

**BROADENING THE GENETIC BASE
OF CROP PRODUCTION**

BROADENING THE GENETIC BASE OF CROP PRODUCTION

Edited by

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CABI Publishing

in association with

Food and Agriculture Organization of the United Nations

and

International Plant Genetic Resources Institute

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A catalogue record for this book is available from the British Library, London, UK.

Library of Congress Cataloging-in-Publication Data

Broadening the genetic base of crop production / edited by H.D. Cooper, C. Spillane, and T. Hodgkin.

p. cm.

Includes bibliographical references.

ISBN 0-85199-411-3 (alk. paper)

1. Food crops--Germplasm resources. 2. Plant genetics. 3. Genebanks, Plant. I. Cooper, H. D. (H. David) II. Spillane, Charlie. III. Hodgkin, T. IV. Food and Agriculture Organization of the United Nations. V. International Plant Genetic Resources Institute.

SB123.3.B76 2000

333.95434--dc21

00-044455

Published jointly by:

CABI *Publishing*, a division of CAB *International*

CABI Publishing, CAB International, Wallingford, Oxon OX10 8DE, UK

Tel.: +44(0)1491 832111; Fax: +44 (0)1491 833508;

Email: cabi@cabi.org; Web site: www.cabi.org

CABI Publishing, 10 E 40th Street, Suite 3203, New York, NY 10016, USA

Tel: +1 212 481 7018; Fax: +1 212 686 7993; Email: cabi-nao@cabi.org

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ISBN 0 85199 411 3 (CABI)

ISBN 92 5 104438 4 (FAO)

ISBN 92 9043 458 9 (IPGRI)

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Typeset in 10/12pt Garamond by Columns Design Ltd, Reading

Printed and bound in the UK by Biddles Ltd, Guildford and King's Lynn

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Foreword

The world's political leaders, meeting in Rome at the 1996 World Food Summit, made a public commitment to halve the number of under-nourished people by 2015. The World Summit Plan of Action sets out a component of this task: 'to pursue, through participatory means, sustainable, intensified and diversified food production'. The better use of plant genetic diversity and resources will be a prerequisite to meeting this challenge. Greater use of plant genetic diversity will be required in order to produce varieties adapted to the extreme and highly variable environments of low-productivity or marginal areas. The need to combine sustainable productivity increases with mounting pressure to reduce the use of agrochemicals, and make more efficient use of water and nutrients, is likely to place even greater reliance on the utilization of a wider range of plant genetic resources in high-productivity areas.

The importance of improving conservation and use of the genetic diversity of useful plants has been recognized in a variety of ways over the last decade. The Convention on Biological Diversity reflected a strengthened global recognition of the importance of maintaining biodiversity for development. The Global Plan of Action for the Conservation and Sustainable Use of Plant Genetic Resources for Food and Agriculture, which was adopted by 150 countries at the International Technical Conference on Plant Genetic Resources (held in Leipzig in June 1996), identified a series of specific ways in which conservation and use of plant genetic diversity could be improved. The Conference of Parties to the Convention on Biological Diversity in November, 1996, highlighted key elements of the Global Plan of Action. These are: broadening the genetic base of major crops; increasing the range of genetic diversity available to farmers; strengthening the capacity to develop new crops and varieties that are specifically adapted to local environments; exploring and promoting the use of under-utilized crops; and strategies that deploy genetic diversity to reduce crop vulnerability.

This emphasis on the wise use of genetic resources, and the contribution that this can make to socioeconomic development and food security, is reflected in the strategy and programmes of the Food and Agriculture Organization and the International Plant Genetic Resources Institute.

The very limited amounts of plant genetic variation that are present in modern varieties of some crops has been identified as an area of major concern by a number of international and national bodies and expert commentators. Substantial losses in production have resulted from the narrow genetic base present in some crops, the loss of many millions of tons of production of maize in the USA in the early 1970s being one of the most famous examples. Increasingly, production tends to depend on fewer varieties drawn from a narrower genetic base. Additionally, farmers' choice of varieties to plant is often limited by poor access to genetic resources, particularly in developing countries.

Concerned with the limited use of the available genetic diversity, the FAO Global Plan of Action identified broadening the genetic base of crops as a key element of the activities that should support improved use of plant genetic resources. The plan is concerned to see genetic vulnerability reduced and increased amounts of diversity made available to farmers. It recognizes that ways need to be found whereby increased amounts of useful genetic diversity can be brought into breeding programmes and into crop production systems. The ways in which this might be done are many and varied, and this book examines the rationale and need for activities to broaden the genetic base of crop production, and examines past experience and discusses new methodologies. We hope that it will stimulate more research and practical activities in this area.

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Preface

Plant breeding and the production of new cultivars is widely regarded as underpinning agriculture and the development of society. Yet crop failures and risks associated with genetic uniformity on large cultivated areas, yield stagnation (below potentially attainable levels), and persistent failures to achieve sustainable production increases in important local ecologies are widespread problems. What is frequently not recognized is that continuing success requires a long-term and sustainable commitment to the effective utilization of plant genetic resources by enhancing and expanding the genetic base from which future cultivars will be generated.

This is not a question of more collecting, storage and evaluation – we have more than 6 million accessions in the world's genebanks. Nor is it enough to introduce selectively a few genes. Indeed, the future needs for an enhanced base cannot be predicted and the particular needs of farming systems should not be prejudged.

Because of this, and of the short term interests of many involved in current national and international breeding programmes, there is a clear need for an international commitment by FAO and others to take a lead in championing base broadening of the world's food and fibre crops. This commitment should take many forms: initiating specific crop programmes; promoting awareness; and supporting and linking local, national and regional activities. It should be aimed at ensuring that farmers and breeders have increased access to useable diversity.

The commitment should be an essential component of an ecologically sound approach to agricultural production based on the more effective use of genetic diversity, employing, as appropriate, decentralized plant breeding driven by the specific needs of farmers and consumers. Strengthening the participation of farmers' communities is vital to achieving these goals.

The above statement was prepared by a group of experts meeting in Rome, September 1997, to examine ways to further the objectives of Activity 10 of the FAO Global Plan of Action for the Conservation and Sustainable Use of Plant Genetic Resources for Food and Agriculture: 'Increasing genetic enhancement and base-broadening efforts'. The full statement, with recommendations, and a list of participants, is provided on p. 437.

Following that meeting, it was decided to produce the present book, to bring together, in one volume, a number of papers on various approaches which contribute to broadening the genetic base of crops. By broadening the genetic base of crops we mean, in particular, increasing the amount of genetic diversity used to produce new crop varieties or used in agricultural production. This reflects a continuing concern with the fact that much crop production depends on very limited amounts of genetic variation and that, in many cases, the genetic diversity present in a crop is not easily available to the plant breeder or the producer interested in making use of it.

The book has a similar title to one published 20 years ago (A.M. van Harten and A.C. Zeven (1979), *Broadening the Genetic Base of Crops*. Proceedings of the conference, PUDOC, Wageningen, The Netherlands). The earlier book, and the conference on which it was based, emphasized collecting and evaluating germplasm, and methods for overcoming barriers to the use of wild relatives. The present book focuses more on the ways in which the amounts of genetic diversity in production can be increased and the ways in which breeding programmes can make use of greater amounts of genetic variation. A number of papers describe 'incorporation' work (*sensu* Simmonds, *Biological Reviews* 66, 189–241, 1991), that is, the large-scale development of locally adapted populations from unimproved or exotic sources, through long-term population-based approaches. It also reflects the many developments that have taken place over this period in participatory plant breeding and *in situ* conservation of genetic resources.

This book could not have been prepared without the help of the many individuals who generously contributed their time, energy and expertise to its writing and production. Above all, the authors of the various chapters are thanked for their contributions as well as for their patience and forbearance in adapting to changing deadlines. Special acknowledgement is due to Norman Simmonds, whose seminal paper on 'Introgression and incorporation: strategies for the use of genetic resources' (*Biological Reviews* (1993) 68, 539–562) stimulated the development of a specific activity on the issue in the Global Plan of Action. In the Food and Agriculture Organization (FAO), particular thanks go to Mahmud Duwayri, Niek van der Graaf, Helena Gomez, Erik Kueneman, Tony Putter, Marcio Porto and Peter Kenmore, for encouraging and guiding the initiative. Nina Dudnik worked tirelessly in keeping the editors more organized than they otherwise would have been. Finally, thanks go to Paul Stapleton of the International Plant Genetic Resources Institute, Shalini Dewan of FAO and Tim Hardwick of CABI Publishing for their cooperation in publishing this work.

Acronyms and Abbreviations

ACMV	African cassava mosaic virus
ADG	Andigena group
AFLP	amplified fragment length polymorphism
APIC	Association of Potato Intergenebank Collaborators
ARI	advanced research institute
ASTA	American Seed Trade Association
BAZ	Bundesanstalt für Züchtungsforschung an Kulturpflanzen (Federal Centre for Breeding Research on Cultivated Plants), Germany
BCMV	bean common mosaic virus
BRG	Bureau des Ressources Génétiques, France
BTI	Boyce Thompson Institute
BUCAP	Biodiversity Use and Conservation in Asia Programme
CBD	Convention on Biological Diversity
CENARGEN	Centro Nacionalde de Recursos Genéticos e Biotecnologia (of EMBRAPA), Brazil
CGIAR	Consultative Group on International Agricultural Research
CIAL	local committee for agricultural research
CIAT	Centro Internacional de Agricultura Tropical
CILSS	Comité Permanent Inter-Etats de Lutte contre la Sècheresse dans le Sahel
CIMMYT	Centro Internacional de Mejoramiento de Maíz y Trigo, Mexico (International Wheat and Maize Improvement Centre)
CIP	Centro Internacional de la Papa, Peru (International Potato Center)
CIRAD	Centre de Coopération Internationale en Recherches Agronomiques pour le Développement, France
cms	cytoplasmic male sterility
CORAF	Conférence des responsables de recherche agronomique africains
CORPOICA	Corporación Colombiana para la Investigación en Agricultura, Colombia

CRBP	Centre des Recherches Régionales sur Bananiers et Plantains, Cameroon
CRSP	collaborative research support programmes
DGER	Direction Générale de l'Enseignement et de la Recherche, France
DM	dynamic management
DUS	distinctiveness, uniformity and stability
EBN	endosperm balance number
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuaria
ESD	equal seed descent
FAO	Food and Agriculture Organization of the United Nations
FFS	farmer field school
FHIA	Fundación Hondureña de Investigación Agrícola
GCA	general combining ability
g-cms	genic-cytoplasmic male sterility
GE	genotype \times environment
GEM	Genetic Enhancement of Maize Project
GILB	Global Initiative on Late Blight
HOPE	hierarchical, open-ended population enrichment
HR	horizontal resistance
HYE	high-yielding environments
HYV	high-yielding variety
IAEA	International Atomic Energy Agency
IARC	International Agricultural Research Centre
IBPGR	International Board for Plant Genetic Resources
ICA	Instituto Colombiano Agropecuario
ICARDA	International Center for Agricultural Research in Dry Areas
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
ICTA	Imperial College of Tropical Agriculture
IDRC	International Development Research Centre
IIRB	International Institute of Sugarbeet Research, Belgium
IITA	International Institute for Tropical Agriculture
INIBAP	International Network for the Improvement of Banana and Plantain
INIFAP	Instituto Nacional de Investigaciones Forestales y Agropecuarias
INRA	Institut National de la Recherche Agronomique, France
INSAH	Institute for the Sahel
INTA	Instituto Nacional de Tecnología Agropecuaria, Argentina
IPGRI	International Plant Genetic Resources Institute
IPR	intellectual property rights
IRAT	Institut de Recherches Agronomiques Tropicales et de Cultures Vivrières, France
IRRI	International Rice Research Institute
ISNAR	International Service for National Agricultural Research
ISO	International Standards Organization
ISWYN	International Spring Yield Wheat Nursery
ITC	INIBAP Transit Centre
IWIS	International Wheat Information System
KUL	Katholieke Universiteit Leuven, Belgium

LAMP	Latin American Maize Program
LSC	Lancaster Sure Crop
LYE	low-yielding environments
MBP	modified bulk population
MGIS	<i>Musa</i> Germplasm Information System
NARS	National Agricultural Research System
NCRPIS	North Central Regional Plant Introduction Station, USA
NGO	non-governmental organization
NSSL	National Seed Storage Laboratory, USA
NTB	Neotuberosum
OFM	on-farm management
OPV	open-pollinated variety
PBR	plant breeder's rights
PCIM	Programa Cooperativo de Investigaciones en Maíz
PGRFA	plant genetic resources for food and agriculture
PLRV	potato leaf roll virus
PPB	participatory plant breeding
PPRI	Plant Protection Research Institute
PRACIPA	Programa Andino Cooperativo de Investigación en Papa
PRAPACE	Programme Régional de l'Amélioration de la Culture de la Pomme de Terre et de la Patate Douce
PRECODEPA	Programa Regional Cooperativo de Papa
PROCIPA	Programa Cooperativo de Investigaciones en Papa
PVP	plant variety protection
PVS	participatory varietal selection
QDPI	Queensland Department of Primary Industry, Australia
QTL	quantitative trait loci
QUT	Queensland University of Technology, Australia
RAPD	random amplified polymorphic DNA
R&D	research and development
RFLP	restriction fragment length polymorphism
RRS	reciprocal recurrent selection
RYD	Reid Yellow Dent
SCA	specific combining ability
SCRI	Scottish Crop Research Institute, UK
SEARICE	South East Asia Regional Institute for Community Education
SI	self-incompatible
SIFT	standard international field trial
SMBR	Sierra de Manantlan Biosphere Reserve
SSR	simple sequence repeats
TBG	tuberosum group
TBRI	Taiwan Banana Research Institute
TRIPs	Trade Related Intellectual Property Rights
TSG	technical steering group
UNALM	Universidad Nacional Agraria–La Molina, Peru
UPOV	International Union for the Protection of New Varieties of Plants
UPWARD	Users' Perspective with Agricultural Research and Development

USDA	United States Department of Agriculture
VCU	value for cultivation and use
VR	vertical resistance
WBN	World Beta Network
WISBEN	West Indies Sugarcane Breeding and Evaluation Network

1

Broadening the Genetic Base of Crops: an Overview

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Introduction

Crop improvement through plant breeding, like crop evolution in general, occurs through selection operating on genetic variability. Selection by plant breeders or by farmers can be intense and has resulted in major improvements in our crops. However, continued success in plant breeding can only be realized in so far as new variability is available for selection. Such variability provides adaptability, that is the capacity for genetic change in response to selection. Genetic diversity is therefore essential for crop improvement.

In many crops the amount of variability that is available for selection is rather limited. A number of crops have an intrinsically narrow genetic base caused by bottlenecks at domestication, by migration or by epistatic and disease effects. Others have a narrow genetic base arising from a lack of diversity in previous breeding practices. Plant breeders tend to use favoured existing cultivars as the basis for generating new ones, because they need to generate short-term gains, and because, often, they are forced to meet stringent market requirements for uniformity. In fact, there is a tendency to give more attention to adaptation through selection than to the generation of new variability or the maintenance of adaptability (Simmonds, 1962). This represents opportunities lost in terms of the utilization of genetic resources, and in its worst manifestations can lead to a progressively narrower genetic base, slower progress (genetic gain) in plant breeding and increased risk of crop vulnerability.

Clearly visible consequences of this have been limited to relatively few calamitous events such as the Irish potato famine, caused by late blight, and the southern leaf blight epidemic in the US maize crop in 1970, which was the result of cytoplasmic uniformity. The latter event led to a major report by the US Academy of Sciences on the 'Genetic Vulnerability of Major Crops' (National Research Council, 1972) which recommended a broadening of the genetic base of major staple crops. However, to date there have been few concerted genetic base-broadening efforts. One reason for this may be the perception that, even in crops with a narrow genetic base, there remains

sufficient genetic variability within breeding populations to continue making improvements (Duvick, 1984; Rasmusson and Phillips, 1997).

Since the 1970s, work on the conservation of crop genetic resources has increasingly become a large-scale independent activity detached from crop improvement efforts. A substantial germplasm collecting effort was launched in the 1970s in response to concerns about genetic erosion and crop vulnerability. Over 1000 genebanks have been established, holding about 6 million accessions (FAO, 1998). Much has been invested in characterization, evaluation and documentation, yet, for various reasons, the use of many collections has actually been rather limited (FAO, 1998). This situation has led to criticism by some, including both plant breeders (e.g. Simmonds, 1993) and non-governmental organizations (e.g. Cooper *et al.*, 1992), that the genetic resources maintained in genebanks could be more usefully deployed in both plant breeding and farmers' fields.

In more industrial agricultural systems, the separation between genetic resources conservation and crop improvement is also reflected at field level. Most modern cropping systems do not contain substantial crop diversity at field level, but rather rely on diversity 'in reserve' (Duvick, 1984). More traditional farming systems, on the other hand, often possess considerable diversity in production systems both within individual crops and through use of a wider variety of crops. Indeed the within-crop variability, acted upon by farmer selection (conscious and unconscious), was the basis for crop evolution from the beginnings of agriculture until the advent of modern plant breeding. On-farm crop improvement remains essential to many farmers today, particularly in more economically marginal areas.

In recent years there has been growing awareness of the role played by farmers, especially women, in crop improvement and genetic resources management, and a renewed emphasis on strengthening the links between the conservation of genetic resources and their use. These trends are reflected in the Global Plan of Action for the conservation and sustainable use of plant genetic resources for food and agriculture (PGRFA) adopted at the International Technical Conference on Plant Genetic Resources held in 1996 (FAO, 1996). The Plan includes, among its priority activities, 'increasing genetic enhancement and base-broadening efforts', 'promoting sustainable agriculture through diversification of crop production and broader diversity in crops' and 'supporting on farm management and improvement of PGRFA'.

The importance of maintaining diversity in crop production systems was highlighted by the Conference of Parties of the Convention on Biological Diversity, when it considered agricultural biological diversity in 1996. Countries agreed to develop national strategies, programmes and plans, 'which should focus on, *inter alia*, the key elements of the Global Plan of Action, such as broadening the genetic base of major crops; increasing the range of genetic diversity available to farmers; strengthening the capacity to develop new crops and varieties that are specifically adapted to local environments; exploring and promoting the use of underutilized crops; and deploying genetic diversity to reduce crop vulnerability' (UNEP, 1997).

Thus, there is a perception and concern that genetic diversity is limited, both within production systems and in breeding programmes, and that there is a need for continuing and concerted efforts to broaden the genetic base of crops. In the wide sense used here, broadening the genetic base of crops can be considered at three levels:

1. Increasing the extent of useful diversity available to breeders, that is broadening the genetic base of breeders' material through genetic enhancement, or pre-breeding.
2. Increasing the range of useful diversity available to farmers as planting material.
3. Increasing the diversity of crops and varieties grown in the field.

In this book we have brought together papers on all of three of these areas. The book seeks to present and explore the main concepts related to broadening the genetic base of crops (see, in particular, Part I), and discuss the extent to which some recent trends (including the greater use of participatory plant breeding and on-farm genetic resources conservation) can contribute to these base-broadening goals. This chapter introduces the topic, provides an overview of the main concepts and surveys some examples, drawing upon the various chapters of the book, as well as the results of meetings on the topic held in 1997 and 1999 (FAO, 1999, 2000).

The Rationale for Broadening the Genetic Base of Crops

Variability, adaptability and the genetic base

Adaptability is the capacity for genetic response to selection that results in adaptation (Simmonds, 1962). There is an inherent conflict between adaptation and adaptability, since the more completely a population or variety is adapted to its environment the less adaptability it is likely to have for evolutionary change. Adaptability is essential for continued crop improvement through selection by farmers or in plant breeding programmes, but tends to be reduced by such selection. There is a continuing need to balance this tendency.

Adaptability is dependent on the presence of genetic diversity within a population or crop. The extent of genetic diversity can vary substantially depending on the crop or population under consideration and not all of it contributes to adaptability. None the less, variation is an essential prerequisite of adaptability.

Genetic diversity in crop plant populations does not occur at random but is structured in ways that depend on crop biology, distribution and the environment in which the crop occurs. Levels of diversity between and within plants can vary dramatically from virtual absence in a pure variety of modern rice to extremely high levels in populations of outbreeding forest trees.

From the perspective of the user, whether a farmer or a breeder in the formal sector, the genetic base of a crop includes all the genetic diversity that is readily available to them for adaptation to any particular environment(s) of interest. It includes the genetic diversity of varieties, both traditional and modern, already in use in any one production environment, as well as the materials currently being used to develop new varieties for that environment. Less readily available material exists in different environments (*in situ*) and in genebanks (*ex situ*) and wild gene pools. This exotic, unadapted material is generally not considered part of the genetic base, but can be brought into it through genetic enhancement or base-broadening programmes.

The genetic diversity of locally adapted varieties includes variation within and between varieties as well as variation that is temporarily concealed as recessives in heterozygotes. It is supplemented by mutation (in the short term, to a low extent) and by

introduction of material from other populations. Recombination and selection allow new combinations of this variability to be exposed.

In many traditional agricultural systems such variability allows crop evolution to continue, on-farm. Chapter 4 by Berthaud *et al.* provides examples of this.

In traditional varieties of outcrossing annual crops such as maize (for example in Mesoamerica) and millet (West Africa), very high levels of variation are present within varieties (Simmonds, 1962). There is substantial variability between genotypes, which are themselves highly heterozygous. The recombination that results from outcrossing allows continued adaptation, through selection, at the level of the population, such that gene frequencies continually change, but gene combinations do not become fixed. Within this diverse genetic background, farmers maintain a number of varieties that are phenotypically distinct for characteristics of importance to them (such as colour and end-product quality). While these characteristics are maintained by selection, there may be an enormous flux of other genetic characteristics between and within these varieties.

As shown by Louette and colleagues (Louette, 1994; Louette *et al.*, 1997) and by Berthaud *et al.* (Chapter 4, this volume), introgression of new genetic material can occur continually as a result of cross-pollination with material from neighbouring farms, and material brought in from other areas. Recombination of locally adapted material, together with introgression of material from other areas, continuously replenishes the available variability, and may help to balance ongoing selection by nature and farmer.

Similar situations are observed for outbreeding perennials that are propagated by seed (such as coconuts and oil palm). Even crops which are usually clonally propagated, such as potatoes (in the Andes), bananas (in Uganda and Southeast Asia), sugar cane (in New Guinea) and cassava (in South America), can show high heterogeneity between clones. As shown by Second and Iglesias (Chapter 11, this volume), in some traditional cropping systems new cassava genotypes may be obtained when the latter are produced from seed.

In inbreeding annuals such as rice (in Asia), wheat and barley (in the Mediterranean and the near East), heterozygosity is low, but in traditional agricultural systems there is substantial variability both within and between varieties. Though the extent of outcrossing is low compared with crops such as maize and millet, it is large enough to allow continuous recombination and crop improvement through selection over time. Such processes have allowed a large number of local varieties to evolve, as in the case of rice, where there are estimated to be over 100,000 known varieties (FAO, 1998). Outcrossing can also be significant over short time periods as demonstrated in the work on dynamic management of wheat populations by Goldringer *et al.* (Chapter 13, this volume).

Despite the presence of locally adapted variability on-farm, there may, nevertheless, be a need for influxes of new material. This will be the case especially in areas outside the centres of diversity, and where the market imposes demands for new traits. Increasing the range of genetic material available to farmers can often be important even in areas where diversity levels are already high.

In modern, 'industrial' agricultural systems, locally adapted variability is very much reduced. The diverse varieties of outbred annual crops have been largely replaced by uniform F_1 hybrids, as is the case with maize. Though substantial variability can still be present, as heterozygotes, in practice there is a major disincentive to its use by the

farmer, since second generation crops would give reduced yields and insufficient uniformity. Single clones of crops such as potatoes, banana and rubber are often grown on a large scale in agribusiness-oriented agriculture. Similarly, many local varieties of crops such as wheat, barley and rice have been replaced, to a large extent, by uniform stands of single lines which have low adaptability (Simmonds, 1962).

The new crop varieties are highly adapted to their production environments (which, in parallel, have often also been 'improved' through fertilizers and irrigation), and are highly productive. They often show broad adaptation to a very wide geographical range. However, the low levels of locally available variability have two major implications for plant breeding and genetic resources management.

Firstly, crop evolution is separated from production – in modern agricultural systems it no longer takes place on-farm, but in breeding programmes. To respond to changing needs and circumstances (such as changes in market requirements, or the emergence of a new or newly resistant pest or disease), farmers in such systems are dependent on a stream of new varieties produced in plant breeding programmes. This has been described as provision of 'diversity in time' by Duvick (1984). This phenomenon is of course very advanced and widely accepted in many parts of the world, where it represents a rational and economically efficient division of labour. But it has not yet taken place in many marginal areas. In fact, in many such areas the incentives, capacity and infrastructure required to produce and distribute new varieties are not present. The loss of variability on-farm also reduces population adaptation as a factor in production (that is, the positive interactions between the components of varietal mixtures (Simmonds, 1962)), and might raise problems of crop variety vulnerability in the face of attacks by new pathogen races (Smale, 1997).

Secondly, crop breeders tend to rely increasingly on a narrow set of improved elite materials for future plant breeding. Broadening the base of these materials through genetic enhancement becomes an increasingly important and increasingly difficult proposition. For a variety of reasons, including biological and economic constraints, there is a tendency to give this low priority. Additionally, as industrial agriculture expands, there are fewer reserves of crop genetic variability *in situ*, and an increasing need, therefore, to rely on *ex situ* collections.

Base-broadening and breeding programmes

Most modern varieties, and the populations with which breeders work, consist of elite germplasm which has been carefully built up over periods of perhaps 10–50 years of research, hybridization and selection. These outstanding genotypes are destroyed by crosses with unimproved exotic germplasm (Duvick, 1984). Moreover, breeders usually find that, even within a narrow genetic base, improvements can continue to be made from further crossing and selection (Wych and Rasmusson, 1983). Thus, there is a major disincentive for breeders to access other germplasm sources that appear to be agronomically inferior. Unless outside sources of germplasm are considered absolutely necessary and possess specific desirable traits, breeders will usually try to find new genetic material within their own breeding lines. Over the long term, this can lead to a dependence on a narrower and narrower elite germplasm base for crop improvement.

The variability of the available material that is likely to be well adapted to any one specific production environment is small in comparison with the variability of any crop as a whole. As pointed out by Simmonds (1962), it seems inconceivable that all of the potentially useful combinations have been assembled in any single group of locally adapted stocks (at least in areas outside the centres of diversity). Exotic materials, even crop wild relatives, often contain potentially useful genes and gene combinations, many of which are not expressed as obvious phenotypes in their original genetic background. Moreover, the immediate performance of exotic material itself is often poor. The problem is that mainstream breeding methods cannot accommodate, at reasonable cost, the numbers of combinations that would need to be examined (Simmonds, 1962).

Instead, therefore, it has been proposed that dedicated programmes of pre-breeding or genetic enhancement are required. While pre-breeding programmes of various types have previously been a well-established component of some publicly funded agricultural research programmes, currently there is concern that the support given to such programmes has declined in recent years. Pre-breeding programmes take different forms depending on the crop and the issues of concern, and include the introduction of new characters from wild relatives or the development of specific selections from which desirable improved inbreds can be obtained. Panmictic populations established on a very broad base, such as the barley composite cross or populations (Harlan and Martini, 1929, 1938), can also constitute pre-breeding programmes. Such mass reservoirs (Simmonds, 1962) of genetic adaptability can also carry out a valuable conservation function (Shands, 1990; Goldringer *et al.*, Chapter 13, this volume).

Simmonds (1993) described approaches that involve the large-scale development of locally adapted populations from unimproved or exotic sources, through long-term population-based approaches, as 'incorporation', distinguishing them from the introgression of single genes (typically for qualitative traits such as disease resistance) into breeders' materials. In contrast to the periodic introgression of a few selected genes or gene complexes from exotic germplasm into elite germplasm, to meet specific pre-identified needs, incorporation approaches are based upon the construction of genetically diverse and dynamic plant populations, which through sequential cycles of genetic recombination and selection are used to develop locally adapted germplasm pools. Initially diversity is maximized by drawing upon material of wide genetic and geographic origins. Selection intensity is initially weak, though progressively increased as the populations are decentralized to the target environments and end-users.

The process of selection is subject to so many constraints that it cannot possibly achieve perfection (Lewontin, 1984; Mayr, 1988; Eriksson *et al.*, 1993). One objective of base-broadening is to facilitate the production of populations of increased adaptive fitness. Wright (1922, 1977) combined migration, drift and selection into a unified process of evolution called the shifting balance theory, which views most populations as being substructured into small, periodically drifting groups where fitness is due to many interacting loci. Wright envisaged a process where a population can be 'trapped' at a certain fitness level where only a limited number of genotypes are well adapted. However, evolutionary rearrangements of allele frequencies due to drift or other factors followed by selection can reassemble the available genes into a new type more fit than the original and which can reach a higher 'adaptive peak'. Adaptive valleys, where the fitness of genotypes is at a minimum, act as constraints to geneflow and to reaching

higher adaptive peaks. While adapted germplasm may be at one type of adaptive peak, by definition corresponding exotic germplasm will be at a different type, with a major maladaptive valley preventing gene flow between them (Whitlock *et al.*, 1995). Base-broadening can be considered as a means of building ridges between different fitness peaks (see also, Spillane and Gepts, Chapter 2, this volume; Goldringer *et al.*, Chapter 13, this volume).

Base-broadening programmes may also be important in maintaining or increasing the current levels of diversity and in avoiding further inadvertent narrowing through plant breeding programmes. Base-broadening programmes may be particularly important as a necessary complement to (or component of) new crop improvement approaches (for example: micropropagation, F₁ hybrid breeding, the possible introduction of apomixis in new crops and recombinant gene transfer) which, depending on the approach taken, may either contribute to broadening, or lead to further narrowing, of the genetic base.

Pre-breeding is often considered to be an activity at the interface between germplasm conservation and utilization. As a result, which sector (private or public) and who (curators or breeders) should be responsible for this activity is not clear. Generally, it is considered a pre-competitive activity which commercial breeders cannot afford in the short term. Private incentives for such activities are few, and pre-breeding is usually regarded as an international or national public good. Indeed, most public research institutions, universities or funding agencies have done pre-breeding in the past, but with the increasing withdrawal of public funding, pre-breeding activities are now often left unfunded or underfunded (Duvick, 1984; Anderson *et al.*, 1993). The scarcity of long-term research funds as well as the lack of academic recognition for such a long-term activity have contributed to the neglect of pre-breeding activities. This neglect has negative long-term implications for maintaining or increasing the use of germplasm stored in genebanks, and needs to be overcome. (Kannenburg and Falk, 1995; FAO, 1998).

Increasing the range of useful diversity available to farmers

Farmers have three possible sources or channels of access for new crop varieties: (i) the private sector; (ii) government seed supply schemes; and (iii) informal farmer to farmer distribution of seed. Type (i) is involved in seed production for commercially viable markets and clients. Because resource-poor farmers express little financial demand, types (ii) and (iii), on the other hand, provide the bulk of the staple crop varietal needs of resource-poor farmers in developing countries (FAO, 1998).

When provided with the opportunity and means to do so, farmers often express a demand for access to a wider range of useful crops and varieties. Traditional farmers and those operating in more industrialized or market-oriented conditions alike are ready to test new varieties whether, for example, it is the latest officially released cultivar, or an interesting local variety observed during a visit to a relative's farm (Johnson, 1972; Grisley, 1994). Access to suitable new varieties at the level of the farm may in fact be considerably limited by a range of factors. These can include poor seed distribution systems (Cromwell and Wiggins, 1993), breakdown in informal seed supply networks (Bellon, personal communication), an inappropriate regulatory framework

(Louwaars, Chapter 5, this volume) and the lack of suitable varieties. This last reason may result from insufficient plant breeding capacity in the country concerned or the use of breeding strategies that do not result in varieties with the traits needed by farmers (Cromwell and Wiggins, 1993; Witcombe, Chapter 26, this volume). Because of these latter factors, improved varieties can often show low adoption rates.

On a local level, it has been suggested that some existing local varieties, or groups of local varieties, may actually have quite narrow genetic bases as a result of a previous genetic bottleneck due to past events or widely fluctuating environmental conditions (Wood and Lenné, 1996). This might be the case particularly where crops have been introduced into a region or locality where they did not previously exist, or where they have been subject to extreme biotic or abiotic stresses which have narrowed the genetic base in particular locations. Such limited genetic diversity in locally adapted materials can limit the response to selection that breeders (or farmers) may achieve.

Often farmers do not have the opportunity to formulate and put forward their need for access to a wider range of planting materials (Spillane *et al.*, 1999). Communities and farmers' organizations have little choice but to accept the materials distributed by national organizations or by private companies. New plant breeding approaches, such as participatory variety selection and participatory plant breeding, seem likely to result in increased ranges of useful material for farmers (Witcombe, Chapter 26, this volume; Sperling *et al.*, Chapter 27, this volume). Other imaginative approaches may be needed to ensure that farmers retain access to the full range of diversity that they have found useful in the past, or get access to a continuing supply of new useful materials.

Increasing the diversity of crops and varieties grown in the field

The diversity of crops and varieties grown in the field can be important for many reasons. It can reduce crop vulnerability, that is the likelihood of crop failure due to pest and disease epidemics or unpredictable climatic effects. More generally, it can provide insurance to farmers against risk and uncertainty. This is especially important for farmers operating in economically marginal areas where there is little alternative provision of such livelihood insurance.

Crop or varietal diversity in the field can also contribute to the conservation of plant genetic resources. Most significantly for the topic of this book, diversity in the field allows crop evolution to continue, and this process can be accelerated through farmer participatory plant breeding, in those cases where farmers select from segregating populations or a mixture of a large number of selfing lines. On-farm crop evolution is important in self- and cross-pollinated crops and in clonal crops (e.g. Berthaud *et al.*, Chapter 4, this volume). The continuous and dynamic patterns of crop variety change and evolution seem to be a major feature of traditional crop production in many areas.

In many industrial farming systems there is very little diversity on farm, at least at the level of a single farm or production unit. In these situations some of the functions of on-farm diversity are replaced by farm inputs such as pest control chemicals, and by alternative strategies for managing risk and uncertainty, such as crop insurance and alternative employment opportunities (Swanson *et al.*, 1994). Nevertheless, in some cases, where large contiguous areas planted to single varieties or varieties with the same

resistance genes, crop vulnerability may be a concern (Smale, 1997). Additionally, as noted earlier in this chapter, in the more industrial farming systems there is a reliance on genetic diversity kept off-farm (in genebanks) and on temporal diversity – the continuing production and introduction of new varieties. It is therefore vital that sufficient attention is provided to the other two aspects of broadening the genetic base, that is to increasing the diversity available to breeders through genetic enhancement, and ensuring that new varieties are actually available to farmers.

Identifying Priorities for Base-broadening

The needs and priorities for base-broadening will vary from crop to crop and also, for any one crop, from production area to production area. There are two main groups of criteria and indicators to determine or predict the likely need for base-broadening for particular crops in particular situations: *ex ante* and *ex post*. Some of these are explored in further detail, using an evolutionary perspective, by Spillane and Gepts, Chapter 2, this volume.

The first group of indicators and criteria refer to evidence of a bottleneck in the availability of genetic diversity historically during domestication or crop migration, or during modern plant breeding, or seed distribution:

- During domestication, only a small proportion of the total diversity of the wild population is likely to be sampled (the ‘founder effect’: Ladizinsky, 1985). Subsequent gene flow between the new cultivar and its wild progenitors might be restricted by breeding barriers, depending on the breeding system of the crop concerned, and nature of the domestication event. Crops which might be expected to have a narrow genetic base because of bottlenecks at domestication include rice, bread and durum wheat, *Phaseolus* beans, tomato, pigeon pea, chickpea, *Citrus*, and possibly *Musa* and yam (Spillane and Gepts, Chapter 2, this volume; Participants in the Rome Workshop, 1997, personal communication).
- Bottlenecks may have arisen through additional ‘founder effects’ when crops were distributed between continents and the initial sample of material from which all material in the new location(s) were derived was very small. During transfer between latitudes, there may be a further narrowing of the genetic base because the population would not be well adapted to the new day-length conditions, and so only a small number of the genotypes would survive (‘epistatic effects’, e.g. potato in temperate areas). Finally, there may be other chance occurrences that narrow the genetic base such as disease epidemics, which may decimate populations. Examples of crops with narrow genetic bases arising during migration may include soybean (in the USA), maize (in Africa and the US; see Tallury and Goodman, Chapter 9, this volume), sorghum and millet (in South Asia), lentil (in South Asia; see Erskine *et al.*, Chapter 21, this volume), cocoa and coffee (Participants in the Rome Workshop, 1997, personal communication).
- Bottlenecks during modern plant breeding might be indicated, for example, by a small number of parents or high degree of relatedness between parents, as elucidated from pedigree analyses. The narrow genetic base of maize in the US is the classic example (Goodman, 1985, 1990; Tallury and Goodman, Chapter 9; Pollack and

Salhuana, Chapter 19, this volume). Another is rice in the US and Japan (Nakagahara *et al.*, 1997; Xu *et al.*, 1997). Further, narrowing of the genetic base may result from specialization within crops: for example, breeding of winter wheat has been mainly done by using only winter germplasm and breeding of spring wheat by using only spring germplasm (Spillane and Gepts, Chapter 2, this volume). The genetic base of hot peppers (*Capsicum annum*) is partitioned by the specialized requirements for distinct uses (e.g. thin pericarp required for drying, whilst fresh use requires small fruit). The genetic base of *Brassica* is similarly partitioned into different morphological types (Pickersgill in FAO, 2000).

- The diversity available in any one locality is inevitably a small fraction of the total available in the crop at large. Both formal and informal (farmer-to-farmer) seed distribution systems are likely to have a major impact in crop geneflow within any country or region (Cromwell and Wiggins, 1993; Sperling *et al.*, 1996; Sthapit *et al.*, 1996; Witcombe *et al.*, 1996). Factors such as harsh topography, lack of transport or communications can limit geneflow between regions and thus farmers who live in peripheral regions are likely to have less access to novel germplasm (Brush and Meng, 1998). Genetic bottlenecks to such geneflow can occur because of social factors such as income status, gender, family, ethnicity or other social groupings (Ferguson, 1992; Sperling *et al.*, 1996). Both the diversity of material made available to farmers and its suitability to their production systems can be limited by inadequate plant breeding capacity, and inappropriate regulations for variety release and seed certification (Louwaars, Chapter 5, this volume).

The second group of indicators and criteria refer to actual evidence that performance of the crop is being limited by a narrow genetic base. These include, for example:

- When a yield plateau or low rate of progress (genetic gain) is apparent in breeding programmes. This has been suggested to be the case for potatoes in northern temperate areas (Simmonds, 1993; Bradshaw in FAO, 2000), and for sugar cane in the Caribbean (Kennedy, Chapter 16, this volume).
- When breeders are increasingly forced to source qualitative genes from the secondary and tertiary gene pools (often using costly high technology approaches).
- When there are repeated instances of crop failure, or crop vulnerability to particular biotic or abiotic stresses. Sugar cane in several islands of the West Indies provides an example of this situation (Rao and Gardiner, 1997). Concerns over the vulnerability of maize in the USA and Europe have led to base-broadening efforts (Pollack and Salhuana, Chapter 19, this volume; Gallais *et al.*, Chapter 20, this volume).
- When the needs of farmers for a sufficiently diverse range of planting material are not being met (this can include the needs of particular groups of farmers or sections of the community such as women, landless farmers, children or the old, and particular needs, such as that for labour-saving crops or crops required for particular products, including those of cultural importance).

Bottlenecks may be: (i) genetic – that is, while the total genetic diversity of the species or genus may not be limiting, barriers to breeding occur between the primary gene pool and other gene pools. Additionally, barriers may arise due to differences in adaptation that have arisen through geographical bottlenecks; (ii) spatial or geographic – that is, while the total genetic diversity worldwide may not be limiting, that available, or

adapted to, particular areas may be; and (iii) institutional or regulatory – that is, that availability is limited by economic, legal or other regulatory factors, such as seed and variety release regulations, access laws or lack of purchasing power. Since the most appropriate way to overcome a suspected bottleneck may depend in part on its cause, the indicators and criteria outlined above may provide initial clues as to the most suitable base-broadening approach to use. Critical assessments of the state of diversity of crops, and of the state of use of diversity of those crops, would help to provide a more objective basis for determining future needs and priorities. Such assessments might include the following components:

- Assessments of the genetic diversity present within the various gene pools of the crop, comparing the *in toto* variation (that is the sum of the variation in the 1°, 2° and 3° gene pools) with that available in the primary gene pool.
- Assessments of the genetic diversity present in the primary gene pool of the crop, comparing that *in situ* (aggregating all areas), with that available (i) in collections, and (ii) in breeding pools.
- Examination of the extent that such available genetic diversity is actually utilized in breeding programmes of the crop, including pedigree analyses.
- Examination of the extent to which such genetic diversity used in breeding programmes is actually available to farmers in the full range of geographical areas and for the full range of purposes (including specific attention to past and ongoing efforts to produce improved varieties of use to farmers in both high-potential and marginal environments).

The chapters in Part II of this book provide information on some of these points: for millet in West Africa (Niangado, Chapter 8), for maize in the USA and sub-Saharan Africa (Tallury and Goodman, Chapter 9), for potato (Ortiz, Chapter 10), for cassava (Second and Iglesias, Chapter 11) and for *Musa* (Sharrock *et al.*, Chapter 12).

Approaches to Broadening of the Genetic Base of Crops

Several approaches to base-broadening are discussed in this book. Many are strategies for genetic enhancement or pre-breeding – with an emphasis on the incorporation approach, as noted earlier. Others also include elements of genetic resource conservation and plant breeding *per se*.

Incorporation programmes, involving the generation and maintenance of populations

The main elements of a base-broadening programme involving incorporation (Simmonds, 1993; Spoor and Simmonds, Chapter 3, this volume), include:

- Making use of the broadest possible starting materials, consistent with the specific objectives of the programme. Evaluation of such material is, in this context, often irrelevant, since most of the starting material is expected to be un-adapted to the target environments anyway. However, for reasons of feasibility, some genetic enhancement programmes start with a subset of material that is selected for likely

usefulness. Core collections may be useful tools to select genetically diverse starting material (Van Hintum *et al.*, 1999).

- A need for extensive recombination. (If natural outcrossing rates are sufficiently high, recombination is easy; otherwise controlled crossing or the use of male sterility genes may be necessary.)
- Weak and progressively decentralized selection. Whenever possible, selection should be based on multiple large populations and carried out over several generations in target environments, in order to exploit genotype by environment interaction; inbreeding should be minimized; simple and cheap methods should be used as far as is possible. (If adaptation is reflected in production, as with seed grain crops, semi-natural selection can be exploited as in the composite cross populations.) Long-term programmes of the order of a decade or more are required in order to generate usable material, though the duration depends on the specific objectives and crop concerned.
- The maintenance of the above process as a programme distinct from conventional breeding programmes, until usable material is produced. At this stage, material may be used directly in formal breeding programmes, crossed with existing adapted material or, potentially, made available for further selection in farmer participatory approaches.

Of course the actual methodologies have to be adapted to the biology of the crop, and to the specific objectives, scale of operation and time horizon of the programme. One way of grouping population-based approaches to base-broadening follows (see also Table 1.1, and Part III of this book).

A: Synthetics and composite cross-populations

Populations are established by crossing a number of genetically different accessions in order to maximize the importance of genetic and geographic origins. These populations are then split into the different locations where a need for new variability has been identified and each sub-population is allowed to adapt progressively to local conditions. Such base-broadening thus involves the evolutionary development over time of different locally adapted populations of genetic resources from an initially genetically diverse pool of unadapted exotic germplasm. Approaches of this type include the classical composite cross populations (Harlan and Martini, 1929, 1938; Ibrahim and Barrett, Chapter 15, this volume). Newer examples include the development of broad-based barley pools for Nordic conditions (Veteläinen and Nissilä, Chapter 14, this volume). Simmonds (1962) considered such composite cross-populations as 'reconstituted local varieties' or 'mass reservoirs' of locally adapted variability, while Suneson (1969) considered that the changes in such populations constituted an evolutionary plant breeding method. Similar concepts have been used for sugarbeet (Frese *et al.*, Chapter 17, this volume). Experiments are now being carried out to explore the use of such populations for the 'dynamic *in situ* management of genetic resources' (Goldringer *et al.*, Chapter 13, this volume). Dynamic management, as practised on composite wheat populations, is also proposed for cassava (Second and Iglesias, Chapter 11, this volume), mimicking the management of cassava cultivars in Amazonian villages. Such on-farm dynamic management is also documented for maize and millet (Berthaud *et al.*, Chapter 4, this volume). In crops where the seed is the harvested product, the normal cycle of planting and harvest may provide sufficient selection to produce agronomically useful material.

Table 1.1. Base-broadening: examples of incorporation programmes involving population management.

Crop and objective	Starting material	Selection process	Status and outputs	References
<i>A: Composite crosses</i>				
Barley (composite crosses, e.g. CCII) To broaden the local genetic base; to produce new varieties; to maintain long-term breeding reserve.	28 lines (15 adapted to N. America, 13 Old World) Selected for promising phenotypic characters from USDA collection. All 378 crosses made; polyallele crossing.	Grown as unselected bulk for 30 generations at Davis, and distributed to barley breeders in various countries.	15 commercial varieties by 1956; more than 50 lines eventually developed into varieties, others used as parents for other varieties.	Harlan and Martini, 1929, 1938.
Barley (Cambridge CCV)	30 diverse varieties, crossed in pairs, followed by pairwise crosses of F ₁ s, for 3 generations. Harvest bulked.	Grown as unselected bulk for 30 generations at Davis; 10,000–15,000 seeds/season. Samples of F ₁₀ , F ₂₀ , F ₃₀ maintained at Cambridge, UK.		Ibrahim and Barrett, Chapter 15, this volume.
Barley (Nordic) To produce broad-based barley gene pools, resistant to various diseases, adapted to Nordic conditions.	Unadapted material: 5 wild barley, 10 landraces from Asia. Adapted material from Sweden or Finland. Selected for disease resistance and wide diversity. Controlled crossing for 6 generations (pairwise and diallel), with selection avoided.	Not yet in progress.	Dynamic gene pools Evaluation data	Veteläinen and Nissilä, Chapter 14, this volume.

continued

Table 1.1. *continued*

Crop and objective	Starting material	Selection process	Status and outputs	References
Wheat (dynamic management, France) To maintain genetic diversity for use in breeding programmes by mimicking natural processes responsible for its diversification and conservation.	Three populations: PA (16 parents, domestic sources); PB (16 parents, exotic sources); and PS (as PA, with male sterility). 3 years of bulk multiplication.	The 3 populations distributed over 7 to 12 locations in France. No conscious selection; 2 levels of management: intensive farming; extensive farming. In latter stages geneflow between locations to be introduced to create metapopulations.	Diverse set of locally adapted populations with mostly agronomically favourable traits.	Goldringer <i>et al.</i> , Chapter 13, this volume.
Cassava (EMBRAPA, Proposed) 1 To conserve diversity in centres of diversity. 2 To produce new, broadly based varieties in new areas mimicking traditional practices.	1 In centre of origin: pool local varieties in single field. 2 In new areas: pool maximum diversity in a single field.	Planting at distances to allow balance between adaptation and geneflow. Selection for tuber quality and productivity. Also, in the case of (2), metapopulation established through periodic and limited exchange between material in a network of sites.	1 Dynamic conservation of varieties. 2 Development of locally adapted varieties.	Second and Iglesias, Chapter 11, this volume.
Sugarbeet (USDA/ARS) To overcome narrow genetic base.	Crosses with wild <i>B. vulgaris</i> germplasm, made in 1986, 1990 and 1994. In 1990: male sterile sugarbeet plants were chosen as the female parent to obtain F ₁ plants. F ₁ s intercrossed. Bulkied to produce F ₃ families. At least two recombination cycles were allowed without selection. No prior selection on useful characters was done.	Mild selection on root shape and bolting resistance. After five cycles of mass selection some of the progenies started to resemble the sugarbeet.	Started in 1986. USDA germplasm releases.	Frese <i>et al.</i> , Chapter 17, this volume.

Sugarbeet (European Breeding companies) To overcome narrow genetic base.	Beet x wild crosses, using 22 different French wild beet populations. 50:50 combination maintained in progeny using 'Dogget' populations.	Subsequently selection for agronomic characters.	Started in 1996; selection for agronomic characters now under way.	Frese <i>et al.</i> , Chapter 17, this volume.
<i>B: Incorporation to overcome historical bottlenecks</i>				
Potato (John Innes/Cornell etc.) To overcome bottlenecks caused by: (i) migration from Andes to northern temperate zones; and (ii) late blight epidemic.	Large number of samples from Andigena cultivars of S. America. No evaluation.	Weak mass selection, over 10 to 20 years, under long days and disease attack, alternating between seedlings and tuber-grown selections.	'Neo-tuberosum': promising selections, especially in crosses with temperate 'tuberosum' cultivars.	Simmonds, 1993; Spoor and Simmonds, Chapter 3, this volume.
Potato (John Innes/North Carolina) As above.	Large number of samples from cultivated diploids of S. America. No evaluation.	As above.	Material to be crossed with temperate cultivars of 'tuberosum' and 'neo-tuberosum' groups.	Carroll and de Maine, 1989; Simmonds, 1993.
Potato (Sturgeon Bay) As above.	Wild diploids of S. America, crossed with dihaploids derived from TBR.		Material of 25% wild and 75% 'tuberosum' germplasm.	Ortiz, Chapter 10, this volume.
Cocoa (BAL/CDC) To overcome narrow genetic base of crop.	Clones from upper Amazon.	Test crosses in well-structured mating designs.	New clones and parents.	Simmonds, 1993.
Rubber (RRI, Malaysia) To overcome the very narrow genetic base derived from very small original population derived from the centre of origin.	Wild Amazonian material.	Weak mass selection, long-term, alternating between seedlings and clonal selections.	Proposed programme. New plantation material.	Simmonds, 1993; Simmonds 1989.

continued

Table 1.1. *continued*

Crop and objective	Starting material	Selection process	Status and outputs	References
Oil palm (PORIM) To re-domesticate crop in Asia from W. African material.	Collections from W. Africa.	Selection in Asia.	Proposed programme. New plantation material.	Simmonds, 1993.
Sugar cane (WISCBS) Repetition, on large genetic base, of substantial part of the crop evolution.	Large range of Noble polycrosses, and over 50 <i>S. spontaneum</i> parents. Crossing at plant breeding station. No evaluation.	Weak selection, on large populations, alternating seed/clonal cycles. Multilocational selection throughout Caribbean.	New parents to cross with existing commercial parents (CM).	Spoor and Simmonds, Chapter 3, this volume; Kennedy, Chapter 16, this volume.
Sorghum ('conversion') To adapt exotic sorghum to long days.	Tropical races.	'Introgression' of long day length into tropical material (i.e. in reverse to normal direction).		Goodman, 1990.
<i>C: Genetic enhancement to overcome effects of intensive breeding and historical bottlenecks</i>				
Maize (NCSU) To overcome extremely narrow genetic base in the USA caused by: (i) daylength bottleneck between tropical and US maize; and (ii) intensive hybrid breeding.	Superior tropical maizes: hybrids or inbred lines. Identified on basis of evaluation. Large diallel cross.	Selection for adaptation to temperate conditions, over 5–6 generations. Resulting material (100% tropical) selfed for 2 generations, and tested by top-cross with elite temperate.	14 inbred lines suitable for breeding or production and 2 lines for breeding only.	Goodman, 1990, 1985; Simmonds, 1993; Tallury and Goodman, Chapter 9, this volume.

<p>Maize (GEM) As above, specifically to improve traits for agronomic productivity, disease and insect resistance; and value-added characteristics such as starch, oil and protein grain composition and qualities. Private/public sector cooperation.</p>	<p>Originally 50 elite tropical and temperate LAMP accessions (identified by evaluation data), and 7 commercial tropical hybrids from DeKalb Genetics.</p>	<p>Selected populations crossed to proprietary inbred lines, under short days, by each private cooperator. Resulting material (50% tropical) selfed. Some also crossed to elite by another cooperator and top-crossed to test, or first, crossed to elite to give 25% tropical.</p>	<p>Breeding crosses (50%, 25%) evaluated by testcrosses. Best used to develop breeding lines by cooperators. Access to this material is limited to GEM cooperators. Data collected are freely available. GEM-enhanced lines and synthetics will be freely available after their public release.</p>	<p>Tallury and Goodman, Chapter 9, this volume; Pollak and Salhuana, Chapter 19, this volume.</p>
<p>Maize (INRA/PROMAIS) To overcome narrow genetic base in France, especially that caused by intensive hybrid breeding Private/public sector cooperation.</p>	<p>1236 accessions from Europe, Asia, and N. and S. America. Mostly landraces (open pollinated varieties); some bred lines from USA. All evaluated (<i>per se</i> and testcross value) at 2 French locations.</p>	<p>Accessions grouped into pools for different uses.</p>	<p>Differentiated breeding pools for different uses. Evaluation and molecular data.</p>	<p>Gallais <i>et al.</i>, Chapter 20, this volume.</p>

continued

Table 1.1. *continued*

Crop and objective	Starting material	Selection process	Status and outputs	References
Maize (HOPE, Guelph) To overcome narrow genetic base in Canada caused by: (i) daylength bottleneck between tropical and temperate maize; and (ii) intensive hybrid breeding.	Open ended: initially 43 entries (adapted OPVs, synthetics, composites, and 4 double-cross hybrids of foreign origin). To date <i>c.</i> 1000 entries included. Worldwide in origin. Includes germplasm with poor agronomic performance. Most short season, suitable for Guelph. Around 5% longer season exotics from elite improved sources (e.g. CIMMYT).	Hierarchical: L level (all introductions): stratified mass selection. H level (from L level, and few introductions): S ₂ progeny selection. E level (from H level, in 2 heterotic blocks): full-sib reciprocal recurrent selection.	HOPE populations that vary considerably among themselves and represent markedly different germplasm from that deployed commercially. 2 Guelph inbreds, CG91 and CG96, released in 1997, contain HOPE germplasm.	Kannenberg, Chapter 18, this volume.

BAL/CDC: BAL plantations Sdn Bhd/Commonwealth Development Corporation; CIMMYT: International Maize and Wheat Improvement Centre; EMBRAPA: Empresa Brasileira de Pesquisa Agropecuaria; GEM: genetic enhancement of maize; HOPE: hierarchical, open-ended population enrichment; INRA: Institut National de la Recherche Agronomique; LAMP: Latin American Maize Programme; NCSU: North Carolina State University; OPV: open-pollinated variety; PORIM: Palm Oil Research Institute of Malaysia; RRI: Rubber Research Institute; USDA: United States Department of Agriculture; WICSCBS: West Indies Central Sugar Cane Breeding Station.

A similar process – the Multiple Population Breeding Strategy – has been proposed for tree species (Namkoong *et al.*, 1980).

B: Incorporation programmes to overcome historical bottlenecks caused during crop migration and/or disease attack

In these cases, diverse material from the centre of diversity of the crop is used as the starting material, and subjected to repeated cycles of recombination and mild selection in the target environment. Thus a stage of the evolution of the selected crop is repeated, in order to overcome genetic bottlenecks that took place during crop evolution through founder effects, epistatic effects or, for example, disease epidemics. The examples of such ‘crop reconstruction’ approaches to date include potato, sugar cane, cocoa, rubber and oil palm (Simmonds, 1993; Spoor and Simmonds, Chapter 3, this volume; Kennedy, Chapter 16, this volume). In the case of potato, the programmes were aimed at overcoming bottlenecks of all three types mentioned. In all of these cases, as in those of category A on page 12, the starting materials are chosen mainly in order to maximize diversity. Evaluation of the starting material is otherwise not practised. A related case, in which an alternative approach is used for the same objective, is the ‘conversion’ of tropical sorghum germplasm to long days through the introgression of genes for short day into tropical material such that it could enter the gene pool of the temperate crop (Goodman, 1990).

C: Genetic enhancement to overcome effects of intensive breeding, as well as historical bottlenecks

As highlighted earlier, temperate commercial maize has a very restricted genetic base for various reasons. In response to this, Goodman (1985) used a base-broadening approach similar to that outlined under Category B – tropical germplasm was crossed, and selected under temperate conditions for several generations. However, in this case the starting material was selected on the basis of productivity. This reflects the exacting requirements for commercial maize production. Similarly, in the Genetic Enhancement of Maize (GEM) programme, material was selected on the basis of the evaluation data of the previous Latin American Maize Programme (LAMP) (Pollak and Salhuana, Chapter 19, this volume). Material in the French INRA/PROMAIS programme was also evaluated (Gallais *et al.*, Chapter 20, this volume). The HOPE programme uses a hierarchical system to separate diverse introductions from elite material (Kannenberg, Chapter 18, this volume). Private sector support is provided in the GEM and PROMAIS programmes. As a consequence, not all of the enhanced products are freely available.

Other approaches to base-broadening

There are various other approaches to broadening of the genetic base of crops. Examples are provided in Part IV of this book. Erskine *et al.* (Chapter 21, this volume), used several approaches to overcome an ancient bottleneck in lentil. Lentils in South Asia are of a specific ecotype and have a narrow genetic base. This was overcome first by the introduction of pre-adapted germplasm from West Asia, and secondly by the production of new hybrids. Baudoin *et al.* (Chapter 23, this volume) used inter-specific

crosses to develop composite populations adapted to maize/bean mixtures. Farmers will practise further selection within these mixtures.

Grando *et al.* (Chapter 22, this volume) highlight the value and importance of barley landraces as a genepool for breeding programmes. Selections from diverse landrace populations can reveal high-yielding genotypes, which can be used directly, crossed in breeding programmes, or used in reconstituted mixtures.

Espinosa *et al.* (Chapter 25, this volume), and Trognitz *et al.* (Chapter 24, this volume) emphasize the importance of a wide genetic base in breeding for horizontal resistance to diseases.

Finally, there are many approaches to increasing the diversity available to farmers through participatory varietal selection, participatory plant breeding and decentralized plant breeding (Ceccarelli *et al.*, Chapter 6; Salazar, Chapter 7; Witcombe, Chapter 26; Sperling *et al.*, Chapter 27, this volume). As discussed by Witcombe, in cases where selection is decentralized, with or without farmer participation, there is likely to be broadening of the genetic base on-farm.

Concluding Remarks

The approach chosen for a base-broadening programme will reflect crop biology, the nature of the perceived problems, the interests and needs of the farmers and, not least, the interests of those involved in developing and managing the programme. Some work will be solely concerned with introducing useful diversity into a plant breeding programme; other work with ensuring that farmers have access to more diverse seed stocks. Neither approach is necessarily more important than the other, and the two are not mutually exclusive. The long-term effect of these different emphases and approaches is equally uncertain both in respect of their impact on production and in respect of their impact on available genetic diversity for crop production systems.

At the present time, a number of new approaches offer advances in crop improvement. These include gene-transfer and the use of marker-assisted selection as tools for managing 'useful' trait diversity and improving the efficiency and scope of both conventional plant breeding and genetic engineering. An increasing range of techniques is available to facilitate wide crosses in order to access germplasm in the secondary and tertiary genepools. There is substantial investment in many of these approaches, although such investments are heavily biased towards the agricultural systems of developed countries and more export-oriented crops (Spillane, 1999). The various chapters in this book show that a range of approaches to crop improvement are available that are expected to generate reasonable results with minimal resources, provided that there is a sufficiently long-term commitment. These approaches may not need expensive inputs from biotechnology or molecular genetics. They can often be carried out in ways that bring together farmers and plant breeders and link together the formal and informal sectors. Such approaches are able to make use of a wider range of crop diversity, and are an important complement to the more high-technology approaches being pursued at the present time.

In this book we have tried to bring together a range of chapters on various different aspects of base-broadening. Part I includes chapters on some of the basic principles and the factors that limit available genetic diversity in plant breeding and crop produc-

tion, both from crop genetic and from socioeconomic and human perspectives. Part II looks critically at the available diversity in selected crop gene pools and in specific production situations. The chapters provide illustrative examples of specific situations and are not in any sense meant to be exhaustive. Part III presents recent work from different incorporation programmes where the emphasis has been on creating and maintaining populations. Part IV includes chapters which cover documented examples of base-broadening in different crops by means of approaches other than the creation and long-term management of composite populations. Both formal plant breeding programmes and farmer participatory approaches are included; wherever possible the emphasis has been on documenting past work and bringing together known cases that reflect different experiences and situations.

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2

Evolutionary and Genetic Perspectives on the Dynamics of Crop Genepools

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‘Nothing makes sense except in the light of evolution’

(T. Dobzhansky)

Introduction

Genetic diversity is not randomly distributed across or within plant populations. Various factors such as reproductive system, life history and gene flow can influence the level and distribution of genetic diversity within and among populations (Hamrick, 1997). Evolutionary and historical information on a particular crop’s domestication, geographic dissemination and the extent of use of its various genepools is extremely valuable for the rational planning of the use of germplasm in any germplasm-enhancement or base-broadening initiatives (Smartt, 1986; Gepts and Debouck, 1991; Gepts, 1993; Simmonds, 1993). However, crop genetic diversity in itself is not necessarily an economically productive goal from a farmer’s perspective. It may even be counterproductive if resources are expended to increase diversity randomly when they instead might have been used to target or adapt available germplasm diversity to situations and locations where it is needed (Smith and Duvick, 1989).

There are instances where significant breeding progress has been made based upon relatively narrow genetic bases (Leng, 1974; Wych and Rasmussen, 1983; Hallauer, 1986; MacKey, 1986; Dudley and Lambert, 1992; Manninen and Nissila, 1997; Rasmussen and Phillips, 1997). Different mechanisms for the endogenous generation of genetic variability have been posited as possible explanations for such instances (Rasmussen and Phillips, 1997). On the other hand, theory predicts that the response to selection diminishes as the genetic variability decreases (Falconer, 1989). Indeed, there are situations where lack of useful genetic variability is considered the potential rate-limiting factor for genetic progress (Shands and Weisner, 1991, 1992; Simmonds, 1993; Kannenberg and Falk, 1995).

For all crops, both farmers and breeders have to date only used a fraction of the

plant genetic resources that are available. Although gains have been achieved from the tapping of this fraction of genetic resources by plant breeding, these gains have been limited (Fehr, 1981; Gepts, 1998). Current breeding efforts, for valid reasons of practical expediency, often tend still to exploit the genetic variability which was inherent in early founder populations and which resulted from early cycles of selection. In such instances breeding progress becomes increasingly difficult with each cycle until a genetic ceiling on improvement is approached, unless significant new variability is introduced into breeding populations (Kannenberg and Falk, 1995; Gepts, 1998).

While yield increases for some crops have been significant in some countries, in other countries (or agroenvironments) they have been much less spectacular. For instance, yields of maize in the Central American region have remained well below the global average since 1961. The same applies to sorghum and millet in East Africa, cassava in Central Africa, potato in South America and sweet potato in East Africa (FAO, 1998). For some crops, there has been little progress in almost all environments. For example, dry bean yields have remained on a plateau globally since the 1950s (McClellan *et al.*, 1993; Gepts, 1998). On a local level, some landraces may actually have a quite narrow genetic base because of genetic bottlenecks due to past events (Wood and Lenné, 1996). Such bottlenecks can limit the response to selection that breeders (or farmers) can achieve in improving their crops.

In some instances there may be a need to facilitate the broadening of breeding or cultivated populations in key staple crops to remove (or reduce) barriers to yield increases due to limited genetic diversity (Simmonds, 1993; Kannenberg and Falk, 1995). For other crops, it may be pointless to broaden the genetic base *per se*. In distinguishing between such instances it is the authors' assertion that it will be useful to initially identify in what geographic regions the genetic base has been narrowed due to its evolutionary history since (and during) domestication, and then look at other factors (yield plateau, yield gain rate, etc.) to determine whether a genetic base-broadening exercise may be warranted or not.

This chapter therefore looks at a range of factors over both time and geography that can affect the levels of genetic diversity found in crop plants. In particular the chapter focuses on factors that can cause genetic bottlenecks or loss of useful genetic diversity to occur. The authors recognize that genetic diversity is lost as a result of anthropogenic or natural selection and do not equate such purging/purifying selection (elimination of deleterious or undesirable alleles) with the largely undefined concept of genetic 'erosion' (Allard, 1996; Smale, 1997; Wood and Lenné, 1997).

Genepools for Crop Improvement

An essential starting point for any meaningful genetic base-broadening effort will be to assess the extent of utilization of the crop's genetic resources to date and whether this can be (or needs to be) improved to meet future socioeconomic needs (Smartt, 1986). The genepool concept of Harlan and de Wet (1971) provides a good basis for categorizing plant genetic resources according to their ease of use for plant breeding or cultivation (see Box 2.1).

Most crop genepools are typically depauperate for some agronomically desirable traits (e.g. protein quality, biotic or abiotic stress tolerance, etc.) that may only be avail-

Box 2.1. Genepools of crop genetic resources.

In the classification of Harlan and de Wet (1971), for each crop species there are three genepools of genetic resources:

- The primary genepool (GP-1), which refers to germplasm within which sexual recombination is readily accomplished as a result of cross-hybridization (i.e. the true biological species). This category includes landraces, cultivars in current use, obsolete cultivars and many breeders lines. This category also includes the conspecific wild progenitor (Dobzhansky, 1937; Mayr, 1963).
- The secondary genepool (GP-2), which refers to germplasm within which crosses with the cultivated species are difficult but can be achieved using conventional plant breeding methods. Hybrids may be weak or partially sterile, chromosomes may pair poorly and there may be differences in ploidy levels. This category includes non-conspecific wild relatives of the cultivated species, as well as other cultivated species belonging to the same genus.
- The tertiary genepool (GP-3), which refers to germplasm where sexual recombination is possible only by advanced breeding or biotechnological techniques. This category would include many distant wild relatives of the cultivated species (or even different genera) from which gene transfer through sexual recombination is possible but is very difficult. Embryo culture of either the hybrid or its offspring may be needed or bridging crosses may be necessary to transfer germplasm from this genepool to GP-1.

able in the sexually inaccessible genepools of other crops or species. Many transgenic approaches to crop improvement hence arise from a lack of suitable conventional approaches to dealing with a particular agronomic problem or need (Spillane, 2000). Where lack of an agronomic trait seriously limits agricultural productivity, transgenic approaches may provide new options for 'phenotypic' base-broadening where current options for trait selection or generation are lacking in their efficacy or existence (Thro and Spillane, 2000). It is now necessary to consider a fourth (or quaternary, GP-4) genepool to reflect recent technological advances in plant molecular biology and genomics. Such a genepool would refer to any useful germplasm, which can be harnessed from species that are sexually incompatible with the crop species.

Plant transformation techniques such as *Agrobacterium*-mediated transformation and biolistics allow the precise transfer of genes from any organism into either plant nuclear (Walden and Wingender, 1995) or chloroplast genomes (Svab and Maliga, 1993; Daniell *et al.*, 1998). The many examples of the application of gene transfer from microorganisms through genetic engineering techniques range from the introduction of vaccine antigen genes to aluminium tolerance genes to food plants (e.g. Mason *et al.*, 1996; de la Fuente, 1997; Arakawa *et al.*, 1998; Cheng *et al.*, 1998). Many isolated plant genes are now also being transferred between sexually incompatible crop plant species (e.g. Whitham *et al.*, 1996; Molvig *et al.*, 1997; Wilkinson *et al.*, 1997).

The evolutionary relationships between sexually compatible (and incompatible) crop genepools are being elucidated. Recent advances in comparative molecular mapping between different crops (e.g. the *Gramineae*) open hitherto unknown possibilities for uniting the genetics of different crop species in the grass family (Bennetzen, 1998; Gale and Devos, 1998; Kellogg, 1998; McCouch, 1998). It may even be possible to develop a unified genetic map of higher plants, which spans both monocots and dicots

(Paterson *et al.*, 1996; Bevan and Murphy, 1999). The application of molecular markers to genetic linkage maps of a wide range of crops is allowing the identification of the chromosomal (physical) locations of genes for improving yield and other complex traits important to agriculture (McCouch *et al.*, 1997). The underlying genetics of a wide range of quantitative agronomic traits is being dissected through the identification of quantitative trait loci (QTLs) using a combination of molecular markers and advanced statistical breeding procedures. These developments will provide increased opportunities for understanding the genetic basis of adaptation across different crop species and applying the knowledge gained from one crop gene pool to promoting the development of adapted germplasm in the primary gene pool of another crop (Hoisington *et al.*, 1996; Devos and Gale, 1997; McCouch, 1998; Sasaki, 1998).

Genomics is a term that is used to describe the development and application of large-scale, high-throughput and parallel-processing approaches to the functional analysis of entire genomes or genetic systems (Bouchez and Hofte, 1998). Genomics technologies include large-scale genome sequencing efforts such as those now completed for *Arabidopsis* and rice (Rounsley *et al.*, 1998). Emerging genomics technologies such as 'DNA chip' and microarray technologies can allow the function of tens of thousands of different genes to be analysed simultaneously in parallel (Baldwin *et al.*, 1999; Kurian *et al.*, 1999; Zweiger, 1999). Genomics initiatives are both generating genetic markers and identifying genes that can be used either for marker/gene-assisted selection, or the development of transgenics with improved novel agronomic properties (Phillips and Freeling, 1998; Dellapenna, 1999; Sommerville and Sommerville, 1999; Suarez *et al.*, 2000). Genomics technologies will provide powerful tools for both the analysis and broadening of the genetic base of crop gene pools (Lee, 1998; Sniegowski, 1999; Spillane, 2000).

Promoting Useful Geneflow for Crop Improvement

Geneflow refers to the movement of genes among populations of crops and related taxa, or the introduction of genes from related taxa into the recipient gene pool of a crop. Such geneflow can be induced by humans (as in plant breeding) or can occur spontaneously between crops and wild relatives. The latter phenomenon is less well understood. Using the Harlan and de Wet (1971) classification, it is evident that geneflow can occur at different taxonomic levels – intraspecific, interspecific and intergeneric. The extent of spontaneous geneflow is governed by many factors such as the breeding system of the crop, the distribution pattern of the crop and its wild relatives, the mode of pollination and dispersal, planting design of the crop, inter-plant distances, longevity of individuals and population sizes (Levin and Kerster, 1974; Klinger *et al.*, 1992; Hamrick *et al.*, 1995). The more geneflow capacity is limited, the more between-population genetic differentiation is predicted to increase (Wright, 1965). High levels of gene flow can homogenize population structure and counteract the effects of drift and diversifying selection. High levels of gene flow into small populations can also reduce local variation, prevent local adaptive differentiation and reduce fitness (Slatkin, 1987).

While both breeders and farmers generally focus their crop improvement efforts on what materials are available to them from the primary gene pool, some plant

breeders and biotechnologists also attempt to move useful genetic resources (i.e. promote geneflow) from the secondary, tertiary and quaternary genepools into the cultivated primary genepools. For most crops, much of the useful genetic diversity available in the primary, secondary, tertiary or quaternary genepools has not, to date, been used over a wide range of agroenvironments either by breeders or by farmers (Smartt, 1984). Table 2.1 provides some examples of the genepools of a number of crop species.

While the direction of geneflow can be both to and from the crop, in this Chapter we are concerned with geneflow into and within the primary gene pool. We do not focus on 'outward' geneflow from the primary gene pool to the secondary and tertiary genepools, which is a topic that has recently become subject to much investigation

Table 2.1. The primary, secondary and tertiary genepools of selected crops.

Crop	Primary gene pool	Secondary gene pool	Tertiary gene pool	References
Barley	<i>Hordeum vulgare</i> <i>H. spontaneum</i>	<i>H. bulbosum</i>	<i>Hordeum</i> spp. Triticeae	Bothmer <i>et al.</i> , 1983; Valkoun <i>et al.</i> , 1997
Bread wheat	<i>Triticum aestivum</i>	<i>Triticum</i> spp. <i>Aegilops</i> <i>Secale</i> <i>Thinopyrum</i> <i>Haynaldia</i> <i>Leymus</i>	Other Triticeae spp.	Dubin <i>et al.</i> , 1997
Cassava	<i>Manihot esculenta</i>	Over 80 wild <i>Manihot</i> spp.		Bonierbale <i>et al.</i> , 1997
Common bean	<i>Phaseolus vulgaris</i>	<i>P. coccineus</i> , <i>P. costaricensis</i> , <i>P. polyanthus</i>	<i>P. acutifolius</i> , <i>P. lunatus</i> and other <i>Phaseolus</i> spp.	Debouck, 1991; Schmit and Debouck, 1991; Schmit <i>et al.</i> , 1993; Llaca <i>et al.</i> , 1994; Freytag and Debouck, 1996; Hidalgo and Beebe, 1997
Chickpea	<i>Cicer arietinum</i> ; <i>C. reticulatum</i> ; <i>C. echinospermum</i>	None	<i>C. bijugum</i> ; <i>C. pinnatifidum</i> ; <i>C. judaicum</i> ; <i>C. chorassanicum</i> ; <i>C. montbretii</i>	Muehlbauer <i>et al.</i> , 1994; Singh <i>et al.</i> , 1997
Groundnut	<i>Arachis hypogaea</i> <i>A. monticola</i>	Section <i>Arachis</i>	<i>Arachis</i> spp.	Smartt, 1984; Singh and Nigam, 1997
Lentil	<i>Lens culinaris</i>	None	<i>L. nigricans</i>	Muehlbauer <i>et al.</i> , 1994; Robertson and Erskine, 1997
Sugar cane	<i>Saccharum officinarum</i> ; <i>S. barberi</i> <i>S. edule</i> ; <i>S. sinense</i> ; spp.; <i>S. robustum</i> ; <i>S. spontaneum</i>	<i>Erianthus</i> spp.; <i>Imperata</i> spp.; <i>Miscanthus</i> spp.; <i>Narenja</i> spp.; <i>Nephia</i> spp.; <i>Neyrudia</i>		Anderson and Miller, 1995
Sweet potato	<i>Ipomoea batatas</i>	Approx. 400 wild <i>Ipomoea</i> spp.		Huaman and Zhang, 1997

because of perceived risks of gene flow from transgenic crops to their wild relatives. Such 'biosafety'-related gene flow continues to be well researched and reviewed elsewhere (Schmitt and Linder, 1994; Lefol *et al.*, 1996; Mikkelsen *et al.*, 1996; Linder *et al.*, 1998). This chapter looks at some of the factors that are barriers to deliberately promoting useful gene flow from the secondary and tertiary gene pools into the primary cultivated gene pool. We also look at barriers to useful gene flow within the primary cultivated gene pool and how this is important for the development of germplasm adapted to specific agroenvironments. All of these barriers can represent constraints to broadening the genetic base of the primary cultivated gene pool of any crop.

Genetic Bottlenecks in the Continuing Evolution of the Primary Cultivated Gene Pool

During their evolutionary history, all crops have been subjected to genetic bottlenecks and subsequent founder effects, over both time and geography. A genetic bottleneck occurs when the genetic diversity of a population is reduced due to a decrease in its population size because of some event (Nei *et al.*, 1975). Founder effects refer to situations where a new effective population is derived from a limited number of individuals representing a small sample of the genetic pool from which they were derived (Mayr, 1942). Smaller population sizes are more prone to loss of rare alleles or allelic combinations because of genetic drift (Wright, 1965). The overall result is decreased genetic variability in the new population.

Founder effects can affect subsequent response to both artificial and natural selection pressures (James, 1971). Founder effects can sometimes lead to a morphologically distinct species or race, when the founder population's gene pool undergoes what Mayr (1954) called a 'genetic revolution' to develop new coadapted gene complexes, in response to new selection pressures (Templeton, 1981). Quantitative variation may harbour potentially strong epistatic components, and such cryptic epistatic variation may become important when allele frequencies are substantially disturbed by selection or a population bottleneck (Goodnight, 1987; Wade, 1992).

Alterations in a small number of key genes could potentially have major effects on the genotype and morphology as a whole (Wilson *et al.*, 1974; Hedrick and McDonald, 1980; Carson and Templeton, 1984; Lande, 1985). This may have been the case in the domestication of some of the cultivated cereals and legumes (Doebley *et al.*, 1995, 1997; Paterson *et al.*, 1995; Koinange *et al.*, 1996). Indeed, recent work further suggests that changes in the regulatory (rather than protein encoding) region of key genes (e.g. *teosinte branched 1*) involved in domestication may be responsible for some of the major phenotypic effects that occurred during domestication (Doebley and Lukens, 1998; Wang *et al.*, 1999).

In any crop's evolutionary history, genetic bottlenecks and subsequent founder effects are likely to have occurred at all levels of geographical scale. For instance, domestication events will have contributed to global bottlenecks for most crops while crop migration events are likely to have contributed to more regional bottlenecks. However, genetic bottlenecks will also have occurred at national and local levels. For many crops, genetic diversity is likely to have been lost over time from what was domesticated due to random genetic drift caused by small population sizes resulting

from either new crop introductions or crop failures. Such founder events will have been an extremely important factor in narrowing the genetic base of many crops, especially where their cultivation has moved beyond their centre of diversity/origin.

The following sections attempt to look at factors that contribute to genetic bottlenecks of crop genetic diversity/resources over time, geography or both.

Founder effect of domestication

As humans migrated over the past 10,000 years, they moved domesticated crops beyond their initial centres of origin and diversity (Smith, 1995; Diamond, 1997). The earliest protocrops are likely to have spread along with the cultural diffusion of the idea of cultivating plants. It is probable that the first farmers chose to grow the first domesticates where they could be grown, rather than domesticate a new set of crop plants for each new location. In many crop plants, the number of genes controlling the essential agronomic traits of non-shattering of seed and reduction of seed dormancy is small. During the domestication process involving the sowing of wild seeds, it is likely that once these agronomic traits had become fixed in a cultivated population there would have been little rationale to continue sowing seeds of the wild plant, once the domesticated type had been established (Ladizinsky, 1985).

Some plant species with good potential in domestication could therefore quite feasibly due to phylogeographic accidents have been totally neglected by the earliest farmers (Smarrt, 1986). The earliest domestication events for instance were biased in favour of annual rather than perennial cereal crops (Francis, 1990; Pimm, 1997). They were also probably biased in favour of sexually reproducing crops which easily generated visible variation in their progeny for subsequent selection (Jefferson and Bicknell, 1997). The proto- or initial domesticates did not inherently have an outstanding agronomic potential nor did they have high levels of genetic diversity. In many locations, this limited initial diversity is likely to have been added to only marginally since (Simmonds, 1993; Rasmusson and Phillips, 1997).

The selection pressures for many traits (e.g. ripening, seed size, germination, non-dehiscence, palatability, etc.) associated with domestication are likely to have fixed alleles of major effect (Knight, 1948; Hilu, 1983; Gottlieb, 1984). Major effect genes are proposed to be the basis for the selection of the tomato 'fruit' (Paterson *et al.*, 1991; Paterson, 1995) and the transformation of the teosinte inflorescence into the maize 'ear' (Doebly *et al.*, 1997). One gene, *Sb1*, accounts for the difference between shattering and non-shattering sorghum types (Paterson *et al.*, 1995). Paterson *et al.* (1995) demonstrated that the domestication of sorghum, rice and maize is due predominantly to a small number of major effect homologous genes conferring phenotypes such as large seed size, seed dispersal and daylength insensitive flowering that were convergently selected for in the three species. Such genetic changes largely define the basic biological differences between wild and cultivated germplasm.

The first genetic bottleneck event, for any crop selected for domestication, is likely to be the actual initial domestication of the crop, the earliest of which took place some 7000–10,000 years ago. Most of our major food crops were initially domesticated by 5000 years ago, at which stage only a small part of the wild gene pool is likely to have been brought under cultivation (Ladizinsky, 1985; Doebly, 1989; Gepts, 1995). The

initial domestication of each crop species by the earliest farmers represented a selection process, which *de facto* would have reduced genetic diversity in the incipient crops (Ladizinsky, 1985; Allard, 1988; Debouck and Tohme, 1989; Doebley, 1992; Gepts, 1995).

Numerous studies of the relative genetic variability found in cultivated versus wild progenitors demonstrate that the wild species are generally more variable than the corresponding crop (Chapman, 1989; Gepts, 1995). Among many crops, this has now been shown for barley (Brown and Clegg, 1983; Petersen *et al.*, 1994), soybean (Doyle, 1988), pearl millet (Gepts and Clegg, 1989), lentil (Havey and Muehlbauer, 1989), sunflower (Arias and Rieseberg, 1995; Cronn *et al.*, 1997) and rice (Cordesse *et al.*, 1990). However, this is not an absolute rule. In comparisons between the cultivated and wild forms of sorghum, few novel alleles were identified in the wild genepool (Deu *et al.*, 1995; de Oliveira *et al.*, 1996). In addition, some parts of the genome may show increased variation caused by selection under domestication (Gepts, 1995).

For most crops, a wild conspecific progenitor species forms part of the primary genepool (GP-1) and crosses of the conspecific progenitor are usually possible with the cultivated forms. Nevertheless, it is likely that much of the available genetic diversity in the wild progenitors of many crops has rarely been used or comprehensively harnessed either by farmers or by breeders since the earliest domestication. Evolutionary studies (Table 2.2), which conclusively identify the wild progenitors of crop plants, therefore provide valuable information for initiatives to broaden the genetic base of the cultivated genepool of crops (Gepts, 1995).

Gene exchange between many crops and their non-conspecific wild relatives is often highly restricted (Harlan, 1965). Various isolating mechanisms prevent natural hybridization between sympatric cultivated and wild plants (e.g. Robert *et al.*, 1991). If gene flow occurs, it may be more likely to occur in the direction from the cultivated to

Table 2.2. Examples of closest wild relative of diploid species identified or confirmed using molecular markers (see Gepts, 1995 for references).

Crop	Cultigen	Closest wild relative
Avocado	<i>Persea americana</i> var. <i>guatemalensis</i>	<i>P. steyermarkii</i> (female) ♀ <i>P. nubigena</i> (male)
Barley	<i>Hordeum vulgare</i> ssp. <i>vulgare</i>	<i>Hordeum spontaneum</i>
Common bean	<i>Phaseolus vulgaris</i> var. <i>vulgaris</i>	<i>P. vulgaris</i> var. <i>aborigineus</i> and <i>mexicanus</i>
Groundnut	<i>Arachis hypogea</i>	<i>A. monticola</i>
Lentil	<i>Lens culinaris</i> ssp. <i>culinaris</i>	<i>L. culinaris</i> ssp. <i>orientalis</i>
Lettuce	<i>Lactuca sativa</i>	<i>L. serriola</i> and other unidentified wild taxa
Maize	<i>Zea mays</i>	<i>Z. mays</i> ssp. <i>parviglumis</i> (Balsas and Jalisco)
Pea	<i>Pisum sativum</i>	<i>P. humile</i>
Pearl millet	<i>Pennisetum glaucum</i>	<i>P. glaucum</i> ssp. <i>monodii</i>
Rice	<i>Oryza sativa</i>	<i>O. rufipogon</i>
Rice	<i>Oryza glaberrima</i>	<i>O. breviligulata</i>
Sorghum	<i>Sorghum bicolor</i>	<i>S. bicolor</i> ssp. <i>arundinaceum</i>
Soybean	<i>Glycine max</i>	<i>G. soja</i>
Tomato	<i>Lycopersicon esculentum</i>	<i>L. exculentum</i> var. <i>cerasiforme</i>

the wild populations, because of farmer selection against wild \times domesticated hybrids. However, spontaneous gene flow between a crop and its wild relatives has been documented for many crops, including barley (Svitashev *et al.*, 1994), beans (Singh *et al.*, 1991a,b; Beebe *et al.*, 1997), carrot (Wijnheijmer *et al.*, 1989), cotton (Brubaker *et al.*, 1993), foxtail millet (Boudry *et al.*, 1993), maize (Doebley, 1990), quinoa (Wilson and Manhart, 1993), radish (Klinger *et al.*, 1992), rice (Langevin *et al.*, 1990), sugarbeet (Boudry *et al.*, 1993), squash (Wilson, 1990), sunflower (Arias and Rieseberg, 1994) and tomato (Rick, 1974). The agronomic significance of such gene flow is unresolved (Wood and Lenné, 1996). Even today, the induced gene flow of genetic resources from both wild relatives and conspecific progenitors via plant breeding into the cultivated gene pools is still limited and often concerns the introgression of a few major genes for disease or pest resistance via recurrent backcrossing (Simmonds, 1993; Rasmusson and Phillips, 1997).

Polyploidy-induced domestication bottlenecks

The adaptive benefit of polyploidy is largely unknown (de Wet, 1979; Leitch and Bennett, 1997; Wendel, 1999). However, almost 80% of crop species are polyploid (Grant, 1963). Some crops, such as wheat, have been domesticated or have arisen as a result of polyploidization events. The fitness of novel polyploids relative to their progenitors can be partially increased if the new polyploid is self-fertile and perennial. Hence, polyploidy is much more common in perennial species than annual ones, and most allopolyploid species are self-fertile (MacKey, 1970; Stebbins, 1971). In general, polyploidization may offer novel avenues for phenotypic response to selection (e.g. Wright *et al.*, 1998). Repeated cycles of hybridization and polyploidy have played an important role in the evolution of wheats, sugar cane, potato, sweet potato, yams and plantain. Wild polyploid complexes can generate variants that are of agricultural value, as in the case of taro where numerous cultivated races have been selected from the wild (Kuruvilla and Singh, 1981).

Where diploid progenitor species produce measureable amounts of unreduced gametes (e.g. in potato, cassava, cotton, strawberry and cherry), it is more likely that derived polyploids will have originated repeatedly in time and geography (Harlan and de Wet, 1975). However, polyploidization events, which have occurred infrequently or over a local scale, can represent a genetic bottleneck to gene flow from the wild progenitors into the cultivated gene pool. Of the two major types of polyploids, this bottleneck effect applies in particular to allopolyploid crops because allopolyploids have originated from chromosome doubling of sterile interspecific diploid hybrids or the union of unreduced gametes (Ladizinsky, 1985). Many important crops such as hexaploid wheats (*Triticum aestivum*), tobacco (*Nicotiana tabacum*), rape (*Brassica napus*) and cotton (*Gossypium hirsutum*) are allopolyploids. Allopolyploids, unlike autopolyploids, can lead to entirely new gene combinations and hence novel phenotypes. Cotton provides a good example of a likely genetic bottleneck due to allopolyploidy. Most commercial cotton varieties belong to *G. hirsutum* L. (upland cotton). The development of upland cotton from hybridization and polyploidization in the New World between *G. raimondi* and the introduced species *G. herbaceum* is likely to have constituted a significant genetic bottleneck event in the domestication of upland cotton (Ladizinsky,

1985). Polyploidization can also lead to new and useful gene interactions. This feature has been suggested by Leitch and Bennett (1997) in general for plants and by Jiang *et al.* (1998) specifically for cotton. The latter authors observed a bias of QTLs for seed fibre traits towards the D genome, although the D genome ancestor does not produce fibres.

While the progenitors of many allopolyploid species are known to possess useful genetic variation, such genetic resources are not easily accessible because of chromosomal and endosperm imbalances in crosses. Hence, they have rarely been used in plant breeding to date. F_1 hybrids between allopolyploids and their progenitors are usually sterile. In most instances, promoting gene flow from the progenitors into the primary gene pool of allopolyploids cannot be done by regular crosses and requires the use of embryo rescue and other wide crossing technologies. However, for some other crops such polyploid barriers are not insurmountable. For instance, many wild *Solanum* species can readily be crossed with the cultivated potato once their ploidy level is experimentally adjusted by chromosome doubling or haploidization. However, accessing genetic variability in some of the wild species such as *S. tuberosum* and *S. brevidens* requires more complex bridging crosses and chromosome adjustment (Hermsen, 1989). Polyploidy may be a barrier to interspecific gene flow in some legumes (e.g. *Phaseolus*) but not in others (e.g. *Arachis*) (Smartt, 1986). Polyploidy can sometimes act as a genetic bridge between different diploid gene pools (Dewey, 1980), as in the case of the wild *Aegilops* species of wheat (Zohary, 1965).

Crossability barriers limit gene flow

While the gene pools of many crop wild relatives may be known to contain agronomically useful germplasm, there are often significant technical barriers to obtaining viable hybrids between the primary gene pool and wild species in the secondary and tertiary gene pools (Muehlbauer *et al.*, 1994). Many types of reproductive isolating barriers can reduce the level of gene flow possible between species or even between populations. Combinations of such barriers can result in reproductive isolation, i.e. no gene flow. A significant element of plant breeding to broaden the genetic bases of crops is concerned with finding ways to overcome such isolating barriers, so as to gain access to novel and useful genetic variation. There may be extensive genetic variation in crossability of some cultivated genotypes with wild relatives, as is the case for wheat (Jiang *et al.*, 1994) and *Phaseolus* sp. (Parker and Michaels, 1986; Koinange and Gepts, 1992). Reproductive isolation, incompatibility barriers, embryo or endosperm abortion, hybrid sterility and limited levels of genetic recombination are significant obstacles to the greater use of wild germplasm. These obstacles are in addition to those of undesirable linkages to non-agronomic traits once gene flow has been achieved.

Reproductive isolating barriers can be of two general types: (i) pre-mating barriers or (ii) post-mating barriers. There can be different types of pre-mating barriers to gene flow between populations of the same or different species. These include ecogeographic, temporal, floral and gametic incompatibility. Ecogeographic barriers exist when habitats are distinct and hence the populations rarely come into contact. For instance, an ecogeographic barrier exists between the common bean, *P. vulgaris*, and the runner bean, *P. coccineus*. The former is found in warm to temperate areas and the

latter is found in the cool, humid uplands of Mexico and Central America (Delgado Salinas *et al.*, 1988; Debouck, 1991). In addition, populations of *P. coccineus* can be reproductively isolated because of differences in pollinator distribution: at higher altitudes, *P. coccineus* flowers are visited by hummingbirds, whereas at lower altitudes they are visited by bumblebees (Búrquez and Sarukhan, 1980). Seasonal isolation can occur when plants mature at different times with little to no overlap between the flowering periods to allow hybrid formation. Gametic incompatibility occurs when foreign pollen grains cannot germinate on another species' stigma or cannot grow down the style to reach the ovaries. Alternatively, pollen grains sometimes do function on an allochthonous stigma or style, but they are less competitive than the autochthonous pollen (e.g. Robert *et al.*, 1991; Carney and Arnold, 1997). A wide range of gametic incompatibility barriers is observed in crosses between white and purple flowered species of *Capsicum* (Zijlstra *et al.*, 1991).

There is also a range of post-mating barriers to gene flow between populations of the same or different species. These include hybrid inviability, hybrid sterility and hybrid breakdown. Hybrid inviability occurs when hybrids are weak and have poor survival, such as occurs with most crosses between species in the secondary and primary crop gene pools. An example of such hybrid inviability is provided by endosperm balance number (EBN) differences between species (Ehlenfeldt and Ortiz, 1995; Spillane *et al.*, 2000). To achieve normal endosperm development, EBNs must typically be in a 2:1 maternal:paternal ratio (Johnston and Hanneman, 1982). EBNs can, however, be manipulated by ploidy changes to overcome endosperm development problems and obtain new hybrids (e.g. Carputo *et al.*, 1997). Hybrid sterility occurs when the hybrids do not produce functional gametes and are hence sterile, as occurs in crosses between the cultivated rices *Oryza sativa* and *O. glaberrima*. Hybrid breakdown is observed when F₂, backcross and later generation hybrids have reduced viability or fertility as is seen in many of the F₂ populations of interspecific bean crosses (Hucl and Scoles, 1985).

Gene flow can be limited by both chromosomal (structural) and genic factors. Rieseberg and colleagues (1995a,b) have provided evidence for both types of barriers in *Helianthus* sp. They showed that rapid genomic reorganization following hybridization appeared to have taken place in *Helianthus anomalus*, relative to its two parental species, *H. annuus* (sunflower) and *H. petiolaris* (Rieseberg *et al.*, 1995a). In effect, this reorganization isolated *H. anomalus* from its parents and allowed it to diverge to become a separate species. Between *H. annuus* and *H. petiolaris* both chromosomal and genic factors play a role, as shown by the level of introgression of mapped markers into advanced backcross populations (Rieseberg *et al.*, 1995b).

Because of such mating barriers, the wild relatives of many crops (e.g. cowpea, chickpea, groundnut, millets) are often organized into sections based on their chromosome numbers, morphology and their crossability with each other and the cultigen(s). The defining feature of a section is often a genetic barrier to crossability with another section. For instance, there are three crossability sections in the *Cicer* genus, which contains the cultivated chickpea *C. arietinum*. Of the 40 species in the *Cicer* genus, only *C. reticulatum* and *C. echinospermum* can be crossed with cultivated chickpea (Singh and Ocampo, 1997). In such instances, major constraints to gene flow exist between different sections (Muehlbauer *et al.*, 1994). Similarly, over 1500 Asian rice cultivars which were classified into six different phyletic groups by molecular analysis exhibit various

levels of sterility in inter-group crosses but not in intra-group crosses (Glaszmann, 1987; Khush, 1997).

The research area of wide hybridization, especially of the less commercial crops, is considered to be a neglected area for research funding and for international coordinated efforts which are strongly linked to breeding programmes (Duvick, 1989). Yet, continuing advances in wide crossing techniques such as hybrid embryo culture (Sharma *et al.*, 1996) and the development of novel crossing strategies (e.g. bridge crosses) are making the wild gene pools of many crops ever more accessible (Stalker, 1980; Muehlbauer *et al.*, 1994). For instance, wide crosses in wheat have become very successful since the advent of successful embryo rescue techniques (Jiang *et al.*, 1994; Sharma, 1995). The success rate of gene transfer in such wide crosses can be increased by knowledge of the chromosome pairing mechanisms and their genetic control. Such knowledge is essential to promote recombination between heterologous or homologous chromosomes if one is to minimize (or maximize) the size of the introgressed chromosome segment(s) (e.g. Luo *et al.*, 1996a,b). It is likely that continuing advances in structural genomics (e.g. comparative mapping) and genetic engineering (e.g. crossability transgenes) will result in new strategies for wide hybridization.

Inbreeding and outbreeding depression affect geneflow

Outbreeding depression (or hybrid dysgenesis) is the population level counterpart to genetic mechanisms separating species or subspecies. Hybrid plants within individual populations of species are usually normal, but hybrids between different populations of the same species are sometimes weak or inviable (Wallace, 1968). Within crop species, this can be a barrier to geneflow between different populations. For example, the large- and small-seeded gene pools of common bean (*P. vulgaris*) from the Andes and Mesoamerica, respectively, sometimes give rise, when crossed, to lethal or weak progeny. In the F_1 , the lethality is due to two complementary loci (Gepts and Bliss, 1985; Gepts, 1988). In subsequent generations, numerous genes appear to be involved (Welsh *et al.*, 1995; Singh and Molina, 1996; W.C. Johnson and P. Gepts, unpublished results).

In cultivated populations that evolved sympatrically with their wild progenitors, mechanisms that prevent or restrict geneflow among populations are selectively advantageous. Marchais (1994) has suggested the existence of a genetic isolating mechanism between pearl millet and its wild relative in West Africa. Nevertheless, efficient reproductive isolating mechanisms are rare within the primary gene pool, even among races/populations that have remained sympatric for thousands of generations. Among differently adapted cultivated and wild populations, disruptive selection is the primary mechanism that restricts geneflow. The most common mechanisms isolating sympatric races of the same crop species from each other are differences in flowering time and gametophytic or sporophytic systems that prevent cross-fertilization. Cultivated fields of African rice (*O. glaberrima*) are often invaded by populations of its wild relative, *O. barthii*. A dominant allele in each species makes hybrid progeny weaker than either parent and hence reduces geneflow from one species to the other (Chu and Oka, 1972).

Inbreeding depression has been documented for most investigated plant species,

even highly selfing species (Charlesworth and Charlesworth, 1987). In plant breeding, inbreeding depression can be an impediment to the increased use of exotic germplasm (Spillane *et al.*, 2000). For example, use of open-pollinated tropical maize populations in a US maize breeding programme indicated that inbreeding depression for yield may be severe in some exotic populations (Goodman, 1992). Plants can also exhibit a phenomenon of 'optimal outcrossing distance' which may have a major bearing on what types of crosses yield the most fit or immediately favourable progeny (Waser, 1993). Such a phenomenon can be associated with either inbreeding or outbreeding depression (Lynch, 1991). These latter two phenomena are still poorly understood genetically yet can affect what germplasm is of more immediate utility in plant breeding (Spillane *et al.*, 2000).

Mating system effects on geneflow

One of the most important evolutionary factors affecting geneflow within a crop gene pool is the mating behaviour of the crop. The mating system of a crop affects the geographic distribution of genetic variation within the crop (Schoen and Brown, 1991). Plants may be either mainly self-fertilized (inbreeding species) or there may be inherent biological barriers to self-compatibility such that an egg cell is normally only capable of being fertilized by pollen of a different genotype of that species (outbreeding species). The mode of reproduction of the crop in farmers' fields may sometimes differ from that of the species from which the crop is derived, as is the case for vegetatively propagated crops such as sugar cane, potato, orchard crops and soft fruits. Most vegetatively propagated crops are outbreeders in which methods of clonal reproduction are used to bypass sexual reproduction. Also, among sexually propagated crops such as tomato there has been a long-term trend towards increase in autogamy (Rick *et al.*, 1977). This trend is attributable to several causes, such as the preference for 'true-to-typeness' and the possible absence of suitable pollinators in areas outside the domestication area.

Some genetic systems limit genetic recombination and therefore can act to maintain coadapted gene complexes. For instance, chromosomal rearrangements and tight genetic linkage can hold coadapted genes together by limiting recombination (Stebbins, 1971). Inbreeding and asexual (apomictic) reproduction can also have the same effect, although these systems tend to fix whole genomes rather than blocks of genes. Asexual reproduction can occur because of agamospermy in which viable seeds arise without fertilization or by vegetative propagation via structures such as stolons, tubers, rhizomes or suckers. Many important crops are vegetatively propagated through tubers (potato, yams, sweet potatoes) or artificially via cuttings (banana and cassava). Very few crops are obligate apomicts. In some crops such as *Bracharia*, sugar cane and some fruit crops, apomixis, polyembryony and predominant asexual reproduction are barriers to geneflow and account for limited utilization of germplasm due to the difficulty of breeding such crops (Savidan, 2000).

Self-pollination is also a barrier to geneflow. While outbreeding crop species are usually characterized by wide genetic polymorphism, high levels of heterozygosity and recombination in each sexual cycle, self-fertilization brings about drastic reductions in recombination and the splitting of the progeny population into homozygous, true

breeding lines (genotypes), which maintain genetic variation in tight multilocus gene combinations (Allard, 1996; Pérez de la Vega, 1996). While selection operates mainly at the level of the individual genes in outcrossing plants, it operates at the level of the individual genotypes in the case of self-fertilizing plants. The multilocus genotypes in selfing plants can be very tightly associated with definable micro-niches, soil types and climatic conditions.

In populations of selfing plants, genetic variability is maintained by the coexistence of different homozygous lines and genetic flexibility is maintained by low levels of outcrossing, which result in the recombination and production of numerous new homozygous combinations (Allard, 1996; Pérez de la Vega, 1996). On the other hand, an outcrossed, heterozygous species has a considerable amount of genic flexibility with which to meet environmental change, but selfing homozygous species may be better adapted to specific unchanging conditions. An intermediate strategy with variable outcrossing rates may yield the greatest long-term success in an unpredictable world; this may be why few extreme selfers or outcrossers are found (Allard, 1988).

Founder effects of geographic movements of crops

Since the advent of agriculture, long-distance crop movements or dissemination have always occurred and continue to this day. By their nature, such crop movements do not lead to the even distribution of the genetic variability of crops, and many crops are likely to have been subjected to significant genetic bottlenecks during movement from one location to another (Simmonds, 1995). Crop migration followed by natural selection over time in the new environment can lead to ecogeographic differentiation of the genetic variation at the new environment (e.g. Allard, 1990; Saghai-Marooft *et al.*, 1990; Zhang *et al.*, 1990). Major crop movements occurred in pre-Columbian times: for example, the movement of African crops such as sorghum, millet (*Panicum* spp.), cowpea (*Vigna unguiculata*), sesame (*Sesamum indicum*) and niger seed (*Guizota abyssinica*) to semi-arid areas of India (Simmonds, 1995). For instance, bananas (*Musa* spp.) had probably reached parts of upland East Africa from their centre of diversity in Asia by the first millennium AD. The dissemination of mung bean (*Vigna radiata*) from its centre of origin in western Asia to Southeast Asia led to a reduction in seed protein diversity (Tomooka *et al.*, 1992).

The Columbian exchange after 1492 was a process which led to an increase in crop movements, in particular of crops previously unknown either within or outside of the Americas or Europe (maize, potato, cassava, sugar cane, banana, tomato, squash, etc.) (Bermejo and León, 1994; Butzer, 1995). Maize emerged as an essential staple in Africa and as a minor staple in India and parts of China. Cassava, sweet potato and groundnut dispersed across Africa. Sweet potato became an extremely important food crop both within and outside of its primary centre of diversity in the Andean region (FAO, 1998). Since its spread beyond Latin America from the 16th century onwards, sweet potato is likely to have undergone many major geographical genetic bottlenecks, especially in its dissemination between smaller islands (Huaman and Zhang, 1997). Much of the genetic diversity available in Latin America has never been used outside Latin America (Z. Huaman, personal communication).

Amaranth (*Amaranthus hypochondriacus*) represents a crop that only reached Asia

(via Europe) in the early 19th century. It has been subjected to significant bottlenecks since its migration from its centre of diversity in the Andean region in the 16th century. Spread of amaranths to higher latitudes in Asia has left behind any races that have flowering delayed by long days. Although far more amaranth is now produced in Asia than in the Americas, most production has relied on a few broadly adapted Mexican *A. hypochondriacus* and *A. cruentus* selections. The extensive diversity present in Latin America appears to have played a limited role in developing regionally adapted germplasm (Kauffman and Weber, 1990).

Genetic bottlenecks due to geographic movements may also have occurred very recently. For instance, present-day US sunflower cultivars may be derived from a number of movement-related bottlenecks. These occurred when sunflower was bred for a variety of uses in Europe and subsequently re-imported back to America, its centre of domestication, during the latter half of the 19th century (Cronn *et al.*, 1997). Similarly, while cultivated soybean (*Glycine max*) originated in China at least 3000 years ago, it was not widely grown outside of Asia until the 1900s and its diffusion was subject to major genetic bottlenecks (Hymowitz and Kaizuma, 1981). The genetic base of cultivated soybean outside of Asia is considered to still be extremely narrow (Shoemaker *et al.*, 1986; FAO, 1998; Dashiell and Fatokun, 1997).

In some regions it is thought that initial crop introductions were based upon extremely narrow genetic bases, such as for potato (Europe), banana (Caribbean) and sugar cane (Caribbean) (Simmonds, 1995). However, it is likely that crops in most locations have been subjected to recurrent introductions of new germplasm following the initial introductions (Simmonds, 1995). Examples include sugar cane to the Americas and potato to the northern temperate environments of Europe and the USA. In some instances, crop movements may have reached the same destination via different routes or from different locations, resulting in different samplings of the primary gene pool. The coconut is thought to have reached Mesoamerica independently via two routes, one trans-Atlantic from Africa and the other trans-Pacific, with the result that the coconuts of the two coasts of Mesoamerica are different (Simmonds, 1995).

It is unlikely that such initial introductions represented anywhere near a full or optimal sampling of the genetic diversity available in the primary gene pool of the crops concerned. In addition, the initial introductions are most likely to have led to genetic and phenotypic inertia effects which may have had 'knock on' effects on dictating which new germplasm was subsequently useful for addition to the crop gene pool at that location.

In some instances, domesticated plants came into contact and hybridized through cultivation in new locations with previously isolated wild or cultivated relatives. The apple, *Malus pumila*, was originally cultivated in the region between the Caspian and Black seas and as its cultivation spread to new locations it hybridized with wild relatives, such as *M. sylvestris* (Europe) and *M. baccata* (East Asia). Interspecific hybridization with wild species following human migration also played an important role in developing better adapted germplasm of grape (*Vitis vinifera*) and peach (*Prunus persica*). The modern strawberry cultivars are the result of the accidental cross in France between two octoploid species introduced from the Americas – *Fragaria chiloense* and *F. virginiana*. In spite of subsequent introgression of additional genetic diversity by breeders, the modern cultivated strawberry gene pool is quite narrow, given the effect of polyploidization and long-distance human dispersal (Graham *et al.*, 1996). For

Table 2.3. Some molecular genetic studies which demonstrate a narrower cultivated genetic base in one region/race relative to another.

Crop	Scientific name	Narrower genetic base region/race/type	Broader genetic base region/race/type	Reference
Cocoa	<i>Theobroma cacao</i>	Nacional type	Forastero, Criollo and Trinitario types	Lerceteau <i>et al.</i> , 1997; Whitkus <i>et al.</i> , 1998
Sweet potato	<i>Ipomoea batatas</i>	USA cultivars	Papua New Guinea cultivars	He <i>et al.</i> , 1995
Wheat	<i>Triticum aestivum</i>	USA hard red spring wheat cultivars	Other USA hexaploid wheat cultivar classes	Chen <i>et al.</i> , 1994
Amaranth	<i>Amaranthus</i> spp.	<i>A. hypochondriacus</i> <i>A. caudatus</i>	<i>A. cruentus</i>	Transue <i>et al.</i> , 1994

example, only two plants of *E. chilense* were introduced initially in France (Sauer, 1993). Many modern plantation crops such as oil palm, coffee, cocoa and rubber have relatively narrow genetic bases due to inadequate initial genetic diversity sampling (Sauer, 1993; Smartt and Simmonds, 1995).

Phenology is an important factor in the success of new crop germplasm introductions. Phenology refers to the study of how periodic biological events – such as flowering, seed dormancy, etc. – relate to climate and other environmental factors. Germplasm from different latitudes and altitudes often has specific temperature and photoperiod requirements and hence will not flower when grown in new locations. Soybean provides an interesting example of a daylength-sensitive crop for which east–west movement is much easier than north–south. Therefore, movement of soybean across latitudes has been very limited (Hymowitz and Kaizuma, 1981). Novel germplasm can only be of utility in a new location if its phenology is well matched to the resources and constraints of its new production environment (Shorter *et al.*, 1991). The timing of phenological events is generally modulated by responsiveness to photoperiod and temperature, with much variation in responsiveness between genotypes (Summerfield *et al.*, 1996). Yet, durations from sowing to flowering are of critical importance if crops are to have the potential to yield well in a new environment (Summerfield *et al.*, 1997). Efforts to broaden the genetic base of lentil in South Asia have had to address phenology as a barrier to gene flow (Erskine and Muehlbauer, 1991; Erskine, 1997). In many instances, unless such germplasm is subjected to sexual recombination (or gene transfer) and then re-selected, the genetic variability is not usually accessible in the new location.

It is now known that important phenological traits may not necessarily be under complex genetic control. For instance, flowering time genes have a major effect on adaptation of genotypes to specific environments. In wheat, these include the genes that control vernalization (*Vrn* genes), response to photoperiod (*Ppd* genes) and ‘developmental rate’ genes (Snape, 1996). There are multiple alleles at all of these loci: for example, the winter versus spring habit in wheat varieties is controlled by one to four major loci; in *Pisum*, four major loci control flowering time (Snape *et al.*, 1976; Murfet, 1977). As a result of increased understanding of the underlying genetics of phenological traits, there may now be some potential to fine-tune the flowering time of

crops to specific environments (Laurie, 1997). For instance, Snape *et al.* (1995) have converted a UK winter wheat into a spring wheat by transferring a vernalization-insensitive allele at the *Vrn1* locus. Such work may open new routes for gene flow between crop gene pools previously isolated as a result of phenological barriers.

Disease-induced genetic bottlenecks

Even where several resistance genes are available for combatting specific pests or pathogens, there is often a reliance at the field level on a few such genes when farmers exhibit preferences for the most successful varieties (Heisey *et al.*, 1997). This results in a risk of crop genetic vulnerability if large areas are planted to a few of the most popular crop varieties which have identical genes for resistance against particular pests or diseases (Smale, 1997). In such instances, neo-virulent pathogens that arise through natural selection or immigration can lead to serious losses of all susceptible genotypes (Mundt, 1994). Crop epidemics due to genetic vulnerability can lead to genetic bottlenecks at the regional or local level and the loss of locally adaptive traits in susceptible varieties. Such an event occurred in the USA when a chestnut blight (*Cryphonectria parasitica*) epidemic destroyed large numbers of chestnut trees which exhibited significant overall genetic heterogeneity but were uniformly homogenous at susceptible genetic loci (Anagnostakis, 1982). European and North American potatoes are also likely to have passed through a major (*Phytophthora infestans*) disease-induced bottleneck in the 1840s (Simmonds, 1993).

For some important crops there is little to no effective resistance in the cultivated gene pool against important pests and diseases. Examples include leaf roll virus in potato (Corsini *et al.*, 1994), black sigatoka in plantains (Swennen and Vuylsteke, 1991), bruchids and weevils in coffee, rice grassy stunt virus (Swaminathan, 1982), rice hoja blanca virus (Madriz *et al.*, 1998) and bean golden mosaic virus (Hidalgo and Beebe, 1997). For instance, an epidemic of African cassava mosaic virus (ACMV) suddenly occurred in Madagascar in 1934–1936 in which all of the susceptible local varieties were largely destroyed (Cours *et al.*, 1997). Sufficient levels of ACMV resistance were not found in the available *Manihot esculenta* gene pool (Jennings, 1994; Cours *et al.*, 1997). Subsequently, this disease-imposed bottleneck necessitated an ultimately successful exercise to develop ACMV-resistant varieties by interspecific crossing of cultivated cassava (*M. esculenta*) with ceara rubber (*M. glaziovii*). However, ACMV still causes serious crop losses in much of sub-Saharan Africa and has recently reached epidemic levels in Uganda (Otim-Nape *et al.*, 1997).

To counter such problems, Lenné and Wood (1991) have emphasized the importance of broadening the genetic base of disease resistance in crops, including through the use of wild germplasm and gene deployment strategies (Smale, 1997).

Gene flow in and between farmers' fields

There have been few systematic studies of gene flow at the farmer's field level as either a result of germplasm exchange between farmers or other modes of transmission (Brush, 1995; Louette *et al.*, 1997). However, farmer management of crop varieties can be

highly dynamic and open systems with a high turnover of local and introduced germplasm over even a few crop generations (Louette *et al.*, 1997; Rice *et al.*, 1997). The lack of studies of this process may reflect the complexity of undertaking such studies as such gene flow can be conditioned by biological, physical and social factors. Yet there is much potential for such local-level gene flow occurring whether it is between landraces, modern varieties and/or sympatric wild relatives.

Little of predictive scientific value is known of how farmers may consciously or unconsciously affect (or effect) local-level gene flow. Yet recent genetic studies of farmers' landraces of pearl millet in West Africa have demonstrated that the crop management practices of neighbouring farmers led to the selection of different genotypes of the same named landrace and similar genotypes of different named landraces (Busso *et al.*, 2000). In this instance, while the phenotypic characteristics which identified a landrace were maintained across farmers, it was found that the genotypes of two different landraces grown by the same farmer were more similar than those of the same landrace grown by two different farmers (Busso *et al.*, 2000).

Both formal and informal (farmer-to-farmer) seed distribution systems are likely to have a major impact on crop gene flow within any country or region (Cromwell *et al.*, 1993; Sperling *et al.*, 1996; Sthapit *et al.*, 1996; Witcombe *et al.*, 1996). Genetic bottlenecks to such gene flow can occur because of social factors such as income status, gender, family, ethnicity or other social groupings. Local-level crop gene flow can be affected by the relative wealth of farmers (Ferguson, 1992; Sperling *et al.*, 1996). Factors such as harsh topography, lack of transport or communications can limit gene flow between regions, and farmers who live in peripheral regions are likely to have less access to novel germplasm (Brush and Meng, 1998). A study of the partitioning of genetic diversity in Andean potato landraces demonstrated high levels of gene flow between commercial landrace populations as a result of seed tuber exchange among farmers. This gene flow was of such magnitude that it counteracted ecogeographic partitioning and local adaptation (Zimmerer and Douches, 1991). However, lower levels of gene flow were inferred for those potato types used solely for subsistence (Zimmerer and Douches, 1991). In some instances, gene flow can occur between introduced modern varieties and local landraces, leading to the 'rustication' of the introduced varieties (Wood and Lenné, 1996; Louette *et al.*, 1997).

While the detrimental effects of weeds on agriculture are well known, little is known of the evolutionary or agronomic role of weed forms or companion weeds. These could act as natural bridges to useful gene flow between conspecific wild progenitors and crops (Pickersgill, 1981; Harlan, 1992; Wood and Lenné, 1996; Linder *et al.*, 1998). In most modern agricultural practices, companion weeds and crops are now only likely to coincide at the boundaries of the cultivated crops (Cubero, 1997). There are some examples of traditional cultural practices that can promote gene flow between fruit crops and their wild relatives (Zohary and Hopf, 1993; Hanelt, 1997). Conversely, farmers can actively select against any crop × wild relative hybrids because of their undesirable seed, phenological and other characteristics (R. Papa, A. Delgado Salinas, J. Acosta and P. Gepts, unpublished results). These traits are likely to show up already in the F₁ generation because they are generally controlled by dominant genes. If undesirable hybrids can be recognized by farmers before flowering, negative selection can strongly limit gene flow towards the crop. If such selection can only operate during and after flowering, selection will only be partially effective. The existence of farmer

selection can actually lead to asymmetric gene flow whereby gene flow from the crop has a stronger effect than gene flow to the crop (R. Papa and P. Gepts, unpublished results).

The breeding system of a farmer's crop can have a strong influence on gene flow at the local level (Allard, 1975). While plant species may range from obligate outcrossers to completely selfed, most species will lie somewhere in between. However, even strongly self-pollinating crops such as rice, barley, wheat and oats will have some degree (e.g. 1–5%) of outcrossing (Allard and Kahler, 1971). Local geographic separation of populations can therefore be a significant barrier to gene flow between different populations of the same crop species. In plants, gene flow is usually effected by two carriers: seed and pollen. The bulk of pollen from both wind- and insect-pollinated plant species can often only travel 5–10 m (Golenberg, 1987). On the other hand, pollen of some species (e.g. beet) can be dispersed at distances up to 1 km (Ellstrand and Hoffmann, 1990; Klinger *et al.*, 1991). Unaided seed dispersal is often limited to several metres (Levin and Kerster, 1969), yet much seed dispersal is via artificial means (animals, trade, soil, transport) as has been well demonstrated for companion weeds of crops (Mack, 1991; Boudry *et al.*, 1993). Even within a population, limited gene flow may result in a highly substructured population in which only adjacent plants have a high likelihood of mating. Local-level gene flow within plant populations can and does occur (Ellstrand, 1992; Hamrick *et al.*, 1995; Ellstrand *et al.*, 1996). As expected, the extent of local-level gene flow between populations is likely to be affected by the relative sizes of each population (Klinger *et al.*, 1991). It is possible that farmers manipulate distance between crops to regulate undesirable gene flow.

New strategies for promoting useful gene flow between exotic and adapted genepools

Hallauer and Miranda (1981) cogently defined exotic germplasm as all germplasm that does not have immediate usefulness without selection for adaptation to a given environment. The definition of what is adapted or exotic material within the cultivated primary gene pool is perspective dependent – i.e. what is adapted germplasm for one grower may be unadapted for another depending on their relative environmental locations. The definition of exotic germplasm therefore also implies a parallel definition of an environment where an extreme or unsuitable environment is one to which the germplasm in question is poorly adapted. Both elite and landrace material within the primary gene pool can be adapted or unadapted (exotic) depending on the environment in question. However, regarding the utility of wild germplasm to farmers or breeders, all such germplasm is exotic according to the definition of Hallauer and Miranda (1981).

Most plant breeders are reluctant to utilize exotic or unadapted material due to its initial detrimental effects on elite breeding material (Kannenberg and Falk, 1995). Breeders seldom explore much of the genetic variability contained within wild relatives for useful traits since the use of such unadapted materials presents major practical problems in breeding (Duvick, 1996). Crosses with exotic material can result in the concurrent introduction of inferior alleles and disruption of useful co-adapted gene complexes in the elite material. Even after 20 or more years of conventional breeding, a single gene transferred by backcrossing from a wild species could be associated with enough linked chromosomal DNA to contain more than 100 other potentially undesirable genes

(Young and Tanksley, 1990). Exotic germplasm, whether cultivated or wild, can negatively affect adaptedness when introduced into a locally adapted genetic base. The 'linkage drag' inherent in elite or locally adapted breeding material is a major constraint to increased utilization of unadapted or exotic germplasm over the longer term. Although it may be desirable over the longer term, there are major barriers (both genetic and practical) to promoting useful gene flow from exotic gene pools into the adapted gene pools of different breeders and farmers.

Before exotic germplasm can be of utility, in many instances it must undergo 'conversion' or 'pre-breeding' such as was performed for sorghum and maize in the USA (Simmonds, 1993). Despite such isolated efforts, it is thought for most crops that the genetic gap between elite adapted gene pools and exotic pools is growing larger with each breeding cycle (Holley and Goodman, 1988; Martin *et al.*, 1991). Yet it is well known that exotic germplasm contains useful alleles that could further improve elite germplasm or be used to develop *de novo* adapted germplasm (Harlan, 1976; Hawkes, 1977; Stalker, 1980; Rick, 1982). For instance, Uhr and Goodman (1995a,b) were able to identify maize inbreds derived from tropical germplasm that had inbred or testcross yields comparable with that of temperate inbreds. Better knowledge of the underlying genetic differences between adapted and exotic germplasm could help to overcome such barriers to gene flow.

The genetic basis of adaptation is poorly understood (Barton and Turelli, 1989; Orr and Coyne, 1992; Milligan *et al.*, 1994; Hawtin *et al.*, 1996). The phenotypic traits conferring adaptation to novel environments were traditionally considered to have a polygenic basis composed of many loci of small effect (e.g. Falconer, 1989). However, it is now accepted that often a few of these loci can account for a major portion of the observed genetic variance (e.g. Edwards *et al.*, 1987). Such loci have been termed quantitative trait loci (QTL) because they control a quantitatively inherited trait (e.g. Tanksley, 1993). The recent use of DNA marker-assisted mapping in conjunction with new statistical methods (e.g. Lander and Botstein, 1989) has provided an efficient means of identifying major-effect QTLs underlying quantitative agronomic traits (e.g. Hayes *et al.*, 1993; Nodari *et al.*, 1993; Lu *et al.*, 1997; McMullen *et al.*, 1998). While little is yet known of the genetic origins or basis of adaptedness, it is now considered that marker-assisted dissection of the genetic basis of adaptedness is feasible (Allard, 1996).

Some important 'adaptive' traits (flowering time, vernalization requirement, etc.) in both domesticated and wild plants can be due to a few genes or QTLs of major effect. This has been found for both domesticated (Ferreira *et al.*, 1995; Teutonico and Osborn, 1995) and wild plants (Coupland, 1995; Mitchell-Olds, 1996; Kuitinen *et al.*, 1997). For instance, comparative QTL analysis has demonstrated that the 'conversion' of exotic sorghum races into more agronomically desirable genotypes could largely be attributed to fewer than ten QTLs imparting reduced height or earlier flowering (Lin *et al.*, 1995). However, there are also some instances where many QTLs have been found to be responsible for such 'adaptive' traits (Jansen *et al.*, 1995).

While QTL mapping holds great promise for crop improvement, such techniques require adequate levels of genetic variation to work optimally. Most of the breeding-related QTL studies undertaken to date have been based on the manipulation of quantitative trait variation already existing within elite or adapted germplasm (Tanksley and Nelson, 1996). Frequently, elite germplasm (e.g. in self-pollinated crops) has reduced

levels of polymorphism making QTL analysis difficult (Helentjaris *et al.*, 1985; Miller and Tanksley, 1990; Wang *et al.*, 1992; Anderson *et al.*, 1993). A more long-term and broader focus on the germplasm starting materials (including exotic germplasm) is necessary to avoid a situation where molecular markers are being used to manipulate the same alleles that breeders have been manipulating for many years through classical breeding procedures (Tanksley and Nelson, 1996). One approach may be more proactively to select genetically diverse genotypes from existing or 'QTL-mapping tailored' crop core collections for inclusion in such QTL analysis studies (Van Hintum *et al.*, 1998).

Where previously the use of exotic germplasm was limited mainly to prospecting (through evaluation) for monogenic qualitative traits such as disease resistance genes (e.g. Lenné and Wood, 1991), it is now clearly the case that exotic wild germplasm can contain useful loci for many quantitative agronomic traits (Tanksley and McCouch, 1997). It has been known for some time that such 'hidden' or cryptic wild loci contributing to quantitative traits cannot be screened for unless evaluated in the genetic background of the cultivated gene pool – i.e. cultivars or breeders' lines (Frey *et al.*, 1984; Bramel-Cox and Cox, 1988; Vetelainen, 1994; Tanksley and McCouch, 1997). It is most likely that wild relatives, regardless of their phenotype, contain alleles that can improve most quantitative traits of interest (Frey, 1975; Cox *et al.*, 1984; Singh *et al.*, 1995; Tanksley and McCouch, 1997).

Unfortunately, until recently there has been no effective strategy for identifying and recombining the few agronomically favourable alleles, which are masked by the preponderance of undesirable alleles, in wild relatives (Tanksley and McCouch, 1997). However, exciting new strategies, combining an appropriate mating system with marker-assisted selection, are now emerging for the identification of agronomically important QTLs in phenotypically inferior wild relatives and for their precise transfer into the primary gene pools of crops (Haghighi and Ascher, 1988; deVicente and Tanksley, 1993; Anderson *et al.*, 1996; Tanksley and Nelson, 1996; Tanksley *et al.*, 1996; Tanksley and McCouch, 1997). The selection of superior lines may also be aided by the availability of molecular markers that are linked to genes for the quantitative trait of interest or to deleterious traits (lack of viability or fertility, lack of adaptation, etc.). Positive selection for the former ('foreground' selection) and selection against the latter ('background' selection) can accelerate the selection process (Tanksley *et al.*, 1989; Paterson *et al.*, 1991; Edwards, 1992; Lee, 1995). This innovative use of molecular maps and markers is likely radically to alter and improve the way that exotic germplasm is utilized in plant breeding and genetic enhancement in the decades ahead (McCouch, 1998).

Geneflow constraints in plant breeding

Plant breeding as a science is in a constant state of flux in its efforts to maintain or increase food production levels in the face of continually changing biotic and abiotic stresses. All plant breeding is based upon the application of artificial selection pressures to select improved germplasm from unimproved (Duvick, 1996). By its very definition, such selection, whether natural or human selection, generally leads to a reduction in the genetic diversity of the population undergoing selection at a particular location.

This is a necessary aspect of plant breeding and crop improvement (e.g. Burton *et al.*, 1990; Marocco *et al.*, 1992). Indeed, high selection intensity breeding of crop varieties may have narrowed the adapted or cultivated genepool of many of the major crops (Tanksley and Nelson, 1995). Such a phenomenon may be especially acute in self-pollinated crops where the level of genetic variation in cultivated varieties is often only a small fraction of that available in the overall genepool (Miller and Tanksley, 1990; Wang *et al.*, 1992).

Recent genetic diversity studies of the varieties in production of crops as diverse as strawberry (Graham *et al.*, 1996), hard spring wheat (Mercado *et al.*, 1996), rice (Yu and Nguyen, 1994) and peppers (Izioka *et al.*, 1997) have indicated a general need to broaden the genetic base of the crops concerned. A number of comparative studies have shown greater levels of genetic diversity in landraces compared with modern cultivars (Sonnante *et al.*, 1994; Jo *et al.*, 1997). For example, a comparison of the levels of gene diversity in US commercial common bean cultivars gives an indication of the high level of selection intensity that have been applied to the primary genepool of bean in the USA (Sonnante *et al.*, 1994) (see Table 2.4). The existence of a relatively broader genetic base for less productive landraces may not on its own be sufficient justification to warrant the broadening of the genetic base of more productive elite germplasm. A wider range of factors (e.g. yield plateaus, lack of useful traits, past bottlenecking events, recurrent disease problems) should be considered in deciding whether the elite germplasm of a crop requires aggregate infusions of novel genetic variability, or not.

Sonnante *et al.* (1994) show that modern plant breeding *per se* is not the only culprit in the reduced genetic diversity levels in the primary genepools of crops. The domestication of crops by the earliest farmers is likely to have involved only a small sample of the available genetic diversity in the wild relative genepool(s) from which the crop was selected. Informal mass selection efforts by farmers followed by widespread adoption of popular landraces can also have a narrowing effect on genetic diversity. Areas such as secondary centres of diversity which exhibit high levels of phenotypic diversity may in some instances actually have low levels of genetic diversity (Wood and Lenné, 1996).

The data presented in Table 2.4 are based on molecular diversity analyses. When considering phenotypic data (growth habit, seed colour, etc.), a trend in the opposite direction is often observed, namely cultivated materials can show increased phenotypic diversity compared with their wild counterparts. This discrepancy can be attributed to genome sampling effects. Phenotypic data for genetic diversity are often (but not exclusively) based on traits with high heritability (e.g. seed weight) or controlled by major genes. This type of inheritance probably reflects the type of selection practised during domestication. In contrast, unlinked molecular marker loci are generally neutral (i.e. they have a small or neutral phenotypic effect) and are therefore much less likely to sur-

Table 2.4. Levels of gene diversity in US commercial common bean germplasm classes and Latin American germplasm from which they were derived (Sonnante *et al.*, 1994).

Genepool	Wild ancestor	Landrace group	US commercial class
Middle American	0.24	0.09 (Durango)	0.00 (Pink)
Andean	0.20	0.17 (Nueva Granada)	0.06 (Kidney)

vive in populations than genes with a strong selective advantage (Crow and Kimura, 1970). Molecular markers, because of their small or neutral phenotypic effect, are therefore much more representative of the majority of genes in the genome that have small phenotypic effects. Therefore, the downward trend revealed by molecular markers is thought to represent more accurately the reduction in genetic diversity in crop genomes.

Initial successes with conventional plant breeding, coupled to the fact that genetic progress can be made on a relatively narrow genetic base, are likely to lead to inertia effects in the pedigree history of modern varieties (Duvick, 1984; Rasmussen and Phillips, 1997). The 'inertia effect' of existing adapted germplasm can have a major effect on what exotic germplasm can now be chosen for recombination with existing adapted germplasm. Of the 250–300 described races of maize, only one forms the basis of US agriculture, 2% provide the foundation for the temperate zones and less than 5% have been used in maize breeding globally (Goodman, 1985). The estimation of general (GCA) and specific combining ability (SCA) can dictate what germplasm can be used for incorporation of multigenic traits (Griffing, 1956; Holland and Goodman, 1994). Some heterotic groups of inbreds are used preferentially over others in hybrid seed production (Mumm and Dudley, 1994). It is also likely that parents used for initial crosses were chosen for their adaptation traits of most utility in the defined target environment.

In many cases plant breeders have confined their efforts to using genetic variation within defined intraspecific groups. Breeding of winter wheat has been mainly done by using only winter germplasm and breeding of spring wheat by using only spring germplasm. Similar examples occur in other crops, such as rice, groundnut, common bean, chickpea, rape seed and mustard. In European barley, a few studies have demonstrated that genetic variation in the cultivated gene pool has not increased significantly since scientific plant breeding began (Linde-Laursen *et al.*, 1987; Fischbeck, 1992; Melchinger *et al.*, 1994). This was considered to be mainly due to the use of a few superior landraces as the founder materials (in the 1880s–1920s) and the further recurrent use of genetically derived elite cultivars since (Fischbeck, 1992). Since 1900, no more than 20 sources of exotic germplasm have contributed to varieties that make up the largest proportion of US barley acreage (Hayes *et al.*, 1997).

Similarly, the genetic base of the US rice industry is considered to be narrow and can be largely traced to 22 plant introductions in the southern rice belt and to 23 plant introductions in the western rice belt (Xu *et al.*, 1997). Japanese rice cultivation is also considered to have a relatively narrow genetic base (Nakagahara *et al.*, 1997). A recent study of soft winter wheat (*T. aestivum*) breeding lines showed that the eastern US soft winter wheat gene pool had been developed from a narrow genetic background, mainly due to the recurrent use of a small number of the same parents in breeding (Kim and Ward, 1997). Diversity studies of cotton (*G. hirsutum*) cultivars from Pakistan (Iqbal *et al.*, 1997) and Australia (Multani and Lyon, 1995) have indicated high levels of genetic similarities between most of the varieties tested. The level of genetic diversity found in a range of *G. hirsutum* cultivars was also found to be low (Brubaker and Wendel, 1994). Most such examples relate to comparatively narrow genetic bases in specific environments or regions as identified by molecular diversity analyses at a particular point in time.

However, for some crops and regions there are examples based on pedigree analysis

over time which suggest that the numbers of exotic landraces introgressed into elite germplasm can be increasing over time. CIMMYT's International Wheat Information System (IWIS) has yielded data that show that the number of parental landraces in CIMMYT's bread wheats has increased over the past four decades, from six ancestors in Yaqui 50 to 68 ancestors in Weaver. The IWIS has also been used to show that the cytoplasmic diversity in CIMMYT wheats was restricted and that landraces from certain regions of wheat's centre of origin rarely appear in the pedigrees of modern wheats (Dubin *et al.*, 1997). It has also been shown that in the major wheat-growing areas of the world, the concentration among leading cultivars has tended to decline as agricultural research and seed systems have matured (Smale and McBride, 1996; Smale, 1997). Pedigree analysis, based on systems such as IWIS, is a highly useful and cost-effective tool for designing rational strategies to broaden the genetic base of cultivated gene pools, where such broadening may be needed.

In plant breeding it is likely that selection intensity is correlated to some extent with the time horizon the plant breeder faces in providing germplasm that is marketable or acceptable to his or her client farmers. In the past, public-sector plant breeders may have had a longer time horizon than private-sector breeders and subsequently could play a larger role in pre-breeding and genetic enhancement. Ironically, just at the time when improved research tools for genetic enhancement and pre-breeding are becoming increasingly available, declining public sector support for plant breeding may result in a serious and widening pre-breeding gap between the exotic germplasm in genebanks and the elite germplasm actually used in breeding programmes (FAO, 1998).

Recombination rates – the effect of mating and selection strategies on geneflow

Mating and selection strategies employed in breeding affect the evolutionary trajectory of primary crop gene pools over time. Breeding (or mating) strategies depend on the reproductive biology of the crops and generally on what has been successful in the past (Jensen, 1988). The practical recombination of genetic variability is an issue that can be neglected relative to selection and isolation in plant breeding. Simmonds (1962) stated that the recombination phase of a breeding programme is often thought of 'as something to be passed as quickly as possible by rigorous inbreeding or backcrossing'. Stebbins (1959) argued that, because of the low endogenous mutation rate, genetic recombination was the most likely source of novel genetic variability for breeding and that recombination-generated diversity could be maximized by hybridization between populations with different adaptive norms. Intragenic recombination coupled to epistatic effects has been suggested to be an important source of novel and potentially useful genetic variability in developing elite germplasm (Schnable *et al.*, 1996; Rasmusson and Phillips, 1997).

Crop plant genomes will differ in their 'permeability' to introgression of different genes or chromosomal regions by wide cross recombination with different wild relatives (Rieseberg *et al.*, 1996). This is a problem for accessing exotic rice germplasm (Brar and Khush, 1997). Recombination rates are typically reduced in crosses between divergent taxa of maize/teosinte (Doebly and Stec, 1993), rice species (Causse *et al.*, 1994) and tomato species (Paterson *et al.*, 1988). In addition, inbreeding following a cross may

also reduce recombination rates (Srivastava, 1980). The movement of alleles across reproductive barriers can be enhanced by increasing recombination rates between parental linkage blocks (Hanson, 1959a,b; Wall, 1970; Rieseberg *et al.*, 1996). The fact that some mating strategies promote higher levels of recombination than others has important implications for genetic enhancement and genetic base-broadening schemes if inadvertent bottlenecks to geneflow are to be avoided.

Recurrent backcrossing is often considered the most inefficient mechanism for breaking up parental linkage blocks (Hanson, 1959a,b). Two mating designs that enhance recombination between parental genomes are selfing and sib-mating. Unfortunately, populations resulting from either selfing or sib-mating will generally exhibit lower levels of fertility than progeny from recurrent backcrossing (Wall, 1970). Mating designs employing one or more generations of sib-mating interspersed with backcrossing may be an effective strategy for efficient geneflow from wild relatives into the primary genepool (Wall, 1970; Rieseberg *et al.*, 1996). Because the two parents are usually quite different, a backcrossing programme to one or the other parent is generally necessary to increase the overall frequency of favourable alleles (Dudley, 1982).

Such mating strategies may be important for genetic enhancement or pre-breeding, especially in situations where the resources to conduct marker-assisted introgression are not currently available. Recombination rates are also a vital consideration in the development of inbred lines in breeding for heterosis. Use of slow rates of inbreeding via sib-mating strategies which promoted higher recombination rates has been considered to be a more effective method than selfing for extracting inbred lines from tropical maize germplasm (Holley and Goodman, 1988). However, mating strategies based on sib-crossing will disrupt favourable coadapted multilocus combinations more than selfing and hence require longer periods of breeding to reselect for more favourable multilocus combinations (Allard, 1996). This has led to suggestions to combine backcross and inbreeding to retain useful parental gene combinations while concurrently generating new, potentially useful gene combinations. Additional backcrossing schemes that have actually been used include the recurrent, inbred and congruity backcross methods:

1. In the recurrent backcross, as illustrated by the introgression of small seed size from *Glycine soja* into *G. max* (LeRoy *et al.*, 1991), successive backcrosses are performed to the same parent with or without selection between backcross generations. This mating and selection scheme is more effective for traits with higher heritability, which are often mono- or oligogenic and segregate in qualitative fashion.
2. In the inbred backcross method, a limited number of backcrosses (usually one to three) are performed, followed by several generations of selfing (Wehrhahn and Allard, 1965). The inbred backcross method results in a population of more than 50 lines that are homozygous, have a common genetic background similar to that of the recurrent parent, but differ for specific genomic regions inherited from the unadapted donor parent. Because the lines can be used in replicated trials, this method has been used successfully to transfer quantitative traits from exotic germplasm into elite, adapted germplasm as illustrated by improvement of nitrogen fixation and seed protein content in common bean (Bliss, 1985).
3. The congruity backcross, originally proposed by Haghghi and Ascher (1988), involves backcrossing to both parents in alternate generations. This method was used to recover progeny with increased fertility from *P. vulgaris* × *P. acutifolius* crosses that are

normally highly sterile (Haghighi and Ascher, 1988). In the progeny of these crosses, it was possible to obtain progenies with intermediate seed morphologies rather than morphologies resembling one or the other parent (Anderson *et al.*, 1996). The recovery of these morphologically intermediate yet viable and fertile individuals was attributed to the increased levels of effective recombination through the increased levels of heterozygosity.

Urrea and Singh (1995) compared the inbred backcross and the congruity backcross in an intraspecific *P. vulgaris* cross between two diverged common bean cultivars, belonging to races Mesoamerica and Durango, respectively, of the Mesoamerican gene pool. Their results showed that the congruity backcross generated progenies which were intermediate between the two parents, whereas the inbred backcross led to progenies resembling very much the recurrent parent even after a single backcross. Their results suggested that further recombination among advanced, superior backcross lines may be needed to ensure sufficient recombination, as illustrated by St Clair and Bliss (1991).

Factors contributing to bottlenecks in crop cytoplasmic genetic diversity

The genomes of cytoplasmic organelles (chloroplast and mitochondria) of most crop plant species also exhibit significant genetic diversity (e.g. Kemble *et al.*, 1983; Komarnitsky *et al.*, 1990; Belhassen *et al.*, 1991) and hence can also be subjected to genetic bottlenecks, drift and founder events (Rieseberg and Soltis, 1991). In most angiosperms, cytoplasmic organelles are maternally inherited (Sears, 1980). In general, chloroplast DNA has proved to be less genetically variable than mitochondrial DNA (Palmer, 1987).

Repetitive use of the same female parents in breeding programmes can lead to a bottleneck in cytoplasmic genetic diversity among cultivars, where all cultivars share similar maternally inherited cytoplasmic DNA. For instance, in the case of all commercial sugar cane (*Saccharum officinarum*) hybrids, cytoplasmic genetic diversity is derived only from *S. officinarum*. Nuclear genetic diversity is derived from *S. officinarum* and one or more of *S. spontaneum*, *S. sinense*, *S. barberi* and *S. robustum* (Irvine, personal communication). Although *S. spontaneum* contains the most significant levels of cytoplasmic genetic diversity, it has rarely been used as a female parent in crosses.

Cytoplasmic bottleneck effects may be common in crops where the cytoplasmic genomes can, among many other traits, confer cytoplasmic male sterility (cms), which in conjunction with nuclear restorer genes is of immense practical value in plant breeding (Horner and Palmer, 1995). For instance, in maize three different genetic types of genic-cytoplasmic male sterility (g-cms) have been described (g-cms-T, g-cms-S and g-cms-C) on the basis of specific nuclear restorer genes capable of restoring fertility (Horner and Palmer, 1995). While such g-cms traits are extremely useful, for example in recurrent selection or hybrid seed production, the use of the same male sterile parents in pedigree breeding schemes can lead to a situation where many cultivars contain genetically identical cytoplasmic genomes.

The geographic distribution of genes for fertility restoration in hybrid rice based on cytoplasmic male sterile germplasm has been studied from this perspective (Li and Zhu, 1989). The US maize blight epidemic of 1969/70 (where 15% of the crop was

lost) was caused by the use of the same Texas (or T) cytoplasmic male sterility in developing many maize varieties which were – inadvertently – uniformly susceptible to a race of the southern leaf blight fungus, *Helminthosporium maydis*, as a result of a mitochondrial disease susceptibility locus (NRC, 1972). More recently, breeding schemes that limit the contribution of the cytoplasm of the male sterile to the progeny have been devised and are important in avoiding breeding-induced cytoplasmic bottlenecks (Horner and Palmer, 1995). Nevertheless, F₁ rice hybrids today grown over 18 million hectares in China contain a single source of cytoplasmic male sterility (WA) (R.S. Paroda, personal communication).

Recent analyses of genetic variation in the cytoplasmic genomes (chloroplast, mitochondria) of *Triticum* (wheat) and *Aegilops* have suggested that *Aegilops speltoides* is the cytoplasmic donor/progenitor (i.e. female parent) of all polyploid wheats (Wang *et al.*, 1997). Interestingly, the same study showed that the evolution of the two organellar genomes has been parallel only to a limited extent, even though they have been maternally inherited as a set. Similarly, a study of chloroplast DNA diversity in populations of wild and cultivated barley indicated that the great majority of the cultivated samples tested had chloroplast DNA derived from only one wild progenitor (Neale *et al.*, 1988).

Changing agricultural practices and consumer preferences

The changing nature of food supply, consumer preferences and agricultural modernization can also affect the levels of genetic diversity in crop production. In many instances, this is inevitable and necessary, especially from a farmer's perspective. Consumer and trader preferences for uniformity of produce that has been graded into particular categories can exert selection pressures for particular sizes, shapes, colours, tastes, etc., of crop produce. Consumer preferences which are developed over generations in any given sociocultural context can also have a significant effect on which alleles (or allelic combinations) – contributing to quality traits such as palatability, cooking time and storability before and after cooking – are acceptable to different groups of consumers. It may often be difficult to introduce novel germplasm which does not meet such consumer criteria. For instance, tequila is made from a single clone of agave away from which tequila producers are reticent to diversify genetically in case tequila quality suffers.

Selecting for specific genes which confer 'quality' traits can lead to overall reductions in allelic diversity at particular loci in a crop gene pool. This may account for the regional predominance of only a few glutenin subunits which are controlled by specific alleles on the long arm of wheat group 1 chromosomes (Morgunov *et al.*, 1993; Pena, 1995). Similarly, the quality requirements for good malting barley are wholly different from those for good feed barley. The special quality requirements for malting barley have been shown to have significant effects on the genetic diversity of malting barley cultivars (Wych and Rasmusson, 1983; Saghai-Marooif *et al.*, 1994). On the other hand, consumer preferences for a steady supply of locally produced fresh products can result in the selection of a wide range of maturity times in certain crops (e.g. *Brassica*). For example, the cauliflower crop in Italy occurs as distinct types in several regions, differing in curd colour and conformation, and in leaf and plant type (Crisp and Astley,

1985). These examples indicate that overall breeding-induced reduction in genetic diversity is due in part to producer- and consumer-driven requirements.

Due to globalization and comparative advantages in crop production, crop products are increasingly traded and hence transported over large distances. This necessarily imposes selection pressures for non-spoilage of transported varieties/produce, with a concomitant bias against genetic variation conferring early or sequential ripening, which may not be such a problem for produce that is quickly consumed or processed at a more local level. Agricultural mechanization involving more precise seeding and harvesting requires varieties with more uniform phenotypes to work efficiently, and large-scale cultivation of such varieties is necessary to realize economies of scale relating to the use of such machinery. The standardization of agricultural machinery for harvesting by institutions such as the International Standards Organization (e.g. ISO 6689 on combine harvesters or ISO 11520 on grain dryers) may have selection effects on the phenotypic requirements of crop varieties (Duranton and Abram, 1996). While some types of food processing (e.g. malting barley for brewing) may require strict phenotypic standards, others such as starch production may require less stringent phenotypic criteria. Hence, some types of food processing may promote genetic diversity in crop production.

Conclusions

Many factors conspire to reduce the genetic diversity of crop gene pools. While diversity is not a breeding objective *per se*, it is useful to remember that genetic diversity needs to be maintained or enhanced in order to obtain significant future progress from selection. Given the small fraction of total genetic diversity that has been included since domestication in the domesticated gene pool of most crops, there is probably a need to re-domesticate or further domesticate most crops, i.e. to reconstitute or regenerate the domesticated gene pools through introgression or incorporation of genetic diversity from exotic, wild and/or cultivated gene pools. However, what is not clear is whether the necessary public-sector funding will be available from governments for such long-term germplasm enhancement work. To ensure that enhanced germplasm is actually used, any such pre-breeding or base-broadening work would have to be closely integrated from the outset with existing, more 'downstream', breeding efforts and seed supply channels.

Yet the payoffs to society of long-term germplasm enhancement could be substantial (Hoisington *et al.*, 1999). Of relevance to planning future evolutionary change in crop gene pools will be shifts towards substituting genetic resources (genes and gene complexes) for chemical inputs wherever it is possible agronomically (Harwood, 1989; Coffmann and Smith, 1991). Breeding for sustainability is likely to become increasingly a process of fitting cultivars to an environment rather than altering the environment by adding inputs such as fertilizer, water and pesticides (Coffmann and Smith, 1991). The beneficial social, economic and energy externalities and spillovers of moving agriculture towards a more biological resource intensive activity will be significant.

Since developing a long-term base-broadening programme will incur costs and planning by comparison is cheap, it is essential that any such germplasm-enhancement

or base-broadening programmes take into account all available evolutionary and historical information on the crop which is of relevance to the geographical scale of the programme. This applies whether the genetic base broadening is to be undertaken at the global, regional, national or local level.

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3

Base-broadening: Introgression and Incorporation

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Introduction

Serious attention was paid to genetic resources of crops and to genetic diversity in general only after the beginnings made in the 1920s by the Russian school of plant collection led by N.I. Vavilov. Considerable collections of a few crops were built up locally and scattered round the world in the following decades, but really serious efforts were only begun in the 1960s; they were followed by the foundation of the International Board for Plant Genetic Resources (IBPGR, now IPGRI) in 1974, which has since played a leading role in work on genetic resources of crops. Though collections were widely regarded, in both Consultative Group on International Agricultural Research (CGIAR) and Food and Agriculture Organization (FAO) circles, as being highly desirable, even necessary, there was little understanding of how they might be used and to what purpose.

In the 1970s and 1980s, indeed, there was widespread confusion about the function of curators of collections, who might themselves both characterize (i.e. identify) and evaluate (i.e. determine the utility of) items in their care. It took a long time for the genetic resources community to realize that this idea was unworkable. In the longer run the point was taken that evaluation can only be for plant breeders working locally, because evaluation is beset by genotype × environment problems, which cannot possibly be resolved, even understood, at a single (usually distant) place. It is now universally agreed that collections are best accumulated, cared for, maintained and characterized at chosen central sites but that utility/usefulness can only be determined by plant breeders working in distant places, in the sites to which adaptation is desired. Holden *et al.* (1984, 1993) and Bretting and Widrelechner (1995) comprehensively review the essentials.

The foregoing does not mean, however, that collections went completely unused in earlier times. From the 1920s there were many examples of what we call introgression (borrowing a genecological word); that is, items from collections were chosen as having some desirable character (nearly always a disease resistance) and crossed and backcrossed to breeding stocks in the hope of transferring the desired character. This

sometimes worked but sometimes did not. All too often, the desired character was either polygenic or was a vertical resistance (VR), due to a major gene, readily nullified by evolution of a new pathogenicity in the pathogen. The wheat rusts, potato late blight, and leaf diseases of rice barley and grain legumes provide scores of examples. Generally, introgression has been widely practised but has only very rarely been useful. Thus, at least 11 R-genes have been backcrossed from *Solanum demissum* into cultivated potatoes, to no useful effect. To the plant breeder they are merely nuisances.

Recognition of Wider Functions

Recognition of the need to go beyond introgression to widen the genetic bases of diverse crops, either narrow at the start or seriously narrowed by subsequent selection, came much later and even now the concept has not been fully assimilated. The first plain statement was that of Simmonds (1962), which coincided with the initiation of the Andigena–Neotuberosum potato project described later. The principle was simply to recognize that the large-scale loss of genetic variability due to response to selection had to be repaired somehow and that the best and most economical approach was to adopt a very widely founded base-broadening attack. The approach aims at wide incorporation of genetic variability which, of its very nature, cannot be pre-selected. It generally turns out that the earlier evolutionary history of the crop must be reconstructed if good new parents are to be synthesized.

In effect, then, we recognize two basic ways of using a crop collection, namely: (i) introgression, adopting a pairwise crossing and backcrossing technique to introduce specific genes and (presumptively useful) characters; and (ii) incorporation, which attempts a wide-scale incorporation of genetic variability, the value of which cannot be known until the incorporation has been nearly achieved. In contrast to the preceding, incorporation must go forward on a wide genetic base, must in a sense repeat crop evolution and must usually be regarded as a continuing process. Figures 3.1 and 3.2 provide general illustrations: the former treats both introgression and incorporation; the latter elaborates on the theme of incorporation.

Functions of the Two Approaches

Introgression will have its uses but it will commonly continue to fail in future, as it has failed in the past. Either the desired character is not simply monogenic (and therefore not readily backcrossable), or it is a VR susceptible to the emergence of a new pathotype. It may be that major-gene virus resistances will prove to be more useful and 'durable' than others because the agents may be less liable to generate new pathotypes, but this is quite speculative and far from certain as a generalization. By contrast, incorporation has indefinitely wide applications and has yet been but little explored. The need sometimes arises from a narrow base *ab initio*, sometimes from a base narrowed by prolonged selection. A good deal is known about its application to potatoes, sugar cane and maize (Simmonds, 1993; and Figs 3.3 and 3.4; see also Kennedy, Chapter 16, this volume). Its use for barleys is plainly foreshadowed by the great Californian Composite Cross experiments, and its application to several tropical tree crops has been outlined

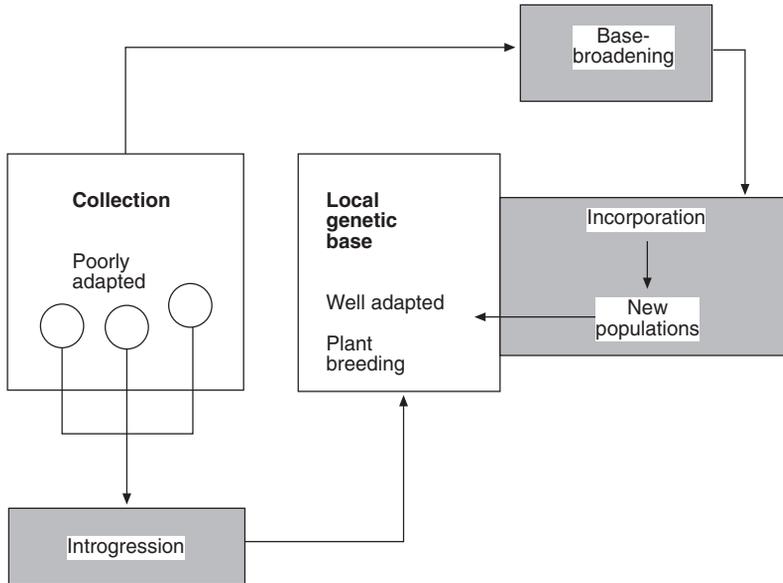


Fig. 3.1. The general pattern of introgression and incorporation in crop improvement. From *Biological Reviews of the Cambridge Philosophical Society* (68, 542, 1993) by kind permission of the Editor and Cambridge University Press.

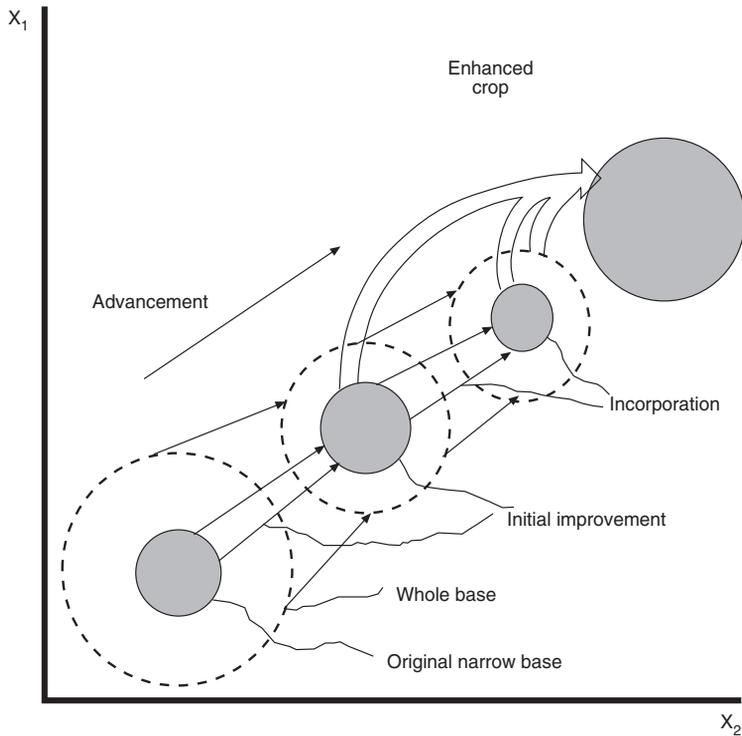


Fig. 3.2. The general pattern of incorporation in crop improvement. Two arbitrary 'characters', X_1 and X_2 , are plotted; they might well be major components of an index of 'general worth'. Widths of circles roughly represent genetic variances.

in, for example, rubber (Fig. 3.5), cocoa and oil palm. However, the great array of other crops, both temperate and tropical, that would benefit from incorporation remain untouched, both experimentally and even conceptually. There has been very little awareness and thinking; the small grain cereals such as wheats, rices and millets and the inbred grain legumes are conspicuous examples of neglect. There have, however, been some signs of interest in soybeans.

Genetic Principles of Incorporation

The genetic principles underlying introgression are simple and obvious; those underlying incorporation are not. The latter may be listed as follows:

1. Large scale of operation is essential if a wide range of variability is to be caught in the net; a narrow start simply ensures an even narrower finish.
2. Non-adaptation of the introduced materials will usually have to be assumed, even if the assumption is sometimes mistaken. The 'primitive' potatoes and sugar canes looked

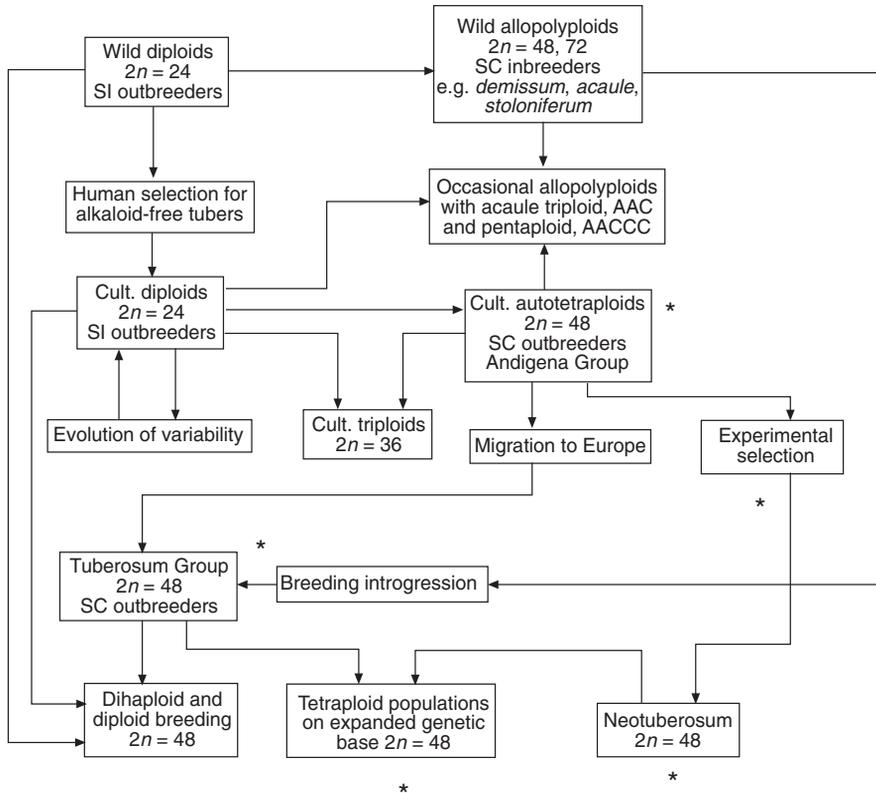


Fig. 3.3. The long-term place of base-broadening (= incorporation) as a feature of potato evolution and current improvement.

Entries of a special consequence for incorporation are marked with an asterisk. From Smartt and Simmonds (1995, p. 467), by kind permission of Blackwell Scientific.

useless but many 'primitive'-looking cereals and tree crops have attractions. The cereal pot trials described by Spoor and Simmonds (1993) provided some surprises: examined barleys generally appeared to have no value but this concealed a substantial minority that were intrinsically well adapted to Scotland

3. The process must be complementary to conventional breeding: testcrosses may sometimes be undertaken, but any general crossing with adapted materials is not only inappropriate but also inappropriate because it must corrupt the process of adaptation itself and will tend to corrupt, even destroy, the base-broadening effort.

4. The methods and breeding patterns to be adopted will depend on the biology of the crop, its breeding system and reproductive behaviour. The general rule must be 'quick and dirty' but always within the bounds of security and reliability. The crops already at least partly understood, all demanded different methods (Simmonds, 1993). An attractive possibility, if it could be proved to be useful, would be to exploit pot tests (e.g. in barley: Spoor and Simmonds, 1993).

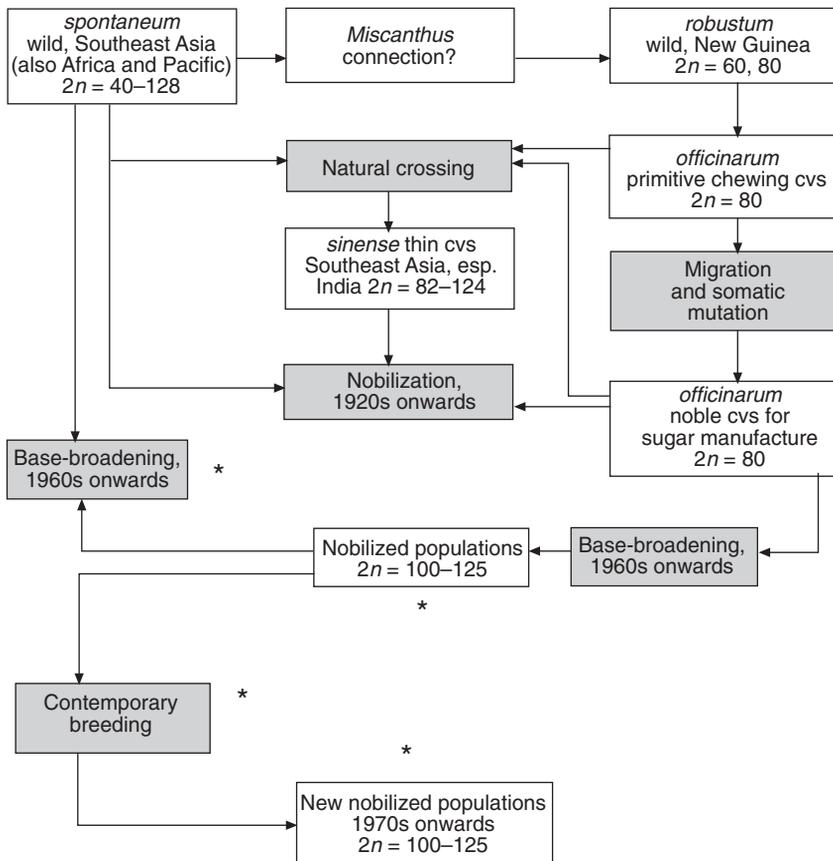


Fig. 3.4. The long-term place of base-broadening (= incorporation) as a feature of evolution and current improvement of sugar cane. (See also Kennedy, Chapter 16, this volume.)

Entries of a special consequence for incorporation are marked with an asterisk. From Simmonds (1976, p. 106), by kind permission of Blackwell Scientific.

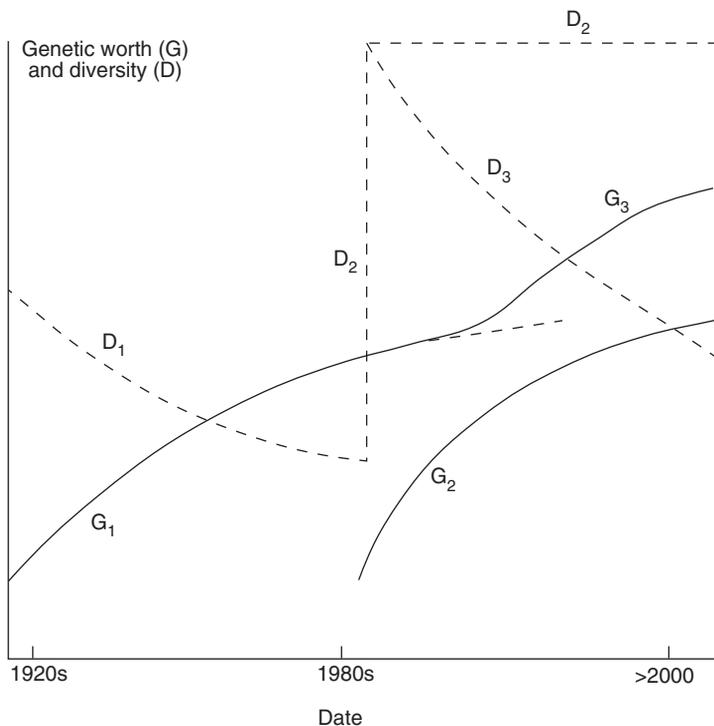
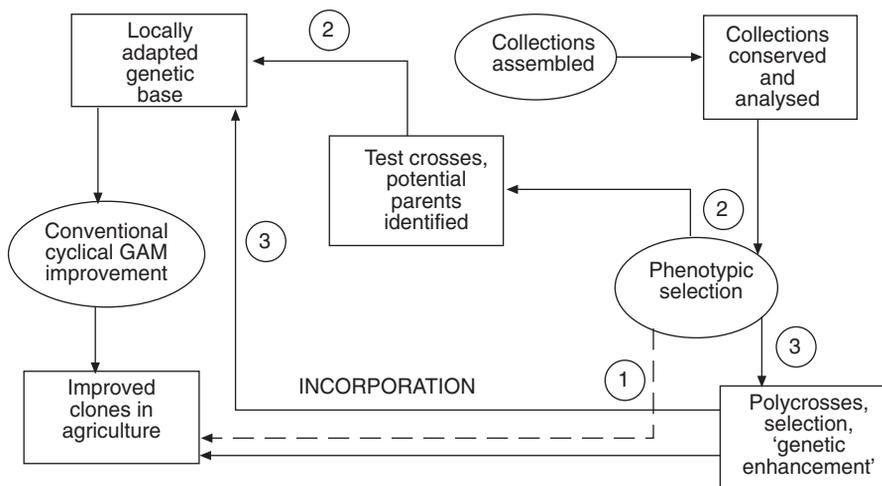


Fig. 3.5. The genetic base and use of base-broadening (= incorporation) in rubber breeding.

This programme is projected rather than actually realized but it observes the principles set out on pages 74–77 and the analogy with potatoes and sugar canes (Figs 3.3 and 3.4) will be clear. From Webster and Baukwill (1989, pp. 116–117) by kind permission of Blackwell Scientific. GAM:

5. It is prudent to assume little inherent adaptation in the material, and therefore to use large populations, to maximize recombination (by cyclical crossing if necessary) and to maintain only weak selection. Rigorous selection can only narrow the base unnecessarily, but usually without concomitant gain.
6. Utilization of such broadly based populations will require considerable development of local adaptation before true potential can be recognized. To minimize undue narrowing of the base and further genetic loss, replication over several diverse sites is highly desirable.
7. An important feature of local genetic adaptation is horizontal resistance (HR) to disease. Most important crops have 5–10 (or more) more or less serious diseases, and new ones regularly appear (as in sugar cane). Usually, it will be sufficient to grow populations in disease ‘hot-spots’ and let natural selection do the work; sometimes, however (as in potatoes and sugar cane), some intervention by the plant breeder is needed. The profound importance of HR (generally, but especially for the small farmer) has been strongly emphasized by FAO (1986, 1988) and genetic features have been reviewed by Simmonds (1991).
8. Progress may well be remarkably rapid on evolutionary time-scales (it was in potatoes and sugar canes) but seemingly rather slow on human/plant breeding time-scales. This is unavoidable but it implies a long-term commitment and assured continuity in relevant programmes. But, even in years, time scales are not always long and both potatoes and canes showed major advances in a decade: a mere moment in crop evolutionary time (Figs 3.3 and 3.4). Strictly annual crops could well be quicker.
9. The outcome of an effective base-broadening programme will be enhanced genetic variance in economic characters (Figs 3.1, 3.2 and 3.5) and either good materials *per se* or good parents for crossing into established programmes. Both outcomes are known and both are to be expected.

A closing comment is justified because it is often a source of difficulty. The term ‘pre-breeding’ is used in various senses and should, in our opinion, usually be avoided. It may refer to the development of potential parents either from adapted stocks or from what might be regarded as a base-broadening programme. Only confusion follows from loose usage.

An Example from Potatoes

Frequent reference has been made above to base-broadening of potatoes, perhaps the leading example of incorporation because it was the earliest and arguably the most successful.

The work was summarized, with references, in Simmonds (1993). Figure 3.3 herein illustrates the evolution of the group, including base-broadening.

The potatoes are ancient Andean cultivars which started as diploids ($2x = 24$) from diploid ancestors; they are all outbred and self-incompatible (SI). In the Andes, at great altitudes, autotetraploid derivatives ($4x = 48$), the Andigena group (ADG), came to dominate and still do. They are adapted to short tropical days but to cool weather. A few ADG cvs were taken to Europe in the 16th century and slowly became adapted to temperate climates though they tended to be ‘late’ (because of short-day

adaptation) and were very susceptible to diseases. In Europe, and also in North America, local adaptation emerged in the Tuberosum group (TBR), which is effectively Andigena with minor morphological differences and adaptation to long summer days. The importance of day-length adaptation cannot be over-emphasized. Very few ADG were brought to the north and the crop made good genetic progress on a very narrow genetic base up to the middle 19th century when it was catastrophically attacked by the newly introduced late-blight fungus, *Phytophthora infestans*, introduced from Mexico to Europe and North America in the 1840s. By then, TBR was a major food crop. Blight still further narrowed the base, though the crop responded well to selection. Pedigree information showed that millions of hectares of a few clones all went back to half a dozen or so introductions. Attempts to use ADG for direct crossing to TBR were useless; products were sometimes vigorous but had many bad features, including disease susceptibility.

The only solution, and the method in fact adopted, was to recreate the TBR group from ADG stocks, of which a large sample was available in the Commonwealth Potato Collection at the John Innes Institute, Hertford, England. An initial sample (1959) of about 3300 seedlings was grown, selected roughly and the selections carried on vegetatively in the next year. Thereafter seedling and tuber propagation alternated; seed was collected from isolated tuber plots in the hope that it was mostly crossed, even though the ADG potatoes are fairly self-fertile. This was a mistake, later remedied by making crosses, when it was found that selfing predominated. Little conscious selection was practised, though plots were deliberately grown every year in a blight 'hot-spot'. Responses were very largely to natural selection for survival, growth and yield (i.e. tolerance of long days), with minimal interference by the breeder.

Daylength adaptation and disease resistance improved very rapidly and in three 2-year generations (i.e. before 1970), the better materials rivalled TBR in performance, had a great range of tuber types, cooking qualities and resistances in them and showed some truly spectacular heterosis in crosses with TBR. So good were they that the name Neotuberosum (NTB) was invented for them. In the 1970s about 60,000 plants were grown, so the demands, though non-trivial, were not great.

The work was carried on in Scotland in later years and many crosses made into a conventional breeding programme. Stocks were widely distributed round the world. A few current commercial varieties in the UK, Europe and North America are half NTB in constitution and many more are in prospect. The material is, of course, freely available to *bona fide* potato breeders and, if wisely used, can hardly fail to revolutionize potato breeding, temperate and tropical. It may be that the greatest potential of all will be in the tropics, for Third World agriculture (Simmonds, 1997). Diploid selections can readily be introduced into the programme if required (Fig. 3.3).

Summary and Conclusions

Many crop plant collections were built up and maintained in various places over the last 60–70 years of the 20th century. They have provided some interesting scientific data but have been but little exploited for plant breeding. The evidence of the need for base-broadening of a crop plant lies in historical information, pedigrees and poor progress under selection.

Two means of using a collection may, broadly, be distinguished: introgression implies the introduction of a character by backcrossing a single gene or a small group of polygenes; incorporation implies the large-scale introduction of genetic variability by mass crossing followed by mass selection under some approximation to random mating. The former has been widely used for monogenic disease resistances (usually VR) which have generally failed, for obvious reasons. The latter has been successfully exploited in potatoes and sugar cane and is being ever more widely adopted as a longer-term strategic measure for the improvement of other crops. In principle, it is applicable to all crops, and a great many (e.g. all the inbred cereals) would benefit if so treated.

Incorporation, if correctly exploited, generates substantial reserves of adapted parental materials for incorporation in plant breeding programmes. It may itself generate new crop varieties but is not primarily intended to do so: its function is to widen the genetic base.

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4

The Role of Local-level Geneflow in Enhancing and Maintaining Genetic Diversity

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Introduction

In traditional agricultural systems, it is often thought that plant varieties are conserved without evolution over long periods of time by farmers because local-level geneflow and its role in maintaining and enhancing genetic diversity of crops is often underestimated. Local-level geneflow can be defined as gene exchange between varieties at the local level, i.e. within farmers' fields and rural communities. In this chapter we present a few case studies of seed management by farmers in different locations and production systems which demonstrate the impact of farmer activity in the management of plant diversity.

Knowledge related to farmer management is still limited but is required when we want to propose strategies for broadening the genetic base of crops which take advantage of this existing farmer management or which produce new genetic material to be included in such management. The selected cases are not typical of all the situations encountered but offer the opportunity to stress specific and important points. Some of these cases were presented in Bamako during the workshop: 'Genetic resources management in savannah of Africa' in March 1997 (Anonymous, 1997).

Case Studies

Maize in a traditional community in Mexico

The valley of Cuzalapa and the Sierra de Manantlán Biosphere Reserve (SMBR)

This biosphere reserve was established in a area where teosinte, the wild parent of maize, is found, and especially where the species called *Zea diploperennis* occurs. It is an area of traditional agriculture in a centre of maize diversity. The indigenous community of Cuzalapa is located in a valley in the southern section of the buffer zone of the Sierra de Manantlán Biosphere Reserve (SMBR), in the municipality of Cuautitlán, in the state of Jalisco, on the Pacific Coast of Mexico. The Cuzalapa watershed covers nearly 24,000 ha (most of which lie within the boundary of the biosphere reserve) of mountainous land of extremely irregular topography, ranging from an elevation of 550 m to 2660 m. Each year, about 1000 ha of maize may be sown in Cuzalapa; of this area, 600 ha are irrigated (Martinez and Sandoval, 1993) using traditional techniques based on gravity. Cultural practices continue to be relatively traditional when compared with those found outside the Sierra de Manantlán. Maize (*Zea mays* ssp. *mays*) is the dominant crop in the valley. It is grown during the rainy season from June to November, associated with squash (*Cucurbita* spp.), on an average of 2 ha per farmer. It is also planted under irrigation in the dry season, extending from December to May, intercropped with beans (*Phaseolus vulgaris*), on an average of more than 2 ha per farmer. Irrigation and intercropping are reported to have been a feature of agriculture in Cuzalapa in pre-colonial times (Laitner and Benz, 1994). Maize and beans are produced essentially for home consumption; some surplus is sold at local markets, yet the Cuzalapa community is poorly linked to commercial markets.

Cuzalapa is located in one of the most marginalized municipalities of the region, in terms of housing quality and level of education (Rosales and Graf, 1995). At the time of the study (1989–1991), these localities were all remote from main roads and urban areas. Based on its farming and socioeconomic characteristics, Cuzalapa is broadly representative of many indigenous, poor and isolated rural areas in Mexico. It is one of the many traditional communities which are being slowly incorporated into commercial marketing systems while maintaining features of indigenous society.

Documenting the exchange of seed lots and varieties

To document which maize varieties are cultivated and to record the exchange of seeds and varieties in the community and between the valley of Cuzalapa and other regions, 39 farmers (one-fifth of Cuzalapa farmers) were surveyed during six cropping seasons covering three calendar years (the 1989, 1990 and 1991 rainy and dry seasons). For each farmer and cropping season, data were collected on varieties cultivated and seed sources. Varieties included those grown on farmers' own fields, on rented fields and shared cropping fields. Each variety was recorded with the name given by the farmer.

The seed source was classified into three classes: (1) own seed (seed selected by farmers from their own harvest); (2) seed acquired in Cuzalapa (seed obtained in the valley of Cuzalapa from another farmer); and (3) introduced or foreign seed (acquired outside the Cuzalapa watershed). The data therefore give a clear representation of the

extent of seed exchange and of local level of geneflow, but they understate the importance of seed of foreign origin introduced in Cuzalapa because seeds acquired in Cuzalapa can be of foreign origin in the previous generation.

Regular introduction of new varieties

This community does not function as an isolated area. On the contrary, foreign varieties are regularly introduced to be tested. From the 26 varieties identified, only the varieties Blanco, Amarillo ancho, Negro, Tabloncillo, Perla and Chianquiahuitl are local (Table 4.1); the other varieties are foreign. Local means that varieties had been grown continuously for at least one farmer generation in the valley of Cuzalapa. Only the introduction date of the Chianquiahuitl can be traced back to the 1950s and all the varieties can be classified as Tabloncillo race. Although few in number, the local varieties cover more than 80% of the area planted with maize. Blanco, Tabloncillo and Perla are white-grained and used essentially to make tortillas, the Mexican staple food. Amarillo ancho is yellow-grained and used for feeding poultry. Negro is purple-grained and is essentially consumed roasted at the milky stage.

The remaining 20 of the 26 varieties that Cuzalapa farmers were growing during the survey period are classified as *foreign*. Each foreign variety covered less than 5% of the maize area planted in each season, and most varieties were cultivated by only a few farmers at a time. The composition of this group of varieties changed from season to season. Only three of these varieties (Argentino, Enano and Amarillo) had been regularly cultivated over the preceding 4 or 5 years by a significant percentage of farmers (10–12%). Most varieties had been used for the first time recently or during the survey period and had only been planted once or twice.

The origin of the foreign varieties is often difficult to ascertain. Farmers are able to indicate in which community they acquired a variety, but not its original source. Even the original name of the variety can disappear or take on a different meaning when farmers exchange seed. Based on the information collected, foreign varieties can be

Table 4.1. Importance of 26 varieties cultivated in Cuzalapa (Mexico).

Varieties	% maize area	% farmers	Grain colour
Six local			
Blanco	51	59	White
Chianquiahuitl	12	23	White
Tabloncillo	5	6	White
Perla	0.4	0.2	White
Amarillo ancho	8	23	Yellow
Negro	3	34	Purple
20 foreign			
3 most cultivated			
Argentino	5	10	White
Enano	3	12	White
Amarillo	3	11	Yellow
17 minor varieties	< 3 per variety	< 4 per variety	Mainly white

classified into three groups: 15 farmers' varieties (landraces); four farmers' advanced generations of improved varieties; and one variety which was a recent generation of an improved variety. The group of foreign varieties is morphologically diverse, including white-, yellow- and purple-grained material. Representatives of different races are found in this group. Most varieties were introduced from communities of south-western Jalisco, less than 100 km from Cuzalapa, although a variety cultivated by one farmer originated in the United States.

Variable composition of a variety

Significant differences in origin were associated with the dominance of the variety in terms of planted area (Fig. 4.1). Seed of the most widely grown varieties – including the local varieties and the three most important foreign varieties – is less likely to have been obtained from farmers outside Cuzalapa than seed of the more minor foreign varieties (7.9% of local varieties and 5.3% of important foreign varieties seed lots were introduced, compared with 36.4% of minor foreign varieties seed lots). Nevertheless, it is difficult to establish a pattern for the minor foreign varieties, because each variety appears to be a special case, defined by the time of its introduction and the number of farmers planting it.

Seed of local varieties is essentially reproduced by each farmer. Among local varieties, farmers manage the seed for Chianquiahuitl and Negro more conservatively. More than 70% of the seed for these varieties is selected from farmers' own maize harvests. In fact, farmers plant such a small area with the variety Negro that, on average, seed equivalent to only 27 ears is required per farmer to plant their area (Louette, 1994). This amount of seed, if in good condition, is carried over easily from one cycle to the next, and farmers do not need to get seed from another farmer. Chianquiahuitl is a variety of unknown origin that is believed to be no longer widely cultivated outside the study zone, and farmers in the Cuzalapa Valley must rely on their own stocks.

The case of Blanco contrasts with that of Chianquiahuitl. Of all the local varieties, Blanco has the highest proportion of seed obtained from farmers outside the study zone (15%). This result reflects the importance of Blanco in terms of area cultivated in Cuzalapa and regions nearby. Because Blanco is important for household subsistence, an insufficient number of ears suitable for seed may remain at planting time. Farmers then search for seed from other farmers in and outside the community.

We have considered as a 'seed lot' all kernels of a specific type of maize selected by a farmer and sown during a cropping season to reproduce this particular type of maize. Farmers use an important percentage of their own seed lots for both major and minor foreign varieties (42.1 and 39.4%, respectively), in the first case to reproduce them and in the second case to test foreign varieties over several seasons. Major and minor foreign varieties can be distinguished by their pattern of diffusion. The percentage of seed brought from other regions is small for the most widely grown foreign varieties (5.3%), while for some of the minor varieties introduced late in the survey period all seed lots were introduced (average 36.4%). On the other hand, farmers in the valley much more frequently exchange seed of the major (52.6%) than of the minor foreign varieties (24.2%). Major varieties were introduced some years ago by these local farmers and, because they have demonstrated characteristics of value, their seed is redistributed to other farmers in Cuzalapa. In contrast, survey farmers who did not plant the minor

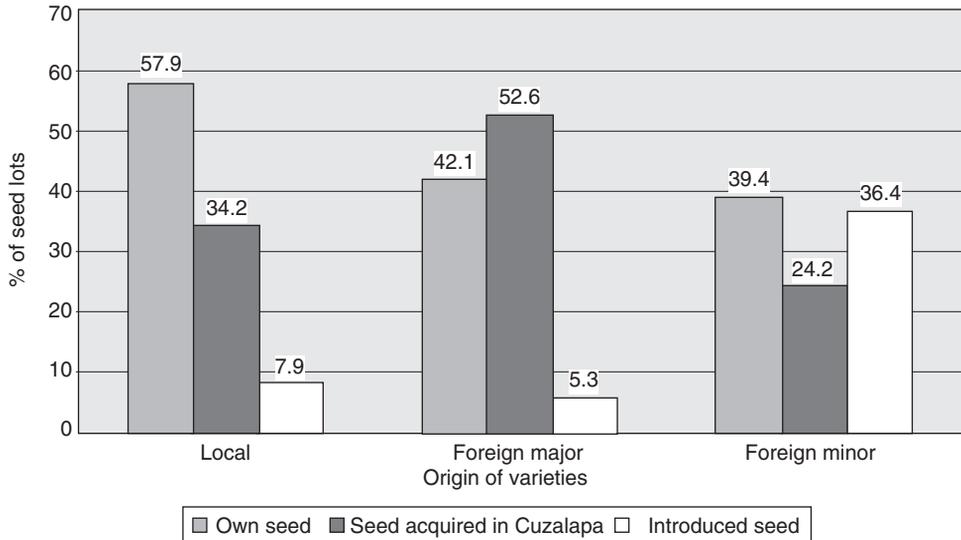


Fig. 4.1. Origin of seed planted in Cuzalapa by origin of variety.

varieties during the study period may not yet be convinced of their advantages and do not look for seed.

In summary, for the local varieties, there is a moderate level of diffusion inside the watershed and little infusion from other regions. Recently introduced foreign varieties are infused from outside the valley. Older foreign varieties that have attained a moderate level of acceptance are also diffused inside the watershed. The pattern of diffusion of the varieties is therefore linked essentially to the local acceptance of the variety, the time it has been introduced in the region, and the availability of seed inside and outside the region.

The general patterns of maize seed exchange that we have just described conceal major differences among survey farmers. Three major groups can be identified.

At one extreme, we find 17 farmers who always use seed selected from their own maize harvests. They sow the same varieties regularly and only modify the proportion of maize area planted with each variety in every cropping season. These farmers are considered suppliers of seed of local varieties ('they always have seed').

Fourteen farmers use their own seed lots in addition to seed acquired in the community or introduced from other regions, and the proportion of each type of seed varies from season to season depending on each farmer's objectives and constraints. These farmers are generally regarded as suppliers of introduced seed, and some are known in the community for their curiosity concerning new varieties.

At the other end of the spectrum are six farmers who have never used their own seed lots (0% of own seed lots) and had recourse throughout the study period to seed acquired within and outside the Cuzalapa community. This group of farmers includes those who do not have rights to land and cannot plant maize each season and those who farm small areas on which they cannot harvest enough maize for both family con-

sumption and seed. Farmers in this group are obliged to look for seed from other farmers when they want to plant maize.

Geneflow

The survey and the observation of the sowing pattern in an area of 10 ha during three cultivation seasons indicate that there is no traditional strategy to actively prevent the sowing of seed lots of different varieties in contiguous areas. Farmers sow on average 2.5 varieties (one to seven) per cycle in the same field, independently of those sown on the contiguous fields. There is no physical isolation between local and foreign varieties and between locally reproduced seed lots and seed lots originating from other areas.

In addition, the date of sowing does not lead to a sufficient difference of flowering dates to permit reproductive isolation

Phenotypic observations on six farmers' fields confirmed the presence of geneflow and gave an idea of the level at which it occurs. It was observed, as indicated by literature (Paterniani and Stort, 1974), that the level of introgression of one variety by another diminished rapidly with distance. We observed the presence of 10–20% of purple grains in the first row of the white or yellow variety, levelling down to 1% after the first 2 or 3 m. The level then stabilized over a great distance.

In Cuzalapa, the traditional management of sowing, leading to the development of different varieties on contiguous areas, favours genetic exchange between all variety types, independently of the origin and growing cycle of the different varieties.

Maize in Burkina Faso

Crop management

Maize is cultivated in Burkina Faso in the southern region where the annual rainfall is over 900 mm and in a secondary zone with a lower annual rainfall of 600–800 mm. According to FAO, during the last decade, maize has been cultivated on 200,000 ha with an average of 1.3–1.6 t ha⁻¹. The crop was introduced in Africa in the 16th century from germplasm of various origins (Chastenet, 1998). Since then, this crop evolved in this region and became locally adapted. New introductions have been very limited before this century. Surveys and collections in Burkina Faso have shown that maize varieties are strongly structured, based on genetic and cultural components (Sanou *et al.*, 1997). Based on several criteria (Table 4.2), three types of fields have been characterized:

1. Backyard fields, very small, high organic fertilization (manure from cattle). These fields are cultivated by women farmers. Varieties in these field are specific, called household type, very early maturing and used to bridge the gap between main harvests.
2. Bush fields. They can be located far away from the village, are of a large size, 3–10 ha, and are relied upon for the main maize production. They are managed by men. The corresponding varieties are late maturing and produce grain for local consumption and for urban markets. They are of the open-field type.
3. Village fields. They are intermediate, in size and location, between the two former types. In these fields, open-field, late-maturing varieties are also used.

Table 4.2. Main characteristics of the fields cultivated with maize in Burkina Faso.

	Field typology		
	Backyard field (0.1–0.5 ha)	Village field (2–5 ha)	Bush field (3–10 ha)
Area	Main and secondary zone	Main and secondary zone	Main zone
Fertilization	+++	++	+
Type of cultivation	Intercropping	Intercropping or single crop	Single crop or intercropping
Maize variety types	Household CV	Open field CV	Open field CV
Competition between local and elite varieties or cash crops	–	++	+++
Sex of farmers	Female	Male	Male

–, Absent; +, some; ++, high; +++, very high.

Maize is mainly intercropped with cowpea and groundnut, but also with cotton, pearl millet or yam.

Origin of varieties

Both open-field and household types of varieties are considered family heritage and are transmitted through the male lineage, but in some cases they can be exchanged or borrowed. Weddings offer such opportunities: women introduce the household varieties of their family into the collection of varieties of their family-in-law. In other cases, it is a specific trait of a variety that leads to the exchange (early maturing, culinary properties, etc.). Many of these exchanges involve household varieties for cultivation in backyard fields and transfer is mostly from the marginal to the main (southwest of Burkina Faso) area of cultivation.

Elite varieties and local varieties

Experiments were conducted in Burkina Faso to compare elite varieties (SR22 from the International Maize and Wheat Improvement Centre (CIMMYT), Maka, Irat 171, from the Centre de Coopération Internationale en Recherches Agronomiques pour le Développement (CIRAD)) with local household (early maturing) and local open-field varieties in conditions comparable to traditional agriculture (with no fertilizer) and intercropping on one hand, and to intensive agriculture (using fertilizers, single crop and high density planting) on the other hand (Sanou, 1996). In the conditions of traditional agriculture, most of the local varieties had a better productivity than the best elite variety (SR22) selected in a single-crop environment. In the conditions of intensive agriculture, many local varieties (60%) had a production very similar to the elite variety. This was especially true for the early maturing varieties. However, a higher planting density (from 50,000 to 100,000 plants/ha) affected the local varieties more than the elite variety. Intensifying the maize cropping system with local varieties could bring lodging problems. Complex hybrids produced between local varieties and the elite variety SR22 showed an improvement of productivity of 1–2 t ha⁻¹, a small

increase in height (less than 20% for ear height) and a better reaction to Maize Streak virus when compared with their respective local variety parents. This improvement is produced by the favourable traits existing in the elite variety.

Gene flow between elite and local varieties

Differences were already mentioned between local household and open-field varieties. Almost no substitution from elite varieties is observed in this group. Elite varieties are selected for traits in relation to their commercial interest: productivity, grain colour, late maturing. They can substitute for field varieties but not the household varieties.

Gene flow was evaluated by:

1. Observation of cultivation practices (Fig. 4.2). Backyard, village and bush fields constitute separated entities but it was observed that farmers establish temporary shelters in their bush fields and plant household varieties around them for their own consumption before the harvest of bush fields. It is an opportunity for the dissemination of genes of the household early material.
2. Use of isozyme markers. The elite variety SR22 has some specific isozyme alleles – IDH1-2 and IDH2-4,2 – which are not found in the local varieties. On 100 local varieties tested, ten showed introgression from the elite variety. These ten varieties were found in villages where the elite variety was widely distributed and grown in rotation with cotton or where the extension service had established demonstration fields. Contrary to what might have been predicted by observation of cultivation practices, introgression from the elite variety into the household varieties occurred (Sanou, 1996).

Evolution in this system

In Burkina Faso, the local varieties are structured in two groups. Gene flow facilitates gene transfer from one group to the other to a limited extent. The household variety group is relatively autonomous when compared with the field varieties, but within each group gene exchange can be very extensive.

In planning to produce new genetic material for this crop management system, it is important to take into account the gene flow pattern. The final product (i.e. new varieties) has to meet the criteria used by farmers to choose their existing varieties (maturing time, culinary quality, etc.). Dynamic management of this diversity and participatory breeding should therefore be conducted on both pools separately.

To broaden the genetic base for utilization outside the area, it is possible to put these two pools together. However, the new products will be very different from what currently exists in this production area.

Conclusion

The genetic structure we observed for maize varieties in this area is derived from the social structure of the communities that use them. This social structure surely buffers possible changes at the level of the genetic material to be used by farmers. At the same time, it does not freeze evolution of these varieties but promotes a gradual and continuous crop evolution.

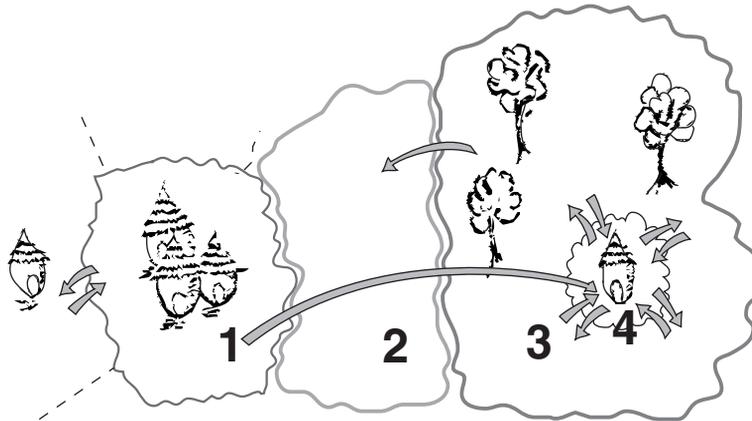


Fig. 4.2. Typical maize field distribution and gene flow in the main cultivation area in Burkina Faso. 1, Backyard fields with household cultivars; 2, village fields with open field cultivars; 3, bush fields with open field cultivars; 4, household cultivars around temporary settlements.

Pearl millet landraces in West Africa

The results in this section are based on surveys conducted by one of the authors (J.-C. Clément) in the Sahelian region of West Africa, from Mauritania to Chad, over a 20-year period to collect pearl millet landraces (Clément, 1985, 1997) and complement the work by Niangado (Chapter 9, this volume).

During these surveys, both genetic material and information from the farmers of this area were collected; in several regions, collections were made several times between 1968 and 1988. During this period, this part of Africa experienced very severe droughts. From the available data we can describe the factors that had most impact on stability and variation in this plant material. The large intra- and intervarietal polymorphism noted in pearl millet varieties of this region is expressed in traits which are used as selection criteria by farmers. They are mainly inflorescence agromorphological traits and include: inflorescence shape, grain colour, size and vitrosity and non-shattering of spikelets. These traits can be seen by the naked eye and used to distinguish the main phenotypes at the local and regional scale. Another trait, the duration of the sowing to harvest period, is also useful for discriminating between varieties and relates to the daylength sensitivity of the varieties. Early maturing varieties do not respond to photoperiod, while late-maturing varieties are quite sensitive to daylength. Millet landraces of Mali display a unique range of maturity in West Africa. In the area of Kolokani (Mali), farmers cultivate several varieties independently in adjacent plots: early-maturing varieties called 'sounas' (souna dié, souna boabâ) maturing in 75–95 days, and three late-maturing varieties called 'sanios' maturing in 100–160 days (sanio titioni, sanio makangoulou, sanio boabâ). This range of maturity is associated with some overlapping of flowering times which could facilitate gene exchange between cultivated varieties (early and late maturing) as well as with wild and weedy forms of this species.

Stability of cultivated types and areas

When data from the surveys from the 1980s and from older sources are compared, two facts are worth noting: a stability in the area of cultivation of the main types and a surprising phenotypic stability of the various types cultivated in these areas.

This stability is especially noted in the central area – Mali, Burkina, Niger – where the largest West African varietal diversity is found. In this area, landraces and families of varieties are still cultivated with their former characteristics.

Generally, the main varietal types in this central area are still morphologically distinct despite adjacent or overlapping areas of cultivation. This can be explained by farmers selecting seed only from inflorescences corresponding to the types they are interested in. In fact, the farmer strategy for seed production is related to a mass selection within each type of variety, renewed at each generation. The on-going search for better food security (i.e. to lower the consequences of climate variation on production) leads to the utilization and the maintenance of the broadest range of varieties and maturity times, making these crop management systems *in situ* genetic reservoirs.

Genetic isolation can also exist. In southeast Burkina Faso, North Togo and Benin a variety named Iniadi is cultivated: its inflorescence is short and conical and it matures quickly, in 90 days. This variety is the only early one within a set of late varieties that are well adapted to a climate with more than 1100 mm rainfall. The genetic isolation conferred by this different flowering time could explain the stability of this landrace and its specificity, which makes it one of the main genetic groups used for F₁ hybrid production in pearl millet. Andrews and Kumar (1996) have described the use of this variety in the F₁ hybrid production in the USA, India and Africa. Using isozyme markers, Sédogo and Tostain (1996) have shown that this variety has strongly diverged from the others found in this area.

Variation and evolution of landraces in relation to climatic changes

Monitoring changes in the crop management systems and varieties is possible in this region where many surveys were conducted over several decades.

EVOLUTION TOWARDS EARLINESS In areas where early, semi-early and late varieties are planted, the latter two types usually evolve toward a shorter maturing time. This is a farmer strategy to adapt to climatic changes. This strategy favours progressive genetic changes within varieties more than a substitution of varieties. In pearl millet, the genetic control of maturity is relatively simple and selection can be quite effective for this trait (Bilquez, 1963; Bilquez and Clément, 1963). In Senegal the sanio landrace is no longer cultivated with its former maturity time of 140–160 days. However, it can still be found in some areas such as the Serere country, where farmers modified it for a shorter maturity time of 120–130 days maintaining all the other traits typical of this landrace. In southeast Niger, the semi-early variety ‘maewa’ (120–130 days) has become a 100–120 days variety and grain colour has changed from blue-grey to yellow or grey-yellow.

DROUGHT AND INTRAPOPULATION MIXING In Mauritania, due to the severe drought, farmers stopped cultivating pearl millet and replaced it with sorghum. Their millet seeds were lost. When climate became more favourable, they planted their fields with

varieties from adjacent areas where the cultivation had been maintained or from a souna landrace cultivated in West Senegal and distributed by the relief teams. Landraces cultivated in the south and west part of Mauritania were related to sounas from the Senegal river; those cultivated in the east were related to sounas from Mali. Loss of seed due to drought promoted a new mixing of genes in the area when the pearl millet cultivation was re-established from these two souna types and their intermixing. In Niger, a similar phenomenon was noted, where cultivation favoured a mixing within groups of varieties along a north–south axis.

GENETIC CHANGE AND CLIMATE Severe drought was experienced by farmers from 1968 to 1973, 1976 to 1979 and 1983 to 1985, and caused substantial losses of millet types. However, its consequences should be placed in perspective with other factors. In the area of Toubouro in Cameroon and Bossangoa in the north of the Central African Republic, the disappearance of pearl millet is due to a change in agricultural activity redirected towards cotton production. In Guinea, in the Kankan area and in the south of Sigiri, pearl millet is being abandoned and replaced by rice and maize. A similar case can be observed in the east of Senegal. In the area of the Senegal river, from Bakel to Saint Louis, the 'tiotande', an 'after flood' (decrue) specific ecotype, is now almost a relict. It is replaced by maize and sorghum with a higher production potential and a better resistance to pests and diseases. Sorghum is also replacing pearl millet in many typical Sahelian areas (500 to 600 mm rainfall) in Mali.

Conclusion

For pearl millet, detailed surveys have been conducted on a very large area and over a long period of time. This area, the Sahel, with its low rainfall is relatively marginal for agriculture and often suffers climatic crises (drought). In this harsh environment, farmers have been able to maintain most of their pearl millet varieties. This apparent stability does not preclude genetic evolution. Exploiting intravarietal diversity, farmers have been able to shorten the maturing time of some of their varieties leading to a better adaptation to a drier climate. They have also recreated their varieties exploiting intervarietal diversity with introductions from adjacent areas, and by favouring geneflow and selection.

The main characteristic of this management is the existence of a large amount of genetic diversity and extensive geneflow in this crop. If one of these elements, i.e. diversity or geneflow, is reduced, the system will be affected. Modifications of this system can arise from farmers changing their main crop from pearl millet to another crop due to the many cultural and economic changes that occur in this region. Up to now, farmers have demonstrated their ability to overcome crises, managing their varieties as dynamic entities, a concept that could be used when we think of strategies to broaden the genetic basis of some of our crops.

Cassava in Amazon (Rio Negro, Brazil)

This case study has been described in detail by Emperaire *et al.* (1998). A general discussion of the use of diversity in this crop is given by Second and Iglesias in this volume, Chapter 11.

Study site location

In Brazil, Suápiranga is a village located on the Rio Negro, between Barcelos and Santa Isabel, where nine families live. These families are of very different ethnic origin (Tukano, Desana, Pira-Tapuia, Tariano, Baré). Slash-and-burn cultivation of cassava is the basis of the production system in this village. Cassava flour is very strategic in home economics, local exchanges and regional markets, and cassava plots are located in a radius of 2–3 km around the farmers' homes. Every year, men clear a plot of 0.5–1 ha in the more than 10-year-old regrown forest. Mostly women then take care of the plot and the harvest. A plot is kept under cultivation for 2–3 years, i.e. two cassava cultivation cycles, and then enriched with fruit trees before being abandoned for the forest to re-grow.

Farmer selection criteria of varieties (Table 4.3)

In this study, a variety is defined as a group of plants which are given the same name by farmers. As cassava is a vegetatively propagated crop, it can be assumed that most of the plants with the same name are of unique genetic origin.

USAGE SELECTION CRITERIA Today, in Suápiranga, cassava is mostly eaten or sold as flour (*farinha*), as pancake made from the mixture of grated meal and starch (*beijus*) and sometimes of pure starch (*curadás*). Colour is a very important attribute of the food, and especially of the flour. It has a specific value but is also considered as an integrated meta-trait to describe other characteristics, related to nutritional and culinary values, such as starch, water and fibre contents.

AGRICULTURAL SELECTION CRITERIA Selecting varieties is also a part of the production strategy that promotes food security. Combining varieties with various maturing and

Table 4.3. Selection criteria used by farmers from Suápiranga.

Use criteria	Yield criteria	Non-use criteria
<i>Colour = integrated criterion for :</i>	<i>Yield = integrated criterion for :</i>	<i>Symbolic value</i>
Starch content	Yield potential	<i>Emotional value</i>
Fibre content	Broad adaptation	<i>Filiation value</i>
Water content	Resistance to pests and diseases	<i>Novelty value</i>
Yield	Resistance to splitting	<i>Purple-red colour</i>
Production	Resistance to lodging	<i>Unusual shape</i>
Colour of processed products	Yield stability	
<i>Ease of peeling</i>	<i>Propagation rate</i>	
<i>Ease of uprooting</i>	<i>Branching</i>	
	<i>Height</i>	
	<i>Maturity time</i>	
	<i>Storage time</i>	
	<i>Drought tolerance of cuttings</i>	

storage times helps to ensure a stable production over the year in the cultivated plots (roças). Early maturing varieties (6–7 months) are systematically planted in newly established plots. Tuber storage underground varies from 10 to 36 months and offers farmers the opportunity of abandoning the plot for a few months and carrying out other activities (e.g. forest product harvesting and staying in town). Factors related to cultivation, either to the genetic material (yield capacity, pest and disease resistance, ecological adaptation, lodging resistance) or to knowledge of the agricultural techniques (evaluation of the state of a plot, cutting, maintenance) are rarely identified by farmers but are globally assessed through yield. Boster (1984) had already perceived the same behaviour in relation to the management of the cassava variety diversity by the Aguaruna in Brazil.

AESTHETIC SELECTION CRITERIA Farmers combine non-use value or aesthetic selection criteria with the previous criteria. A variety can be appreciated for its origin: e.g. it was cultivated by a mother or a grandmother, and becomes an element of family continuity. A collection of varieties is also the backdrop to a woman's working life: a cassava field with some purple-red plants or with varieties of an unusual shape can give proud, aesthetic pleasure and entertainment as can a well cleaned plot or healthy plants. These aesthetic aspects of establishing a variety collection are real factors involved in the selection process.

Local management of variety collections

The number of varieties cultivated per family is relatively homogeneous, and varies between 28 and 40. From a total of 61 varieties found in the area, only five (8%) are cultivated by all the five families studied, 13 are cultivated by four of them, nine by three families, 20 by two families, but 14 by only one family. These figures show the specificity of each family variety portfolio and the individual management level of these portfolios. Different families prefer different selection criteria.

The very rare or very frequent varieties are found in the three main categories of bitter cassava (*mandiocas*): white, semi-yellow and yellow. However, a comparison based on plant frequency within varieties leads to a general scheme for the distribution of diversity in these portfolios:

- Half the plants belong to two to three yellow or semi-yellow varieties.
- White varieties represent only 2–15% of the plants.

Within this framework, each farming woman manages her own variety portfolio according to her own preferences and cutting availability.

Selection criteria have been modified in search of a better adaptation to a specific market based on non-timber forest products in the Brazilian Amazon. This change in variety diversity occurred during one human generation and had already been noted by Dufour (1993) for the Tukano of the Colombian Amazon.

Vegetative propagation

Cassava varieties are distributed in the field in small spots, which allow, during the two or three production cycles, a serial harvesting from the centre to the border. It is a way of preserving the field (roça) centre where some medicinal and magic species are cultivated away from prying eyes and spiteful actions. Every 15 days, some tens of square

metres containing a limited number of varieties are harvested (Dufour, 1993 noted an average of 4.3 varieties per harvest). This part of the field is almost immediately replanted with new cuttings taken from cassava stem bundles of the harvested varieties (*feixes*). By this technique, the spatial distribution is maintained unchanged throughout the cultivation period.

Ecological conditions required for sexual seed production, dispersal and germination are not very well defined. It is possible that not all varieties are equally fitted for seed production, in which case the genetic broadening of varieties would rely only on a few of them. Our own data and information gathered from farmers indicate that the frequency of plants grown from sexually recombined seed is one or two per new roça, i.e. every 5 years: a low but significant frequency. This sexually induced broadening of diversity has already been described by other authors (Chernela, 1986; McKey and Beckerman, 1993) in the context of low pressure for land use, as in Suápiranga. A possible link between modes of land management and production of new varieties through sexual seeds should be evaluated.

The social origin of the cuttings is very different from one family to another. Some individuals received varieties from their mother or mother-in-law during their wedding ceremony: these varieties give the couple the capacity to be self-sufficient and to become integrated into the community when they start their first field. The cuttings of the initial variety portfolio are an important element of the process of social reproduction, being a legacy from the women and recognized as a patrimony by men, representative of the past and valuable for the future (Chastel, 1986). These cuttings are also a form of identity assertion. Those who make the choice of favouring agriculture take great care of this genetic patrimony and try to broaden it by practices that relate to the social as well as the agricultural environment.

Genetic diversity

The genetic diversity of this material was studied using DNA markers to test the significance of the high diversity index existing among the varieties when estimated by the many attributed names. Several questions had to be answered:

- What is the degree of diversity of cassava from Suápiranga compared with a representative cassava world collection?
- Are two plants with the same name genetically distinct? Cassava is vegetatively propagated and one expects to find identical plants under one name. How frequently can exceptions be found?
- When two plants with the same name are found to be genetically different, how different are they? And how does this difference compare with the genetic differences between different varieties?

Universal markers (restriction fragment length polymorphism (RAPD) and amplified fragment length polymorphism (AFLP)TM) were used. We analysed the diversity among 42 plants representing 18 names, including three plants *sem nome* (with no name), presumably directly grown from germination, all planted in one field of this village. The plants were also compared with 40 accessions from a world collection at CIAT. Two series of analyses were conducted using the same DNA extracts and AFLP (Second *et al.*, 1997) or RAPD (Colombo, 1997) markers. The main results of these studies reviewed in Emperaire *et al.* (1998) show that the genetic diversity found in this

cassava field compared well with the tested world-collection diversity but that there was no overlap. This shows that the diversity maintained in the Amazon is very large and that some specific alleles and gene combinations are maintained in this area. Through these analyses, 25 genotypes were distinguished between the 42 plants of the single Amazonian field. This shows that many of the plants with the same name are genetically identical, that all names represent different genotypes, and that the plants with no name (*sem nome*) were all distinct. These three *sem nome* plants are genetically related and their sexual origin is confirmed. Genotypes with the same name appeared as genetically related as compared with total diversity.

These preliminary results show that farmers recognized the interest and utilized the process of sexual recombination, which is favoured by the grouping of several varieties in a field. This management of variety diversity was something not expected for a vegetatively propagated crop. A traditional variety can be considered a family of clones sharing: (i) some traits of direct interest for the farmers: quality, productivity, resistance to pests, diseases and other stress; and (ii) some morphological traits useful for their identification. However, the full description of a variety should incorporate the culinary and post-harvest quality. These findings are being confirmed by work currently in progress.

Main points from this cassava case study

A vegetatively propagated crop such as cassava can go through steps of sexual reproduction under farmer management. Both natural selection and farmer selection are applied after genetic recombination, i.e. after new associations of genes are produced. The impact of farmers on the evolution of varieties is quite strong.

Modification of food habits and economic exchanges bring changes to the content of the individual cassava variety portfolios. The evolution of this traditional agriculture is still active and translates into an evolution of the plant material at all levels including the individual farmer level. During our current study, we observed that the unit for the management of diversity is the variety portfolio and not the variety. This shows that farmers are aware of the diversity existing in their plant material and that, to fit their needs, they require various varieties, each sharing some interesting traits.

Social and exchange networks are basic factors for the conservation and management of cassava in Brazil. Through these networks, varieties are maintained even when catastrophic events occur. These networks are at the root of the establishment of the variety portfolios.

Farmers select their activities according to complex motivations, based on food, social and economic interests. All these motivations lead to the maintenance of a large choice of varieties and to a broad cassava variety portfolio. They have a structuring effect on biological diversity of this crop at the village level we studied, but this effect should also be found at a higher level.

These farmers surviving in a traditional system of agriculture and using a vegetatively reproduced crop could in theory have been involved in a perfectly genetically frozen system. The study conducted showed that, on the contrary, there is a strong dynamism promoted by the social system and, as a consequence, a strong dynamic equilibrium for the genetic diversity involved in the production system.

Gene flow between varieties and wild relatives

Situations of maize-teosinte introgression

BALSA AREA Most of the F_1 hybrids between maize and teosinte are fully fertile. In the Balsa region, teosinte is a wild plant that can be found along roads and outside maize fields. Wilkes (1967) recognized both spatial and temporal isolation of teosinte and maize, and noted that teosinte flowers 2–3 weeks later than maize. However, when teosinte is found beside maize fields, F_1 hybrids are detected. In their collections of Balsa teosinte, Sanchez and Ordaz (1987) reported that ten out of 55 populations showed F_1 hybrids. So, in this area, there are situations where teosinte and maize are not as isolated as is currently reported.

VALLEY OF MEXICO In the valley of Mexico, teosinte belongs to the race Chalco, a representative of *Zea mays* ssp. *mexicana*. In this area, teosinte has all the traits of a weed. It is almost only found within and along the cultivated maize fields. In some fields, teosinte accounts for 10% of the plants (Wilkes, 1967) or more (J. Berthaud, personal observation). There is no spatial isolation, and temporal isolation is 'only partially operative' (Wilkes, 1967, p. 73). Flowering of teosinte is about 2 weeks later than maize, and Wilkes (1967) noted a proportion of F_1 maize \times teosinte hybrids of 2–5% within teosinte and teosinte-like plants.

CENTRAL PLATEAU Teosinte found in this area (north of state of Michoacan and south of state of Guanajuato) belongs to the same subspecies as in the Chalco area: *Zea mays* ssp. *mexicana*. This subspecies also includes the populations discovered around the town of Durango.

In this region, populations of teosinte are found wild or as weeds, and plants grow both in maize fields and in places where there is no maize (Wilkes, 1967). There is no spatial isolation, but there is temporal isolation, with teosinte flowering 2 weeks after maize.

Wilkes (1967, pp. 80–81) mentioned that in some small populations teosinte plants exhibited non-brittle rachis and paired spikelets, which are maize traits. This suggests that introgression from maize occurred in these small populations and that teosinte populations can survive with some domestication traits. Another case of introgression is described by Doebley (1990) when he found that the chloroplast DNA in a CMS-S cytoplasmic male-sterile maize was only shared by three populations of Central Plateau teosinte, from Copandaro. This CMS-S maize also shared the same mitochondrial type as the three teosinte populations: further evidence that introgression has occurred. In this case, introgression would have started on a teosinte plant, and successive backcrosses from maize pollen would have resulted in a plant with maize nuclear genes in a teosinte cytoplasm.

ZEA DIPLOPERENNIS, A WILD ZEA SPECIES CONSERVED IN SITU The perennial and diploid teosinte, *Zea diploperennis*, was discovered by R. Guzman in 1977 and described by Iltis *et al.* (1979). It is only found in the Sierra de Manantlán (state of Jalisco, Mexico). Four populations are reported, at an altitude extending from 1350 to 2440 m above sea level. Populations from Manantlán and Rincon de Manantlán are small, with a recent origin, while populations from La Joya and Valley of San Miguel are distributed over 40 and 320 ha respectively.

The ecological requirements of *Zea diploperennis* make it quite dependent on human activity. Its populations grow on former maize fields or on intermittently grazed areas. Manantlán and Rincon de Manantlán populations were most probably established by farmers for pasture. In San Miguel, the teosinte population is actively managed: farmers sow seeds where density of teosinte is low. A 'genetic' use of this population is also reported by Benz *et al.* (1990). A controlled introgression of maize by *Zea diploperennis* is promoted by farmers planting some teosinte along maize fields. They plant the F₁ hybrids the following year and the backcrosses the next years. The 4th year, these seeds are mixed with those of the local varieties. Farmers say that it is a way to improve maize, especially for disease resistance. However, actual introgression is yet to be confirmed.

A biosphere reserve was created which protects this *Zea* species and conserves it *in situ*. At the beginning, this implied preserving the wild populations in their original localities. Later observations have shown that survival of these populations is linked to the activity of farmers who keep their land open through cultivation. When land is left fallow, forest regenerates after less than 30 years, trees and shrubs compete with teosinte for light and the teosinte is eliminated. This example of *in situ* conservation underlines the strong link existing between a 'wild' species and human activities. In this case, when geneflow exists between wild and cultivated forms of the species, it is largely due to the activity of farmers, who are the key element of the system.

Genetic differentiation in maize and teosinte populations

Studies already carried out by Smith *et al.* (1984, 1985) and Doebley *et al.* (1984, 1987) based on isozyme diversity have shown:

- Plants from section Luxuriantes – *Z. diploperennis*, *Z. perennis*, *Z. luxurians* – form a group different from the Mexican annual teosintes.
- The race Balsa, *Z. mays* ssp. *parviglumis*, has a wider range of variation. Accessions from Central Guerrero are close to accessions from Central Plateau, taxonomically belonging to *Z. mays* ssp. *mexicana*.
- A closer similarity between Balsa and maize could be due in part to the existence of more alleles (in low frequencies) in this race. As a consequence, Balsa would have more alleles in common with maize.

From these studies, several genetic parameters have been estimated (Doebley *et al.*, 1984). Diversity in populations of teosinte is quite comparable with diversity of Mexican maize accessions (Eyre-Walker *et al.*, 1998), and a lot of variation is retained within populations.

Does introgression occur between maize and teosinte ?

Doebley (1990) has already discussed this issue. The most convincing example given is from *Z. diploperennis*, where he found a plant with alleles from maize at two linked loci. Frequency of these alleles was 0.01, which can be considered as high.

Kato (1984) did not find knob distribution in maize and teosinte that would have suggested introgression. For example, abnormal chromosome 10 type 2 is only found in teosinte and not in sympatric maize.

In conclusion, presence in the fields of F₁ hybrids between maize and teosinte has been well documented (Wilkes, 1967; Sanchez and Ordaz, 1987) but there is still a

need to set up experiments to follow the evolution of F_1 hybrids when they are back-crossed by maize or by teosinte, and estimate the size of gene exchange between these forms of *Zea*.

Geneflow, Farmers and the Base-broadening Process

Comparison of dynamic (DM) and on-farm management (OFM) of genetic resources

The dynamic management of genetic resources (DM: Goldringer *et al.*, Chapter 13, this volume) consists of distributing the genepool to be conserved in a number of small populations, representing a metapopulation. In so doing, processes of genetic drift and selection are favoured. This system promotes the conservation of alleles at the population level – but not at that of genotypes or individuals – and it takes advantage of the effects of genetic drift and natural selection to enrich the small populations with locally advantageous genes and gene combinations. Dynamic management can also be seen as a base-broadening or pre-breeding technique. When we compare this DM with what we described as on-farm management (OFM), we see that in OFM the selection process depends on natural selection and on selection exerted by farmers (mainly directed to traits useful to the farmers). OFM is conducted on many farms and the total population size is much greater than that of the more controlled condition of DM, and can explore many more niches. However, the two types of management are similar because both are more directed at the conservation of alleles than the conservation of genotypes.

Evaluating the bread-wheat dynamic management in France over a 13-year period, Goldringer *et al.* (Chapter 13, this volume) draw the conclusion that morphological characters evolved differently from site to site during this period, and that evolution also occurred for the relationship between plants and pathogens. A comparable evolution is expected within OFM of genetic resources: direction of selection is always changing and genetic material evolving due to geneflow and recombination. Equilibrium is seldom reached but this dynamic maintains genetic diversity.

In OFM, some varieties are used in different conditions in different sites: for instance, the Blanco variety of maize in Cuzalapa or the backyard varieties in Burkina Faso and cassava in Amazonia. These varieties experience varied selection pressures and even selection cycles, for example from rain-fed cultivation to irrigated cultivation and back. A broader adaptation can be expected from these varieties compared with genetic material produced through dynamic management alone.

OFM goes beyond dynamic management as it takes into account management at the level of a collection (variety set or portfolio) which can enable more diversity to be conserved than DM and can also enable a complementary type of diversity management to be carried out. OFM is an open system that allows complementary introductions of varieties and a rapid evolution and genetic adaptation when needed. However, the system is susceptible to replacement of varieties by new introductions, i.e. new varieties or new crops that totally replace the landraces. This is one way farmers deal with changing conditions in production systems and it can lead to the disappearance of some local varieties when they are not cultivated in many different places. It is the strength and weakness of this system that it responds to economic and social forces.

The broadening of the genetic base of some crops could be obtained by introgression from wild ancestors or related weeds. The management of this type of introgression requires almost necessarily a monitoring of geneflow. It will be more easily established and run in a dynamic management system than in the OFM system where it could be difficult for farmers to assess the introgression process. However, this may not always be the case, and situations have been described where geneflow between wild relatives and crops are under the control of farmers (see page 97).

Promoting geneflow through farmer participation

In the cases studied, several types of genetic exchange have been observed which are generated by the activity of farmers on their farms. The three levels of exchange described are as follows:

1. Exchange, introduction and loss of varieties in farmers' collections leading to a change in the number of varieties available to the farmers in a specific place.
2. Genetic exchange between landraces and modern varieties, and between wild and cultivated plants.
3. Genetic exchange within varieties as the varieties are usually seed reproducing and are not genetically fixed.

The base-broadening activities could be modelled according to the situation described on-farm.

Exchange between collections of varieties

The first level of farmer management of genetic resources is that of the collection of varieties maintained. The diversity within these collections (the portfolio) is a farmer's answer to agricultural uncertainty and to varying needs, according to productivity and usage criteria.

When defining strategies for base-broadening, we should take into consideration that the new products (varieties) will be used in association with others and managed as portfolios of varieties. These new products will have to complement the diversity already existing in these collections, which implies a very delicate combination of new traits and adaptation to different requirements. Base-broadening could also play a role in restoring the farmers' collections where they have disappeared for such reasons as war or drought.

Exchange between varieties

Exchanges occur between different types of material, i.e. between wild and cultivated plants, between modern and traditional varieties, or between traditional landraces.

This intervarietal diversity and close proximity of varieties in the farmers' fields favour gene exchange between varieties. The varieties generally have very distinct morphological and genetic traits and farmers maintain through selection the most important characteristics that identify these varieties and are the basis for their agricultural interest. Gene exchange can also allow farmers to select for different characteristics, such as a shortening of the time to maturity of a crop. It is quite important to recognize the existence of such a management system, which is certainly a process promoting the genetic diversity found in landraces.

Base-broadening can use this gradual introgression as a model. It can also take advantage of this existing OFM to propose new progenitors to farmers for incorporating new genes into their own varieties. This should be a way for farmers to obtain new (modified) landraces which respond better to their changing needs.

Exchange within varieties

Farmers recognize their varieties by certain agronomic and morphological traits and apply selection pressure for these traits. Varieties are more or less stable for these traits but not for others. Each variety is far from being genetically homogeneous and this makes them a potential reservoir for genetic progress. Base-broadening actions should consider diversity not only at the intervariety level but also at the intravariety level when it comes to decide on base-broadening strategy. This is also true for crops with vegetative propagation such as yam and cassava: their varieties are often polyclonal, and genetic recombination is a mechanism exploited by the farmers. This reservoir of diversity within varieties also offers a possibility for breeding progress or for developing broad adaptation. We have seen that the variety Blanco is cultivated in Cuzalapa under irrigation but also in other villages under rainfed conditions. Seeds of this variety are exchanged between these villages. This management confers a broad adaptation to the variety and, at the same time, favours the maintenance of a within-variety genetic diversity.

General Conclusion

Peasant farming systems have been considered as crop evolutionary laboratories (Brush and Meng, 1998). Our case studies have shown three levels of complexity in these laboratories – between collections of varieties, between varieties and within varieties – with gene flow occurring at these three levels. Maintenance of these varieties or landraces is not based only on interest for maximum yield but also on their private value and their comparative advantage due to relatively small advantages (Brush and Meng, 1998).

In their concept of variety, farmers integrate a dynamic component; we are very often far away from the concept of a commercial variety with its constraints of distinctness, homogeneity and stability. The concept of a dynamic variety is well in agreement with biological models of metapopulations, which consider sets of populations with history of extinction and migrations (Hanski, 1998). An evolution of farmers' varieties towards more stability and homogeneity, i.e. closer to the concept of commercial variety, would introduce an erosion of the gene flow and lead to a loss in our capability to maintain genetic diversity and a broad genetic base for our crops.

The dynamic of the biological structure of genetic material, farmers' varieties and landraces is strongly dependent on the social structure organizing the life of the farmers: we can consider that the former is a reflection of the latter. Selection of seeds as a continuous and iterative process is emphasized by Rice *et al.* (1998) for maize. We could define plant varieties in these farming systems as continuous cultural constructions which integrate constraints from yield, use and aesthetic criteria, but these activities come at a biological and social cost. More detailed studies should be conducted and theoretical approaches completed to evaluate and compare different strategies, taking into account genetic load and other biological constraints.

How can we take advantage of this system to conduct base-broadening of our crops?

We saw that varieties managed by farmers are open genetic systems. Farmers are very active in experimenting with new genetic material and they have a strong interest in innovation. This is a very favourable situation for experimenting with base-broadening involving farmers in this process. The dynamic of these systems can be used as models when we define base-broadening strategies. As a result, it should produce varieties and populations of progenitors dynamically maintained. When we want farmers to be part of the process, we have to look beyond biological criteria and take into account the social and farming systems in and/or for which the base-broadening will be carried out. Incentives to promote this base-broadening will have to be compatible with the main component of these integrated systems.

As a very general conclusion for our study, it can be said that OFM of seeds and varieties is a complex system with many different options chosen by farmers. When we propose systems of improvement and conservation of plant varieties we should be careful that they are not too simplistic and not very far away from what is being done by these traditional farmers.

Continuing to document this complex system will certainly reveal even more sophisticated relationships between people and their crops, challenging our strategies for broadening the genetic base of our crop and the conservation of their genetic resources.

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5

Regulatory Aspects of Breeding for Diversity

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Introduction

Seed regulatory frameworks aim to promote varietal and seed quality, and thereby to protect farmers from planting sub-standard seed. Seed laws commonly regulate variety testing and release, seed certification and seed quality control, and they establish the institutional framework of national seed councils and certification agencies.

Variety release systems aim at making only varieties of proven value available to farmers. Seed certification aims at controlling the varietal identity and purity throughout the seed chain. Seed quality control checks on seed quality such as viability, purity and health. Seed quality control also protects *bona fide* seed producers from competition by less scrupulous colleagues. Additionally, intellectual property rights on varieties are included in seed laws of some countries in order to protect the breeder from competitors that may provide seed without any R&D investment through the granting of an exclusive right over the exploitation of the variety.

The regulatory frameworks that have been developed in various countries reflect different levels of state involvement. For example, in North America certification is, in many cases, a voluntary service, and variety release is fully the responsibility of the company. This reflects the general confidence in the regulatory effects of the free market itself: suppliers of poor quality seed would be punished by the customers through declining demand for their products. In various European countries, on the other hand, public institutions have developed a significant mandate for 'policing' seed quality. In some countries such as The Netherlands, certification agencies have developed as independent foundations managed by farmers, seed producers and breeders, but they operate within a legal framework.

In most developing countries, formal seed production has developed as part of a strategy based on the Green Revolution paradigm of agricultural development in which plant breeding would increase yield potential under optimum growing conditions, and seed production would therefore be a necessary vehicle for technology transfer. Seed and other inputs have often been heavily subsidized in order to increase adoption of the

new technologies. Within this paradigm, centralized seed production units have been built to resemble the successful European and North American seed industries. These formal seed systems subsequently developed specialized seed quality control institutions to create a quality awareness and to safeguard the interests of farmers, similar to the official seed certification agencies in the north. Especially in the era of privatization of public institutions at the end of the 1980s, these seed quality control institutions became the driving force behind the development of seed legislation (Louwaars and van Marrewijk, 1996). Such legislation would give these institutions a legal backing necessary to perform its police tasks *vis-à-vis* (private) seed producers. The result of this development is that many seed laws in the south strongly resemble those in the north. However, whereas in the north the farmers' interest was often represented by a strong voice in the seed quality control systems, in several countries in the south seed regulations fit into the existing bureaucratic structures and are imposed upon both seed producers and users.

Seed laws are not usually intended to influence the direction of plant breeding. However, there are significant indirect effects of the variety release systems and of seed certification requirements on plant breeding methodologies and the resulting varieties. Breeders tend to target favourable farming conditions, wide adaptation and varietal uniformity as a result.

This chapter analyses the effects of seed regulatory frameworks in relation to the objectives of broadening the genetic base of plant breeding, with particular focus on the role of alternative breeding strategies.

Effects of the Various Components of the Regulatory Framework on Breeding

Variety registration and testing

Variety release may become a goal in itself when regulatory systems are too rigid. Release is the yardstick by which the effectiveness of public plant breeding is measured. The reward system for breeders is commonly based on the number of varieties released, not on their widespread use by farmers. Hence, the objectives of plant breeders are likely to be adapted to the variety release procedure instead of the farmers' needs.

A variety release system commonly incorporates the following steps:

1. Application with a formal variety release committee and variety registration, including a variety description.
2. Testing for the value for cultivation and use (VCU) of the variety involving a prescribed number of sites and seasons.
3. Testing for distinctiveness, uniformity and stability (DUS).
4. Analysis of the test results by the committee leading to approval or rejection for formal release.

In each of these stages there can be a bias favouring particular types of varieties.

Application for variety release commonly includes payment of a fee. The global trend of reducing public expenditures has raised the financial contribution by the breeder to the testing system in most countries. The result is that both public and

private breeders reduce the number of varieties submitted for official release to those that are likely to perform well in all test locations and to pass other registration standards such as the DSU requirement. Varieties with specific adaptation to particular agroecological niches or uses are less likely to be presented.

The management of many variety testing systems further reduces the number of approved varieties and delays release. High input levels are often used to improve the trial from a statistical point of view. Sometimes, this is also a deliberate policy to represent the conditions of the 'better farmers' and to motivate other farmers to follow; also, high input levels give 'beautiful crops' that make a trial presentable to visitors. But high inputs such as fertilizers conceal environmental variations in the trial, thus reducing residual variance. Poor trial design and management increases residual variances and thus reduces the chance that actual differences in quantitative traits are identified. This may require additional trials to be performed, which delays release, or it may obstruct release altogether. Moreover, poor site selection and high input levels make it doubtful whether the trial results have any value for most farmers. For example, it is unlikely that the official sorghum trial results in India are valuable for the majority of farmers where average yields in the 1989/90 trials were three times the farmers' average yields (Virk *et al.*, 1996). Breeding for favourable agroecological conditions and for monoculture is encouraged.

The evaluation of trials using simple statistical analysis methods leads to a bias in favour of breeding approaches for wide adaptation. Since trials are pooled in one calculation, the variety having the highest average yield is considered the best. However, this may not be the best variety in any of the testing sites. Standard variety release procedures rarely accept a variety that is specifically adapted to particular conditions, even though national variety lists may contain regional recommendations.

The trial system is biased against breeding for partial (horizontal) resistance, which is in most cases polygenic and more durable. Such varieties are resistant, but not immune to disease and thus they commonly carry disease symptoms, and for this reason are liable to be rejected in a release system, even if uniform. Additionally, the small size of the research plots makes it difficult to identify horizontal resistance (Ceccarelli, 1989).

Evaluation of variety trials by release committees is usually totally dependent on figures, with the result that only yield becomes the decisive characteristic, and important characteristics for smaller-scale farmers may not be taken into account. These include, for example, aptitude to intercropping, shattering (e.g. soybean), lodging when harvesting is delayed (e.g. maize), cooking time of the produce (e.g. beans), and the yield and quality of secondary products (e.g. straw for construction or fodder). Breeding thus tends to concentrate on yield only, without giving credit to the diverse needs of farmers.

Variety release committees commonly consider the appropriateness for the production of certified seed as an important criterion. A variety needs to be morphologically identifiable, and thus distinct from existing varieties, and stable. Both factors contribute to the need for a certain level of genetic uniformity. The uniformity standards of seed certification systems are commonly very high (allowing only one dozen or a few dozens off-type plants per hectare); much higher even than International Union for the Protection of New Varieties of Plants (UPOV) standards for plant variety protection (see page 109). Releasing varieties to a seed certification system thus implies breeding for uniformity, even where this has no agronomic advantage.

Finally, lack of participation and transparency in the closed system of formal variety release leads to conservative trial designs and management. Parallel (demonstration) trials by the extension service, non-governmental organizations (NGOs) or private seed companies are rarely taken into account in the release decision. Official on-farm variety trials are becoming increasingly popular with variety release systems. This positive development, however, hardly ever contributes to releasing more adapted varieties because such on-farm trials are either completely researcher managed, and thus similar to station trials, or the results cannot be easily analysed statistically, leading to denial of such results: the non-numerical comments by farmers are difficult to include in reports. In developing countries, farmers are rarely well represented in the variety release committee, or in the evaluation of varieties. Improved representation would be likely to lead to a higher transparency of the system.

In conclusion, standard variety release procedures commonly result in the approval of few, uniform and widely adapted varieties that often do not respond to the diverse needs of farmers.

Seed certification and quality control

Seed certification, being the check on varietal identity and purity, has a marked effect on breeding strategies. Varieties have to be stable in order to guarantee varietal identity; only uniform varieties can supply the required level of stability.

Further effects on breeding largely depend on the definitions and interpretation of the seed law. In some countries all seed planted falls within the scope of the law. Examples can be found in the former Soviet Union and various countries in Africa and Asia. In other countries 'all seed in the market' fall within the definition of the law, thus basically making any exchange of seed of non-tested seed and non-released variety seed strictly illegal. More recently some more 'open' seed regulatory systems are being designed in developing countries. Examples are the regulation of seed of so-called 'notified crops' only in Bangladesh, and the specific rules to (de-)regulate the local and formal production of landrace seed in the draft Eritrean seed law.

Strict seed laws can mean that the distribution of non-regulated seed is illegal, thus participatory plant breeding strategies that rely on informal dissemination of new selections may not be legal in a strict interpretation of many seed laws. Even on-farm testing of non-released varieties has been obstructed in some countries (e.g. Uganda at the end of the 1980s) on these grounds. It also discourages the emergence of small-scale seed enterprises that find a niche market by selling seed of locally preferred varieties.

In conclusion, seed quality control regulations tend to limit the number of varieties of seed that can be multiplied, and reduces the possibilities for alternative breeding and seed production strategies.

Intellectual property rights

Intellectual property rights (IPRs) can be considered as a contract between the inventor (author, breeder, etc.) and society, by which an exclusive right to use or commercialize the protected subject matter is granted in return for public disclosure. Plant varieties

can, in some countries, be protected by a special type of IPR, called plant variety protection (PVP) or plant breeder's rights (PBR); in some others by patents. The many countries that do not protect plant varieties, but are members of the World Trade Organization, are required to do so 'by patents or by an effective *sui generis* system' through Article 27.3(b) of the Agreement on Trade Related Intellectual Property Rights (TRIPs). Furthermore, in a growing number of countries, gene constructs and biotechnological methods can now be patented.

Implications for plant breeding and particularly for broadening the genetic base can be envisaged and are described in the following paragraphs.

The term plant variety protection is commonly used in connection with the UPOV, but it may be used for any '*sui generis*' system to protect plant varieties. Under the UPOV convention, an exclusive right is granted to the breeder or discoverer of a variety that is distinct, homogeneous (uniform), stable and new (novelty relates to the marketing of seed of the variety). This means that the breeder is likely to be granted benefits only for those varieties that conform with these 'DUS-N' standards. Applying for PVP is only useful if the variety will be commercialized, i.e. multiplied and sold to a fairly wide range of customers.

Homogeneity standards are not extremely strict compared with seed certification standards. However, as the number of varieties of any one crop species registered increases, a larger number of characteristics have to be uniform in order to distinguish a new application. A landrace of a crop for which few varieties have been registered so far could thus comply with the homogeneity requirement, but it would not pass the novelty requirement. It may, in fact, not be worthwhile to have PVP for most landraces since it is unlikely that there would be a large-scale commercial market.

Specific to PVP amongst IPRs, are the breeders' exemption and the farmers' privilege. The breeders' exemption rules that any protected variety may at any time be used to produce a new variety on which PVP can be granted. This means that PVP does not monopolize the genetic base of plant breeding. Revisions introduced in the most recent UPOV Convention (1991) may even have a positive effect on broadening the genetic base of plant breeding, since, in its clause on 'essentially derived varieties', varieties that have been developed by small manipulations in a protected variety are considered 'dependent', i.e. that the rights on the new variety are shared with the holder of the rights of the original one. This means that in order to reap the full benefit of the PVP system, a breeder has to develop a new variety through more substantial changes, such as through a crossing programme, preferably with more distant parents.

The farmers' privilege rules that farmers are allowed to produce seed of a protected variety without consent from the owner of the variety either for his own planting, or for non-commercial purposes (the details differ according to national laws, some of which include an allowance for 'over-the-fence' trading of seed). The farmers' privilege is particularly important in developing countries where by far the largest quantities of seeds are produced within the local informal seed system (that is, saving of seed on-farm, and local diffusion of seed through farmer-to-farmer exchange: Almekinders and Louwaars, 1999). This privilege has, however, been tightened in the latest UPOV Convention (1991), and now requires a positive act by national authorities to permit it, on a crop-by-crop basis. Depending on its application then, PVP may thus restrict the use of protected varieties in local seed systems.

Though designed to stimulate conventional plant breeding, PVP does not restrict

alternative breeding strategies. Indeed the breeders' privilege allows for any protected variety to be used in any breeding programme, including alternative ones. However, most products of alternative breeding are either likely to be ineligible for protection, or are unlikely to benefit from such protection since they are mostly intended to be fed into local seed systems.

The patent system was designed for industrial inventions. Living matter had been explicitly excluded from the system for ethical and practical reasons. The practical reason was mainly that plants could not be described as methods or articles in the inanimate world. However, it is now widely considered that genes can be described, and some countries allow genes and methods for gene manipulation to be patented. Since existing patent systems do not make provision for a farmers' privilege and the research exemption of the patent system is narrowly defined (compared with the breeder's exemption in PVP), germplasm containing patented genes is not freely available for breeding even if the patented gene has entered a plant through natural crossing. Patents thus can cause a serious limitation in the availability of parent material in a breeding programme. Arguably, in alternative breeding programmes where a wide range of genetic resources are being used, this problem may even become more serious than in a conventional programme.

In conclusion, IPRs designed to promote commercial plant breeding may sometimes be at the cost of public plant breeding for less endowed farmers, but may stimulate the use of a wider genetic base in conventional plant breeding. Strong IPRs are likely to create obstacles in the use of germplasm in alternative breeding programmes.

Regulations governing access to genetic resources, the sharing of benefits and farmers' rights

Finally, implementation of the Convention on Biological Diversity (CBD) and the revised International Undertaking on Plant Genetic Resources for Agriculture will have implications for the availability of genetic resources. Regulations on access to genetic resources, and IPR-type arrangements for the protection of the genetic resources of local and indigenous communities, are being introduced or considered in a number of countries, and are being discussed both under the CBD, and in the Commission on Genetic Resources for Food and Agriculture. This includes, in the latter forum, elaboration of the concept of farmers' rights – a term introduced by the Food and Agriculture Organization (FAO) to recognize the contributions of farmers in the development of the materials that are the basis of modern plant breeding.

Under the CBD, national governments have the authority to determine access to genetic resources, which is subject to national legislation and should be on mutually agreed terms. Unless determined otherwise, access is subject to prior informed consent of the providing country. Major restrictions on access to genetic resources could lead to serious obstacles for the broadening of the genetic base of plant breeding, and hamper alternative breeding strategies. As indicated in other chapters (Berthaud *et al.*, Chapter 4; Salazar, Chapter 7, both this volume), there is often substantial gene flow within and between farmers' crop varieties. In certain circumstances, restrictions on access could, in fact, harm efforts by farmers themselves to improve their own varieties. The wider the parental materials used in breeding, the more barriers that may be encountered.

Farmers' rights are meant to stimulate the conservation and use of plant genetic resources through recognition and remuneration. Farmers' rights are as yet insufficiently defined to fully analyse their impact on plant breeding. If farmers' rights are interpreted as the rights of farmers to continue their traditional saving and exchanging of seed, and the right to receive a remuneration for the continued use of diversity, the concept can strongly support strategies for broad-based plant breeding. On the other hand, IPR-like interpretations of the concept would be likely to impede gene flow and thus, in fact, be contrary to the principle of farmers' rights. The same considerations apply to the elaboration of mechanisms to respect, preserve and maintain the knowledge, innovations and practices of indigenous and local communities, as required under Article 8j of the CBD.

In conclusion, the full control over germplasm by communities or nations, though inspired by thoroughly ethical concerns, may in fact reduce genetic diversity and hinder farmers' own efforts at plant breeding. Such restrictions could also result in it being easier to use modern varieties as sources of genetic material (because of the breeders' exemption) than to take local landraces as a starting point of breeding.

Macro-economic policies that promote the narrowing of the genetic base

While seed laws and IPRs greatly influence the economics of plant breeding and seed supply, other economic factors are also important, and thus are briefly mentioned here (McGuire, 1997).

Fundamental changes have occurred in the organization of plant breeding in developed countries since the 1980s. The privatization of plant breeding research (as in the case of the Plant Breeding Institute, Cambridge, UK), or its commercialization (as in the case of many universities and research departments), has increased the influence of economic forces on plant breeding. Competitive plant breeding is likely to have a positive effect on the rate of development of new finished varieties, but it may reduce the opportunities for commercial breeders to invest in new approaches to breeding. Base-broadening or genetic enhancement programmes are typical examples: the investment in the use of more diverse germplasm means a high initial cost and risk for the company, whereas successful results would be available to all competitors as soon as the first variety is released. Competitive plant breeding, where crossing the two best varieties in the market at any particular moment is likely to yield a slightly better one in a short period, thus results in a narrowing of the genepool that is used for actual breeding. This applies particularly to self-fertilizing species such as wheat and barley, where commercial prospects for the sale of seed are poor.

In developing countries also there is a trend towards the commercialization of public agricultural research as research institutions increasingly have to compete for public funds and concentrate on earning revenues in the market. Since they produce concrete products, breeding departments of national agricultural research systems (NARS) are particularly susceptible to these pressures. The result is that such breeding programmes concentrate even more on those sectors of the farming economy likely to afford to pay a seed price that includes a research bonus. This again strengthens the trend of producing varieties that fit the variety release and seed certification systems and relatively uniform farming conditions.

Impact of Regulatory Frameworks on Alternative Breeding Methods

Where conventional breeding methods may be very successful to develop varieties for uniform and favourable farming conditions, they rarely manage to develop varieties that are adapted to ecologically diverse and marginal conditions. Farmers' breeding methods for such conditions generally result in genetically diverse landraces. Such landraces are maintained through a combination of conscious and unintentional selection by both the farmers themselves and the biotic and abiotic environment. Farmers may also consciously look out for off types in their crop and experiment with them. Improvement of landraces through mixing introduced materials into a landrace, or promotion of cross-fertilization by planting different materials close to each other, is also part of the traditional process of landrace development.

To benefit from the value of genetic diversity in particular farming systems, scientific breeders are emulating some traditional methods. Strategies broadly include:

- Breeding for plasticity within a variety, e.g. genes or gene combinations that respond to multiple stresses.
- Breeding for diversity within varieties, e.g. many alleles of one gene in one genotype.
- Breeding for specific adaptation, i.e. for diversity among varieties.

In order to be effective, participatory methods have to be used, especially in the latter two strategies.

The importance of breeding for diversity can be illustrated in the case of breeding for disease resistance (Louwaars, 1997). A monogenic (vertical) resistance can be broken by the pathogen, causing massive losses. Such losses are more disastrous for risk-prone, small-scale farmers in low external input farming conditions, compared with their more commercial colleagues. The seed replacement rate in commercial farming is high, so when a resistance is broken farmers can purchase seeds of a new variety the next season, assuming that the breeders have done their job in being 'ahead of nature'. Their loss has to be absorbed for 1 or 2 years only, which can be done in the presence of effective rural credit. This was the case for the massive destruction of maize due to blight in the early 1970s in the USA.

Breeders for low external input farmers, who are mostly in the public sector, have different responsibilities. Their clients obtain seed to a large extent through the local seed exchange mechanisms, and variety replacement is slow. In the absence of effective rural credit schemes and commercial seed supply systems, a serious outbreak of a disease cannot be tackled by the market. Durability of resistances to diseases is therefore even more important in such systems. Breeding for polygenic resistance or multilines should be promoted, even though the methodologies are more complex. This is currently discouraged due to very ineffective variety release systems. Breeding for partial (horizontal) resistance, for example, is biased against, since, as explained on page 107, such varieties commonly do carry some disease symptoms and are rejected by the release system.

Breeding multilines can also encounter problems. An illustrative case is a multiline wheat variety bred by The Netherlands' cooperative seed company Zelder in the late 1970s. This novelty put a lot of pressure on The Netherlands' variety release system. The variety, aptly named 'Tumult' (Dutch for 'commotion'), was insufficiently uniform, and thereby could not be released. The final option was to register the con-

stituent lines as separate varieties. These are hardly distinctive because they are different only for the resistance gene. Moreover, testing of the lines for VCU would cause problems: the resistance to yellow rust of individual lines was below standard, but when tested as a multiline the variety was superior. Eventually the registration authority was convinced by the breeder to test the multiline variety as one entity. Commercially, however, 'Tumult' turned out to be a failure. The breeding and release procedure caused the multiline variety to be outdated before it even appeared on the market. Additionally, maintaining the lines and producing the seed separately were too expensive. The Zelder seed company has not produced multiline varieties since.

In breeding for diversity among varieties, conventional variety release systems provide quite effective sieves that allow only a very limited number of varieties to reach the farmers. Where the number of different (uniform) varieties has to constitute genetic diversity in the field, any regulated system is going to frustrate such strategies.

Breeding for diversity among varieties basically means the selection of many different lines for many different conditions. Participatory plant breeding commonly leads to such results, when farmers are stimulated to select from wide germplasm in on-station or regional nurseries. Again, the physical release of the material is not connected with subsequent formal seed production, so in this case strategies are obstructed not supported. The main risk of the use of wide germplasm in such breeding programmes is that in the future more and more proprietary material will enter the scene, which may create restrictions. The same accounts for strong farmers' rights or strict implementation of national sovereignty.

The importance of such regulatory frameworks in breeding strategies has been acknowledged only very recently. Regulations are an impediment to novel approaches, such as breeding for specific adaptation and participatory plant breeding, which are very valuable tools for targeting less endowed farmers.

Conclusions and Recommendations

There are a variety of reasons why current public seed regulation is unsatisfactory: it is not efficiently organized, often uses inappropriate standards, does not offer opportunities for farmer and seed producer participation, and is not sufficiently transparent. Thus, adjustment to seed regulatory frameworks is necessary because of significant changes in national seed systems, including reductions in budget for public agricultural research; the failure of many seed parastatals; pressure for the establishment of plant variety protection; the increasing contributions of commercial seed enterprises; and the emergence of innovative local-level variety development and seed production initiatives, as well as increasing concern about plant genetic diversity (Tripp, 1997; Tripp *et al.*, 1997).

There are a number of options for regulatory reform. In plant breeding, more emphasis should be placed on decentralizing variety testing, breeding for particular niches, and making site selection, trial management and analysis more representative of farmers' conditions. In variety regulation, simpler registration procedures are required, and the demands of plant variety protection should not be allowed to bias or limit the development and use of public and farmer varieties. Variety performance testing for release should be made more flexible. In seed quality control, standards should be

re-examined for their relevance to particular farming conditions, and much of the responsibility for monitoring seed quality should be passed to seed producers and merchants, accompanied by well-defined public oversight and enforcement mechanisms. Introduction of intellectual property rights, rules on access to genetic resources, and mechanisms to reward local communities should be done in such a way as to avoid or minimize negative impacts on the use of genetic diversity.

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6

Decentralized and Participatory Plant Breeding for Marginal Environments

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Introduction

Formal plant breeding has been beneficial to farmers in favourable environments, and to those who could profitably modify their environment to suit new cultivars. It has been less beneficial to those farmers, the poorest, who cannot afford to modify their environment through the application of additional inputs (Byerlee and Husain, 1993; Eyzaguirre and Iwanaga, 1996; Trutmann, 1996). Poor farmers in marginal environments continue to suffer from chronically low yields, crop failures and, in the worse situations, malnutrition and famine, while farmers in favourable environments who use large quantities of inputs are now concerned with the adverse environmental effects and the reduction of genetic diversity.

Because of the successes in favourable environments, plant breeders have tried to solve the problems of poor farmers living in unfavourable environments by simply extending the same methodologies and philosophies applied to favourable, high-potential environments, without considering the possible limitations associated with the presence of large genotype \times environment (GE) interactions.

In unfavourable environments, progress with empirical breeding has been negligible, with Australia – where most of the selection takes place in the target environments – as one well-known exception. As a result, the yield of some important staple crops has shown only modest increase or remained virtually unchanged. This has been attributed to the difficult nature of the target environment (Passioura, 1986; Blum, 1988), and has led to the widespread habit of conducting most selection work in favourable conditions (Simmonds, 1991). Rather than questioning the dangers of selecting in an environment different from the target environment, much research has been done, and resources spent, to seek alternatives, such as physiological traits, to empirical breeding for unfavourable conditions.

GE interactions are almost unanimously considered to be among the main factors limiting response to selection and the efficiency of breeding programmes in general. GE interactions become important when the rank of breeding lines changes in different environments ('crossover GE interaction' Baker: 1988).

GE interactions in general, and GE interactions of crossover type in particular, have a negative impact on the progress of breeding programmes, particularly when breeders try to avoid them by searching for widely adapted cultivars. However, breeders may exploit GE interactions by selecting for specific adaptation (Ceccarelli, 1989; Hildebrand, 1990; Stroup *et al.*, 1993). This is particularly relevant when breeding for adaptation to unfavourable environments and subsistence agriculture.

Throughout this chapter, unfavourable environments are defined as those where crop yields are commonly low due to the concomitant effects of several abiotic and biotic stresses. The semi-arid areas of Syria, where barley is the predominant rain-fed crop, are a good example of such environments where not only low annual rainfall, but also rainfall distribution, low winter temperatures, and high temperatures and hot winds from anthesis to grain-filling are important abiotic stresses. Although the frequency, timing, intensity and duration of each of these stresses, as well as their specific combinations, vary from year to year, pre-anthesis water stress is common and post-anthesis water stress is the rule (Fig. 6.1).

Because of the high probability of low yields and crop failures in unfavourable environments, the use of inputs such as fertilizers, pesticides and weed control is seen by farmers as risky. Therefore, the adoption of improved agronomic practices has been limited, and the only economic solution to increase crop yields in unfavourable environments is through breeding. However, empirical plant breeding for these environments has been historically much less successful than it has for more favourable or for high-potential environments.

This chapter describes a strategy to exploit GE interactions in national and international breeding programmes for such areas. Issues such as the choice of the selection environment, specific versus wide adaptation, and genetic uniformity versus genetic diversity are discussed, and some implications for the genetic base are noted.

Challenging Conventional Breeding Concepts

Most plant breeders assume that breeding for environments where drought and other stresses are unpredictable and variable is too slow and too difficult. The target is hard to define; heritabilities, and hence responses to selection, are too low to achieve

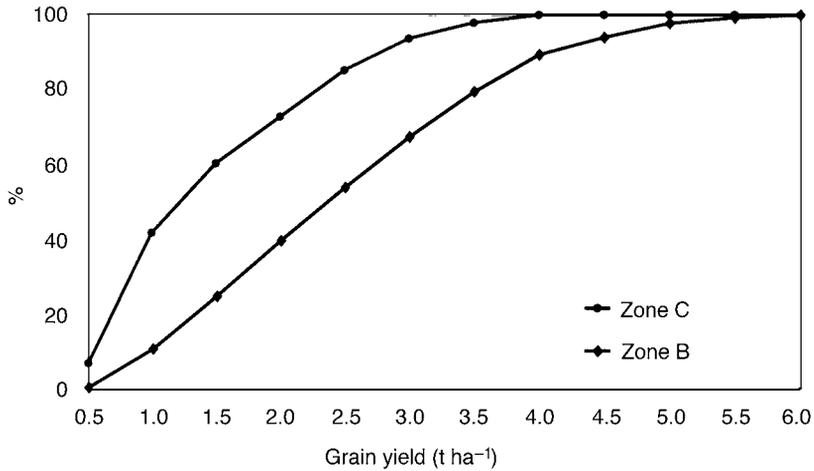


Fig. 6.1. Cumulative frequency distribution of barley yields in two climatic zones of Syria (zone C receiving less than 250–300 mm annual rainfall, and zone B receiving 300–350 mm annual rainfall) between 1982/83 and 1996/97. The distributions are based on 97 and 134 location–year combinations for zones C and B, respectively. In zone C, low yields of barley are common, crop failures occur one year out of 10, and yields above 2.5 t ha⁻¹ are expected about 15% of the time. In zone B, yields of 1 t ha⁻¹ or less have a frequency of about 7%, and yields above 2.5 t ha⁻¹ occur about 45% of the time.

meaningful results. Therefore, most of the breeding for stress environments has actually been conducted using the same basic approach that has been very successful in areas where lack of water (and other abiotic stresses) is seldom important.

With few exceptions, many breeding programmes share the following concepts:

- Selection has to be conducted under the high-input conditions of research stations, where environmental ‘noises’ can be kept under control, error variances are smaller and response to selection are higher.
- Cultivars must be genetically homogenous (pure lines, hybrids, clones) and must be widely adapted over large geographical areas; locally adapted landraces must be replaced because they are low-yielding and disease-susceptible.
- Seed of improved cultivars must be disseminated through mechanisms and institutions such as variety release committees, seed certification schemes and governmental seed-production organizations.
- The end-users of new cultivars are not involved in selection; they are only involved at the end of the consolidated routine (breeding, researcher-managed trials, verification trials), to verify whether the choices made for them by others are appropriate or not.

Until recently, breeders seldom questioned these assumptions. When they have, it has been found that:

- Selection in high-input research stations tends to produce cultivars that are superior to local landraces only under improved management, not under the low-input conditions typical of the farming systems of stress environments. The result is that

although many new cultivars out-yield local landraces on research stations and some are released few (if any) are actually grown by farmers in difficult environments.

- Poor farmers in stress environments tend to maintain genetic diversity in the form of different crops, different cultivars within the same crop, and/or heterogeneous cultivars to retain adaptability (Simmonds, 1962), i.e. to maximize adaptation over time (stability or dependability), rather than adaptation over space (Martin and Adams, 1987). Diversity and heterogeneity serve to disperse or buffer the risk of total crop failure due to environmental variation. This is in sharp contrast with the trend of modern plant breeding towards uniformity.
- Resource-poor farmers seldom use the formal seed-supply systems. They frequently rely on their own or on neighbours' seed (Almekinders *et al.*, 1994). Therefore, when the appropriate cultivar is selected, adoption is much faster through non-market methods of seed distribution (Grisley, 1993).
- When farmers are involved in the selection process, their selection criteria may be different from those of the breeder (Hardon and de Boef, 1993; Sperling *et al.*, 1993; Sperling *et al.*, Chapter 27, this volume). Typical examples are crops used as animal feed – such as barley, where breeders often use grain yield as the sole selection criterion – while farmers are usually equally concerned with forage yield and the palatability of both grain and straw.

Because the concepts of conventional plant breeding are not questioned, the blame for the non-adoption of new cultivars is variously attributed to the ignorance of farmers, the inefficiency of extension services and the unavailability of seed of improved cultivars. Thus, enormous resources continue to be invested in a model of breeding which is unlikely to succeed in unfavourable agroclimatic conditions.

The contrast between the reality of the farming systems and the plant breeding philosophies is particularly striking in developing countries. This is not surprising: most of the breeders from developing countries have received their training in those rarely questioned breeding principles enshrined in developed countries.

Genotype by environment interactions of crossover type

Since GE interactions of crossover type pose major problems in conventional breeding programmes, the question of how frequently these interactions occur is important. In general, when different lines or cultivars of a given crop are evaluated in a sufficiently wide range of environments, GE interactions of crossover type seem to be very common.

Examples of GE interactions of crossover type can be found in the literature in a range of crops and environments, and for drought, temperature and salinity stresses: Blum and Pnuel (1990) and Calhoun *et al.* (1994) in wheat; Breese (1969) in cocksfoot; Arboleda-Rivera and Compton (1974), Muruli and Paulsen (1981), Hildebrand (1984), Loffler *et al.* (1986), Lafitte and Edmeades (1994), Byrne *et al.* (1995) and Bänziger *et al.* (1997) in maize; Simmonds (1984a) in sugar cane; Lawn (1988) in chickpea; Ceccarelli (1989), Ceccarelli and Grando (1991), Jackson *et al.* (1993) and Muñoz *et al.* (1998) in barley; Virk and Mangat (1991) in pearl millet; Chisi *et al.* (1966) in sorghum; and Shannon and Francois (1978) in muskmelon.

In the barley breeding programme of the International Center for Agricultural Research in Dry Areas (ICARDA), the breeding material is routinely tested in sites differing in total rainfall, soil fertility and winter temperatures, with an average fourfold difference in mean yields between the two most contrasting sites. When we compared different lines at each of the two most contrasting sites, a consistent pattern was observed over a period of 14 years (Table 6.1). When compared in low-yielding sites (LYE), those lines which had the highest yield in high-yielding sites (G_H) yielded significantly less than the lines which had the highest yield in low-yielding sites (G_L). When the comparison was made in high-yielding sites (HYE), those lines which had the highest yield in the lowest-yielding sites (G_L) yielded significantly less than the lines which had the highest yield in high-yielding sites (G_H).

A similar picture emerges from the few published data on genetic correlation between yield measured in high- and low-yielding conditions (Atlin and Frey, 1989, 1990; Ceccarelli *et al.*, 1992; Ud-Din *et al.*, 1992; Cooper and DeLacy, 1994). This indicates that, as a general phenomenon, high-yielding lines under optimum growing conditions do not perform well under poor growing conditions, and vice versa. This is hardly surprising. Physiologists have long recognized, with specific reference to drought, that different physiological mechanisms and different phenologies are associated with high yield in favourable conditions and high yield in unfavourable conditions (Hsiao, 1982; Blum, 1993).

Figure 6.2 shows an example of GE interactions of crossover type in barley. Lines selected for high grain yield in high-yielding sites (YP) yielded more than lines selected in low-yielding sites (YD) in the medium- to high-yielding location-year combinations, and the YD lines yielded more than the YP lines in the low- and very low-yielding location-year combinations (Ceccarelli *et al.*, 1998). Between the medium- and

Table 6.1. Average grain yield ($t\ ha^{-1}$) in the lowest (LYE) and highest (HYE) yielding sites in each of 13 cropping seasons, of the 5% highest-yielding lines in the lowest-yielding site (G_L), and of the 5% highest-yielding lines in the highest-yielding site (G_H).

Year	LYE		HYE	
	G_L	G_H	G_L	G_H
1985	1.283±0.073	0.767±0.076	3.462±0.121	4.139±0.029
1986	1.935±0.026	1.340±0.079	4.139±0.078	4.970±0.070
1987	1.076±0.013	0.633±0.050	2.687±0.090	3.547±0.037
1988	4.199±0.048	3.383±0.131	4.672±0.173	6.100±0.067
1989	1.287±0.018	0.658±0.052	4.874±0.315	7.814±0.107
1990	0.794±0.017	0.429 ±0.046	3.066±0.118	4.122±0.027
1991	1.693±0.024	0.953±0.110	4.705±0.254	6.073±0.065
1992	1.305±0.026	1.030±0.046	4.799±0.171	5.793±0.099
1993	0.851±0.018	0.531±0.041	3.769±0.107	4.074±0.085
1994	1.702±0.024	1.377±0.081	3.210±0.107	3.663±0.047
1995	0.680±0.10	0.451±0.085	3.872±0.317	5.109±0.068
1996	1.860±0.032	1.370±0.093	4.089±0.425	5.214±0.078
1997	1.456±0.005	0.873±0.091	3.673±0.058	6.218±0.061
1998	1.273±0.066	0.320±0.051	4.000±0.538	7.033±0.155
Mean	1.528	1.008	3.930	5.276

low-yielding location–year combinations the YP and YD lines cross over (note that the range of environments in Fig. 6.2, and their associated yield levels, may represent either variation over time within one given geographical area or variation over space, i.e. between different geographical areas within or across countries).

Four points emerge from the analysis of multi-environment trials such as those illustrated in Table 6.1 and Fig. 6.2.

First, the definition of unfavourable environments plays a key role in determining breeding strategies. Defining as unfavourable environment an environment with an average yield at or above the crossover point is often justified for some crops. Taking Syria as an example again, bread wheat is cultivated only in areas with more than 300 mm annual rainfall, and the probability of yields lower than 2 t ha⁻¹ is considerably less than for barley: this may result in the absence of crossover and hence in different breeding strategies for the two crops (Calhoun *et al.*, 1994).

Secondly, crossover may be affected by the type of comparisons made in multi-environment trials. The superiority of lines such as the YP lines in Fig. 6.2 over the mean of all the lines in the trial, or against a local check, may be taken as an indication of broad adaptation. Very rarely is the comparison made with lines specifically selected in stress environments below the crossover point (such as the YD lines) because few breeding programmes select specifically for performance under stress conditions. When this is done, the YP lines are still broadly adapted, but to a narrower range of environments.

Thirdly, the presence of a crossover GE interaction is often neglected by conducting selection and testing only above the crossover point, and particularly in high-input research stations. When breeding materials are evaluated in many locations and selec-

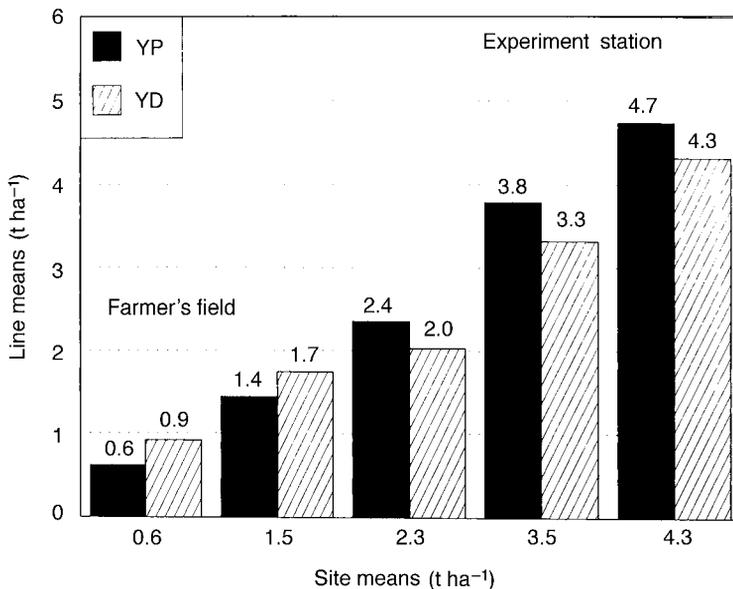


Fig. 6.2. Crossover type of GE interaction: YP and YD are lines selected on the basis of the 1988–1990 data in high- and low-yielding environments respectively; and then tested in 21 location–year combinations between 1991 and 1994.

tion is made for high average yield across locations, this is equivalent to selection for responsiveness to favourable conditions (Simmonds, 1991). Even shuttle breeding between two contrasting environments can miss the presence of crossover GE interactions if both environments are above the crossover point.

Fourthly, while the existence of a crossover GE interaction has been allegedly disproved by the release of cultivars for low-yielding environments (Byerlee, 1994), this argument neglects the fact that many of these cultivars have never been adopted by farmers in the intended environment (Maurya *et al.*, 1988; Jansen *et al.*, 1990; Byerlee and Husain, 1993).

An argument commonly used in favour of selecting in good environments is that heritabilities are higher there than in poor environments (Blum, 1988). But the experimental evidence does not consistently suggest that heritability in low-yielding conditions is lower than that in high-yielding conditions (Table 6.2), and even when it is lower, it is often not sufficiently lower to offset the effect of a low correlation coefficient. Our own experience with barley (Singh and Ceccarelli, 1995) also suggests that there is no relationship between yield level and magnitude of heritability.

Table 6.2. Heritability estimates of grain yield at low and high yield levels and ratio between the root squares of the two heritabilities in different crops (modified from Ceccarelli, 1994).

Crop	High (h_y)	Low (h_x)	Ratio h_y/h_x	Reference
Wheat	0.25	0.03	2.89	Roy and Murty (1970)
Wheat	0.78	0.32	1.56	Allen <i>et al.</i> (1978)
Wheat	0.33	0.68	0.70	Pederson and Rathjen (1981)
Wheat	0.89	0.74	1.10	Pfeiffer (1988)
Wheat	0.93	0.43	1.47	Cooper <i>et al.</i> (1997)
Cocksfoot	0.89	0.50	1.33	Breese (1969)
Common bean	0.59	0.55	1.04	Schneider <i>et al.</i> (1997)
Common bean	0.19	0.20	0.97	Schneider <i>et al.</i> (1997)
Flax	0.44	0.56	0.89	Allen <i>et al.</i> (1978)
Maize	0.52	0.71	0.86	Selmani and Wassom (1993)
Maize	0.46	0.58	0.89	Lafitte and Edmeades (1994)
Maize	0.62	0.44	1.19	Bänziger <i>et al.</i> (1997)
Barley	0.47	0.54	0.93	Allen <i>et al.</i> (1978)
Barley	0.65	0.66	0.99	Weltzien and Fischbeck (1990)
Barley	0.47	0.68	0.83	Singh and Ceccarelli (1995)
Oat	0.56	0.63	0.94	Allen <i>et al.</i> (1978)
Oat	0.45	0.32	1.18	Frey (1964)
Oat	0.38	0.52	0.85	Johnson and Frey (1967)
Oat	0.67	0.32	1.45	Atlin and Frey (1990)
Sunflower	0.86	0.57	1.23	Alza and Fernandez-Martinez (1997)
Sunflower	0.74	0.44	1.3	Alza and Fernandez-Martinez (1997)
Sunflower	0.79	0.24	1.81	Alza and Fernandez-Martinez (1997)
Sorghum	0.63	0.43	1.21	Zavala-Garcia <i>et al.</i> (1992)
Sorghum	0.17	0.58	0.54	Chisi <i>et al.</i> (1996)
Sorghum	0.69	0.32	1.47	Zavala-Garcia <i>et al.</i> (1992)
Soybean	0.56	0.31	1.34	Allen <i>et al.</i> (1978)

A positive interpretation of GE interactions (Ceccarelli, 1989, 1994; Hildebrand, 1990; Stroup *et al.*, 1993; Gauch and Zobel, 1997) recognizes the importance of specific adaptation and leads to the selection of lines specifically adapted to favourable environments (such as the YP lines in Fig. 6.2), and of lines specifically adapted to unfavourable environments (such as the YD lines in Fig. 6.2). Cooper and De Lacy (1994) and Cooper *et al.* (1996) use a similar strategy in the presence of large and repeatable GE interactions.

The ICARDA barley breeding programme has shown (see Grando *et al.*, Chapter 22, this volume) that it is indeed possible to improve the production of a typically low-input crop such as barley, grown in environments with low and poorly distributed rainfall, low temperatures in winter, high temperatures and drought during grain-filling, low soil-fertility and poor agronomic management by using strategies and methodologies based on: (i) decentralized selection for specific adaptation in the target environment; (ii) use of locally adapted germplasm; (iii) use of suitable plot techniques and experimental designs to control environmental variation; and (iv) participation of farmers in selection. These strategies and methodologies have been described in detail by Ceccarelli and Grando (1996), and the rest of this chapter will concentrate on how to use the concept of specific adaptation in international plant breeding programmes.

Decentralization: using specific adaptation in international breeding programmes

International breeding programmes aim to assist national programmes to increase agricultural production by developing superior cultivars. This is traditionally done through very large breeding programmes that develop fixed or semi-fixed lines with an average good performance across many environments (often high-input research stations).

This type of interaction between international and national plant breeding programmes has been largely a one-way, 'top-down' process (Simmonds and Talbot, 1992) where international programmes develop germplasm, distribute it as 'international nurseries', and national programmes test and eventually release selections as cultivars. This 'top-down' approach has excluded the use of locally adapted germplasm, which is specifically adapted to particular conditions and often performs poorly in the favourable conditions of research stations, and has, in fact, encouraged its displacement.

The distribution of germplasm from international centres to national breeding programmes has indeed historically included segregating populations. However, such segregating populations were derived from crosses designed by the international breeders, were the same for all the countries and were not targeted to a specific environment.

The adoption of a positive interpretation of GE interaction by international breeding programmes has been advocated as a way to address the need of smallholder, resource-poor farmers, who have been bypassed by the Green Revolution (Stroup *et al.*, 1993).

To exploit specific adaptation fully and make positive use of GE interactions, Ceccarelli *et al.* (1994) propose that international breeding programmes should decentralize (that paper uses the term devolution; decentralization is a better term) most of the selection work to national programmes by gradually replacing the traditional international nurseries either with targeted segregating populations, or with nurseries that

contain material selected only for highly heritable traits. Early distribution of breeding material reduces the danger of useful lines being discarded because of their relatively poor performance at some test sites.

This problem is illustrated by 288 barley lines evaluated both in the Maghreb countries (Libya, Tunisia, Algeria, Morocco) and in ICARDA's preliminary yield trials grown at three sites in Syria (ranging from moderately favourable to unfavourable) in 1991/92. In Syria, 103 entries were selected and in the Maghreb 154; but only 49 were selected in both. More than half of the lines selected in Syria were discarded in the Maghreb, and almost 70% of those selected in the Maghreb were discarded in Syria. This gives a measure of the danger, in a centralized breeding programme, of discarding lines potentially useful in other areas.

In 1991, ICARDA's barley breeding programme started a gradual process of decentralization of selection work to the four Maghreb countries (Ceccarelli *et al.*, 1994). This was extended to Iraq in 1992, to Egypt in 1995, and it is gradually being implemented in the Mediterranean highlands of Turkey and Iran.

When the term decentralization is used in a plant breeding context and it is referred to as decentralized breeding, it may actually refer to two fundamentally different processes, namely decentralized selection and/or decentralized testing.

Decentralized selection is a term first used by Simmonds (1984a) and defined as selection in the target environment(s). In the case of self-pollinated crops, it consists of selection of early segregating populations (such as F_2) in a number of locations representing the target environment(s) (climate, soil, farming system and management) the breeding programme aims to serve. Decentralized selection becomes selection for specific adaptation when the selection criterion is the performance in specific environments rather than the mean performance across environments.

Decentralized selection is different from decentralized testing, which is a common feature of breeding programmes and takes place, usually in the form of multilocation trials and on-farm trials, after a number of cycles of selection in one or a few environments (usually with high levels of inputs).

In the type of decentralization implemented in North Africa (Fig. 6.3), national-programme scientists identify suitable parents, crosses are made at ICARDA, the material is advanced as bulks (without any selection) to the F_3 generation, and then distributed to the national programmes. The reason for advancing material to F_3 is to ensure the availability of sufficient seed for distribution. Selection between populations is made in the target environments in each country.

Since barley is mostly used as an animal feed in most of the countries in North Africa and the Near East, uniform cultivars are not required, and successful bulks could, in theory, be released directly as cultivars after adequate testing. Unfortunately, however, a high degree of genetic uniformity is still required for variety release, even in those countries where farmers grow heterogeneous landraces. To meet these requirements, selection within the best populations is done within each country and at ICARDA through single seed descent, and the best lines are used for further cycles of crosses.

The decentralization to Iraq is similar, in principle, to the one described for North Africa, but much simpler in its implementation. Two types of targeted crosses are made at ICARDA with elite germplasm identified in Iraq, one for the Baghdad-type of environment (irrigated areas, warm winters, high temperature and salinity stress, barley used for dual purpose) and one for the Mosul-type of environment (low rainfall,

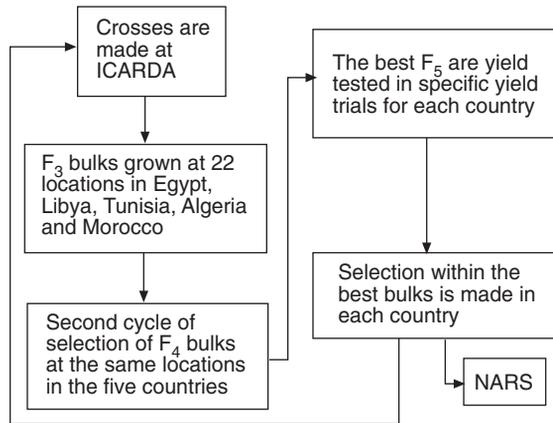


Fig. 6.3. Scheme of decentralized barley breeding between ICARDA and five national programmes in North Africa.

ICARDA: International Center for Agricultural Research in Dry Areas.

continental climate with cold winters). The F_2 s are sent to Iraq and all the successive stages of selection are conducted in Iraq without backup from ICARDA. Released cultivars and/or promising lines are sent back to ICARDA for crosses.

Other breeding activities at ICARDA, such as lentil breeding for the Anatolian plateau in Turkey and for South Asia, are based on the same philosophy (see Erskine *et al.*, Chapter 21, this volume).

These examples show that decentralization does not have to follow a recipe, but can take several forms depending on the nature, the strength and the expertise of the national programmes.

Since it started, the process of decentralizing the barley breeding programme has been gradually extended to other countries and regions (Table 6.3). For each country and/or region where the two most important conditions for decentralized breeding exist – namely large GE interactions with ICARDA research station(s) and availability of local expertise in plant breeding – decentralization generally follows three steps: first, we send a special nursery to identify suitable parents; secondly, we start a specific crossing programme aimed at developing a specific germplasm pool for that country/region; and, thirdly, we distribute the segregating populations.

When fully implemented, the first step is replaced by the routine in-country screening of various germplasm sources. This, together with the decentralized screening for resistance to pests and diseases, ensures that more and more parental material is supplied by the individual countries.

Another type of decentralization has been practised in Ethiopia, where, in 1984, the barley breeding programme was almost entirely based on exotic germplasm, and where, now, the major thrust is on Ethiopian landraces, tested in farmers' fields at low input levels. In this case we have decentralized a methodology (selection of landraces in the target environment) rather than a germplasm (Berhane *et al.*, 1997; Yitbarek *et al.*, 1998).

Decentralized selection is very powerful in maintaining genetic diversity. As an

Table 6.3. Countries and regions where decentralized barley breeding has been initiated.

Country/region	Countries/area	Status
North Africa	(Egypt, Lybia, Tunisia, Algeria, Morocco)	Fully implemented
Near East	Central Iraq (Baghdad area)	Fully implemented
Near East	Nortern Iraq (Gezira)	Fully implemented
East Africa/Red Sea	(Yemen, Eritrea, Tigray)	First crosses made in 1998
Ethiopia	The whole country except Tigray	Use of local landraces fully implemented; first crosses in 1998
Central Asia	Uzbekistan, Kirgystan, Kazakhstan, Armenia	First special nursery in 1997
Turkey	—	First nursery planned for 1999
Cyprus	—	First special nursery in 1995; first crosses in 1998
Far East	(India, Thailand, China)	First special nursery in 1996, first crosses in 1997
Pakistan	—	First special nursery in 1997
Gulf countries	(Saudi Arabia, Qatar, Oman)	First crosses made in 1992
Ecuador	—	First nursery planned for 1999

example, we show the frequency of F_4 bulks and of F_5 bulks which were selected from the F_3 bulks distributed in 1994, 1995 and 1996 (Table 6.4) following the scheme shown in Fig. 6.3. The selection pressures used in decentralized selection appear much milder than those commonly applied in breeding programmes, so that much of the original diversity present in the original sets of F_3 bulks is still present in the subsequent cycles, with as much as 80% of the bulks still being retained after two cycles of selection in the sets distributed in 1994 and 1995. In the third set, the frequency of bulks after two cycles of selection drops to 56% (mostly because no data were returned from Algeria, and consequently those bulks that would have been selected only in Algeria are missing).

While the national programmes were accepting decentralization very positively, we started recognizing that decentralization *per se* will not necessarily respond to the needs of resource-poor farmers in less-favoured areas, if it is only a decentralization from the research station(s) of ICARDA to the research stations of the national programmes, and if the research stations of the national programmes do not represent, as is often the case, the difficult environments where the crop is predominantly grown. To exploit the potential gains from specific adaptation to low-input conditions, breeding must be

Table 6.4. Number and frequency of bulks selected in two successive cycles of selection in four North African countries starting from F_3 bulks distributed in 1994, 1995 and 1996.

F_3 bulks		F_4 bulks			F_5 bulks		
Year	No.	Year	No.	%	Year	No.	%
1994	224	1995	197	87.9	1996	180	80.4
1995	208	1996	185	88.9	1997	169	81.3
1996	269	1997	257	95.5	1998	151	56.1

decentralized from research stations to farmers' fields. Although decentralization and farmer participation are unrelated concepts, decentralization to farmers' fields almost inevitably leads to the participation of farmers in the selection process. Therefore, the ICARDA barley programme initially considered farmer participation as a type of decentralized selection to exploit GE interactions and to make use, within a formal breeding programme, of the farmers' knowledge about the crop, its specific uses and its specific adaptation.

Maximizing Specific Adaptation Farmers' Participation

The idea of farmers participating in the development of new technologies is neither new nor revolutionary (Rhoades and Booth, 1982; Sperling, *et al.*, 1993; Farrington, 1996). It was introduced in 1982 (Rhoades and Booth, 1982) as 'the farmer-back-to-farmer model', later modified into the 'farmer-first-and-last model' (Chambers and Ghildyal, 1985) and more recently discussed by Sperling *et al.* (1993), Stroup *et al.* (1993) and Ceccarelli *et al.* (1996, 1997). Using Sperling's terminology, 'formal breeding programmes' can be described as a sequential and cyclical process in which: (i) an extremely large amount of genetic variability is continuously created; (ii) this variability is drastically reduced through cycles of selection (we have seen that this is often done in conditions which have little in common with those of resource-poor farmers); and (iii) the few lines surviving step (ii) are presented to farmers who are asked to verify if the choices made for them are appropriate.

Besides GE interactions discussed earlier, there is evidence that when farmers are involved in the selection process their selection criteria may be different from those of the breeder (Hardon and de Boef, 1993; Sperling *et al.*, 1993). This is shown by the data of Table 6.5. One of the special nurseries distributed to Tunisia as part of the decentralized barley breeding, described above, was planted near Tejerouine, a village in southern Tunisia close to the border with Algeria. The nursery included 207 barley types, mostly early segregating populations (F_4), together with check cultivars. The latter were both the landraces grown in North Africa and improved cultivars.

The farmer was more selective than the breeder. This is expected since breeders usually select not only lines that could become cultivars, but also those with some other potentially useful specific traits, while farmers are presumably only interested in lines that could become cultivars.

The type of material selected was of interest. Martin, the local landrace, was present once among the 40 lines selected by the breeder, twice among the 13 lines selected

Table 6.5. Number and percentage of lines selected by a breeder, a farmer and the farmer's wife, from a nursery of 207 barley breeding lines (Tejerouine, Tunisia, 1996).

Selected by	No. (%)	In common with:	
		Farmer	Farmer's wife
Breeder	40 (19.3)	2	3
Farmer	13 (6.3)	—	0
Farmer's wife	14 (6.8)	—	—

by the farmer, and was never selected by the farmer's wife. She was the only one to select twice one of the two Algerian landraces, Tichedrette, and once the other Algerian landrace, Saida. The farmer also selected Saida twice, but from two plots not selected by his wife (Saida was present three times in the nursery). Therefore, although chosen from different plots, the farmer and his wife eventually agreed on at least one cultivar. Neither the farmer nor his wife selected improved cultivars.

Examples of different selection criteria between farmers and breeders can be expected in crops used as animal feed, such as barley. Breeders often use grain yield as the sole selection criterion – which usually brings with it high harvest index and lodging resistance. However, in unfavourable environments lodging is seldom a problem because of moisture stress, and farmers are interested not only in grain yield, but also in straw yield and in the palatability of both grain and straw.

A drastic difference between the breeder's and farmers' selection criteria was found during the initial stages of farmers' participation in the ICARDA barley breeding programme. This informal participation led to the formulation of a farmers' barley ideotype for dry areas characterized by tall plants and soft straw. A crop which remains tall even in very dry years is important to farmers, because it reduces their dependence on costly hand-harvesting (Ceccarelli *et al.*, 1995), while soft straw is considered important for palatability. It is obvious that these two characteristics represent a drastic departure from the typical selection criteria used in breeding modern cultivars of cereal crops – short plants with stiff straw and high harvest index. It is also obvious that cultivars possessing the two characteristics considered important by farmers in dry areas will not be suited for cultivation in high-yielding environments because of their lodging susceptibility – a further indication of the importance of specific adaptation.

There is also evidence that, when breeders and farmers select in the same environment, farmers' selection can be effective, implying that farmers possess considerable knowledge which is almost totally neglected in formal plant breeding programmes. Data from Rwanda illustrate the results of the participation of farmers in bush bean (*Phaseolus vulgaris*). Even though the selection was conducted on-station, the farmers were able to select a number of cultivars which kept their superiority when evaluated on-farm, while the professional breeders failed to do so.

A participatory barley-breeding research project started in Syria in 1997 with 208 barley lines and populations planted in nine farmers' fields and on two research stations. Selection was conducted by the farmers and a breeder both in farmers' fields and on-station. This has shown that farmers can be effective in identifying high-yielding entries both in their fields (Table 6.6) and on the research stations. The lines selected by the farmers in six out of the nine locations had a significantly higher average grain yield than the population mean (Table 6.6); the breeder's selections were also significantly higher yielding than the population mean in six out of the nine farmers' fields and on the two research stations. The lines selected by the farmers and by the breeder in the nine locations never differed significantly in grain yield with the exception of one village (Al Bab), where the farmer's selections yielded significantly more grain and more biomass than the breeder's selections.

On the research stations (Tel Hadya and Breda), we used the frequency of the 20 top-yielding lines included among the selected lines as a measure of selection efficiency. This frequency was 14.3% and 16.4% among the breeder's selections in Tel Hadya and Breda, respectively. Among the farmers' selections in Tel Hadya, in only one case was

Table 6.6. Grain yield (kg ha⁻¹) and total biological yield (kg ha⁻¹) of the lines selected by the farmers and by the breeder in nine farmers' fields in Syria.

Location (code)	Grain yield			Biological yield		
	Farmer	Breeder	\bar{y}^a	Farmer	Breeder	\bar{y}^a
Ibbin (01)	4,615***	3,971***	n.s.	10,687**	9,686***	n.s.
Ebla (02)	3,498*	3,199**	n.s.	8,743	8,233	n.s.
Tel Brak (03)	4,235	4,020*	n.s.	8,729*	8,036	n.s.
Jurn El-Aswad (04)	2,049*	1,724**	n.s.	10,535**	8,429*	n.s.
Baylonan (05)	454*	324	n.s.	3,198	2,816	n.s.
Al Bab (06)	649***	488***	***	2,272***	1,787***	***
Melabya (07)	915	920***	n.s.	4,127**	3,246*	n.s.
Bari Sharki (08)	1,366*	1,129	n.s.	5,276	4,708	n.s.
Sauran (09)	2,561	2,654	n.s.	6,796	7,257	n.s.

Source: Ceccarelli *et al.* (2000).

n.s. = non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ relative to the comparisons with the population mean.

^aComparison between breeder's and farmers' selections based on *t*-test for samples of unequal size; *** $P < 0.001$ relative to the comparisons between farmer and breeder selections.

the frequency of the highest-yielding lines higher than that of the breeder, while in Breda the frequency of the highest-yielding lines among the farmers' selections was higher than that of the breeder in seven out of nine cases; in Breda the differences between entries were much more obvious at the time the selection was made.

One of the hypotheses tested with these experiments on participatory plant breeding was that farmers' selection will contribute more to maintain and/or enhance diversity than breeder selection does. In the case of the experiment in Syria, the similarity of selection done in different environments by the breeder and by the individual farmers was evaluated with the similarity analysis based on the dice coefficient (Czekanowski, 1917). Figure 6.4 shows the dendrogram of the nine farmers and of the breeder based on cluster analysis of their selections in the nine farmers' fields. There was a high degree of similarity among the selections done by the breeder in the various farmers' fields, with dice coefficients always higher than 0.57, and a much lower degree of similarity among the selections done by the farmers in their fields, with dice coefficient always lower than 0.33. Also there was little similarity between the selections done by the breeder and the farmer in the same field. The large dissimilarity between the lines selected by the farmers in different locations should result in a higher diversity in the breeding material after one cycle of selection by the farmers than after one cycle of selection by the breeder. These data show that decentralized breeding can give different results depending on whether it is participatory or not.

Decentralized selection is a powerful way of maintaining a high level of diversity. Table 6.7 shows the number and the percentage of different entries selected in all four possible combinations of centralized versus decentralized and of participatory versus non-participatory selection. Participation nearly doubles the percentage of lines retained after one cycle of centralized selection (from 34% to 61%), probably as a consequence of more people being involved in participatory than non-participatory selection. Decentralization further increases the percentages of lines retained after one cycle of selection to about three-quarters, and with minor differences due to participation.

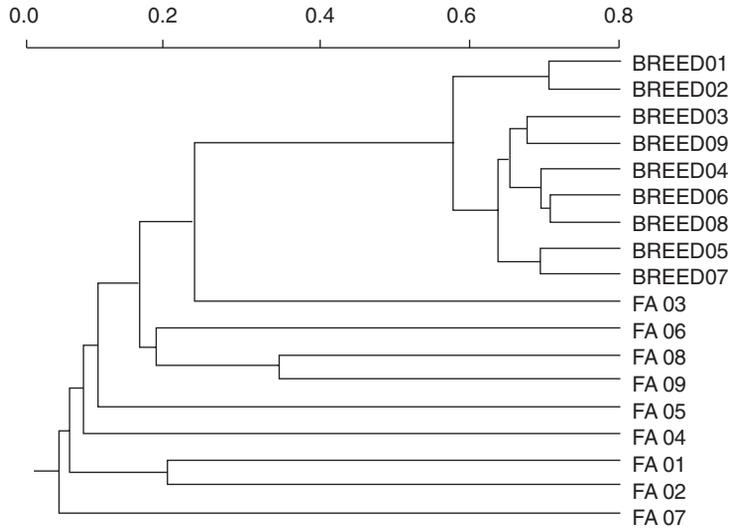


Fig. 6.4. Dendrogram of nine farmers and of a breeder based on cluster analysis of their selections in farmers' fields (FA = farmer, BREED = breeder). Individual locations are indicated with the location code used in Table 6.6.

Table 6.7. Number and percentage of entries selected after one cycle of different types of selection from a population of 208 barley entries.

Type of selection ^a	No. of selected entries	% of selected entries
Centralized, non-participatory	70	33.7
Centralized, participatory	127	61.1
Decentralized, non-participatory	164	78.8
Decentralized, participatory	154	74.0

Source: Ceccarelli *et al.* (2000).

^aParticipatory selection was done by nine farmers, while non-participatory selection was done by one breeder.

These data indicate not only that farmers are expert, but that they predominantly select for specific adaptation. In contrast with breeders, who usually search for a small number of widely adapted cultivars, farmers in different areas need different cultivars to meet specific requirements, either in relation to crop utilization or to the particular environment of their farms. Decentralized, participatory selection – intended as selection done by farmers in their fields and in the early stages of selection – inevitably leads to the selection of a large number of different cultivars, with obvious advantages for the maintenance of genetic diversity within a crop.

However, what has been described so far, not only in this chapter but also in most of the literature on farmer participation, is not participatory plant breeding, but an experiment on participatory plant breeding that lacks the cyclical nature of plant breeding. This means that a truly participatory breeding programme is very complex, with farmers growing different cycles of selection, until the identification and adoption of

new cultivars. These are then utilized by the formal breeding programme in further cycles of recombination, and by the farmers in further cycles of selection. The seed production of the new cultivars can be done either by the formal seed system or by the farmers themselves (informal seed system) depending on the crop and the infrastructures.

The entire process may require too much land to be hosted by individual farmers at each location. The important role of the selection environment, the interest shown by neighbouring farmers in visiting the plots, and the theoretical advantage of testing in more locations with less replications in each location suggest that community participation (Ashby *et al.*, 1996), intended as participation of several farmers in a given geographical area, rather than individual participation, could be a more realistic and feasible way to implement a decentralized-participatory plant breeding programme.

This not only has the advantage of a much wider awareness among the farmers of the newest genetic material available, but it allows the use of different experimental designs and plot sizes that is usual in formal breeding programmes. A schematic example of a decentralized-participatory breeding programme is shown in Fig. 6.5 for one target environment. The same scheme can be applied to any number of target environments.

The first level of selection (new breeding material generated by the formal breeding programme) could be grown each year, and used for selection, by one farmer (level 1 farmers) in each of n areas representative of the target population of environments. The breeding lines selected in the first cycle of selection could then be grown, within the same area, by a number of farmers (between five and ten) neighbouring the level 1 farmer. These will be the level 2 farmers and will probably grow between ten and 20

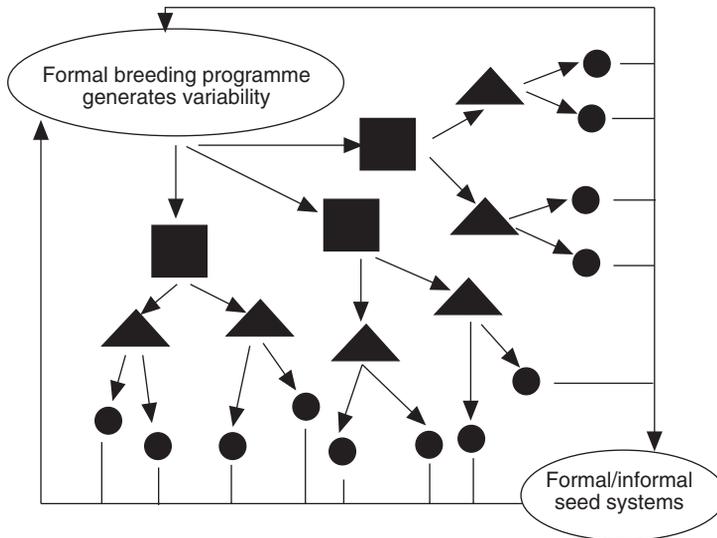


Fig. 6.5. Decentralized-participatory plant breeding. The figure is a simplification of the text.

■ indicates the level 1 farmers, ▲ indicates level 2 farmers, and ● indicates level 3 farmers.

new breeding lines each year. At this level of selection, all lines could be replicated at each location, or different farmers could host either different replications or different incomplete blocks (if an incomplete block design is used).

At the third level, the lines selected by each of the level 2 farmers could be grown in larger plots by five to ten farmers neighbouring the level 2 farmers. As for the level 2 selection, there is a wide choice of experimental designs and field layout at this level. Adoption and seed multiplication of superior bulks can begin at this stage (only 5 years after the crosses are made), but at the same time the formal breeding programme can purify the superior bulks (by single seed descent or double-haploids) in those cases (crops and/or countries) where uniform cultivars are needed by farmers and for future use as parental material in the crossing programme.

The formal breeding programme will continue to generate the new breeding material distributed to the level 1 farmers, produce seed for the trials at the different levels, and recycle the best populations and/or lines from level 3 selection both for crossing and for re-selection. Therefore, the new breeding lines distributed each year to level 1 farmers will be both early segregating populations and pure lines selected from the more successful bulk identified in the previous 3-year selection period.

Conclusions

Decentralized breeding, intended as decentralized selection and testing in the target environment by the users of the future cultivars using the genetic variability created by a formal breeding programme, is a powerful means of maintaining genetic diversity. This is due to concomitant effects of differences between selection environments and between different users which result in the selection of different breeding material in different selection sites. In addition to the most obvious type of genetic diversity, i.e. the presence of different cultivars of the same crop grown in the same country or geographical area at the same time, decentralized selection between early segregating populations done directly by farmers may lead to the adoption and cultivation of bulks, i.e. of genetically heterogeneous cultivars similar to the landraces which are currently grown in many marginal environments.

Because marginal environments tend to be more heterogeneous than favourable environments (Ceccarelli *et al.*, 2000), the effect of decentralized selection on genetic variability is likely to be larger in marginal environments. However, decentralized selection might also be useful in favourable environments to obtain a better adaptation of crops to the physical environment and therefore to rely less on the use of inputs.

In addition to the maintenance of different types of genetic variability, decentralized selection in international agricultural research centres is a powerful means of creating true partnership with the scientists in the national programmes. In a decentralized breeding programme the role of national programme scientists changes from merely testing material selected elsewhere, to selecting from within segregating populations derived from crosses that they decided. In decentralized and participatory breeding, farmers can play a similar role.

Eventually, and because decentralized breeding based on decentralized selection is a highly dynamic process, it is also an efficient way to continuously adapt the breeding material to a continuously changing agricultural environment.

Acknowledgements

The authors thank the OPEC Fund for International Development for supporting the decentralized barley breeding in North Africa, the Government of The Netherlands for supporting the barley breeding programme in Ethiopia, the Government of Italy for supporting the barley breeding programme at ICARDA, Der Bundesminister für Wirtschaftliche Zusammenarbeit (BMZ) for supporting farmer participation in Syria, and the International Development Research Centre (IDRC) for supporting farmer participation in Tunisia and Morocco. The authors thank Dr R.H. Booth, former Assistant Director General for International Cooperation at ICARDA, for his strong support during the first stages of decentralized breeding.

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7

Empowering Farmers and Broadening the Genetic Base: Agricultural Research and Resource Management

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Introduction

Farmers' struggle for access and control of land is inviolable. Genuine agrarian reform remains the basis for rural and national development. However, the increasing dominance of technology in agricultural production requires that rural communities also need to act on the issue of access and control in the development of agricultural technologies. This concern is becoming decisive as technological development makes information – and its higher form, knowledge – a major economic resource, or factor of production. Power and wealth now, and more so in the future, will be determined by those who own and control information and knowledge. This covers all economic sectors, including agriculture.

Intellectual innovation in agriculture has been in the hands of farmers for millennia. It was only in the last 30 years of the 20th century in developing countries, and from 1900 onwards in industrial countries, that agricultural research was transferred from farmers' fields into the laboratories of the formal and centralized research institutions in the public and private sectors (Berg *et al.*, 1991; Fowler, 1994).

For farmers, these developments can constitute a disempowering process: they can become mere objects of research, passive receivers of the 'finished products' of research institutions, and, being tied thus, have changed into labourers on their own lands (Lewontin, 1998). They have become end-users or consumers, rather than active creators. This contributes to the mystification of agricultural science, which becomes something esoteric, beyond the reach of farming communities, beyond understanding and therefore powerful. As usual, language reinforces this disempowerment. Farmers' knowledge is considered 'backward' while products of institutional research are called 'modern', no matter if they are inappropriate. Farmers' varieties are called 'primitive cultivars'; those of formal research institutions are 'advanced materials'.

Since formal agricultural research is not controlled by the farmers, they therefore cannot ensure that the research questions are relevant to their needs. Public research institutions and well-meaning scientists can only approximate farmers' needs and

objectives. Commercial research institutions are straightforward: their research is for profit. These corporations will try to fit their research to the needs and objectives of their target farmer market – that is simple business sense – but in the end both these research approaches are top-down. Most top-down approaches end up mainly benefiting those at the top. Most importantly, top-down research centralizes power at the top.

Understanding the negative implications of centralized and formal research institutions does not mean that these institutions are not important. In fact, this chapter will argue that these institutions will continue to have important and distinct roles: in particular, in ensuring a supply of genetic materials and other public goods. These institutions become counterproductive only when they attempt to disregard the role of farmers' research and try to replace rather than strengthen farmers' intellectual innovation.

The most decisive areas in agricultural innovation are related to the use of plant genetic resources through plant breeding, seed distribution and, now, biotechnology. Seed is the most important key to agricultural production: it is therefore a major arena of battle for control of the different sectors and interests involved in agriculture, from the small farmers in the South to transnational corporations mostly based in the North (Kloppenburg, 1988).

Farmers' traditional innovation created the crops the world depends on today. The great diversity of these crops and the diversity within crop species are products of the different agroecological conditions where these crops are grown, and are results of the intellectual innovation of farmers all over the world (Fowler and Mooney, 1990). These traditional systems of plant genetic resource (PGR) conservation and improvement largely remain today: for example, almost all of the upland rice varieties cultivated in Asia today are farmers' varieties. The general rule is that the varieties used by farmers under less favourable conditions are their own varieties.

For so-called minor crops or crops of local importance, such as traditional vegetables and small grain cereals, almost all of the varieties are farmer varieties. Practically all taro, yams and sweet potato varieties in the Philippines and throughout Southeast Asia are farmer varieties. New and diverse sweet potato varieties are periodically created by Filipino farmers, not by formal research institutions.

More generally, small-scale farming is a conspicuous feature of agriculture today and is likely to remain so (Whitten and Settle, 1998). There are about 4.5 million small-scale farmers worldwide, including about 2 million who are using mainly traditional technologies (Pretty, 1995). They have the potential to play a major role in maintaining a broad genetic base in production systems.

The Asian Irrigated Rice Farming System

The irrigated rice farming system is strongly linked to the market economy; rice is grown not only for subsistence but mostly for cash income. The year long availability of water through irrigation canals radically altered the ecosystem that now allows for at least two agricultural seasons. Farmers' varieties that were bred for subsistence systems and for one agricultural season per year were easily replaced by modern cultivars.

The initial results of the use of modern rice high-yielding varieties (HYVs), produced by the International Rice Research Institute (IRRI) in the Green Revolution,

and the package of technologies that came with it was quite positive, or even dramatic. Yield increases of 30–70% were reached. Countries predicted to suffer serious food shortages and even famine, such as India, reversed the trend and produced enough food. While this chapter will provide criticism on some of the policies that promoted the use of rice HYVs, in the shorter term it is also true that ‘farmers voted for it with their farms’.

In fact, it was only a matter of time before limits to the sustainability of the approach became apparent. The limited number of varieties that can be produced by research institutions narrowed the genetic base of irrigated rice and made it extremely susceptible to pests and diseases. The tungro virus wiped out rice production in Asia in 1972 and 1973, and the virus continues to be the most devastating disease today. The brown plant hoppers reduced the harvest of Vietnam by 20% in 1992. Rice blast fungus destroys wide areas on a scale never known before genetically narrow rice HYVs were widely used. Pests and diseases are able to evolve around the vertical resistance developed by centralized breeding centres (Gallagher, 1988); the massive use of chemicals only accelerated this process (Gallagher *et al.*, 1994; Heinrichs *et al.*, 1994; Settle *et al.*, 1996).

Even more alarming, the breeding programmes of formal research institutions are often losing the race against biotic stresses (Robertson, 1996). Increasingly, disease resistance and other desirable traits bred into the rice plant break down sooner than the successful breeding of new varieties, so farmers in irrigated areas all over the region are clamouring for more and newer varieties.

For example, farmers in central and northern Vietnam, during a random survey conducted in preparation for the Biodiversity Use and Conservation in Asia Programme (BUCAP), unanimously complained that the modern cultivars they cultivate are fast deteriorating and that they are not receiving enough varieties from their research institutions.

Working with farmers in the Philippines

The Philippines had around 3500 rice cultivars before the use of Green Revolution seeds and technologies. Traditionally, each farmer family would cultivate two to five rice varieties per season and there could be 50–100 rice varieties in a 5000 ha area. Today, five to seven related varieties can cover several thousands of hectares. At one point, almost 50% of the rice farms were planted to IR36. In the beginning, productivity also increased by at least 30%; however, as noted above, problems related to the narrowing of the genetic base of the rice varieties, most of which share a common pedigree, surfaced.

Farmers started to select and evolve new varieties to respond to their needs and to adapt the varieties to the conditions of their farms. In the island province of Bohol in the Philippines, all rice varieties released by the government soon developed red grain types as the people of the island prefer red rices. Thus, there are ‘red 36’, ‘red 64’, ‘red 66’, etc., that traced their origin from IRRI releases as well as local germplasm. All over the country, rice farmers and the environmental conditions of their farms selected and evolved new varieties from what they received. In 1991 in the province of North Cotabato in southern Philippines, 30% of the irrigated rice lands were planted to a

farmer variety called 'bordagol'. Bordagol was preferred because it was resistant to the 'tungro' virus, and required less fertilizer. It also had superior eating quality and fetched a higher price in the market. In the same province, around ten farmer varieties less popular than 'bordagol' were cultivated by the farmers for other traits that 'bordagol' and the rice HYVs did not have (Salazar, 1992a).

The same developments can be observed in all irrigated rice areas in Southeast Asia. Rice farmers have been breeding their own varieties using both modern introduced cultivars and traditional cultivars as raw materials. The South East Asia Regional Institute for Community Education (SEARICE), a Philippines-based non-governmental organization (NGO), has been promoting farmer-management of plant genetic resources. Its work is mainly focused on the irrigated prime rice lands where diversity has been lost and where the knowledge system of local farmers has been displaced. The objectives were to recover diversity and strengthen the role of local farmers as PGR managers and researchers.

SEARICE selected a town in North Cotabato province mentioned above with a contiguous irrigated rice area of around 3500 ha in 1993. SEARICE also set up an NGO called CONSERVE to assist the local farmers. More than ten varieties (collected outside the town and from nearby provinces) were distributed to the farmers for observation and adaptation. In 1995, the project CONSERVE assisted the distribution of 18 'bulk-bred' populations from an 'alternative' breeding programme called MASIPAG. Eight new lines (F_7) bred at CONSERVE were also distributed.

MASIPAG or Farmer-Scientist Partnership for Development Association, established in 1986, comprises 21 people's organizations, ten NGOs, three national farmer movements and scientists from three educational institutions. The group collects local rice varieties and teaches farmers how to perform hybridization and subsequent seed selection themselves (Salazar, 1992b). New seeds coming out of this programme are rapidly spreading throughout the Philippines and over 10,000 farmers are estimated to be using such seeds (Zamora, 1993).

At the same time, in the CONSERVE project, local farmers were trained in cross-hybridization including the enhancement of their traditional selection techniques. Out of more than 200 farmers trained in hybridization and selection, only four became effective and committed in continuing hybridization work and working on highly segregating materials, and 31 families continue to be involved in intensive selection work.

As of the first season of 1998, 60% of the 3500 ha irrigated area was planted to varieties that were adapted and selected by local farmers. The 'bordagol' variety, which had 'deteriorated', was planted to less than 3% of the rice lands. The rest of the area was planted to government-released varieties. The number of varieties in the whole area increased to 32 (although eight varieties, four from the government and four from the farmers, are the most dominant and popular varieties).

At the same time, new lines with high potential are emerging from the breeding and selection efforts of those trained by the project and from farmer neighbours who learned from those who were trained. It is estimated that these new farmer varieties will spread in the community over the coming years. Farmers in the area are again playing a major role in plant genetic resource management, creating and conserving diversity.

The project has started the process of broadening the genetic base of the rice crop in the irrigated ecosystem, increasing the number of varieties from a few modern cultivars to 32. More importantly, and intimately linked with broadening the genetic base,

is the process of broadening the actors involved in plant genetic resource research and development. Broadening the actors also means empowering these actors at the sociopolitical and technical levels.

It is also important to note shortcomings of our work at CONSERVE. The project initially had a strong conservation bias, as a reaction to the ongoing problem of genetic erosion. However, the conservation, for its own sake, of specific traditional cultivars in a production system that was increasingly linked to the market – where the agro-ecosystem had been altered by year-round availability of water, and where farmers' economic conditions, pressures and needs were rapidly changing – proved not to be viable. Farmers conserve only by utilizing resources that respond to their needs. Thus, except for a few glutinous local rice varieties that were continually planted because they had distinct desirable traits, most of the varieties that the farms cultivated were either introduced from research institutions, or were developed by themselves or other local farmers from such introductions (and most possibly from their local varieties too). It is clear that the conservation of specific materials for the far future must be a strategic concern of institutions such as governments and international research centres and other international organizations. Small farmers can only conserve through active utilization and constant improvement of these materials. While long-term *in situ* conservation is necessary (for its distinct function) to complement the *ex situ* genebanks, this approach may require constant support and subsidy in so far as some of the materials may not be useful to small farmers as conditions change (see also Wood and Lenné, 1997).

The second shortcoming was the lack of systematic pre-breeding or access to diverse materials to effectively provide the raw materials for farmers' use when the project shifted to participatory plant breeding. While the farmers were enthusiastic, the materials they had in hand were very few. Furthermore, the sources of germplasm were limited to materials in the province, and to materials from other farmer organizations and NGOs in the country. The rich source of PGR diversity, the national and international research institutions, was not tapped.

Building from the farmer field school approach of integrated pest management

CONSERVE built from the successes and lessons of related efforts to assist local farmers. On sociological principles and approaches, the project benefited from a number of community organizing and consciousness raising experiences in the Philippines. The most important contribution at the technical level came from the experiences of the Food and Agriculture Organization (FAO) integrated pest management (IPM) programme.

The FAO IPM programme, based on farmer field schools (FFS), is one of the earliest efforts to merge scientific soundness with a research and education process that empowers farmers. FFS are held in the rice fields throughout the season, from land preparation to harvest time. Every week, insect populations are monitored and the rice plant is assessed in all its major stages. The data are gathered and analysed by a community of farmers with simple research instruments developed by the IPM programme.

This approach builds on local knowledge systems and relies on the farmers as researchers. The approach therefore induces farmers to learn. First, it avoids the 'banking approach' to education where farmers are mere receivers of knowledge. Secondly,

the approach is premised on 'praxis'. Praxis is an 'action–reflection' method where knowledge is gained through experience (Habermas, 1987). Thirdly, FFS relies on collective approaches where experience and knowledge are gained by a community, not by a select few. Farmers can become experts in applying ecological principles to crop management; some become trainers or genuine scientific researchers (Dilts, 1999).

The FFS approach does not idealize but is realistic about farmers' capacities. Practical research tools and instruments are provided to: (i) help farmers plan their research objectives; (ii) gather data more systematically; and (iii) analyse the data. Additional data and information not normally reached by local communities but by research institutions are added.

One of the results of the IPM programme is that pesticide use in the same area has been reduced by more than 50%, and the use of insecticides has almost been eliminated. This reduction is directly due to the enhanced level of biodiversity of natural enemies of plant pests and of other components of biodiversity, including the food sources of these natural enemies. These farmers may be considered, therefore, to be managing biodiversity in ecosystems in support of sustainable agriculture (Settle *et al.*, 1996; Whitten and Settle, 1999).

To date, over 1,000,000 Indonesian farmers have graduated from FFS: over 400,000 in Vietnam, and over 170,000 in the Philippines. The programme has been extended to several other Asian countries, and more recently to many countries in Africa and elsewhere. It has also been extended to other crops such as vegetables, maize and cotton. Work is consolidated through the development of community IPM programmes (Dilts, 1999).

The IPM approach has been adapted to include plant genetic resource and sustainable soil management concerns. Using the farmer-field-school participatory and experimental approach, the science of plant breeding is slowly being returned to farmers' control, in the same manner that the IPM approach was returning the science of pest management to farming communities.

Lessons Learnt

The need for institutional support and access to germplasm

The presence of an institution, in this case SEARICE and CONSERVE, is needed for technical assistance and links to formal-sector institutions. One of its most important functions was to provide the farmers with access to diverse genetic resources. Farmers' traditional systems of access to genetic resources are too limited to be effective compared with that offered by formal research institutions. The other important role was to link and provide the local farmers with related technologies such as IPM, and selecting and breeding. The third role that must be mentioned is the assistance provided in the conduct of on-farm research with local farmers. In short, local farmers in their on-farm PGR research and development efforts also require institutional support.

Pre-breeding, including the selection of parental lines, is a major supportive function requiring institutional support. While the analysis of the state of the plant genetic resources in the community can be undertaken by the local farmers as a basis for determining breeding objectives, the resources required are mostly beyond the means of the

small farmers. While the local farmers can efficiently evaluate their local materials, they will have little knowledge about plant genetic resources outside their area and those in the hands of national and international research institutions. As reported above, only four farmers continued with hybridization and in the handling of early generation materials, yet the number of farmers interested in later generation lines was significant.

As noted earlier, conservation, on-farm, needs to be linked to utilization if it is to be successful: it is not possible for farmers to maintain varieties that are no longer useful. In the end, the majority of the varieties introduced should also be deposited in the national rice genebank, in a black-box arrangement.

More efforts to adapt formal research systems to farmers' realities and capacities are needed. Replication of varietal trials in small plots is too laborious and maybe too complicated for farmers' management. The number of breeding lines a farmer family can handle is low compared with the capacity of research institutions. Estimating varietal performance by using mathematical extrapolation (needed for small test plots) is less effective in demonstrating results compared with the conclusions farmers can reach observing a new variety cultivated at a production scale. These few examples highlight the need for more creative development of research approaches and instruments for on-farm participatory PGR management.

Building from the local knowledge system, the need to strengthen this, using both traditional and institutional science, is an important task. There is a need to develop methodologies, research instruments and techniques that are appropriate to on-farm research by local farmers. Again, the model of the farmer field schools of the IPM approach can be used as a guide. Under the FFS, simplified research instruments have been developed so that farmers are able to gather the data, and to analyse these data themselves. The research instruments for an ecological pest management approach under the IPM programme need to be developed further.

Farmers practising on-farm PGR research and development require wider and free access to genetic resources. The pressures that bear on the lives of farmers' families and the stresses faced by their farms are not only local but global as well. They need many sources of raw material to be able to respond and succeed.

Farmers' breeding efforts need to be formally recognized. For example, SEARICE and CONSERVE convinced the provincial government to honour and award the farmer who developed the 'bordagol' variety. Community gatherings are used to recognize families that bred or are breeding new varieties. This recognition should include the qualification of farmers' varieties to avail their developers with agricultural credit and insurance.

Related to the issue of recognition is the issue of benefit sharing when and if farmers' varieties are used in successful commercial breeding. The absence of international and national agreements and legislation on this matter is creating a tension in farming communities. First, farmers traditionally exchanged seeds freely. Their traditional system depended on free exchange and it is imbedded in farming cultures. Yet developments today of proprietary ownership of genetic resources, and of national restrictions on the exchange of germplasm, threaten to prevent them from doing so. Both the farmers and agricultural development in general will lose out from this situation.

We know that farmers' traditional systems depended on free exchange of PGR, and that these resources move from village to village and great distances, and were continually improved. Thus seeds and the knowledge about them had always been

exchanged freely, and this is part of the culture (or maybe 'ethos') of small farmers. While a single individual may be recognized, by naming a good variety after him or her, the seeds and the knowledge had always been collectively owned.

The experience at CONSERVE was that as the information about the commercial privatization of seeds was discussed with farmers – that seeds and the knowledge that goes with them have become a potential source of wealth – there was some confusion. Many complained that it is unthinkable for them, as farmers, not to share seeds when they are asked to do so. The idea that these can be a source of wealth was not easy to handle either. A few of the farmers trained in participatory plant breeding had begun naming the varieties after themselves (which is not too problematic), and some did not want to share early generation materials and/or breeding lines, preferring instead to release only finished varieties (which could be a problem). We are thus faced with two opposing reactions. The first of these shows that bringing the farmers' system into the commercial sphere could undermine the system that created and maintained this diversity. The second reaction, although very insignificant at the moment, shows that some farmers will change and adapt to the commercial framework. We do not know at this stage whether or not farmers working within this framework will be able to continue to create and maintain diversity.

There is a need to revise the seed certification systems of the country. Farmers' varieties are frequently non-uniform populations, for obvious reasons. Farmers also like to select and evolve their varieties. This contradicts the traditional seed certification requirement of 'stability' and 'uniformity'. However, the multilocation trials required for nationwide adaptation do not always apply to farmer varieties that have more specific adaptation to microenvironments (see Louwaars, Chapter 5, this volume).

There is a need to support the post-production requirements of farmers' PGR management: the drying, milling, bagging and storage system that exists today in the country and in the region is designed for genetically uniform harvests. There is also a need for marketing development that will support the genetically diverse output of farmer breeding. This is a longer-term investment, and appropriate research and 'modelling' are required.

Many of these issues will be explored further in the Biodiversity Use and Conservation in Asia Programme (BUCAP) mentioned above. BUCAP will use the participatory research and development approach of the FFS and community IPM programmes to develop a model of farmer-led plant genetic resource research and breeding, which, *inter alia*, will help maintain genetic diversity on-farm, focusing on areas shifting from subsistence to market-based production; or, where the genetic base has been narrowed (for example in irrigated areas), attempt to restore genetic diversity.

Related sociopolitical concerns

It is important to note that the area in North Cotabato province where this project was conducted is an area with strong farmers' organizations. These organizations were born and grew in the farmers' struggle for agrarian reform and against the Marcos government; village-level formal and informal organizations exist with leaders tested in the past. The highest form of this organization in the project area is the farmers' cooperative, which has more than 2000 families as formal members.

Reliance on their own strengths and capabilities and the capacity to be critical of top-down approaches and technologies is part of the farmers' history and tradition. The decision to seek alternative agricultural technologies was already taken by their organizations even before SEARICE and CONSERVE arrived: the farmers in this town had sent petitions for the banning from the market of endosulfan pesticide compounds; they have signified their opposition to the genetic engineering of rice with Bt.

The same is true of the farmers working on a similar project in the island province of Bohol: the initial effort was within the umbrella of a province-wide alliance of peasant organizations working for agrarian reform, for democratic rights, and for peasant concerns. One of the strongest PGR conservation and development efforts by local farmers of yams and sweet potato goes hand-in-hand with their opposition to the construction of an airport in their town.

This chapter highlights these social and political bases and processes to emphasize the point that they are needed in on-farm PGR conservation and development catering to the interest of local and poor people.

The presence of a strong farmers' multipurpose 'cooperative', especially its credit programme, allowed farmers to use their own varieties. The farmers' varieties qualify for the cooperative's production credit programme. Even before the project of SEARICE and CONSERVE, the farmers were widely planting the 'bordagol' variety (developed by one of the members of the farmers' cooperative) and a few other local varieties because it was encouraged by the cooperative. Moreover, the cooperative promoted and marketed 'bordagol', which was fetching a higher price because of its eating quality, creating more income for the farmers.

In general, there is a need for an 'alternative social infrastructure' that will serve as the power base for on-farm research. Without this, the research problems and directions will be determined by the richer sectors of the rural population, and scientists who are supposed only to assist will end up dominating the interaction.

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8

The State of Millet Diversity and its Use in West Africa

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Introduction

Africa is an important centre of diversity for several crops including millet, sorghum and rice as well as local crops such as fonio. The great variation in rainfall regimes and soil types has led to a wide range of production systems (Spencer and Sivakumar, 1987).

Pearl millet, *Pennisetum glaucum* (L.), was domesticated in the Sahelian belt about 3000–4000 years ago. Portères (1976) suggested that it arose through multiple domestications from the wild progenitor, *P. glaucum* spp. *monodii*, and isoenzyme studies provide evidence to support this theory (Tostain and Marchais, 1989). African farmers have selected crop varieties adapted to a wide range of conditions; the large diversity of millet is the result of this work (Bono, 1973). Major movements between ethnic groups have also contributed to the growth of diversity.

Pearl millet is the most widely cultivated cereal in Africa, south of the Sahara. In Western Africa, 17 countries grow pearl millet on 10.8 million ha (Mha), but five countries account for 90% of the area: Niger (3.5 Mha), Nigeria (3.2 Mha), Burkina Faso (1.1 Mha), Mali (1.0 Mha) and Senegal (0.9 Mha). The other main area of production is South Asia, particularly India which accounts for 10.5 million of the 11.2 Mha total production in this region.

In West Africa, production is in the hands of small farmers and yields are low and variable, rarely passing 1000 kg ha⁻¹. A number of constraints, primarily climatic and soil-related, are responsible for this poor performance.

Various crop improvement programmes have been put in place in West Africa but, while significant gains have been made with cash crops, very little progress has been achieved for subsistence crops. For millet, it is estimated that only 5% of the cultivated area is sown to improved varieties (Matlon, 1985).

This contrasts with the situation in India where there have been major gains, with high adoption rates for hybrid varieties. However, it is important to note that in India varieties are adopted in relatively high production areas: soil and climatic factors are

much less favourable in West Africa than in India (Stoop *et al.*, 1982; Matlon, 1985).

This chapter describes the diversity available in the millet gene pool, and the characteristics of millet varieties; surveys plant breeding programmes in West Africa and reviews their degree of success; describes the institutional arrangements for millet breeding in the sub-region at national and sub-regional levels; and, finally, draws some conclusions concerning the use of millet diversity in the region.

Millet Diversity

Millet gene pools

The genus *Pennisetum* consists of more than 140 species (Clayton, 1972). Stapf and Hubbard (1934) recognized 13 cultivated species, six annual wild relatives and 15 intermediate forms. The number of species was reduced by Clayton (1972) and Brunken *et al.* (1997). Though the name *P. americanum* was used by these authors, the name *P. glaucum* is preferred (de Wet, 1987). Thus, the primary gene pool includes:

- The cultivated form: *P. glaucum*, including the races Typhoides, Nigritarium, Globosum and Léonis, characterized on the basis of seed shape (Brunken *et al.*, 1977).
- The wild form: *P. glaucum* ssp. *monodii* (= *violaceum*) with three races: Mollissium, Violaceum and Fallax.
- An intermediary, hybrid, form: *P. glaucum* ssp. *stenostachyum*, which possesses some features of the cultivated form, but, like the wild form, is characterized by the non-persistence of the husks.

The secondary gene pool includes those species that can be artificially crossed with millet, such as elephant grass (*P. purpureum*), which is resistant to numerous diseases.

The tertiary gene pool includes other wild species such as *P. orientale* and *P. villosum*. Some of these species possess potentially useful characteristics such as apomixy, cold and drought resistance, and cytoplasmic diversity. Gene transfer is not possible using classical techniques (Hanna, 1987).

Collections

The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in collaboration with the International Plant Genetic Resources Institute (IPGRI) and national programmes has conducted a number of collecting missions in 15 countries of Africa (22 missions, 1654 accessions) and in India (14 missions, 2690 accessions). According to Kumar and Rao (1987), ICRISAT held over 17,000 accessions including 11,000 accessions of local varieties, 600 of wild relatives and 6000 from breeding programmes. A more recent estimate puts the ICRISAT collection at 21,000, representing 58% of the world collection. Other important collections are held by the USA, France, Canada and Uganda (FAO, 1998).

Overall, African material constitutes more than half of the world collection, and is fairly well represented in it. Nevertheless gaps remain: priority areas for collecting as

identified by ICRISAT include Benin, Chad, Guinea-Bissau, Côte D'Ivoire and Mauritania (FAO, 1998).

Variability within the cultivated form

P. glaucum shows great phenotypic variability for a number of characters (Bono, 1977; Grouzis, 1980; Marchais *et al.*, 1993).

- Length of the panicle: the greatest variation is found in Nigeria where it varies from 8 to 20 cm. The conical form is the most widespread.
- The vitosity of the grain: this is very important in indicating organoleptic and conservation properties. Early varieties have higher vitosity.
- Colour: dominant grain colours are yellow (especially in Niger) and grey. Except for Ghanaian and Togolaise varieties, the early types are yellow, and the later types from Mali and Senegal are more grey.
- Taste: a very important characteristic.
- Presence or absence of awns ('bearded grain'): in Senegal this allows early types to be distinguished from late ones. Elsewhere, presence of the awn is independent of length of the growing cycle.
- Root systems: generally, local varieties have efficient root systems which facilitate nutrient uptake even from poor soils (Raymond, 1962; Jacquinet, 1972). Relatively strong tillering allows adaptation to rainfall variations and compensation from disease attacks.

Isoenzyme studies by IRD (formerly ORSTOM) of 188 populations have distinguished five groups in West Africa. The same studies have identified the following major groups (Tostain, 1987, 1992; Tostain and Marchais, 1993):

- late millets of West Africa;
- millets of East and southern Africa;
- millets of south Asia.

Length of the growing season

In many villages it is not unusual to find four to seven millet varieties. Matlon's (1985) analysis of data collected by ICRISAT in Burkina Faso shows that farmers use this diversity according to the season, soil types and food preferences.

Classification of cultivated millet varieties is usually made according to the length of the growing season and sensitivity to photoperiod.

Most farmers maintain both early ('souna') and late ('sanio') varieties to ensure some stability in production (and to cover the 'hungry period'). Clement (1985) groups cultivated millet varieties into three groups: early varieties with a growing period of 70–90 days, intermediate types with 90–120 days, and late types of 120–180 days. However, earliness and lateness are relative concepts, depending on the region. There is in fact a north–south gradient: the varieties with the shortest season, in an absolute sense, occur in the drier north (the Sahelian zone), while the varieties with the longest growing period occur in the south (the Sudanian zone).

Millet varieties of Mali show particularly high levels of diversity between regions (Marchais, 1982): this is especially marked in one particular range with respect to the length of the growing season. In the region of Kolokani, farmers cultivate two 'sounas' or early varieties ('souna die' with a growing period of 75–85 days, and 'souna boaba' of 85–95 days), and three 'sanios' or late varieties ('sanio totioni', 100–110 days; 'sanio makangoulou', 115–140 days; and 'sania boaba', 130–160 days). These are grown in separate fields that are nevertheless in close proximity to each other and thus there is a large amount of gene flow between these varieties, as well as between cultivated and wild varieties. Despite this gene flow, farmers maintain distinct phenotypes by selecting for visible characteristics such as length and thickness of the panicle, colour, size and vitrosity of the grain, as well as the length of the growing period (Clement, 1997; see also Berthaud *et al.*, Chapter 4, this volume).

Photoperiodism

In some varieties, flowering occurs when the day-length falls below a certain number of hours critical for each variety (millets are short-day plants). In fact, flowering typically occurs 20 days before the end of the rainy season, though this varies, such that there are 'early' or 'late' varieties, which are none the less photoperiodic.

This phenomenon is important in the millet-growing areas of West Africa, where rainfall, besides being low, is also highly variable, both in terms of annual precipitation and timing of the rains. In fact, for areas of similar total precipitation, the growing season is 20–30 days shorter in West Africa than in India (Oran, 1977; Vaksman and Traoré, 1994). The major constraint is the variability of the date of the start of the rainy season, which leads to great uncertainty over the date of sowing. Photoperiodism allows the length of the growing season to be adjusted, by photosensitivity of flowering time, such that the varieties mature at the end of the rainy season (Vaksman *et al.*, 1996).

Thus, photoperiodism provides great phenotypic plasticity, allowing adjustment of the cycle with the duration of the rainy season and providing farmers with much greater flexibility in choosing the date of sowing. The earlier sowing this allows makes the crop more competitive in relation to weeds and makes better use of the peaks of nutrients that are released by mineralization from soil organic matter at the start of the rains.

However, in order to have more control over the length of the cycle and, indirectly, over plant height (early-sown seeds would give rise to taller plants), as well as to overcome constraints on the use of the same genetic material in different ecologies or in different seasons, the elimination of daylength sensitivity has generally been a major objective of plant breeding programmes. The great droughts of the 1970s reinforced these objectives because it seemed that direct reduction of the cycle could facilitate drought tolerance. However, evaluation of the impact of agricultural research on rural development has shown that the improved varieties which resulted from such approaches are not well adapted to the existing production systems, due, perhaps, to their lack of flexibility in the face of variable environments (Lambert, 1983).

In fact the countries of this region are characterized by a large climatic variation combined with very low soil fertility. Farmers have domesticated and selected millet varieties that, while low yielding, are adapted to the environments. Stability of produc-

tion and resistance to environmental stresses are the main characteristics of the ecotypes of this region (Stoop *et al.*, 1981; Matlon, 1985). The major challenge now faced by plant breeding programmes is to integrate these important characteristics in future varieties of higher yield potential.

Use of Millet Diversity

Worldwide, there are extensive millet breeding programmes, but nevertheless only a small fraction of the available diversity has been utilized. Photoperiod-sensitive material has been particularly under-utilized (Rai *et al.*, 1997).

Millet breeding has been more or less successful in India, and also in breeding for Namibia and other smaller areas throughout southern Africa. The successful varieties such as Okashana 1 were developed at ICRISAT in India using material derived from Togo in West Africa (Andrews and Kumar, 1996). There has been much less success, however, in developing improved varieties for West Africa itself.

The following paragraphs describe crop improvement efforts in West Africa. Three main types of approach were taken: (i) improvement of local populations; (ii) creation of composite populations and synthetic varieties using local and/or introduced materials, and the descendants of other crosses; and (iii) improvement of the harvest index through the introduction of the dwarfing gene.

Improvement of local populations

Local populations were improved for characteristics such as earliness, length of the panicle, grain size and tillering. This is possible because of the substantial genetic variation that exists, and because many of these traits appear to be controlled by genes with additive effects (Bono and Leclerc, 1963; Lambert, 1983). A range of selection methods was used. For example, mass selection was used in Niger in 1967 to improve the local variety 'Haini Kirei', producing both 'normal' and early varieties. In Mali the populations M9D3 and M12D1 were produced in this way.

In Senegal, from 1961, recurrent selection was used to improve five populations (three early and two late). The best progeny of the three early populations were combined to give a synthetic population 'souana 2', which was used as the basis of a new selection programme. The best in topcross were used to develop the 'souana 3' synthetic, which is actually in use in some countries of the Sahelian region. Similar methods were used to improve the local variety 'Zongo' in Niger, and to produce the synthetic varieties PS71 in Mali and 'saria' in Burkina Faso.

This approach has provided the majority of the local improved varieties in West Africa and some are still being promoted in the sub-region. But, in general, they have not shown better production, on farmers' fields, than the original local varieties (Matlon, 1983). Only rarely, have they been widely diffused. This lack of success may have many causes, but probably the main one is environmental variation: it is necessary to select for each ecological niche.

Creation of composite populations and synthetic varieties using local and/or introduced materials, and the descendants of other crosses

Some workers have considered that the variability in local varieties is limited (Kumar and Rao, 1987; Clement, 1985). For this reason, composite populations have been developed in a number of countries, including over 50 such populations developed by ICRISAT (Rai *et al.*, 1997). For example:

- ‘Nigerian Composite’, developed at the Institute for Agricultural Research in Nigeria, made up from 200 S_1 derived from 275 accessions from Nigeria and 54 from other areas of West Africa.
- A ‘World Composite’, composed of 144 S_4 derived from 1000 accessions of the world collection, including material from East Africa, and Nigeria (the ‘Gero’ collection). This has been successfully used in the development of successful varieties for India (Andrews, 1986).
- ‘Compel’ (Composite à épis longs), created for Mali from six ecotypes, with long panicles, from Mali and Niger.
- ‘Genetic Pools’ also developed for Mali, composed of crosses between varieties from Mali and other countries of West Africa. These include the ‘SoxSa’ composites of early (‘souna’) and late (‘sanio’) varieties (Niangado and Kumar, 1989). Further improvement through recurrent selection produced the variety ‘Soxsat’, which is being promoted in Nigeria and Mali.

These methods have been shown to be efficient in improving millet for various traits (such as grain weight, tillering, length of the ear, resistance to mildew). Nevertheless, the varieties produced have not generally been accepted on farms in West Africa. Again this is probably due to genotype \times environment interactions between sites, as well as differences in farmer preferences.

Improvement of the harvest index through the introduction of the dwarfing gene

Early work by Blondel (1967) showed that, among millet varieties, some are more responsive to nitrogen fertilizers. According to Jacquinet (1972), traditional millet varieties have characteristics that are useful to traditional agriculture (hardiness and adaptation to traditional agricultural practices) but are poorly adapted to intensification (Etasse, 1972). In order to produce short-straw varieties, more adapted to the use of inputs, the dwarfing gene D2 from Indian material was introduced at the Institute of tropical agricultural research (IRAT) into several local varieties in Mali, Niger, Nigeria and Senegal. A more elaborate programme, financed by the European Development Fund, was later carried out.

None of the varieties produced was acceptable on-farm. In the light of the results it has to be questioned whether it is appropriate to go to such lengths to develop dwarf varieties. The normal intensive conditions for such varieties – high fertilization, high planting density, mechanical harvesting – are far from those present in West Africa. In any case, much diversity for grain:straw ratio exists among local varieties. Selection among such varieties may be more fruitful since the material would, in general, be better adapted to local conditions. On the other hand, it may be that the reserves accumu-

lated in the long stems of traditional varieties are important in sustaining grain development in the case of water stress, as is the case for maize (Duncan, 1975) and rice (Reyniers *et al.*, 1982).

Conclusions

According to Matlon (1985), of some 3000 improved varieties examined by ICRISAT, none superior to the local types has been identified. In fact, in West Africa, millet yields have barely increased since the 1960s (FAO, 1988). Given the diversity in production environments as well as large year-to-year variation in climatic conditions, it is perhaps not surprising that the formal plant breeding efforts based on 'wide adaptation' have failed (see also Ceccarelli *et al.*, Chapter 6, this volume). The removal of the photoperiodic response and concentration of the dwarf varieties of high yield potential (but low yield under farmers' actual conditions) have proven to be equally inappropriate.

Institutional Arrangements for Millet Breeding in West Africa

National programmes

In francophone West Africa, formal millet plant breeding programmes were initiated in 1931 at the agronomy research centre of Bambey, Senegal, under the auspices of IRAT. The Bambey station served the entire francophone sub-region. Another programme was initiated at the Institute for Agricultural Research in Nigeria.

In the 1960s, national research structures began to be developed. At the same time, ICRISAT and CILSS (Permanent Inter-state Committee for Drought Control in the Sahel) were established. In the 1980s, a major regional project was initiated for the improvement of millets, sorghum, cowpea and maize. At this time the regional organization CORAF (Conférence des Responsables de Recherche Agronomique Africains, later Conseil Ouest et Centre Africain pour la Recherche et le Développement Agricole) was also established.

In most of Africa, the organization of research programmes and institutions continues to follow the colonial model: research is still organized by product, with one station per crop, and programmes are therefore centralized.

Recently, however, some countries of West Africa have decided to decentralize certain aspects of their work. In Mali, regional centres have been developed with participation of users facilitated by a non-governmental organization: the Regional Commission of Research Users (Niangado, 1997). In Benin, INRAB also developed its strategic plan on a regional basis. However, the plant breeding programme remains national.

Collaborative research

Following independence in the West African states, a number of efforts have been initiated for networking at the sub-regional level:

- The Institute for the Sahel (INSAH), operating under the auspices of CILSS, and with funding from the European Community, which has developed a network for the evaluation of new millet varieties in the region. Since INSAH has ceased activities, ICRISAT has held a number of annual workshops in various countries of the region.
- The Intsormil network, following the model of the Collaborative Research Support Programmes (CRSP) funded by USAID, focused on capacity building in the national agricultural research systems. A number of national scientists have been trained at US universities, but there has been little attention paid to building links within the sub-region.
- Rocafremi, the Millet Research network for West and Central Africa, modelled on the other networks promoted by the International Agricultural Research Centres. This network, created in 1990, involves the NARS of all countries of the sub-region. It has the objectives, with regard to millet, to: strengthen the NARS; promote training; develop multilateral collaboration; ensure the circulation of scientific information among the scientists of the sub-region; define common constraints and research priorities; facilitate the exchange of technologies between countries, and internationally; encourage the transfer of results to farmers by means of trials and demonstrations in farmers' fields; and encourage collaboration between existing networks in the sub-region. It is governed by a general assembly of all participating countries.

ICRISAT has played an important role in strengthening the capacity of millet scientists in the region and the implementation of the millet network. The ICRISAT Sahelian Centre has been a centre of excellence in networking with its NARS partners. The centre has provided germplasm to the breeders in the region. While materials developed by the centre have generally been too early, some of these materials, mostly from the various bilateral projects, have been released in the region.

Collaborative research networks allow participating countries to evaluate the varieties developed in other countries and to select and keep those better adapted to their own situation. Unfortunately, no network is currently engaged in the elaboration of a large genetic base material with a view of making it available to the NARS of the region; rather, countries tend to contribute by providing finished products (local improved varieties, synthetics or composites) which may not be adapted to other localities.

Conclusions

West Africa is part of the centre of origin of pearl millet. The great variability of millets in West Africa should constitute a great asset for the development of adapted varieties of higher potential, but after decades of effort there have been few improvements in production in the region. The progress made to date shows no indication of any ceiling having been reached in the genetic improvement of this crop. The great variability available in the cultivated handcars and their wild relatives is a good basis for genetic improvement in grain yield and should provide optimism about opportunities for future adaptation. The main thrust of research in the region has been to produce

varieties that would respond well to improved agronomic conditions, and these varieties have not been well received by farmers since they are not adapted to their specific environments. To avoid this kind of problem, it will be necessary to integrate the farmers in the breeding process, by implementing a 'participatory plant breeding' process.

A major mechanism for adaptation to variable agroclimatic conditions – photoperiodism – has been selected *against* in most formal breeding programmes. There has been little use of local diversity, and where diversity from the region has been used, for example in creating composite populations, there has been little or no attention to selection for specific adaptation to local environments.

It is clear that a change of emphasis is necessary if farmers are to benefit from improved varieties in the region. First, there is a need to make maximum use of locally available diversity, including factors such as photoperiodism that facilitate adaptation to the variable climatic conditions. Secondly, efforts to broaden the genetic base, through the use of composites, must be complemented by decentralized selection in the target environments to allow for specific adaptation. This is especially important in marginal environments such as those of the Sahelian zone and must take place on farmers' fields (see also Ceccarelli *et al.*, Chapter 6, this volume).

This has institutional implications. Global, regional and sub-regional networks, and international centres, are important in order to access a wide diversity and to develop composite populations. Selection, however, must be decentralized to, and within, national systems. There is, therefore, a need for both centralized and decentralized structures. Existing networks, such as Rocafremi, could be refocused to promote and facilitate such approaches to these activities.

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9

The State of the Use of Maize Genetic Diversity in the USA and Sub-Saharan Africa

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Introduction

Globally, maize (*Zea mays* L.) is the most widely grown of all the cereal grain crops. It is unique in its adaptation to diverse ecological regions of the world, ranging from cool temperate to hot tropical and sub-tropical zones, from tropical highlands to lowland regions. It is cultivated in about 70 countries, including 53 developing countries (Timothy *et al.*, 1988; Dowsell *et al.*, 1996). The developing countries constitute about 64% of world maize area and 43% of world production. The United States produces about 40% of the crop on only 20% of world maize area and is the world's leading national producer, with average yields of 8.0 t ha⁻¹ (Dowsell *et al.*, 1996; USDA, 1999). The average per hectare maize yield of the African continent as a whole (about 40 maize-growing countries) is only about 1.6 t (USDA, 1999). Further, the average yields of the developed nations is about 2.5–3 times that of the developing countries. This disparity is mainly due to the lack of improved production technology and unfavourable environment that have influenced maize production in developing countries. Maize is mostly consumed as staple human food in Latin America, Africa and Asia, whereas, in the developed countries it is mostly fed to animals. It is also used in a myriad of manufactured products, including, for example, breakfast cereals, sweeteners, ethanol fuel and beer.

Increasing and stabilizing grain yield has been the principal concern for maize breeders around the world. Pandey and Gardner (1992) reported that, among 48 maize researchers spread over four continents, all but two emphasized yield improvement as a high-priority objective and invested about 46% of their resources toward production of high-yielding populations or hybrids. This is particularly true in developing countries where urbanization is taking away land from agricultural production. As a result, increased yield per unit area is the most viable option to sustain maize production.

The best materials available to achieve this objective are popular elite lines developed in the target environments where hybrids are employed. Recurrent selection of segregating progenies from elite × elite line crosses has been used to develop superior

inbred lines to produce high-yielding hybrids. Maize breeders realized that this approach would lead to the narrowing of the germplasm base. However, most are disinclined to introduce unadapted germplasm into existing breeding programmes, principal reasons being that sufficient genetic progress is made using elite line crosses, the longer time period involved with exotic materials to achieve progress because of undesirable linkage drag, and the fear that the introduction of exotic germplasm might dilute the genetic make-up of the existing cultivars (Kannenberg and Falk, 1995).

Beginning in the early 1900s, in developed countries, high-yielding varieties (HYVs) and hybrids gradually replaced the landraces and farmer cultivars of maize. The sprouting of commercial seed companies and improved technology coupled with the discovery of hybrid vigour played a major role in the shift from open-pollinated varieties to hybrids. This led to genetic uniformity and narrowing of the gene base which, in turn, resulted in genetic vulnerability to insect pests and fungal pathogens. A striking example of the effect of genetic uniformity leading to genetic vulnerability involved the susceptibility of maize with T-cytoplasm to southern leaf blight in 1970 in the USA. Since that time, US maize breeding efforts, both private and public, have recognized and emphasized the need to widen the genetic base of commercial maize germplasm. In spite of this emphasis, Goodman (1998a) indicated that US commercial maize contains only 2.9% exotic germplasm, which includes both temperate and tropical, and that exotic tropical germplasm is about a tenth of that. The exotic tropical germplasm includes introduced tropical germplasm that has undergone extensive selection and testing for adaptation to temperate US conditions and usually constitutes at most 25% of the exotic tropical germplasm of any one inbred line (and most often constitutes 1–2%).

However, it is not genetic diversity *per se* that is needed to make progress in maize. Breeders are interested in useful genetic diversity, which depends upon the target environments and grower's preferences. Although genetic diversity in time (newer cultivars replacing older ones) has occurred, these newer cultivars are still closely related to the ones they replaced, and thus the genetic base of commercial maize has remained narrow (Duvick, 1984).

The scenario is different in developing countries where landraces and open-pollinated varieties (OPVs) are still being grown by farmers. Recently, Taba (1997a) indicated that landraces still account for about 42% of the developing country maize area. However, this trend is gradually changing as more and more HYVs and hybrids adapted to different ecologies are becoming available, primarily through the efforts of International Agricultural Research Centres (IARCs), such as the International Maize and Wheat Improvement Centre (CIMMYT), the International Institute for Tropical Agriculture (IITA) and multinational commercial seed companies.

Maize and its Genepools

Origin

Maize (*Zea mays* L.) is a monocotyledonous species and belongs to the family Gramineae in the tribe Maydeae. It is native to the Americas, with the centre of origin in southcentral Mexico. The earliest archaeological samples – consisting of small eight-

rowed soft cobs, often a little larger than an ordinary pencil eraser – were discovered in the caves of Tehuacán in highland southcentral Mexico (Goodman, 1988; Taba, 1997a). These were later identified as the remains of the earliest cultivated maize. Nevertheless, maize has left an evolutionary trail obscured by complexity as there are no extant intermediate forms between wild maize and the approximately 50 Mexican maize landraces, many of which are still being cultivated in Mexico (Wilkes and Goodman, 1995).

The tribe Maydeae contains seven genera and some have been proposed to fill the obscurity surrounding the progenitor(s) of maize. Three (*Zea*, *Euchlaena* and *Tripsacum*) are native to the New World whereas the remaining four (*Coix*, *Sclerachne*, *Polytoca* and *Chionachne*) are of Asiatic origin (Hallauer and Miranda, 1988; Goodman, 1995). All seven genera, however, share the common trait of monoecy, i.e. separate male and female inflorescences on the same plant. Although the Asiatic genera have not been studied as intensively as the New World genera, there has been an occasional speculation that *Coix* (Job's tears) is more closely related to maize than the other Asiatic genera.

Several hypotheses have been proposed for the origin and evolution of maize, but no convincing, definitive evidence exists, although teosinte may have played an important role in its lineage (Galinat, 1995). According to Goodman (1995), two hypotheses have gained approval from several researchers for the origin of the New World Maydeae members. One hypothesis suggests that maize, teosinte and *Tripsacum* are descendants of a common ancestor (Weatherwax, 1955). The other hypothesis suggests that maize is derived from teosinte (Beadle, 1939). Recent advances in molecular systematics using isozymes, chloroplast DNA and quantitative trait loci mapping of kernel weight in maize, teosinte and their hybrids, prompted Doebley (1990) and Doebley *et al.* (1994) to suggest that maize was domesticated from teosinte; teosinte is ancestral to maize and that *Z. mays* L. ssp. *parviglumis* (race Balsas) was the direct ancestor of maize.

Historical and global germplasm movement of maize

There is general agreement that maize was under domestication about 5000–8000 years ago in southcentral or southwestern Mexico (Goodman, 1988). There is also a consensus that following its domestication in Mexico it spread widely throughout the Americas, extending as far north as southeastern Canada, before and after the European colonization. Christopher Columbus first clearly noted the presence of maize on the north coast of Cuba in 1492 (Mangelsdorf, 1974; Goodman, 1988). He later took it with him to Spain where he introduced it into the Old World in the spring of 1493. There is a possibility that earlier European voyages to the New World might have occurred and maize could have been present in the Old World at an earlier date (see Jeffreys, 1967). Maize was widely grown in Spain, Italy and southern France by the end of the 1500s.

In the early 1500s, maize entered Africa from Spain and Italy, mainly through Portuguese traders (Obilana and Asnani, 1978; Taba, 1995a, 1997a; Dowswell *et al.*, 1996). Caribbean yellow flint was the most predominant type in East Africa during the 16th century and by the 1700s became a major food crop in West and Central Africa. Portuguese traders also introduced several lowland tropical races from Brazil, the

Guyanas and the Paraná basin to the West African coast. Also in the mid-17th century, Dutch settlers brought flourey and flint types to southern Africa, and in the late 19th and early 20th centuries, southern dents from the US and northern Mexico were imported into South Africa (Brandolini, 1970; Taba, 1995a, 1997a).

Maize made its entry into south Asia in the early 1500s probably via the Mediterranean traders who introduced it along the western coast of India (Dowswell *et al.*, 1996). By the time of Magellan's voyage in the Pacific, maize had been introduced into the Philippines. By the mid-1600s, it became well established in the Philippines, Indonesia and Thailand (Taba, 1995a, 1997a; Dowswell *et al.*, 1996). From there it spread to China, Japan and Korea by the mid-1700s.

Maize racial diversity

Maize exhibits a tremendous amount of morphological variability among the different races and varieties. From the original collection of 20,000 accessions, assembled under sponsorship of the Rockefeller Foundation and the US National Research Council, a set of typical collections amounting to about 1200 were characterized and grouped into about 250–300 named races (Goodman, 1983). Most of these racial collections trace their origins to the tropics and are estimated to represent about 95% of maize diversity. This vast amount of diversity is housed mainly in germplasm banks at CIMMYT and the Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP) in Mexico, Instituto Colombiano Agropecuario (ICA) in Colombia, Programa Cooperativo de Investigaciones en Maiz (PCIM) in Peru, the United States Department of Agriculture (USDA) North Central Regional Plant Introduction Station (NCRPIS) in Ames, Iowa, the USDA National Seed Storage Laboratory (NSSL) in Fort Collins, Colorado, and the Maize Breeding Program at North Carolina State University in Raleigh.

Brown (1979) estimated that there might be 150–180 distinct racial groups worldwide, of which about 130 come from Latin America. These racial complexes provided a systematic classification of the variability in maize and are a source to broaden the genetic base of commercial maize. They formed the bases for several thousand OPVs and improved populations for commercial use (Brown and Goodman, 1977; Dowswell *et al.*, 1996). It was indicated by Brown (1979) and Goodman (1985a) that, on a racial basis, only 2% of the available germplasm is being used in temperate maize improvement; this includes the races Corn Belt Dent, Northern Flint and Cateto (Argentine) Flints. On a worldwide basis, excluding subsistence farming, at most, 5% of the races are represented in any maize of commerce (Goodman, 1983). Whether genetic diversity is measured by the number of races or racial groups of current commercial importance or by the number of alleles represented among the breeding materials, Goodman (1983) indicated that only a small proportion of the total variability available is currently being used in the temperate breeding programmes, and this is even today.

Brown and Goodman (1977) classified US maize germplasm, excluding the popcorns and sweet corns, into nine broad racial complexes based on plant, ear, kernel characteristics and geographic distribution. Most of these racial complexes have had little impact on temperate maize of commerce, but one of these racial complexes, Corn

Belt Dent, provides essentially all US maize germplasm. The Corn Belt Dents evolved in the eastern US Corn Belt in the late 19th century. They arose from a germplasm pool consisting of about 75–80% Southern Dents and 20–25% Northern Flint materials (Doebley *et al.*, 1988). Presumably, this event occurred by the accidental hybridization in the field when poor stands of the Southern Dents were replanted with early Northern Flints (Wallace and Brown, 1956). Virtually all of the maize now produced in the US and most other temperate regions of the world traces back to the Corn Belt Dents. Some of the most prominent open-pollinated varieties of this racial complex are Reid's Yellow Dent, Lancaster Sure Crop, Leaming, Boone County White, Krug Yellow Dent and Midland Yellow Dent.

Genepools of maize

The racial descriptions by Brown and Goodman (1977) provided a broad grouping of the maize germplasm which forms the most important part of the primary genepool of Harlan and deWet (1971).

Primary genepool

The primary genepool consists of all of the maize and related germplasm that hybridizes freely with cultivated maize. The racial complexes, OPVs, inbreds, tropical, sub-tropical populations and diploid teosintes form the germplasm of this genepool. Teosinte, a weedy annual, has been considered as the closest relative of maize (Doebley, 1990). It shares the same chromosome number of $2n = 2x = 20$, and similar chromosome morphology, although more terminal knobs are seen on teosinte chromosomes. Morphologically, teosinte plants often resemble maize. It crosses relatively freely with maize, and hybrids are fertile and show regular meiotic pairing (Iltis, 1983; Goodman, 1995). The annual Mexican teosintes have been considered as subspecies of maize by Doebley (1990).

Two perennial forms of teosinte, a tetraploid, *Z. perennis* ($2n = 4x = 40$), and a diploid, *Z. diploperennis* ($2n = 2x = 20$), have also been found in Mexico. Although most annual teosinte races are interfertile with maize, *Z. diploperennis* exhibits minor fertilization barriers with maize (Tabata, 1997b).

Teosinte received much attention from maize researchers because of its speculated role in the origin and evolution of maize. Otherwise, it has been of very limited use for maize improvement or hybrid development (Goodman, 1988; Tabata, 1995b, 1997b). According to Goodman (1988), no inbred line, hybrid or variety contains intentionally used teosinte germplasm, although two inbred lines – N159 and N160, derived in part from teosinte germplasm – were released in Nebraska; neither has been used in hybrid development. Additionally, Northrup King once used a privately developed inbred line derived in part from teosinte germplasm (Goodman, 1985a).

Secondary genepool

The species belonging to the genus *Tripsacum* constitute the secondary genepool of maize. *Tripsacum* species are perennials with chromosome numbers in multiples of $x = 18$. Most species exhibit a polyploid series from diploid to tetraploid and in some cases pentaploid and hexaploid (Berthaud *et al.*, 1997), and many are obligate

apomicts. *Tripsacum* can be crossed with maize, generally with difficulty, and the offspring show varying degrees of sterility. Chromosome morphology and knob positions of *Tripsacum* species differ greatly from those of maize (Goodman, 1995). Also, vegetatively, the various *Tripsacum* species are very variable and species identification is laborious.

In general, the main use of *Tripsacum* species has been as fodder, and there is no documented use of *Tripsacum* germplasm in commercial maize production. Galinat (1977) showed that introgression between maize and *Tripsacum* is possible. A research programme, sponsored by the French research organization IRD, to transfer apomixis from polyploid *Tripsacum* populations to maize lines is underway at CIMMYT (Berthaud *et al.*, 1995, 1997); a second such programme exists in the US at a USDA research station in Oklahoma (Kindiger, 1997). The potential benefits of these projects, if and when accomplished, will greatly help farmers in the developing world, who could replant hybrid seed generation after generation.

Tertiary gene pool

The distantly related oriental or Asiatic genera such as *Coix*, *Sclerachne*, *Polytoca* and *Chionachne* constitute this gene pool. *Chionachne* and *Sclerachne* have 20 chromosomes; *Polytoca* has 40; and different species of *Coix* have 10, 20 and 40 chromosomes. Genera in the tribe Andropogoneae can also be considered to form the tertiary gene pool. While wide crosses between maize and other genera have been reported since the 1940s, none of these has ever contributed to maize improvement and none has ever been backcrossed to maize.

Overall, in our opinion, the primary gene pool of maize has substantial genetic diversity for commercial exploitation. We do not foresee any immediate necessity to utilize taxa from secondary and tertiary gene pools for commercial use, although transfer of apomixis from *Tripsacum* to maize would greatly benefit maize growers of the developing countries.

Maize in the United States

Potential sources for broadening the germplasm base in the USA

Between the late 19th century and early 20th century, the US maize production was predominated by thousands of open-pollinated varieties. However, only a few of these are represented in the current US maize breeding programmes, both public and private (Baker, 1984; Goodman, 1998a). Although open-pollinated varieties formed the basis for initial maize research programmes, the concept of heterosis coupled with the development of hybrids beginning in the 1930s, and the epidemic of southern maize blight in 1970, led private and public maize researchers to look for additional sources to diversify cultivated maize germplasm. The following section provides a review of the potential sources for broadening maize germplasm in the US.

Temperate-adapted sources

Historically, OPVs of maize were the source materials used in the temperate maize improvement programmes. Beginning in the early 1900s, the discovery of hybrid

vigour which led to the development of the inbred-hybrid concept (East, 1908; Shull, 1909, 1910; Jones, 1918) revolutionized the maize breeding programmes in the US. The rapid diffusion of the inbred-hybrid development led to the replacement of thousands of OPVs. By the 1960s, production of high-yielding hybrids in temperate breeding programmes was based largely on inbreds from the OPVs Reid Yellow Dent (RYD) and Lancaster Sure Crop (LSC) (Baker, 1984; Smith, 1988; Goodman, 1998a).

The seed parents of present-day high-yielding hybrids are derived from the Iowa Stiff Stalk Synthetic source, which is predominantly of RYD origin, and mostly trace back to four inbred lines (B14, B37, B73, B84). The pollen parents, derived chiefly from C103, Mo17 and Oh43, which often contribute to plant health, are derivatives of LSC. Iodent lines and Minnesota 13 lines have added early dry-down, allowing earlier harvesting with less artificial drying, and permitting hybrid maize to be grown further north than ever before. Midland, Krug, Leaming, Northwestern Dent, Pride of Saline and Jarvis are other important OPVs that have also contributed to current breeding programmes, but at a much lower level than Reid and Lancaster (Gracen, 1986; Goodman, 1998a). Although about 250 or so described maize races constitute the maize genepool, only one of these races, Corn Belt Dent, represents the commercial maize germplasm grown in the entire US and almost all of the temperate regions of the world. Pedigree information on most US germplasm is available in Gerdes *et al.* (1993).

Temperate exotic sources

Most of the exotic germplasm currently employed in the US is temperate in origin and is represented by two specific sources. Maíz Amargo from Argentina was used as a source of insect and disease resistance, mostly via the inbred B68 from Iowa State. The second source of temperate exotic germplasm is represented by two French lines: F2 and F7. These lines have outstanding germinability under adverse (cold, wet, cloudy) environmental conditions and are widely used for breeding and production of hybrid seed across the northern maize-growing parts of both the Old and New World.

Tropical exotic sources

The tropical sources most widely used for inbred line development in the US are the Cuban Flints, the Tusóns and other Caribbean materials (Goodman, 1985b). The most widely used race in the tropical maize breeding, Tuxpeño, has not proved to be a very suitable germplasm source for temperate breeders. Many of the Tuxpeño collections are too late, even under short-day temperate conditions, for effective evaluation. Also, it is presumed to be one of the putative grandparents of the Corn Belt Dents and may not express high heterosis when combined with some US materials. However, direct evaluation of tropical germplasm in the US Corn Belt is virtually impossible, due mainly to the photoperiod sensitivity of the tropical materials in long-day temperate environments.

A wide array of tropical materials are available from national and international maize germplasm banks. These range from OPVs to improved synthetics and are available from CIMMYT or national programmes such as ICA of Colombia. An extension of the Latin American Maize Program (LAMP) called Germplasm Enhancement of Maize (GEM), financed by the USDA and several private seed companies (Pollak and Salhuana, Chapter 19, this volume), has been identifying tropical sources for use in US

maize breeding programs. In the maize breeding programme at North Carolina State University, private and public tropical hybrids from Central and South America have proven useful sources to extract inbred lines of all-tropical origin but adapted to temperate maize breeding conditions (Goodman, 1992).

Theoretically, initiatives similar to LAMP and GEM could be undertaken to broaden the genetic base of maize in the developing countries too. However, we do not foresee an immediate necessity for such an endeavour except in those areas where hybrids have been in extensive use for several decades. Taba (1997a) indicated that open-pollinated landraces and varieties are still cultivated on 42% of the developing country maize area because these OPVs have genetic attributes preferred by the farmers. Although some are inherently low-yielding, these OPVs are genetically diverse and are themselves a source of genetic variability. However, as improved populations and newer hybrids gain popularity among the farmers of the developing countries, the landrace populations may eventually disappear from farmers' fields. As (and when) such a situation is approached, initiatives similar to LAMP and GEM can be undertaken to broaden the genetic base of maize in the developing world. A wealth of materials are available from CIMMYT, IITA and many national programmes, such as in Mexico and Thailand, to help maize farmers from the developing world to meet any such future challenges.

Synthetic sources

Several tropical and sub-tropical composites suitable for US use have been described by Gracen (1986), and several others have been developed by Arnel Hallauer at Iowa State University. These have been used to a limited extent for derivation of inbred lines, but are not used for production.

Biological and Environmental Barriers to the Movement of Maize Germplasm

Maize is an outbreeding species and grows from 58° north to 40° south latitude. It is cultivated in more diverse areas of the world than any other major crop, from sea level to 3800 m elevation, and from desert oases to areas with 11,000 mm of rainfall (Timothy *et al.*, 1988). It is undoubtedly the most widely adapted crop and is cultivated in Canada, northern Europe, Russia, South Africa, the Himalayas, China, India, Southeast Asia and Australia (Hallauer and Miranda, 1988; Timothy *et al.*, 1988). Adaptation to altitude influences the type of maize grown in these areas. As a consequence of its diverse cultivation, several different local races and types have evolved and adapted to each ecological region. Essentially, each of these local types could form a source of exotic germplasm for another maize-growing region. However, attempts to introduce and use these exotic germplasm sources may be hampered by several biological and environmental constraints.

Susceptibility to local insect pests and fungal pathogens is a commonly observed biological constraint. In North Carolina, we often experience this problem in our maize programme with CIMMYT tropical lines and other tropical germplasm sources. During the summer months, the CIMMYT lines become highly susceptible to smut (*Ustilago maydis* (DC.) cda.), other ear-rot fungi and aphids (*Rhopalosiphum maidis*). Similar phenomena occur when temperate materials are introduced into tropical environments.

Of the environmental constraints, sensitivity to day-length (photoperiod) has been observed as the major factor influencing movement of maize from one ecology to another. When tropical materials adapted to short-day lengths (10–12 h daylight) are introduced into long-day (15–18 h daylight) summer growing seasons of temperate areas, they grow extremely tall (12–18 ft/3.7–5.5 m), have more foliage, exhibit poor tassel-silk synchrony, weak root strength and much lodging. Thus, photoperiod can be an impediment for effective evaluation and movement of maize germplasm from one locale to another. Drought and heat susceptibility is the other major environmental barrier that restricts the movement of germplasm. CIMMYT has successfully developed several drought-resistant elite populations. One of them, Tuxpeño Sequia, exhibited outstanding yield increases even under severe moisture stress (Dowswell *et al.*, 1996), although maize is not competitive with such drought-tolerant crops as cotton and sorghum.

Other constraints for the movement of maize across regions include grain characteristics preferred by the consumers such as grain colour (yellow vs. white) and grain texture (flint vs. dent vs. flour).

Heterosis and Development of Heterotic Groups

In the US Corn Belt, heterosis for yield is almost always observed when inbred lines derived from genetically different backgrounds are used to produce hybrids. Following Shull's demonstration of heterosis in the early 1900s, OPVs served as source populations to derive inbred lines for use as parents of double-cross hybrids. Later, especially with the switch of commercial maize production to single-cross hybrids in the 1960s, progenies from elite inbred line crosses became the source populations to derive superior inbred lines. The tremendous yield gains obtained from superior double-cross and single-cross hybrids demonstrated to maize breeders that the identification and maintenance of heterotic groups are valuable in the classification of maize germplasm and a necessity for continued yield improvements. Although heterosis is a manifestation of genetic diversity of the parental lines, Moll *et al.* (1965) clearly showed that there is a limit to this manifestation (there is no notable yield heterosis in teosinte \times maize or *Tripsacum* \times maize hybrids) and, as a result, a knowledge of these relationships will help to increase the efficiency of a breeding programme (Hallauer and Miranda, 1988).

There are several ways to classify and designate the source populations and lines into different heterotic groups. Commonly, establishing inbred lines from already known heterotic patterns is the first step: for example, in temperate regions, inbred lines from Stiff Stalk and Lancaster genetic backgrounds; and in the tropics, lines from Tuxpeño, ETO (Estacion 'Tulio Ospaña), Tusón, etc. The source populations of mixed or unknown assignment, such as the broad germplasm pools of CIMMYT or tropical populations from GEM, can be crossed to a set of standard, well-established inbred lines. The population \times line crosses are then tested in replicated yield trials. Based on the yield data, the source populations can be grouped into corresponding heterotic patterns.

As a corollary, the racial collections or CIMMYT germplasm pools can be intercrossed among themselves and the hybrids tested in replicated trials to identify the most heterotic pools (Crossa *et al.*, 1990; Sinobas and Monteagudo, 1996). Either

intra- or interpopulation recurrent selection procedures can be conducted in these heterotic pools to derive superior inbred lines from each pool. Additionally, if the germplasm pools are broad-based populations, then selection within the pool may also produce lines which can be combined with lines selected from another pool to evaluate heterosis and produce desirable hybrids.

Preliminary data from crosses of broad-based populations are often of little guidance in actual use of inbred lines, since the lines vary greatly. Thus each line developed from a broad-based population must be tested against lines of known heterotic pattern. At North Carolina State University, we screen new lines from broad-based sources (commercial tropical hybrids, synthetics) against B73 \times Mo17 (or an equivalent), then screen survivors against Stiff Stalk and Lancaster lines separately.

Ways of Genetic Base-broadening in the USA

In the US, exotic germplasm includes domestic unadapted germplasm, temperate foreign germplasm, and tropical or semi-tropical germplasm (Goodman, 1985a). However, elite inbred lines are used to produce superior commercial single-cross hybrids. Consequently, any attempt to use exotic germplasm should begin with an approach to tailor it, both phenotypically and genotypically, to acceptable levels for use in commercial production. Therefore, in our view, genetic base-broadening of US maize should proceed as outlined below. More detailed and comprehensive approaches may be found in the chapter on GEM (Pollak and Salhuana, Chapter 19) and that by Kannenberg (Chapter 18) in this volume.

Identify the best materials in the tropics

In our experience of working with exotic germplasm at North Carolina State University, we believe that either private tropical hybrids or public tropical inbred lines are the most promising germplasm sources. Yield trial information or information from tropical breeders can be used to screen tropical hybrids. Also, the LAMP project (Salhuana *et al.*, 1997) provides maize breeders with much of the useful information required to make judicious selection of tropical germplasm accessions. Winter nursery (short-day) conditions can be used to compare maturities with those of current breeding materials with and lodging (a weak point for most tropical materials) can be scored there at the same time as initial crosses are made.

Adaptation of selected tropical materials to temperate conditions

This, in our opinion, is a critical step and could be very frustrating. The day-length sensitivity (photoperiod) of tropical materials when grown in long summer days in the US has been the main bottleneck for their large-scale use in temperate maize-growing areas. We feel that photoperiod sensitivity can be eliminated or at least reduced from segregants of even 100% tropical materials with skill and luck. To do this, we suggest either of two approaches.

One of the approaches is to conduct a long-term programme (five to six generations) of plant-to-plant mating with selection for earlier, shorter, erect plants with good tassel and silk nick and some evidence of prolificacy. The selected plants are then selfed for at least two generations with visual selection to obtain 100% tropical semi-inbred lines adapted to temperate growing conditions. These lines are then topcrossed with elite temperate lines. Replicated testing of the topcrosses with commercial hybrid checks will provide a measure of the performance of these tropically derived temperate-adapted inbred lines.

The second approach is that being used in the GEM project. Selected tropical populations are crossed to elite lines (e.g. private lines such as LH132, FR1064, LH51 or FR697 or other private-company equivalents) under short-day conditions. These 50% exotic populations are selfed and the partially inbred lines are topcrossed with commercial testers from a complementary heterotic group to test in replicated yield trials. Also, selected 50%-exotic lines are crossed to elite lines to derive 25% tropical lines. The lines derived from these 25% exotic crosses can be tested in topcrosses to identify productive inbred lines.

Maize in Sub-Saharan Africa

Maize is the most important staple food crop of sub-Saharan Africa. Although its production has rapidly expanded in the past three decades, its share of total cereal production has remained about 40% since 1970 (Byerlee and Heisey, 1996). An increased demand for maize production of about 3.2% per year will exist in sub-Saharan Africa for the next two decades due to steady population growth, urbanization and economic growth (Byerlee and Saad, 1993).

Maize is an introduced crop in Africa. Several different types were introduced into diverse ecologies of the continent and represent a vast amount of diversity (Brandolini, 1970). Although Jeffreys (1967) suggested that maize was present in southern Africa before Columbus discovered the New World, it clearly arrived in Africa by the 16th century with Portuguese traders who introduced Cateto or Caribbean Flints on both the eastern and western coasts (Obilana and Asnani, 1978; Efron, 1985; Taba, 1995a, 1997a; Byerlee and Heisey, 1996). The Dutch introduced several types into South Africa in the mid-1600s. Brandolini (1970) indicated that the Dutch settlers brought Caribbean Orange Flint, Brazilian Flourey and Hickory King types to South Africa in the 17th century. Southern Dents from the US were introduced into South and East Africa in the early 1900s (Brandolini, 1970; Obilana and Asnani, 1978). In East Africa, the local yellow maize was derived from early introductions of the Caribbean Flint and Yellow Dents from South Africa. It appears that high-altitude Andean maize was the last distinct type to enter East Africa by way of missionaries before the First World War (Obilana and Asnani, 1978). In West Africa, two distinct types, Caribbean Flints and Southern Flours or Coastal Flours (related to flourey types of Central and South America), were observed. As a result of the long-term cultivation with different introduced maize types in Africa, the crop became adapted to several different ecologies, which ultimately led to the isolation of landraces and farmer cultivars.

Useful genetic diversity available to farmers in sub-Saharan Africa

Although maize originated and evolved in the tropics, temperate germplasm has been the most productive for farmers. Temperate germplasm has evolved through cycles of genetic improvement and diverged into heterotic groups, while tropical germplasm has mainly been exploited as open-pollinated populations. With the establishment of CIMMYT and IITA, genetically improved populations (synthetics, composites, etc.) of tropical germplasm became accessible to sub-Saharan African countries. The reader is referred to CIMMYT (1985), Eberhart *et al.* (1988), Timothy *et al.* (1988) and Dowswell *et al.* (1996) for details on improved populations and inbreds developed by IARCs and national programmes in Africa. Dowswell *et al.* (1996) have outlined the most up-to-date and comprehensive description of useful maize genetic diversity available in sub-Saharan Africa and formed the basis for the following description of useful materials for maize researchers in that area.

Inbreds from CIMMYT and IITA

A breeding effort initiated at IITA with later collaboration from CIMMYT resulted in the release of several tropical inbred lines with resistance to maize streak virus and/or to *Striga* and having good stalk and root strength (Kim *et al.*, 1987). Several of these lines contained US germplasm in their lineage (Gracen, 1986; Kim *et al.*, 1987).

Improved populations from IITA

TZSR-W and TZSR-Y were the first high-yielding populations with maize streak resistance released by IITA for lowland tropics. The former is a white semi-flint and the latter is a yellow semi-flint (Dowswell *et al.*, 1996). These two populations were used as donors for streak resistance and led to the release of resistant inbreds for use in sub-Saharan Africa (Kim *et al.*, 1987).

The tropical mid-altitude populations, TZMSR-W and TZEMSR-W, are also good yielding germplasm sources for sub-Saharan Africa. The former is a late-maturing, white, semi-flint population, whereas the latter is an early-maturing white population that performed well in Nigeria, Cameroon and Zaire (Dowswell *et al.*, 1996).

Zimbabwean maize programme

Most of the maize production area in Africa lies within the mid-altitude subtropical environment and requires resistance to streak virus. The national maize programme of Zimbabwe developed some of the best maize germplasm materials from the open-pollinated varieties Southern Cross, Salisbury White and Hickory King for this production environment. The first commercial single-cross hybrid, SR52, was released in 1960. The three-way hybrids, R200, R201 and R205 are also very popular in Zimbabwe (Dowswell *et al.*, 1996). Additionally, CIMMYT's regional programme in Zimbabwe developed several improved populations and inbred lines for mid-altitude areas of sub-Saharan Africa (Dowswell *et al.*, 1996).

Highland transition-zone germplasm

CIMMYT is the major player in the development of improved germplasm for this ecology in eastern and southern Africa. Pool 9A from CIMMYT is the best germplasm source for this ecology. It is a late-maturing, white semi-dent population and is derived

from Kitale Synthetic II, Ecuador 573 and SR52. Another diverse germplasm complex adapted to this ecology was developed cooperatively by IITA and Cameroon's maize improvement programme from materials based on CIMMYT's Pool 9A, TZMSR (IITA), V301, V304 (Guatemalan), DeKalb 690 (US), SR52 and ZS206 (Zimbabwe) (Dowswell *et al.*, 1996).

Kitale highland germplasm

At the Kitale Research Station in Kenya, several breeding populations were assembled from the best local maize varieties, which mostly trace back to Hickory King. These populations, when crossed with Ecuador 573 and Costa Rica 76 (both Latin American accessions), resulted in significant yield increases. Two outstanding germplasm complexes, Kitale I and Kitale II, resulted from intercrosses of local materials with the above Latin American varieties. A variety-cross hybrid, H611 (K II × Ecuador 573), was released for commercial use. Ecuador 573 and Kenya Flat White are very useful sources to develop inbreds in Kenya and eastern Africa (Dowswell *et al.*, 1996).

Constraints to Maize Production in Sub-Saharan Africa

As in most developing countries, many of Africa's agricultural production constraints are a result of complex interactions of man-made and natural calamities. These include drought, infertile soils, insect pests and diseases, combined with lack of improved technology, and indifference of political support for agriculture (Gelaw, 1985; Byerlee and Jewell, 1997). Moreover, the colonial influence in most countries of the continent led to the production of cash crops – such as tobacco, coffee or tea – for export rather than food crops such as maize. Forty-seven countries with different ecological environments, colonial histories and an array of food staples comprise the African continent (Byerlee and Eicher, 1997). It is impossible to design a standard maize production package for such diverse ecologies. Different categories of farmers demand varieties or hybrids that best fit their needs, environmental conditions and subsistence management practices which, in turn, necessitate the development of ecologically specific varieties (Kim and Ajala, 1996). Overall, the major constraints to maize production in sub-Saharan Africa can be classified as environmental, technological, biological, socioeconomic and governmental (Efron, 1985; Gelaw, 1985; Eicher and Byerlee, 1997). However, the following discussion is mainly limited to the genetic (technological) constraints to maize production in sub-Saharan Africa.

The adoption of improved OPVs and hybrids in sub-Saharan Africa has been promising over the past decade, and an estimated 33–50% of maize area is planted with improved materials. However, the availability of these materials to small-scale farmers is patchy and ranges from 20% of maize area in Tanzania and Ethiopia to nearly 100% of the area in Zimbabwe (Byerlee and Heisey, 1996; Byerlee and Jewell, 1997). Moreover, the relative emphasis on improved OPVs versus hybrids varies from Central and West Africa to eastern and southern Africa. Although often inherently low-yielding, OPVs appeal to subsistence farmers because: (i) seed can be stored from year to year; (ii) non-availability, until recently, of hybrids for the lowland and mid-altitude tropics that predominate in this area; and (iii) the principal sources of improved tropical materials for this area have been mostly OPVs bred to provide yield

stability and food security. CIMMYT and IITA have developed several improved populations and hybrids suited to the major ecologies of sub-Saharan Africa, and the reader is referred to Gelaw (1985), Dowswell *et al.* (1996) and Byerlee and Heisey (1996) for additional details.

Overall, the main genetic constraints to yield improvement include: (i) inherently low-yielding OPVs grown on marginal soils; (ii) paucity of good source populations in the national programmes to derive high-combining inbreds; (iii) practice of inadequate and inappropriate breeding methodologies due to the lack of technical knowledge and/or facilities; (iv) improper and/or lack of seed production and maintenance facilities; and (v) pre- and post-harvest susceptibility to insects and diseases.

Maize Improvement Networks Operating in Africa

Although the National Agricultural Research Systems (NARSs) in sub-Saharan Africa have been instrumental in providing resource-poor, subsistence farmers with improved germplasm, they lack the resources necessary for continued and sustained research and training activities. Two of the IARCs, CIMMYT in Mexico and IITA in Nigeria, have been involved in the development of improved maize technology for resource-limited, smallholder farmers of developing nations and provide support to NARSs (Dowswell *et al.*, 1996). CIMMYT has an international mandate for maize research and conducts the largest public maize improvement programme in the world. Its major focus has been on the development of improved populations for use in the developing countries of the world. IITA's maize research has been mainly on developing appropriate improved maize germplasm and production technology in Western and Central Africa. Following on this lead by IITA, CIMMYT established a regional maize research station in Zimbabwe in 1985 (Dowswell *et al.*, 1996). According to Byerlee and Jewell (1997), an estimated 43% of the maize research budget of the IARCs was spent in Africa in the mid-1980s. Many US agricultural universities and the USDA have also been major players in the maize improvement networks for sub-Saharan Africa.

Given the subsistence nature of maize in Africa and the constraints of resources for smallholder farmers, IITA and the regional branches of CIMMYT have become important networks to develop a research pipeline to complement maize research at NARSs. The release within 3 years of semi-flint hybrids, MH17 and MH18, in Malawi by using dent materials from Malawi and flint materials from CIMMYT is an outstanding example of collaboration between Malawian and CIMMYT scientists, which reduced both the time to release and the cost to the national research programme (Smale, 1995). Byerlee and Heisey (1996) indicated that germplasm from the IARCs contributed to about three-quarters of the maize varieties released in Africa, although data on actual use are limited.

CIMMYT's extensive international testing trials in tropical environments indicated environmental similarities across several areas, leading to the concept of mega-environments (Paterniani, 1990). These mega-environments share climatic adaptation, length of growing season, occurrence of specific diseases and pests, and so on. Such environments can be extremely useful for testing germplasm sources. CIMMYT and IITA are instrumental not only in developing improved maize germplasm, but also in the training and education of researchers and farmers through workshops. IITA led the

development of maize germplasm with resistance to streak virus and tolerance to infestation by the parasitic witch weed, *Striga* (Kim *et al.*, 1985).

Recent biotechnological innovations have the potential to help research efforts of the NARSs in most countries of sub-Saharan Africa, particularly in combating insect pests and diseases. Genetic marker techniques can help identify and select resistant genotypes even in the absence of the disease or pests. NARSs can certainly benefit by collaborating with IITA, which has the research infrastructure, technology and personnel to provide training and conduct biotechnological research.

In the past 5 years, an informally developed US maize genome project, an outgrowth of the Maize Genetics Co-op, has provided detailed and extensive genetic linkage maps of maize. A wealth of maize genome information is available for the public on the Internet, and the Maize Database contains current knowledge about the maize genome and its expression. There are several web sites (e.g. www.nal.usda.gov) that can access this information from anywhere in the world.

One of the exciting areas of biotechnological applications in maize is to exploit genomic sequence data to efficiently and effectively utilize naturally occurring variation for agronomically important traits. Recently, John Doebley from the University of Minnesota proposed that once the nucleotide sequence diversity in a set of candidate genes for important traits is determined, this information can then be used to test whether specific DNA sequence polymorphisms are associated with variation in the phenotype for these traits. Consequently, we can pinpoint specific lines in the maize germplasm pool with the desirable variation, and also the regions of maize chromosomes where useful variation is most apt to be found. It is anticipated that such studies will eventually aid in understanding the distribution of genetic diversity within the maize genome.

Sub-Saharan African countries need to develop and promote strong and stable linkage with IITA and collaborate with neighbouring countries with similar environments to develop an improved maize production package for the subsistence farmers of the region. However, as Eicher and Byerlee (1997) indicated, African governments and donors will have to make an extended commitment to support research at IARCs and NARSs with focus on developing locally adapted, improved maize germplasm that can serve African farmers into the next century.

A Proposal for Broadening the Genetic Base of Maize in Sub-Saharan Africa

Background

Population improvement and inbred line development have been the major components of maize breeding programmes. The choice between the two is largely influenced by breeding objectives, available resources and time constraints; however, inbred line development is the major emphasis in private breeding programmes. Maize breeders have used several breeding methods to either improve existing populations or to derive new inbred lines for hybrid production. In sub-Saharan Africa, where OPVs still predominate on farms, the trend is gradually changing toward hybrids. A critical

evaluation of breeding strategies and selection methods is essential to broadening the genetic base and also to providing yield stability for the subsistence farmer.

In our view, the experience and knowledge gained from the research investment to widen the genetic base of temperate maize germplasm could provide the framework to broaden the germplasm base of tropical maize in sub-Saharan Africa. Analogously to the use of tropical germplasm for temperate maize improvement, elite temperate germplasm could be used to widen the sub-Saharan maize germplasm base. The major limitation of this approach is, of course, the susceptibility of temperate sources to tropical insect pests and diseases (especially viruses), in addition to the potential lack of adaptation to low-input, limited rainfall agriculture characteristic of sub-Saharan Africa.

CIMMYT and IITA have been conducting trials to identify and select temperate sources useful to improve tropical germplasm. Gracen (1986) summarized studies of tropical and sub-tropical CIMMYT topcrosses to the two then most widely used US dent inbreds, B73 and Mo17. The highest yielding combinations were Pool 24 (tropical late white dent) \times B73, and Pool 25 (tropical late yellow flint) \times B73. The best combining crosses included Population 21 (Tuxpeño-1) with both B73 and Mo17, and Population 43 (La Posta) \times Mo17. CIMMYT developed these germplasm pools and populations from extensive international testing. The most commonly used CIMMYT populations in Africa are Population 21, which combines well with both Mo17 and B73, Population 30 (Blanco Cristalino-2), Population 32 (ETO Blanco) and Population 43 (La Posta).

While proposing a comprehensive breeding system for African hybrid maize breeding programmes, Eberhart *et al.* (1988) stressed the importance of heterotic patterns in selecting germplasm to maximize population-cross performance. Because this performance determines the rate of improvement of the derived inbreds and hybrids, they expressed the view that the use of a superior common heterotic pattern among maize breeders across countries would facilitate the exchange of elite inbreds and lead to improved commercial maize hybrids. It was observed that excellent population-cross performance resulted from a Tuxpeño Dent with Caribbean Flint heterotic pattern. They also advocated multi-trait improvement, particularly during early generations because a large number of lines can be screened.

Over the years, CIMMYT has developed about 20 elite maize populations adapted to lowland tropics (Dowswell *et al.*, 1996). These materials, including lines and hybrids developed from them, can be good starting germplasm to derive inbred lines adapted to tropical African environments and to widen the sub-Saharan maize germplasm base.

Procedure to derive new inbred lines from elite exotic materials

Basically, any attempt to develop new inbred lines involves choosing suitable donor parental germplasm, continued inbreeding (sib-mating or selfing) with selection, topcross testing of the selected lines and identification of good inbred lines with high combining abilities. However, if elite exotic materials are chosen as source populations, we propose the following scheme to produce new lines. A scheme very similar to this is being followed at North Carolina State University. The time period can be reduced by half if two suitable growing environments (seasons) are available.

1. Grow F_1 hybrids between local and elite exotic materials. Make plant-to-plant crosses (sib-mate). Select the best plants at harvest with desirable traits (usually earlier maturity, insect, disease and lodging resistance, and yield potential) from the donor parent.
2. Grow F_2 ear-to-row progenies. Repeat as before to develop families.
3. Grow F_3 families. Repeat as before.
4. Continue the same procedures (about 5–6 sib-mating generations) with selection for resistances against insects and diseases and until phenotypically acceptable progenies are obtained. Then, self one or two generations with selection to derive S_1 or S_2 lines.
5. Produce topcrosses of these lines in isolation for combining ability. Use an adapted commercial hybrid, related line cross or another inbred (if available from a different heterotic group and adequately vigorous) as a tester.
6. Conduct replicated topcross yield trials in target environments. Select the best yielding topcrosses. Based on yield and other data, select the best lines for release as inbreds.

Goodman (1998b) outlined a scheme on how to maximize the favourable effects of a variable exotic source through incorporation of exotic germplasm into elite maize lines. He emphasized early topcross evaluation (individual F_1 s or F_1S_1 s topcrossed to elite lines) to identify the most promising fraction of a variable source population as quickly as possible and to concentrate line development efforts on that fraction. A similar procedure can be used to derive inbred lines from crosses of elite temperate or tropical materials (from Thailand and Brazil, for example) crossed with improved open-pollinated populations or lines developed at CIMMYT.

Recommendations for Future Maize Research

In our view, the major emphasis in sub-Saharan Africa should be toward the development of varieties and hybrids tolerant to drought, temperature extremes and improved resistance to economically important diseases, pests and parasites, especially to maize streak virus and *Striga*. Additionally, the development of early maturing varieties would expand the area planted to maize, particularly in the drier savannah. As we have indicated in this chapter, these objectives can be achieved with less cost and in a shorter time span by collaborative research efforts between the NARSs and the maize programmes of IITA and CIMMYT.

Another often ignored but important aspect is to pay attention to the needs of small-scale farmers. Low adoption of improved varieties in Africa and elsewhere is often due to lack of attention devoted to their needs. In our opinion, the farmers' role as the sole consumers of the technology should change to their active participation in generating the appropriate technology for their use. Researchers must acknowledge farmers' skills and innovations that have contributed to global agricultural developments and should understand their needs for future improvements of agricultural production. They should develop greater scientific respect for and collaboration with those who have gained the wisdom of generations of non-scientific farming (Haugerud and Collinson, 1990). Often one of their most pressing needs is protection from insect and rodent damage to stored grain.

Conclusions

Conventional maize breeding should continue to provide benefits to small-scale farmers of sub-Saharan Africa. In our view, development of early maturing, locally adapted, disease- and pest-resistant germplasm should provide yield stability and food security for subsistence farmers. Considerable progress has been achieved with IITA and CIMMYT research efforts in the area of developing disease-resistant maize germplasm. Promising preliminary results have been obtained from drought-tolerant germplasm from the IARCs to fight the effects of periodic drought stresses (Byerlee and Heisey, 1996). Drought-tolerant materials from CIMMYT were also more efficient in utilizing available soil nitrogen and performed well even in marginal soils. Although fertilizer consumption has risen in Africa, leading to production increases, the most suitable option for resource-limited subsistence farmers is the use of genetically improved high-yield-potential materials. In conclusion, as increasing population growth exerts pressure on land, genetic improvement of the breeding materials would be the single most valuable input for future maize yield increases in sub-Saharan Africa.

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10 The State of the Use of Potato Genetic Diversity

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Introduction

The potato (*Solanum tuberosum*) belongs to the family Solanaceae. Potatoes are grown in more countries than any other crop except maize, and, with an annual production approaching 300 million t, this crop is the fourth largest crop worldwide (after rice, wheat and maize) (Anonymous, 1998). China is the world's largest potato producer. Nowadays, in excess of one-third of the global potato output comes from the developing world, underlying the importance of potato as a source of food, employment and income in the developing world, whose countries are becoming integrated into the international potato trade of frozen French fries (chips), chips (crisps) and starch.

The yield potential of potato expected from an ideotype adapted to the northern hemisphere has been calculated as 100 t ha⁻¹. However, the actual world yield average for 1996 was 16.1 t ha⁻¹, while one of the highest national average yields (43.7 t ha⁻¹) was recorded in The Netherlands. Potato yields are affected by some major diseases and pests; lack of improved, locally adapted potato cultivars; limited access to chemical fertilizers; and a shortage of a high-quality planting materials (Ghislain *et al.*, 1997).

Late blight (caused by *Phytophthora infestans*) ranks first among constraints for potato production worldwide. Breeders in the northern hemisphere also consider in their programmes resistance to viruses (potato leaf roll luteovirus and potato virus Y potyvirus), cyst nematode (*Globodera pallida*), golden nematode (*G. rostochiensis*) and specific insect pests. Resistance to late blight, viruses, bacterial wilt (*Pseudomonas solanacearum*), cyst and root-knot nematodes (*Meloidogyne* spp.), and potato tuber moth (*Phthorimaea operculella*) are desired characteristics of new cultivars for the tropics. Tuber-bearing *Solanum* spp. have provided resistance genes for most diseases or pests affecting potato. Besides breeding for resistance to these biotic stresses, potato breeders aim to improve yield, adaptation and tuber quality (for a review, see Tarn *et*

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al., 1992). Genes from some wild and landrace genetic resources of potato have been used by potato breeders to improve these characteristics (Innes, 1992).

The aims of this chapter are as follows:

- To discuss the recent evolution of economically important potato species.
- To examine the nature and availability of genetic diversity within the group.
- To assess the utilization of the available genepool within breeding programmes.
- To look for the future needs of the crop.

Genetic Diversity and Resources Available within the Genepools of Potato

Hawkes (1990) indicated that there are 235 wild and cultivated potato species. Most of them are diploids, followed by tetraploids. The basic chromosome number (x) of potato is 12. A polyploid series occurs in the tuber-bearing *Solanum* species. Besides the diploid species ($2n = 2x$), there are seven species of triploid ($3x$), 27 tetraploids ($4x$) and three pentaploids ($5x$), each of which include cultivated species. Hexaploidy ($6x$) also occurs in addition to these ploidy levels in wild species. The most popular among the cultivated species are *S. tuberosum* ssp. *tuberosum* (adapted to long days) and *S. tuberosum* ssp. *andigena* (adapted to short days). Both subspecies are tetraploids with polysomic inheritance.

An endosperm dosage system known as endosperm balance number (EBN) (Johnston *et al.*, 1980) has influenced the speciation of polyploid forms from diploid *Solanum* species. The EBN was defined as a unifying concept to predict endosperm function in intraspecific, interploidy and interspecific crosses (Ortiz and Ehlenfeldt, 1992). Every *Solanum* species has an 'effective ploidy' (the EBN), which must be in a 2:1 maternal to paternal ratio in the endosperm for crosses to succeed. The EBN was determined for most *Solanum* species by crossing each with species of known EBN (Hanneman, 1994). Most North and Central American diploid *Solanum* species are 1EBN, whereas tetraploids are 2EBN and hexaploids are 4EBN. Conversely, most South American diploid species are 2EBN, whereas the polysomic tetraploids are 4EBN. Species of the same ploidy are isolated from each other by EBN, whereas gene-flow may occur between species of different ploidy but similar EBN. Crosses between species with different EBN could be made when one of the species produces $2n$ gametes (or gametes with the sporophytic chromosome number).

Most tuber-bearing *Solanum* species are relatively easy to cross and show little chromosome differentiation between their chromosomes. Accordingly, Ortiz (1998) indicated that the primary genepool of potato consists of old and modern tetraploid cultivars, tetraploid Andean landraces and tetraploid breeding populations. Diploid cultivars or breeding populations, diploid (2EBN) tuber-bearing wild species producing $2n$ gametes and hexaploid (4EBN) species also belong to this primary pool. The secondary genepool consists of disomic tetraploid species (2EBN) and diploid (1EBN) tuber-bearing *Solanum* species. These species may cross with the crop primary genepool after isolation barriers (mainly due to EBN) are overcome. The tertiary potato genepool consists of diploid (1EBN) non-tuber-bearing wild species of the series *Etuberosa* and other *Solanum* species. This tertiary genepool could cross with the primary potato

genepool via bridge species and assisted by special techniques such as embryo rescue.

Most diploid potatoes are self-incompatible due to a gametophytic system. Selfing occurs in tetraploid potatoes, but outcrossing rates vary from 0.10 to 0.74 (Brown, 1993b), which suggests that it would be possible to select for higher outcrossing rates to develop broad-base populations by natural pollination.

The International Potato Centre (CIP, Lima, Peru) holds one of the largest potato collections in the world (Table 10.1). In excess of two-thirds of this collection are cultivated genetic resources. Other important *ex situ* genebanks are the Commonwealth Potato Collection in the Scottish Crop Research Institute (Innes, 1992), the German–Dutch potato genebank of the Braunschweig Genetic Resources Center in Germany and the Center for Genetic Resources in The Netherlands (van Soest *et al.*, 1984; Mix-Wagner, 1996), the US Potato Introduction Project (Hanneman, 1989; Spooner and Bamberg, 1991) and the N.I. Vavilov Institute of Plant Industry in Russia (Budin, 1992). The importance of these *ex situ* genebank collections to preserve diversity of potato landraces has been illustrated by Huaman and Schmiediche (1991).

Table 10.1. Composition of landrace genetic resources held at CIP, and desired characteristics reported in this and other potato germplasm collections.

Species	Number	Characteristics	Origin
Cultivated landrace genetic resources			
Diploids			
<i>S. ¥ ajanhuiri</i>	10	Frost tolerance, bitterness	Bolivia, Peru
<i>S. goniocalyx</i>	48	Flavour, yellow flesh	Bolivia, Costa Rica, Peru
<i>S. phureja</i>	170	Lack tuber dormancy, high dry matter content, resistance to late blight, PVY	Bolivia, Colombia, Ecuador, Mexico, Peru
<i>S. stenotomun</i>	268	Resistance to PVY	Argentina, Bolivia, Colombia, Ecuador, Peru
Triploids			
<i>S. ¥ chaucha</i>	97	Flavour	Argentina, Bolivia, Ecuador, Peru
<i>S. ¥ juzepczukii</i>	31	Frost tolerance, bitterness	Argentina, Bolivia, Peru
Tetraploid (<i>S. tuberosum</i>)			
ssp. <i>andigena</i>	2644	Resistance to many pests and diseases (e.g. late blight, PVX, PVY, nematodes)	Argentina, Bolivia, Chile, Ecuador, Guatemala, Mexico, Peru, Venezuela
ssp. <i>tuberosum</i>	48	Long-day adaptation, tuber appearance, disease resistance (e.g. PVX)	Argentina, Bolivia, Ecuador, Guatemala, Peru
Pentaploids			
<i>S. ¥ curtilobum</i>	11	Frost resistance, bitterness	Argentina, Bolivia, Peru, Venezuela
Wild genetic resources			
93 wild species	1500	Resistance to many pests and diseases, tolerance to abiotic stresses	Bolivia, Brazil, Chile, Colombia, Ecuador, Mexico, Paraguay, Peru, Venezuela

Sources: Hoopes and Plaisted (1987); Jellis (1992); Huaman *et al.* (1997).

PVX: potato virus X.

PVY: potato virus Y.

However, DNA-marker analysis reveals significant genetic differences between accessions preserved in the genebank and those re-collected in the original sites (del Rio *et al.*, 1997b). It seems that a relatively fast evolution occurs in the wild environment owing to more genetic recombination in each season than in the *ex situ* genebanks, in which this recombination takes place only during seed increase. Re-collection of potato genetic resources in areas of host plant–pathogen coevolution may be an alternative approach to obtain desired genetic resources for resistance breeding.

Resistance to specific biotic stresses in wild tuber-bearing *Solanum* species does not appear to be evenly distributed throughout America. For example, North American species are more resistant to pests such as green peach aphid (*Myzus persica*), potato aphid (*Macrosiphum euphorbiae*), potato flea beetle (*Epitrix* spp.) and potato leafhopper (*Empoasca fabae*) (Flanders *et al.*, 1997). Latitude and altitude of the collection site affect insect resistance in wild tuber-bearing *Solanum* species. Species collected in hot and arid areas are associated with resistance to Colorado potato beetle (*Leptinotarsa decemlineata*), potato flea beetle and potato leaf hopper (Flanders *et al.*, 1992).

Accessing *Solanum* Germplasm from the Distinct Potato Genepools

A compatible interspecific cross permits the development of a broad base breeding population. Ploidy manipulations with haploids and $2n$ gametes (Fig. 10.1) offer the best option for incorporation of diploid genetic resources into the cultivated tetraploid genepool (Peloquin and Ortiz, 1992). Mendiburu and Peloquin (1976, 1977a,b) defined the terminology and the method for the systematic utilization of ploidy manipulations for potato breeding. The potato has been regarded as a crop species whose chromosome sets can be easily managed (Peloquin *et al.*, 1989a). The most common germplasm enhancement strategy in potato involves species, haploids, $2n$ gametes and the EBN (Peloquin *et al.*, 1989a). The species are the source of genetic diversity, haploids provide a method for ‘capturing’ the diversity, and $2n$ gametes and EBN are involved in an effective and efficient method of transmitting diversity to cultivars (Jansky *et al.*, 1990). This approach in potato breeding has been reviewed recently by Ortiz (1998).

Pollen with 24 chromosomes (or $2n$ pollen) from diploid species results mostly due to a recessive meiotic mutant known as parallel spindles (*ps*), which appears to be ubiquitous among tuber-bearing *Solanum* species (Ortiz, 1994). Similarly, $2n$ eggs (with 24 chromosomes) are mostly controlled by another recessive meiotic mutant known as omission of second division (*os*) in diploid species (Ortiz and Peloquin, 1991). Haploids (or sporophite with the gametic chromosome number, i.e. $2n = 24$) of the tetraploid potato are easily obtained through interspecific interploidy $4x-2x$ crosses. Tetraploid seed parents (either from *S. tuberosum* ssp. *tuberosum* or ssp. *andigena*) are crossed with a *S. phureja* ‘pollinator’. After such a cross, maternally derived haploids (with 24 chromosomes) are obtained through parthenogenesis (Peloquin *et al.*, 1996). These haploids have 2EBN and are easily crossed with diploid 2EBN species with the desired characteristics. The 2EBN haploid-species hybrids producing $2n$ gametes are crossed directly with 4EBN tetraploid cultivars or advanced selections to obtain 4EBN tetraploid hybrids, or with other 2EBN diploid stocks for further breeding at the diploid level (Ortiz *et al.*, 1994).

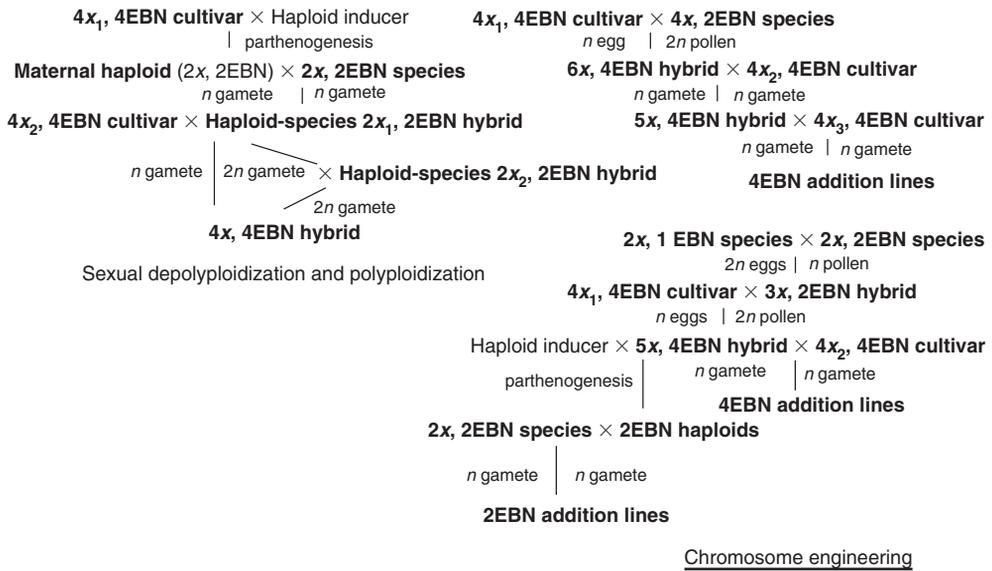


Fig. 10.1. Ploidy manipulations and chromosome engineering for introgression or incorporation of wild and landrace genetic resources of tuber-bearing *Solanum* species into the cultivated potato gene pool.

Sources: Bo Fu *et al.* (1996); Schmediche (1997).

Evolutionary History of Potato: Genetic Bottlenecks in Specific Locally Adapted Germplasm

Cultivated potatoes evolved from wild tuber-bearing *Solanum* species in the high plateau of the Andes between Peru and Bolivia (Simmonds, 1995). The crop was domesticated by ancient farmers in this area owing to its tubers, which contain carbohydrates, proteins, minerals and vitamin C. The Andean tetraploid cultivated species arose by bilateral sexual polyploidization ($2x \times 2x$ cross) between *S. stenotomum* and an unidentified wild species (Grun, 1990). Later, $2n$ pollen of several diploid species fertilized n eggs of *S. tuberosum* spp. *andigena*, which led to extensive gene incorporation from wild or cultivated diploid species into the cultivated tetraploid gene pool of the Andes.

The potato was brought to Europe by the Spaniards in the 16th century. The crop was first harvested at New Hampshire in North America in the early 1700s. In the mid-18th century, potato was extensively grown in England and Ireland, although the crop had been first planted in the late 16th century. Mass selection of early-maturing clones with big tubers among seedlings derived from open pollination was the method to obtain potato germplasm adapted to long days. Brown (1993a) provides a recent review of the adoption of potato as a food in the northern hemisphere.

Late blight hit Ireland in the mid-1840s, destroying most of the potato crop. As a result, 1 million people died due to famine and another 1 million left Ireland. Many researchers have suggested that *S. tuberosum* ssp. *tuberosum* from Chile could have been

the source of the new germplasm adapted to the long days of the northern hemisphere, especially after the late blight outbreak of the 19th century. However, Simmonds (1995) indicates that total crop destruction was unlikely and that perhaps there was a substantial introgression of Chilean germplasm into the cultivated genepool adapted to the northern latitude. One of these exotic accessions was 'Rough Purple Chili', which is in the pedigree of many potato cultivars (Hawkes, 1979).

In the early years of potato breeding, seedlings derived from open pollination were grown for further selection of the most promising clones. With this method, today's number one cultivar of North America 'Russet Burbank' was developed more than 100 years ago (Fig. 10.2). It was assumed initially that such open-pollinated-derived offspring was the result of selfing (Glendinning, 1979; Plaisted and Hoopes, 1989). However, a recent investigation with genetic markers (Douches *et al.*, 1991) suggests a hybrid origin of some of these selected offspring that became new cultivars in the USA.

The genetic structures of *S. tuberosum* ssp. *andigena* from the Andes and ssp. *tuberosum* from Chile were investigated with the aid of isozyme markers (Ortiz and Huaman, unpublished results). These isozymes have been studied in detail in North American cultivars and breeding lines (Douches and Ludlam, 1991; Douches *et al.*, 1991). Further analysis indicated that allozyme frequency changes were not always due

1851: Rev. Goodrich obtained '**Rough Purple Chili**' along with another seven South American landraces via Panama

|
| open pollination

'**Garnet Chili**'¹ selected by Rev. Goodrich

|
| open pollination

1861: long white tuber cultivar '**Early Rose**'¹ selected by Albert Breese

|
| open pollination

1876: Luther Burbank selected a long white potato¹ derived from a seedball found in his mother patch

|
| sport

1914: '**Russet Burbank**' released as new potato cultivar

1990s: 'Russet Burbank' still grown on c. 40% of North American potato acreage

Fig. 10.2. The development of North America's most popular potato cultivar 'Russet Burbank' traces back to exotic germplasm and three generations of selection of hybrid offspring derived from open pollination.

Source: Plaisted and Hoopes (1989).

¹Hybrid origin as revealed by genetic markers (Douches *et al.*, 1991).

to genetic drift, but also to directional selection of a quantitative trait locus affecting an agronomic or quality characteristic, which is linked to a specific isozyme locus, thereby reflecting the genome manipulation by potato breeders (Ortiz, 1999). These allozyme surveys among the potato gene pools suggest that a 'genetic bottleneck', as measured by the number of allozymes per locus, occurred only in certain chromosomes of North American cultivars (Ortiz and Huaman, unpublished results). In contrast, some allozymes not observed in the farmers' selections from the Andes or Chile were identified in the North American cultivars. This result confirmed that potato breeders have incorporated in their improvement programmes genes from wild and other primitive cultivated tuber-bearing *Solanum* species.

Cytoplasm Diversity

Potato breeders prefer *S. tuberosum* ssp. *tuberosum* cytoplasm in crosses with *S. tuberosum* ssp. *andigena* because a tuber yield advantage appears to be associated with the former, especially in northern latitudes (Plaisted, 1977). However, genetic–cytoplasmic male sterility interactions control male sterility in potato (Iwanaga *et al.*, 1991). This male sterility results from the interaction between sensitive factors in the cytoplasm of one species and nuclear genes from another species. There are some species whose cytoplasms are not sensitive, or other species that do not possess genes that interact with sensitive cytoplasm. Ortiz *et al.* (1993b) indicated that tetraploid cultivars differ in their cytoplasm as determined by investigating male sterility in their derived offspring from interspecific crosses.

Early analysis of chloroplast DNA with restriction endonucleases demonstrated that cytoplasm of most cultivated species, except *S. tuberosum* ssp. *tuberosum*, derived from *S. stenotomum* (Hosaka *et al.*, 1984). Extensive research has revealed wide chloroplast diversity in the Andean potatoes (Hosaka and Hanneman, 1988b). Intraspecific chloroplast variation appears to be common in both cultivated and wild species. The variation range of cultivated diploid species corresponds to that of the tetraploid species, which indicated that chloroplast diversity at the tetraploid level originated many times from the diploid populations. A recent investigation determined that the A chloroplast genome arose in central Peru and the T chloroplast genome originated on the Bolivia–Argentina boundary (Hosaka, 1995). Based on this analysis of chloroplast genome, Hosaka (1995) proposed that potatoes were wild species differentiated from time to time and place to place to form an 'ancestral species' complex. Consequently, a wide chloroplast diversity among Andean tetraploid potatoes was formed through sexual polyploidization, and the limited diversity found in Chilean tetraploid potatoes was derived from further selection from this tetraploid Andean gene pool.

The cultivars 'Garnet Chili' and 'Early Rose' (Fig. 10.2) have the same T type as Chilean *S. tuberosum* ssp. *tuberosum*, while the old European cultivar 'Myatt's Ashleaf' has a type A chloroplast genome similar to *S. tuberosum* ssp. *andigena* (Hosaka and Hanneman, 1988a). This finding and other surveys of chloroplast diversity in European tetraploid cultivars (Waugh *et al.*, 1990; Powell *et al.*, 1993) confirm the early introduction to the northern hemisphere of *S. tuberosum* ssp. *andigena* followed by the introduction of *S. tuberosum* ssp. *tuberosum* germplasm after the late blight

epidemics. Most modern Japanese cultivars have a T chloroplast genome, although some cultivars possess a W chloroplast genome derived from *S. demissum*, and very old cultivars an A chloroplast genome (Hosaka, 1993). These results confirm the similar pattern of introduction of potato cytoplasm in the northern hemisphere.

Genetic Diversity in Breeding Programmes

Cross-breeding of potato started after the late blight epidemics, although selection from open pollinated offspring was still performed until the 20th century. Interspecific crosses were made about 1850 (Hawkes, 1979) – however, systematic utilization of wild species in potato breeding did not begin until the 20th century (Simmonds, 1995). Wild species were crossed to different breeding stocks or cultivars, and their selected hybrid offspring backcrossed to the recurrent cultivar parent(s). Table 10.2 lists the most important wild and landrace tuber-bearing *Solanum* genetic resources used during this century to develop modern cultivars in the northern hemisphere. Despite the wealth of genetic resources available for potato breeding, only a few species have been included in the genetic improvement programmes. These species were chosen to introgress resistance genes into the tetraploid cultivated gene pool of North America and Europe (Ross, 1986; Plaisted and Hoopes, 1989). Extra genetic variation was brought into this gene pool together with the chromosomes segments bearing the introgressed gene(s) of interest.

Co-ancestry analyses have been proposed in tetraploid potato cultivars to determine their genetic relationships and inbreeding based on potato pedigrees (Mendoza and Haynes 1974a; Glendinning, 1997). This analysis suggested a narrow genetic base in US cultivars (Mendoza and Haynes, 1974b). Furthermore, Douches *et al.* (1996) reported that genetic yield potential has not improved among the North American cultivars released in the 20th century. Likewise, phenotypic diversity cultivars based on tuber characteristics among selected cultivars do not appear to reflect the year of cultivar release (Fig. 10.3), which might suggest erratic changes owing to breeders' selection during the 20th century. None the less, breeding gains have been reported for chip-

Table 10.2. Most important wild and landrace tuber-bearing *Solanum* genetic resources used in crop breeding of modern potato cultivars in the northern hemisphere.

Ploidy	Europe	North America
Diploid	<i>S. chacoense</i> , <i>S. commersonii</i> <i>S. maglia</i> , <i>S. microdontum</i> , <i>S.</i> <i>phureja</i> , <i>S. sparsipilum</i> , <i>S. vernei</i> , <i>S. verrucosum</i>	<i>S. berthaultii</i> , <i>S. chacoense</i> , <i>S. kurtzianum</i> , <i>S. maglia</i> , <i>S. microdontum</i> , <i>S. phureja</i> , <i>S. raphanifolium</i> , <i>S. spegazzinii</i> , <i>S. stenotomum</i> , <i>S. toralapanum</i> , <i>S. vernei</i>
Tetraploid	<i>S. acaule</i> , <i>S. stoloniferum</i> , <i>S. tuberosum</i> spp. <i>andigena</i>	<i>S. acaule</i> , <i>S. fendleri</i> , <i>S.</i> <i>tuberosum</i> spp. <i>andigena</i>
Hexaploid	<i>S. demissum</i>	<i>S. demissum</i>

Sources: Ross (1986); Plaisted and Hoopes (1989).

processing characteristics in this cultivated North American tetraploid germplasm (Douches *et al.*, 1996), especially after 1960, when attention was given by breeders to potato-chip quality (Love *et al.*, 1998). The release of the cultivar ‘Lenape’ in 1967, which was withdrawn due to its amount of tuber glycoalkaloids, marked the beginning of a sustained increase in tuber solids in most breeding programmes of North America (Love *et al.*, 1998). ‘Lenape’ has *S. chacoense* in its pedigree, and has been the ancestor of ‘Atlantic’ and ‘Snowden’, two of the most important processing cultivars in the North American market. These results also demonstrate that problems associated with tuber glycoalkaloid content could be overcome through conventional cross-breeding in potato.

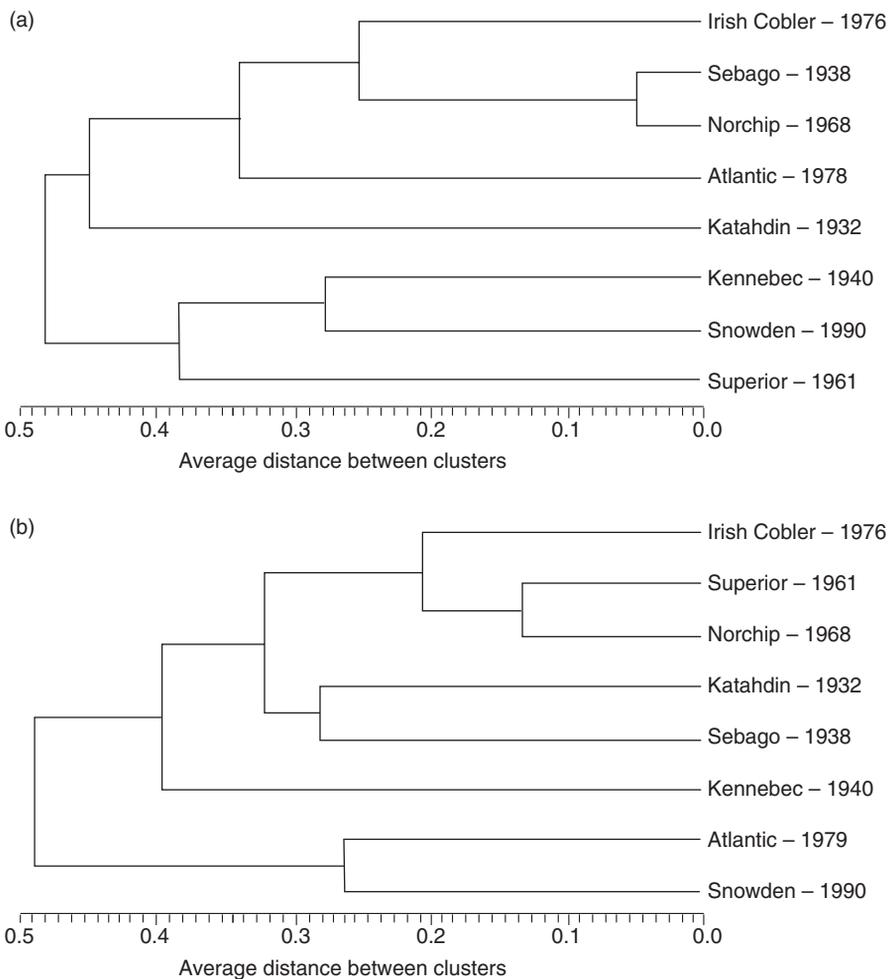


Fig. 10.3. Dendrogram of tetraploid North American potato cultivars based on tuber characteristics recorded in Michigan (a) or Idaho (b). Data for average linkage cluster analysis taken from Douches *et al.* (1996) and Love *et al.* (1998), respectively.

Greater genetic advance for tuber yield may be expected from enhanced genetic diversity in the breeding population. However, maximum heterozygosity appears to be more important in $4x \times 4x$ crosses between adapted breeding lines than in adapted–non-adapted crosses (Bonierbale *et al.*, 1993). As suggested by Amoros and Mendoza (1979), heterosis for yield depends on heterozygosity, but the parental material should be first selected for adaptation.

Different genetic marker systems based on protein or DNA electrophoresis are available to distinguish commercial cultivars and to assess polymorphism in potato (Douches and Ludlam, 1991; Hosaka and Hanneman, 1991; Görg *et al.*, 1992; Hosaka *et al.*, 1994; Demeke *et al.*, 1996; Provan *et al.*, 1996a,b; Sosinski and Douches, 1996; Schneider and Douches, 1997; Kim *et al.*, 1998). Some of these marker systems have demonstrated the important role of wild potato species and exotic germplasm in the development of modern *S. tuberosum* cultivars (Powell *et al.*, 1991).

Utilization of Exotic Landrace and Wild Germplasm in the Northern Hemisphere

Researchers from North America and Scotland developed independently two populations derived from *S. tuberosum* ssp. *andigena* adapted to long-day environments since the 1960s (Glendinning, 1979; Plaisted, 1982). This material has been named as Neotuberosum and provides new sources of adapted genetic resources with desired characteristics to potato breeding programmes of the northern hemisphere. For example, 50% of the genetic composition of the US cultivar ‘Rosa’ derives from this Neotuberosum germplasm (Plaisted *et al.*, 1981). Similarly, long-day-adapted populations of the cultivated diploid species *S. phureja* and *S. stenotomum* were bred in Scotland and the USA. This germplasm adapted to long-day temperate environments has also performed well under the short photoperiods of the tropics (Haynes and Mendoza, 1977; Plaisted *et al.*, 1987).

Selection for tuberization under long days improved the adaptation to the northern hemisphere of cultivated diploid and tetraploid Andean potatoes. In this regard, Fukumoto *et al.* (1991) indicated that selection for adaptation of Andean tetraploid germplasm followed by hybridization with adapted northern germplasm gave a greater rate of improvement in yield than early hybridization between unadapted and adapted germplasm followed by selection for adaptation. Conversely, Jacobsen and Jansky (1989) observed no apparent differences in tuberization response between haploid-species hybrids derived from selected and unselected wild diploid species parents. These researchers reported that some wild diploid species were better than others in producing hybrids that tuberize, whereas there were no differences in the breeding value for this characteristic between haploid parents.

Landraces and *In Situ* Evolution in the Andes

Isozyme surveys revealed that most of the potato genotypic diversity that exists in Cusco (Peru) appears to be between rather than within populations (Brush *et al.*, 1995). This genotype endemism indicates the role of the genotype as the unit for pre-

erving landrace populations. In contrast, the majority of allelic diversity was contained within geographical and landrace populations (Zimmerer and Douches, 1991). Common parentage, shared introgression and high rates of seed–tuber exchange explained these results. These findings suggest that Andean farmers are able to keep most of the potato genetic diversity in their small landholdings.

In situ conservation of cultivated potato genetic resources may be required because econometric analysis suggests that adoption of high-yielding cultivars by Andean farmers in Peru leads to a reduction in but not complete loss of diversity (Brush *et al.*, 1992). Furthermore, insect pollination between cultivated and wild species facilitates the ongoing evolution of the potato in the Andes (Johns and Keen, 1986). Electrophoretic surveys have confirmed this considerable geneflow between diploid, triploid and tetraploid Andean cultivated species (Quiros *et al.*, 1992) or between weedy and cultivated diploid species (Rabinowitz *et al.*, 1990). This was not surprising because botanical seed propagation has been used for disease elimination, stock rejuvenation and generation of new cultivars, despite the fact that Andean farmers also preserve potato genetic diversity by clonal propagation of tubers. Hence, as suggested by Quiros *et al.* (1992), ‘Andean potatoes form a large and plastic genepool amplified and renovated by outcrossing followed in some cases by human selection of desirable genotypes’.

Breeding Potato for Marginal Environments

Adaptation of potato to stressful environments that limit crop performance has been the focus of the breeding programme at CIP. High and low temperature, humidity or drought, and host susceptibility to pests or diseases are among the major constraints for potato production in some agro-ecozones of the developing world. CIP strategy to breed for tolerance or resistance to these stresses and develop locally adapted improved germplasm was based on the concept that the commercial value of a clone depends on genes for adaptation, yield *per se* and resistance to pests and diseases (Mendoza and Rowe, 1977). Population improvement in a highly heterozygous and heterogeneous wide-based germplasm, which was derived from wild or landrace genetic resources and commercial cultivars, has been the breeding tool for genetic enhancement at CIP (Mendoza, 1989). In this way, desired genes or genetic combinations that would be at low frequency or in small segments of the potato genepool were incorporated into tetraploid breeding materials. As a result of this work, advanced tetraploid breeding populations with resistances to pests and diseases were developed for the cool and warm tropics (Golmirzaie *et al.*, 1991). Rapid progress in resistance breeding at CIP depended on efficient screening procedures and high heritability of the characteristic. From these advanced materials many new tetraploid cultivars have been released in the developing world (Mendoza, 1992). The most recent releases combine resistance to two or three stresses.

Diploid potato germplasm was also developed by CIP breeders (Watanabe *et al.*, 1994). This diploid germplasm, which was derived from haploids of tetraploid cultivars or advanced selections, and diploid wild or cultivated species possess specific resistances, acceptable agronomic and tuber characteristics, and $2n$ pollen to transfer the desired gene(s) to the tetraploid level (Ortiz *et al.*, 1994). These selected diploid stocks are another important source for widening the genetic base of potato breeding.

Potato Improvement Networks in the Developing World and Crop Genetic Enhancement

Cooperative research networks in the developing world have been an important partner for CIP success in the genetic betterment of the potato crop. Such networks are, among others, Programa Andino Cooperativo de Investigación en Papa (PRACIPA), Programme Régional de l'Amélioration de la Culture de la Pomme de Terre et de la Patate Douce en Afrique Centrale et de l'Est (PRAPACE), Programa Regional Cooperativo de Papa (PRECODEPA) in Central America and the Caribbean, and Programa Cooperativo de Investigaciones en Papa (PROCIPA) in South America southern cone. Another important network that brings users into the research process is Users' Perspective with Agricultural Research and Development (UPWARD) in Asia. All these networks have received technical support from CIP.

The history of CIP-24 provides an example of research partnership without borders for germplasm exchange and improvement (Bo Fu *et al.*, 1996). Chinese farmers today grow CIP-24 in more than 250,000 ha (Schmiediche, 1997). This cultivar was bred in Argentina with wild and cultivated genetic resources assembled in the northern hemisphere (Fig. 10.4). This success story shows the importance of free availability of potato genetic resources as well as breeders' cooperation for the genetic betterment of the crop.

Cooperation also exists among potato genebank curators. They have formed the Association of Potato Intergenebank Collaborators or APIC (Bamberg *et al.*, 1995), which holds in excess of 13,000 accessions (Huaman, 1998). International, regional and national genebanks are participating in APIC to address common problems and facilitate efficient management of potato genetic resources from a global perspective. APIC has made progress by developing joint passport and evaluation databases, coordinating collecting efforts, preserving germplasm with backup storage, and exchanging technical information on genebank management and in the free but safe movement of potato germplasm. Since 1996, 11 European genebanks are cooperating on the EU project 'Potato genetic resources, including preservation, characterization and use of secondary potato varieties for ecological production systems in Europe' (Schuler and Hoekstra, 1997).

Late blight still remains a top priority in potato breeding, and recently has been the focus for international collaboration among researchers. A Global Initiative on Late Blight (GILB) was launched in March 1996 with participants from 19 nations of Africa, America, Asia and Europe, and CIP. This GILB stimulates, integrates and coordinates research and development on late blight. As a global network, it also assists in developing common efforts that will require funding. For example, researchers of the GILB are studying the genotype \times environment interaction for host response to late blight to determine whether resistance to this disease shows stability across sites.

Outlook: Broadening the Genetic Base of Potato Production via Evolutionary Breeding and Biotechnology

Despite advances in introgression or incorporation of wild species and landrace germplasm in potato breeding populations, new approaches are needed to enhance the

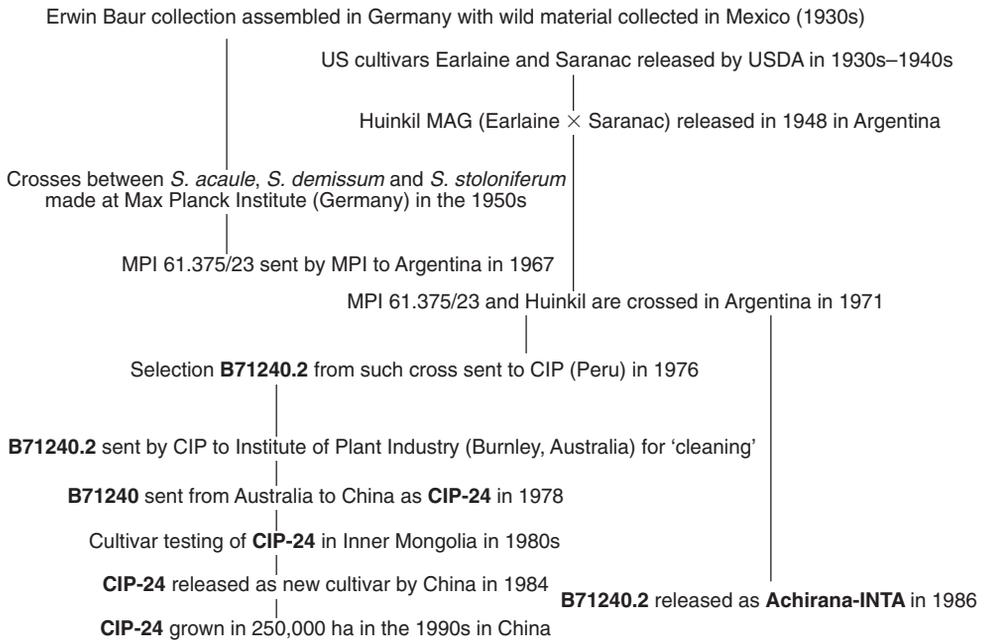


Fig. 10.4. Germplasm sources and development of B-71240.2 (also known as ‘Achirana-INTA’ or CIP-24), a photoperiod-insensitive, early-maturing cultivar with resistance to PLRV, some resistance to late blight, and tolerance to Al. B-71240.2 has been released as a cultivar in 12 further tropical or subtropical countries.

Sources: Peloquin *et al.* (1989a,b); Ortiz (1998).

MPI: Max Planck Institute. CIP: International Potato Centre.

utilization of these genetic resources in the betterment of the cultivated potato genome. Evolutionary crop breeding should be pursued in potato to widen the genetic base of the cultivated germplasm. In this breeding scheme, heterozygous wild species and landraces are the source of allelic diversity, which should be incorporated into locally adapted populations. Owing to the importance of non-additive gene interaction in tetraploid potatoes, selection for specific combining ability (SCA) on segregating populations should result in high-yielding germplasm. This concept of SCA considers both the cross combination and the specific individual within the cross, i.e. outstanding hybrids should be selected from the best crosses.

A true potato seed synthetic cultivar from open pollination may broaden the genetic base of crop production in potato (Ortiz, 1997). Selected tetraploid and diploid parental genotypes, based on their SCA, may be chosen for isolated polycrosses to obtain tetraploid offspring via unilateral or bilateral sexual polyploidization (Ortiz, 1998). Likewise, synthetic breeding populations derived from these polycrosses could be shared with other breeders, who will select in cooperation with their local farmers promising genotypes for further cultivar release. The participation of farmers in the selection process requires that an interesting amount of variation still exists in the

breeding population. Farmers' selection within adapted germplasm may be required for cultivar development in some regions because tuber yield *per se* in optimum environments seems to be a poor indicator of acceptability (Prain *et al.*, 1992), or sometimes breeders' and farmers' choices diverge (Thiele *et al.*, 1997). For example, culinary quality influences choice of new germplasm by farmers and consumers.

A core collection of *Solanum* species will improve the utilization of *Solanum* genetic resources in potato breeding. This core collection must contain chosen wild and cultivated accessions representing with minimum redundancy the genetic variability of the whole tuber-bearing *Solanum* germplasm and closely related non-tuber-bearing *Solanum* species (Ortiz, 1998). CIP has been developing a core collection of Latin American landraces using hierarchical classification based on their taxonomic species, ecogeographical origin, morphological characteristics, molecular markers and host response to diseases and pests (Huaman, 1998). Recently, CIP scientists have defined a core sub-set of *S. tuberosum* ssp. *andigena*, which contains 306 farmers landraces (Huaman *et al.*, 1999). The number of accessions included in the core was determined primarily by the square root of the number of accessions where *andigena* was collected (Huaman *et al.*, 2000a). A phenogram was constructed from the descriptor data using a matching coefficient and the unweighted pair group method using arithmetic averages. Accessions were retained in each cluster considering data on resistance to diseases and pests, dry matter content and number of duplicate accessions identified in the original collection. Allozyme frequencies validated the sampling procedure for this core collection (Huaman *et al.*, 2000b). The most frequent allozymes in the core collection were those observed in the entire collection, and their frequency distributions were homogeneous for most loci. Core sub-sets for other cultivated species will be based on sampling with DNA markers.

There are several cross-breeding methods to incorporate most of the genetic resources into potato breeding populations (Fig. 10.1). Nevertheless, protoplast fusion (or somatic hybrids) offers another means for asexual interspecific gene transfer in potato breeding (Hegelson, 1989). Likewise, genetic engineering provides a source of new alleles, especially for resistance breeding, in potato.

Molecular maps based on DNA and biochemical markers have been developed in potato (Bonierbale *et al.*, 1988; Gebhardt *et al.*, 1989, 1991; Freyre *et al.*, 1994; Eck *et al.*, 1995; Jacobs *et al.*, 1995). The number of genetic markers, available for mapping and assisted breeding, makes potato one of the most fully covered plant genomes (Tanksley *et al.*, 1992). A Solgenes database may be accessed through the World Wide Web interface (<http://probe.nalusda.gov:8300/cgi-bin/browse/solgenes>) maintained by the National Agricultural Library in Beltsville (Maryland, USA).

Genetic-aided analysis with molecular markers proved that quantitative variation for many complex characteristics was under polygenic control. Likewise, resistance gene clusters have been located in chromosomes 5 and 11 after mapping major resistance genes to similar or close chromosome segments. DNA markers may assist gene introgression into breeding pools. Marker-aid selection could facilitate breeding for some quantitative characteristics. However, some markers linked to these characteristics are inconsistent across populations and environments (Bonierbale *et al.*, 1993; Ortiz *et al.*, 1993a; Freyre and Douches, 1994). Hence, candidate markers for assisted selection must be validated in independent populations and across environments.

The lack of common markers among different populations also indicates that

potato breeders have been able to develop improved germplasm by manipulating distinct chromosome regions in their respective populations. This finding suggests that genetically enhanced populations may be developed in potato with the aid of DNA markers by combining specific chromosomal regions controlling the desired characteristic(s). One of the most important targets will be pyramiding available resistance genes to pests and diseases with the aid of these DNA markers in broad-base breeding populations.

Broadening the genetic base of potato with locally adapted, pest- and disease-resistant germplasm will ensure the sustainable and environment-friendly production of this crop. However, as demonstrated by the allozyme surveys reported earlier (Ortiz, 1999), the need for broadening the genetic base in potato may be for specific chromosomes or regions within chromosome arms.

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11 The State of the Use of Cassava Genetic Diversity and a Proposal to Enhance it

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Introduction

Cassava is a perennial arbustive plant cultivated for its tuberous roots and, together with its wild relatives, comprises the widely diverse genus *Manihot*, found across the tropical zones of the American continent. Cassava ranks fifth in the production of world food crops, after maize, rice, wheat and potato. In 1998, the production of fresh roots was estimated at 166 million t (Mt) produced in 92 countries. The largest production was in Africa (51%), followed by Asia (29%) and South America (19%). Five countries produce more than 15 Mt each: Nigeria, Brazil, Thailand, Democratic Republic of Congo and Indonesia (FAO, 1998a).

The areas of production are in the tropical zones where annual rainfall exceeds 600 mm and the mean temperatures 13°C (Raffaillac, 1996). Cassava thrives in light and drained soil, rich in potassium. Nitrogen tends to favour the development of aerial parts, and the presence of endomycorrhiza favours phosphorus nutrition. Cassava tolerates a low soil pH (Howeler, 1991) and long dry seasons (El-Sharkawy, 1993). These characteristics confer adaptation to marginal areas where cereal crops are in decline, as in southern Africa.

Cropping and production systems based on cassava are very diverse. The major part of world production is obtained under traditional cropping systems, with little or no inputs and frequent intercropping practices. Agroindustrial production complexes are rare but cash cropping is also practised.

Cassava can produce large quantities of dry matter under optimal conditions: the total biomass at 12 months can reach 45 t in the south of Côte d'Ivoire, for example. The potential annual yield has been estimated at 30 t of dry matter per hectare (Cock, 1985) and some newly bred cultivars come close to this yield (Raffaillac, 1996). Farmers often grow cassava after other staple food crops because it can produce in soils where other plants cannot.

Cassava production is mainly for human consumption. Only in Asian countries such as Thailand, Indonesia, China and Vietnam is most of the crop produced for

animal feed and industry. International trade accounts for only 11% of the world production. Thailand alone produces 81% of these exports, Indonesia 10% and China 6%.

Some cultivars have 'sweet' flesh in the roots and can be consumed directly after boiling, while others have a 'bitter' flesh and need a specific process to become edible (McKey and Beckerman, 1996). The bitterness is due to cyanhydric acid liberated, after a wound, from cyanoglucosides contained in variable amounts according to the cultivar and environment. Various processes, known from antiquity by the Amerindians and transmitted to Africans, allow the detoxification of the roots of high cyanogenic cultivars. Used separately or in combination, processes such as peeling, crushing, slicing or grating, water expressing, decanting, sun or smoke drying or frying, fermenting by soaking in water, heaping, stacking and boiling or steaming can reduce cyanhydric acid, which is water soluble and volatile. These processes lead to a variety of products for direct consumption or for short- or long-term storage.

Cassava produces a starch appreciated by nutritionists for its excellent digestibility. Cassava roots are low in proteins. Young leaves, rich in proteins, vitamins and minerals are consumed in northeast Brazil as well as in some West and Central African countries. Following recent studies in Brazil, they are now also added as a dry powder to infant foods (Motta *et al.*, 1994).

Research activity in cassava has been relatively scarce, although early work on the selection of clones of cassava dates to 1899 in the Brazilian state of Bahia (Zehntner, 1919). Various breeding programmes were started in the 1930s in Indonesia, Africa, Madagascar, India and Brazil, including the use of wild species. However, with a few exceptions, new cultivars have not had success comparable with improved cultivars of other major food crops. Yet diseases, epidemics and changes in cropping systems imposed upon farmers by the scarcity of arable lands in some areas add to the challenges that could be addressed by new varieties.

Recent work shows that enormous diversity exists for cassava even in a single field in the Amazon basin, and that new cultivars arise from genetic recombination and germination in the same fields.

This chapter reviews the state of cassava genetic diversity available for use, and, based on these observations, proposes new ideas in the management of cassava diversity. Also, some new hypotheses about the basis of cassava domestication and the importance of genetic diversity among the wild *Manihot* relatives of cultivated cassava are addressed.

An Overview of the Genetic Diversity and Resources Available Within the Genepools of Cassava

The whole genepool of cassava is included in the genus *Manihot*. This genus, distributed naturally only in the New World tropics, is part of the family Euphorbiaceae, which is one of the largest in the Dicotyledons, falling within subfamily Crotonoideae, which also includes *Hevea*. The native range of *Manihot* extends from southern Arizona (USA) to northern Argentina. The species of genus *Manihot* are rather sporadic in their distribution and never become dominant members of the local vegetation. Most of them are found in areas with a long dry season but some of them are adapted to rain

forests or their margins, usually proliferating in openings of the forest, whether man-made or naturally caused. They are all perennial but sensitive to frost, and thus their area of distribution does not exceed 2000 m in altitude. They are also found, however, in sub-tropical areas where frost is not rare but predictable. *Manihot* species from these sub-tropical ecosystems become dormant during winter months, as other species do during the dry season in tropical areas. Most of the species are found on acidic soil but some can be found on lime-derived soils.

The limits of the genus *Manihot* are well defined. On the other hand, the limits of the various species within the genus are very controversial. The last available published review (Rogers and Appan, 1973) reduced the number of species from 171 to 98, on the basis of mainly vegetative characteristics. They are grouped into 17 sections, one of which includes the cultivated species only. Cassava is found most closely related to two sections: the central American section *Parvibracteatae*, which includes *M. aesculifolia* (considered as the most closely related wild species); and the South American section *Heterophyllae* which includes most of the wild forms now assembled by Allem (1994) under the species *M. esculenta s.l.*

The main centre of diversity of the *Manihot* genus is found in Brazil, with 77 species out of 80 South American species. Southwest Mexico appears as the other centre of diversity for the 17 Central American species.

Another classification is proposed in a monograph in preparation (A.C. Allem, personal communication). Of the 77 species identified by Rogers and Appan (1973) for Brazil, this new study recognizes only 38, as well as describing a few new species. The lack of correspondence between the two classifications suggests an enormous difficulty in defining a clear line of discontinuity within the genus. This is a case where molecular markers may help to clarify the situation.

Apart from the cassava that was first introduced by the Portuguese from the east coast of Brazil to West Africa, several wild species were introduced to many Old World tropical areas as potential rubber crops (Serie, 1989). In particular, *M. glaziovii* adapted well and subsisted in many places – including Africa, India and Indonesia – as an ornamental or shade tree (Rogers and Appan, 1973). Evidence of its spontaneous introgression into cultivars and the emergence of spontaneous 'wild' hybrid forms was suggested not only in Brazil but also in Africa (see page 204).

The first attempt at molecular characterization of the genus *Manihot* was based on Southern blot restriction fragment length polymorphism (RFLP) analysis of chloroplast and nuclear ribosomal DNA (Bertram, 1993). Representative sets of the Central and North American species were used, but only one wild species from South America: *M. carthaginensis* from Colombia. Cassava was also included. The results showed: (i) a relatively low level of nucleotide divergence for the more divergent species (0.1% for chloroplast DNA); and (ii) that the major divergence found was between *M. carthaginensis* and cassava on one hand, and the Central/North American species on the other hand. They rejected Rogers and Appan's suggestion of *M. aesculifolia* being the species most directly related to cassava, and indirectly pointed to South America as the probable area of domestication of cassava. A survey of a few South and Central American species by Colombo (1997) using the random amplified polymorphic DNA (RAPD) technique also agreed with those findings.

Studies including amplified fragment length polymorphism (AFLP) (Roa *et al.*, 1997) and microsatellites (Roa *et al.*, 1998) characterization of cassava across four

South American species (wild *M. esculenta*, *M. tristis*, *M. carthaginensis* and *M. brachyloba*) and *M. aesculifolia* confirmed the view of Allem (1994) that cassava is closely related to what he considers as wild *M. esculenta*. A small proportion of molecular markers, however, differ between the wild and cultivated forms of *M. esculenta*. The detailed results are consistent with the hypothesis that ancestors of cassava can be found within the Brazilian group of *Manihot* species (Allem, 1994).

Another AFLP survey (Second *et al.*, 1997; Second, 1998) examined all Brazilian species along with cassava and a few other South and Central American species. It demonstrated or confirmed several points in relation to the genetic structure and species relationship within *Manihot* (Fig. 11.1): the wild forms of *M. esculenta* are the most closely related to cassava but do not explain all of its diversity by descent. Most Brazilian species cluster together and are difficult to individualize. Several presumed spontaneous hybrids were confirmed among them, even between species considered

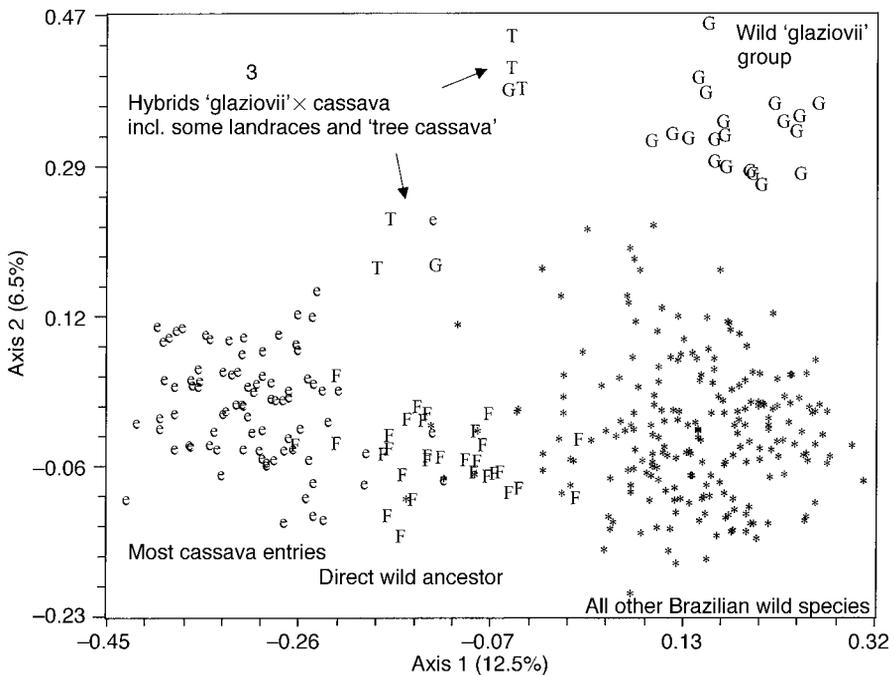


Fig. 11.1. Distribution in the plan defined by the first two eigenvectors of a principal coordinate analysis of the simple matching coefficient matrix of similarities in pairwise comparison of 364 accessions representative of the genus *Manihot*, including cassava. From the bulk of the molecular diversity of genus *Manihot*, the first axis extracts cassava and its direct wild ancestor, while the second axis extracts the 'glaziovii' group. Presumed hybrids are found between cassava and glaziovii, with not only 'tree cassava' but also some cultivars.

e = cassava (the same genotypes as in Fig. 11.2); other symbols = wild species or hybrids; G = *M. carthaginensis* s.l. or wild 'glaziovii' group; T = 'tree cassava' as found in northeast Brazil; F = *M. esculenta* ssp. *flabellifolia* and *peruviana*; * = 217 accessions representing 53 other species, mostly originated in Brazil.

Source: Second *et al.* (1997).

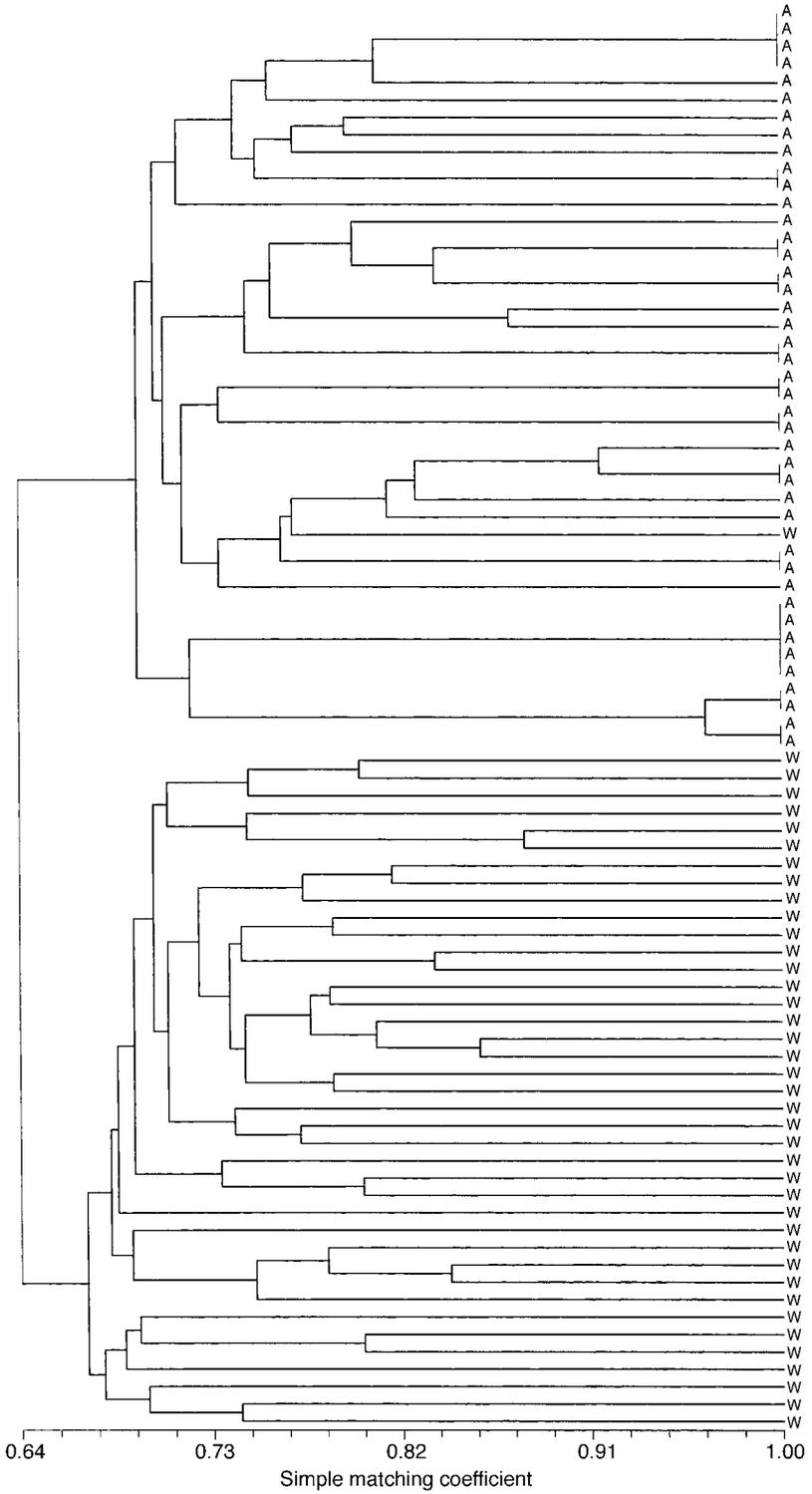
morphologically as the most distant. *M. carthaginensis sensu lato* (including *M. glaziovii*) is most divergent from cassava, among the Brazilian species. It forms, however, spontaneous hybrids with cassava, including some forms recognized as *M. glaziovii*, or 'tree cassava' or even cultivars. This last point is in line with earlier observations made at morphological and isozyme levels on cassava, tree cassava and *M. glaziovii* (Lefèvre, 1989; Wanyera *et al.*, 1994), and validates the hypothesis of a contribution of *M. glaziovii* not only in the domestication of cassava but also in its adaptation to the Old World, in particular Africa where it met the cassava mosaic disease (CMD), which has particular virulence. In this regard, it is interesting to note that *M. aesculifolia* is also morphologically related to *M. carthaginensis* (A.C. Allem, personal communication), although widely divergent at molecular level. A pioneer phylogenetic study based on the non-coding sequence of a single-locus gene further supports the hypothesis that domestication occurred from the wild forms of *M. esculenta* originating from the border of the Amazonian basin forest rather than from the cerrado area (Olsen and Schall, 1999).

Earlier work (that cannot be reviewed in detail here for lack of space available) indicates that in *Manihot*, interspecific hybrids occur frequently and can be obtained relatively easily. In general, no strong reproductive barrier was evidenced between cassava and various wild species tested. Nevertheless, some failures in attempts to hybridize *M. glaziovii* with cassava have been noted in Brazil in the context of other successful hybridizations (Nassar *et al.*, 1986). A partial pollen sterility was also observed in Africa among F_1 hybrids of *M. glaziovii* with cassava (Lefèvre, 1989). However, even in this case, where it appears likely that the wild stocks of *M. glaziovii* presented a strong reproductive barrier with cassava, this was gradually overcome in spontaneous as well as artificial hybridization (the fact that many of the cassava trees around the world are relatively easy to reproduce through cuttings is by itself an indication that they are often hybrid derivatives with cassava, not pure *M. glaziovii*, even if sometimes considered as such). Clearly, the work on this line is incomplete, but available evidence favours the view that most wild *Manihot* species are part of the primary or secondary gene pool of cassava.

Diversity in cassava: evidence from molecular markers

Several reports have addressed the question of the overall genetic diversity of cassava, based mainly on arbitrary molecular markers such as RAPD and AFLP. Collections of both American and African cultivars have been studied, although generally in separate studies, making the comparison between the diversity found on the two continents difficult. Also, Asian cultivars have been covered only marginally in these studies.

Colombo (1997; see also Empereire *et al.*, 1997, and Second *et al.*, 1999) has conducted the most extensive study using RAPD and AFLPTM markers on a set of cultivars combining a representative set of Brazilian collections, a reduced core collection of accessions held in the Centro Internacional de Agricultura Tropical (CIAT) and a small collection extracted from a single traditional field in the Amazon basin. In line with other studies, Colombo's results showed a large amount of variation but little genetic structure. In other words, although such studies allow a comparison of the amount of diversity found in various areas of origin, and suggest certain grouping of cultivars, the



diversity appears to be in complete continuum, with only little genetic linkage disequilibrium, even between extremes in the distribution.

An amazing finding was, however, that a molecular diversity nearly equivalent to that described by Colombo (1997) was evidenced among genotypes extracted from a single field in the Amazon basin. Moreover, the collection from this single field showed, in comparison with the 'world collection', the largest (although relatively minor) divergence found within cassava. In other words, the diversity of cassava in the Amazon basin is large and is not well represented in the available 'world collection' (Fig. 11.2). Further, a traditional cultivar characterized by a local name appears to be often composed of several genetically interrelated but different clones: a concept of a dynamic management of genetic diversity according to an Amerindian tradition emerges from this study (Emperaire *et al.*, 1997). Work on this line is still underway, particularly in Amerindian fields of French Guyana, Guyana, Brazil and Ecuador, confirming these findings while showing that an even more divergent diversity exists on the Guyanian plateau. A confirmation that this little characterized genetic diversity involves not only recombinational diversity but also alleles that are under-represented, or not represented in available collections comes from a study at the level of microsatellite loci that is underway in collaboration with CIAT.

As expected, the few cultivars originated in Africa or Asia included in Colombo's studies did not show any particular divergence from American cultivars. Interestingly, however, this remark also extended to one cultivar (NGA2) known to result from a cross with *M. glaziovii* and used in the construction of the available RFLP genetic map (Fregene *et al.*, 1997). This cultivar clustered with a Colombian cultivar (Col22) and a few other cultivars mostly originated from northeast Brazil. This raised the possibility that *M. glaziovii* – or another species closely related to it such as *M. carthaginensis* – has also spontaneously contributed to the diversity of cassava in America (Second, 1998).

Various studies have addressed the diversity of African cultivars on the basis of isozyme variation (Lefèvre, 1989), RFLP (Beeching *et al.*, 1993) and RAPD (Marmey *et al.*, 1994). All show a large amount of variation comparable with that found among American cultivars. An isozyme marker presumably introgressed from *M. glaziovii* was found generally associated with resistance to CMD. However, this resistance was also found associated with various genetic backgrounds in a different study based on RAPD. It was thus presumed to depend on various combinations of genes (Mignouna and Dixon, 1997). The isozyme study showed that introgression from *M. glaziovii* in Africa has probably contributed to the diversity of cassava on this continent.

At the level of chloroplast DNA only, an RFLP study suggests a relatively large cytoplasmic diversity within cassava, with three different cytotypes, as compared with the diversity found among wild species (Fregene *et al.*, 1994).

The conclusions from this overview are:

Fig. 11.2. A UPGMA dendrogram based on the simple matching coefficient of similarity for the presence or absence of 143 polymorphic fragments (60 AFLP and 83 RAPD) between 82 cassava plants. Forty cultivars are representative of a world collection (W) and 25 genotypes were distinguished among 42 plants collected in a single clearing plot in the Amazon basin (A). The two groups of cultivars form two different clusters, with a similar overall diversity, except for one landrace of the world collection group found among the single plot group. The origin of this landrace is also from the Amazon basin (Para State, Brazil). Source: Emperaire *et al.*, 1997.

- A direct wild ancestor for cassava has been identified. However, domestication included some interspecific events that have not yet been properly characterized.
- Genetic diversity in cassava is high but with little linkage disequilibrium. A high genetic diversity can be found in a single Amerindian field and a traditional cultivar appears to be a family of clones. In spite of the vegetative multiplication generally used to propagate cassava, the domestication process appears to have included: (i) assembling a large diversity in the same field; and (ii) numerous genetic recombination events.
- No clear bottleneck in the transfer of genetic diversity from America to Africa has been evidenced. *De novo* selection of original cultivars in Africa appears to have also included introgressions from the wild species *M. glaziovii*.
- The complete analysis of cassava genetic diversity in America and of its transfer to other continents has not yet been thoroughly accomplished, and there is indication that not all the available diversity is yet assembled in the world collections.
- The genus *Manihot* represents a wide genepool, with most if not all species part of the primary or secondary genepool of cassava.

Extent of Genetic Diversity Utilized to Date

A considerable proportion of the total effort to collect, preserve and characterize *Manihot* genetic resources must have a user-oriented focus. The benefit to final users of *Manihot*'s genetic resources is through crop genetic improvement and the diffusion of cultivars that combine desirable agronomic and quality traits. It is extremely important to have farmers' participation from the onset of germplasm collections, in order to gather most of the information related to traits they consider desirable in the germplasm they possess and characteristics that they judge to be missing or in need of some improvement (Gulick *et al.*, 1983; Fukuda and Guevara, 1996).

Hershey (1994) estimated that close to 10% of the cassava germplasm accessions held at CIAT have been used in the recombination programme to generate genetic diversity that can be used as the basis for breeding programmes. At the same time, he stated that the number that actually has contributed to elite genotypes for release to farmers was considerably less, perhaps around 1%.

Organized breeding for cassava is relatively recent, and it has not had the success that breeding has had in other crops. A great percentage of cassava production is still based on landraces (Hershey, 1987). But landraces themselves are dynamic: each genotype has a relatively short life in production, and is then substituted by other introduced material, or selection from native seedlings.

In most national programmes the initial step in the formulation of a breeding programme is an extensive germplasm collection, to catalogue and evaluate what there is in the country. In large countries (such as Brazil) it is common that landraces introduced from other areas are well adapted and become new cultivars in other areas (e.g. Rosa from Sergipe, recently released in Ceará). In countries where there is considerable variability in the field, we should encourage this type of approach, before resorting to the introduction of foreign germplasm (such as improved populations from international research centres).

Africa, which produces more than 50% of world production (mainly for human consumption), was struck early by CMD, the effects of which were so devastating that

all the national breeding programmes concentrated on obtaining resistance to it. The programmes of the colonial powers (Belgium, France, UK) since the 1930s, and then of the national programmes promoted the collection and exchange of landraces between several agronomic research stations. However, a stage of global exchange was not reached until the international centres (International Institute for Tropical Agriculture (IITA) and CIAT) started to develop and interchange their cassava germplasm collections integrated in their breeding efforts in partnership with the national centres (Dixon *et al.*, 1994; Porto *et al.*, 1994).

The use of genetic diversity from some *Manihot* wild species was promoted in the 1930s in Africa to circumvent the lack of good resistance to CMD in cultivars. Several species were used, including *M. glaziovii*. Germplasm derived from the former East African breeding programme was for a long time the main source of resistance being used (Jennings, 1976; Jennings and Hershey, 1985). Additional useful genetic variability has been detected in the wild relatives of cassava, although it has not been used extensively (Nassar *et al.*, 1986; Bonierbale *et al.*, 1997). IITA has used several *Manihot* species in interspecific hybridization to transfer their desirable genes into cassava (Asiedu *et al.*, 1994). Spontaneous sexual and asexual polyploids from both intra- and interspecific crosses have also been tested for their value as cultivars. These crosses look very promising and represent a new avenue to enlarge the genetic base of cassava cultivars (Hahn *et al.*, 1990, 1994; Sreekumari *et al.*, 1995).

We suggest that this potential for polyploidy in cassava should be put in perspective with various observations that facultative apomixis can be found in interspecific cassava hybrid derivatives (Nassar *et al.*, 1998). In nature, apomixis is generally associated with polyploids (Asker and Jerling, 1992). When facultative, that is when there subsists a small percentage of sexual reproduction, apomixis still allows genetic recombination and breeding to take place in farmers' fields.

There is an inherent risk in the reduction of genetic diversity through the adoption of a single dominant cultivar in an area where cassava represents the basic staple. For example, in the early 1970s, bacterial blight nearly decimated many fields in the Congo that were cultivated with a single traditional cultivar, and created a temporary acute food shortage. On the other hand, not only bacterial blight but also mealybugs and green mites might have been introduced in Africa through importation of cuttings.

There are about 28,000 accessions of cassava held in *ex situ* collections worldwide (Rao *et al.*, 1995; FAO, 1998a). Most are in field genebanks, though IITA and Brazil also hold substantial *in vitro* collections. Most accessions are of landraces. However, the number of discrete landraces may be substantially less than this figure suggests because of recent losses of some collections and duplication between collections: for example, Bonierbale *et al.* (1995) reported 11% duplication within the CIAT collection. Regional estimates of cassava accessions include:

- Costa and Morales (1994) reported a total of 7500 accessions maintained in Latin America; 55% corresponded to Brazilian germplasm and 40% to Colombian accessions.
- In the case of Africa, Msabaha (1994) reported 847 landraces maintained by national programmes in East and southern Africa; Benett-Lartey (1994) reported 2860 for West and Central Africa; while Ng *et al.*, (1994) referred to 350 African accessions maintained at IITA.

- Tan (1994) reported a total of 1110 local landraces being maintained by different national programmes in Asia.

The demand for genetic diversity by breeders still centres on traits such as root yield potential, root dry matter content, earliness, yield stability and reaction to pests and diseases (Fukuda, 1994). Recently, there has been an increasing interest in root quality traits, post-harvest deterioration, sprouting ability under adverse conditions, photosynthetic capacity and nutrient use efficiency. The demand for genetic diversity has been determined by the needs of farmers, processors and consumers. Genetic diversity studies conducted by different scientists show considerable variability among cassava accessions for most of the traits of interest. However, the case of resistance to CMD, derived from an introgression of *M. glaziovii*, and the potential for finding novel genetic variants for starch quality within wild germplasm calls for a greater future need to concentrate on the sections of wild *Manihot* species that are the most promising.

Not all the accessions maintained in cassava germplasm collections have been properly characterized for traits of present importance. This should be a high priority, in order to clarify the needs for further collection, use of wild relatives and resorting to genetic transformation. Even when morphological characterization of cassava germplasm accessions has been completed, basic standardization in the scale of measurement and growing conditions is often lacking. A group of 13 basic descriptors has now been defined (Fukuda and Guevara, 1996). Core collections (Iglesias *et al.*, 1995) provide a more manageable sample of the world cassava collection that can be evaluated across different ecosystems and years in order to determine the genotype \times environment effects for important traits. However, core collections should continually be improved to make them more representative of global cassava genetic diversity (Emperaire *et al.*, 1997).

The agronomic evaluation of germplasm accessions in different ecosystems has resulted in the selection, multiplication and release of cultivars from other regions. Introduction has been one of the most ancient breeding methods, and it has the advantage of dealing with materials that have already passed through the filter of farmers' selection in other places.

Agronomic evaluation usually leads to the selection of accessions with excellent performance for certain traits, but also with weaknesses for other traits. Therefore, after the initial evaluation phase, there is a recombination process to generate segregating progenies from which individuals combining the best of both parents can be selected. The development of these segregating populations constitutes one of the most important steps to link cassava germplasm collection held at international centres or large national programmes with other programmes working in particular regions. The diffusion of genetic diversity from such large programmes to others represented a much larger movement of germplasm in the last decades of the 20th century than had occurred in the previous 450 years.

Table 11.1 presents a summary of cassava cultivars released in Latin America and Asia, and their relationship to accessions in the germplasm collection at CIAT and/or landraces. We can observe that all cultivars can be traced back to a given accession. There have not been more than three or four cycles of selection and recombination for most of the active cassava breeding programmes that started in the early 1970s. The importance of the germplasm collections held at international centres and national pro-

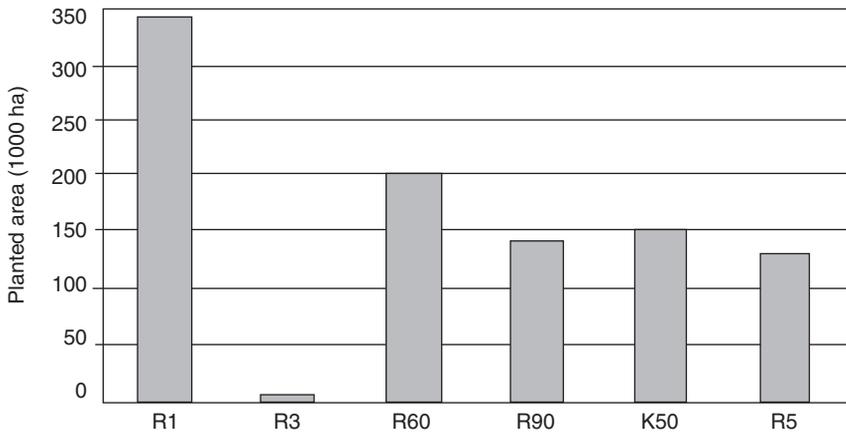


Fig. 11.3. Area planted with the traditional variety (Rayong 1) and alternative new varieties released in the late 1980s and early 1990s in Thailand.

grammes can be pictured through the example of Thailand where, until the mid-1980s, there were more than 1.5 million ha planted to a single cultivar (Rayong 1). Nowadays, farmers have at least three options in terms of improved cassava cultivars, and the area under cassava cultivation has diversified its genetic base (Fig. 11.3), reducing its vulnerability (Kawano *et al.*, 1998). However, it may be stressed that Thailand has relatively quickly adopted new improved cultivars, because cassava is mostly a commercial crop to be exported for animal feed and not a basic staple food in this country. In the case of Nigeria, the emerging possibilities to commercialize cassava associated with advanced processing have been recognized as the main driving force in the adoption of high-yielding cultivars (Nweke *et al.*, 1994). This confirms that farmers are more prone to adopt new cultivars when they have accessible and fluent market channels for their product other than its consumption at the family/community level.

In a breeding programme, clearly not only the quantity but also the quality of the end-product is important. It is paramount to take into consideration the cropping systems as practised by the farmers. The relative importance of single crop or mixed cropping should be taken into consideration. Also, the importance of the aerial part of the plant should not be overlooked, since the success of the following cropping season depends also on the quantity and quality of stem cuttings. Assistance to the farmer in relation to propagation material is rarely provided in a sustainable way. Also, it should be kept in mind that, in various cases, consumption of the leaves can substantially complement the quality of the diet based on cassava.

The extent of available genetic diversity in the future will be broadened by the use of wild genetic resources and the incorporation of genetic transformation protocols. Those two alternatives will help address those traits for which there is restricted genetic diversity (e.g. starch quality) or none available (e.g. resistance to stem borers). In spite of the fact that a very restricted percentage of the total available genetic diversity has been used up to the moment, present work being developed in relation to genetic distances, genome complementation and detection of genomic regions with large effects

Table 11.1. CIAT's cassava germplasm utilization and impact.

Country	Name	Original name or pedigree	Year of release	Main features
a) Landrace provided by CIAT				
Philippines	VC 5	MCOL 1684	1993	High yield
Cuba	CMC-40	MCOL 1468	1981	Early maturity, high yield
Mexico	Costeña	MMEX 59	1981	Drought tolerance, high yield
Mexico	Sabanera	MPAN 51	1981	Disease resistance, acid soil adaptation
Dom. Rep.	M Col 1468	MCOL 1468	1982	High yield, resistant to CBB
Dom. Rep.	M Col 1684	MCOL 1684	1982	High yield, resistant to CBB
Haiti	Mdme Jacques	MCOL 1468	1983	Early maturity, casabe quality
Haiti	M Col 1684	MCOL 1684	1983	Casabe quality
Colombia	Manihoica P-11	MCOL 1468	1984	Early maturity, high yield
Colombia	Manihoica P-12	MCOL 1505	1984	High yield, <i>Diplodia</i> resistance
Brazil	M Mex 59	MMEX 59	1986	High yield
Philippines	VC 2	MCOL 1468	1988	Table use, high yield
Philippines	M Col 1684	MCOL 1684	1989	High yield
Ecuador	Portoviejo 650	MCOL 2215	1992	High starch content
b) CIAT clones introduced to national programmes				
Philippines	VC 1	MCOL 22 × MMEX 59	1986	High yield
China	Nanzhi 188	MCOL 22 × MVEN 270	1987	High yield
Panama	Dayana		1990	High yield
Colombia	ICA-Catumare	MCOL 655A × MCOL 1515	1990	High starch content, CBB resistant
Colombia	ICA-Cebucan	(MCOL 1438 × MCOL 647) × (MCOL 638 × MVEN 218)	1990	High yield, CBB resistant
Colombia	ICA-Costeña	MMEX 11 × MCOL 65	1991	High yield, starch, <i>Diplodia</i> resistant
Colombia	ICA-Negrita	MCOL 22 × (MCOL 655A × MCOL 1515)	1993	High yield and starch content
Vietnam	KM-60	Rayong 60 (MCOL 1684 × R1)	1993	High yield
Vietnam	KM-94	Kasetsart 50 (R1 × R90)	1994	High starch

c) Clones selected from CIAT seed introductions

Thailand	Rayong 3	MMEX 55 × MEVEN 307	1984	High starch content
Thailand	Rayong 2	MCOL 113 × MCOL 22	1985	Good for snack food
Malaysia	Perintis	(MCOL 22 × MVEN 270) × MCOL 1684	1988	High yield on peat soils
Brazil	CNPMF 8339/11	(MVEN 185 × MCOL 22) × (SM 76-66 × MVEN 218)	1989	High yield
Brazil	CNPMF 8347/19	(SM 76-66 × MCOL 638) × (MCOL 655A × MCOL 1515)	1989	High yield
Philippines	VC 3	(MCOL 638 × MCOL 655A) × MCOL 22	1990	Dual purpose
Malaysia	MM-92	(CM 477-3 × MCOL 1684) × (MMEX 55 × MPAN 114)	1992	Early maturity, high yield
Indonesia	Malang 1	CM 4049-2 (CM 105-19 × CM 849-1)	1992	Drought tolerance
Indonesia	Malang 2	CM 4031-10 (CM 922-2 × CM 507-37)	1992	High starch
Philippines	VC 4	CM 4014-3 (CM 728-3 × CM 681-2)	1993	High yield

d) Clones selected from local × CIAT crosses

Thailand	Rayong 60	Rayong 1 × MCOL 1684	1987	High yield, early maturity
Thailand	Rayong 90	MCOL 1505 × V43	1990	High starch content
Thailand	Sriracha 1	MKU2-151 (R1 × CM 305)	1991	High starch
Thailand	Kasersart 50	Rayong 1 × (MCOL 1505 × V43)	1992	High yield and starch content
Thailand	Rayong 5	CMR25-105-112 (27-77-10 × R3)	1994	High yield, early harvest
Vietnam	Rayong 60	21-1 (CMC 76 × V43)	1994	High starch

e) Clones selected from local crosses or landraces with CIAT assistance

Indonesia	Adira 4	M31	1986	High starch yield
China	SC-124	E-24	1989	Cold tolerance
Brazil	Mae Joana	Local landrace Berreiruinha (AM)	1990	Root rot tolerance
Brazil	Zolhundinha	Local landrace Irancuba (AM)	1990	Earliness, intermediate root rot
Brazil	EMBAPA 8	Local landrace Urucará (AM)	1992	Tolerance
China	SC-8002	ZM8002	1995	Root rot resistance
China	SC-8013	ZM8013	1995	High starch

Total	46 cultivars			
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Source: CIAT, Cassava Program, Breeding and Economics Section files (1993, 1995).

upon traits of large importance will boost the use of germplasm that was overlooked from its phenotypic evaluation, as has happened in other crops (Tansley and McCouch, 1997). There will always be a trade-off between the need to gather the most representative sample of cassava germplasm before it disappears, and the need to make the best use of available genetic resources in collections that are expensive to maintain. Cassava genetic resources conservation and utilization is a multi-disciplinary task, which should involve scientists (germplasm specialists, breeders, pathologists, entomologists, food quality specialists, bio-technologists, etc.) as well as final users. From that concept we derive the importance of networking in the collection, preservation and use of cassava genetic resources.

Networks for the Conservation and Use of Cassava Genetic Resources

There are a series of formal and informal networks related to the conservation and use of cassava genetic resources operating in the three continents and other networks with global coverage (Table 11.2). Most of the networks operating in Africa have a formal structure supported by financial resources from special projects (Benett-Lartey, 1994; Msabaha, 1994), facilitated by IITA and furthering their objective of promoting the evaluation, adaptive selection and diffusion of improved cassava germplasm. In the case of Latin America, most of the networks represent potential resources more than effective institutional set-ups. Most of them have depended on CIAT in terms of operational resources and coordination, and lack formal support from donors (Iglesias, 1994). In the case of Asia, the network is informal. While there is considerable support from CIAT in terms of coordination, there are several strong national programmes that can take the lead in coordinating activities in the near future (Kawano, 1995).

The Cassava Genetic Resources Network, which was initially sponsored by the International Plant Genetic Resources Institute (IPGRI), included three key elements in its plan of action: (i) the implementation of an international database on cassava genetic resources; (ii) a worldwide strategy for rational and safe conservation of the germplasm, using available techniques; and (iii) collaborative activities for better use of cassava genetic resources (Perret, 1994). For a crop that lags behind in terms of resources invested for research and development, it is very important to have a network such as this actively working.

A Proposal to Enhance Genetic Base-broadening of Cassava

This proposal is for enhancing the dynamic conservation of cassava, both of wild species and traditional cultivars. Such a dynamic conservation would be associated with cassava breeding, in particular through the evaluation of the useful diversity in agronomic research institutions but also largely through farmer-participatory breeding as initiated by IITA in Nigeria (Robinson, 1996, p. 379). It would complement and, if successful, perhaps partly substitute for the present efforts to exchange, conserve and use germplasm in cassava genetic improvement. The final expected product is to preserve, in a simple yet sustainable way for future generations, a large genetic basis for the

Table 11.2. Cassava research networks operating in Latin America, Africa and Asia.

Region	Network	Type of network	Secured financing
Latin America	Cassava Research and Development Network	Informal	No
	Panamerican Cassava Breeders Network	Informal	No
	Southern Cone Network	Informal	No
Africa	East and Southern Africa Root Crops Research Network (ESARRN)	Formal	Yes
	Collaborative Group on Root and Tuber Improvement and Systems Research (CORTIS)	Formal	Yes
	International Society for Tropical Root Crops – African Branch (ISTRC–AB)	Formal	No
Asia	Cassava Research and Development Users Perspective with Agricultural Research and Development (UPWARD)	Informal	No
		Formal	Yes
Global	Cassava Genetic Resources Network (CGRN)	Formal	No
	Cassava Biotechnology Network (CBN)	Formal	Yes

improvement of cassava from both traditional cultivars and wild species. The scheme includes considerable activities related to intercontinental exchange or introduction of germplasm, making such material available for evaluation in the field and ready for immediate use in breeding initiatives.

From a practical as well as a theoretical point of view, there are several aspects that make the genus *Manihot* and cassava good candidates for dynamic conservation:

- Optimum conditions for the *ex situ* conservation of seeds are not yet known for any of the species, even though most species are apparently orthodox in relation to seed conservation.
- While *in vitro* conservation of plantlets is successful to conserve the cultivars, it is expensive and has limited possibilities for present application with most wild species.
- As evidenced by the difficulty in classifying the genus and difficulties in recognizing limits between species, extensive interspecific hybridization takes place.
- Up to the end of the 20th century, the domestication process of cassava included: (i) gathering a large genetic diversity in the same field; (ii) permanent selection of new genotypes arising through genetic recombination; and (iii) introgression from wild species widely different from the direct ancestor.

Model for dynamic conservation of *Manihot* species

The basic model consists of grouping in an arbitrary order accessions per species, and growing them in the field. Each species is relatively isolated from the others by a minimum of 30 m, but pollination is not controlled.

It is justified to apply the model in different ways according to the biome of the collection's maintenance site, as follows.

An optimal dynamic conservation in the area of origin of the species concerned should not induce excessive genetic recombination but rather conserve the species as they are. Only a relocation of the populations to save them from destruction is advisable. Pooling various populations in a single artificial one can be justified for practical reasons and to save them from disappearing in the wild, rather than to produce new genotypes. Entries pooled should be collected in a relatively small and ecologically homogeneous area. In this case, it will be relatively easy to decide the limits of the species. When some accessions die, it will be preferable to replace them from the same or similar accessions rather than from reintroducing their offspring obtained in exotic locations.

At the other extreme, when introducing the species to an exotic location (different ecology, different continent, etc.) accessions may be pooled from their total area of origin. In this case, the limit between the species is much less well defined. The admixture of such groups of accessions from a large geographic area will lead to large genetic recombinations. Such recombinations should actually boost the chances of successful adaptations to a new environment as exemplified in the most successful cases of domestication of plants.

It is possible to imagine a sustainable, yet relatively simple scheme of dynamic conservation as follows: (i) a network for initialization of the dynamic conservation in the area of origin of the species (defined *sensu stricto*), with grouping of entries for each species found in a certain biome but not introducing accessions from other biomes;

and (ii) a network of dynamic conservation plots in various areas of the tropical world, with species (*sensu lato*) represented by entries originated from their whole area of distribution. On a long-term basis, periodic exchanges of seeds between these various populations from exotic locations in the world should mimic natural gene flow between populations in the wild and maintain a large diversity in each population. This scheme of 'metapopulation' (see Olivieri *et al.*, 1990; Goldringer *et al.*, Chapter 13, this volume) should realize, in a sustainable way, the conservation of the genus *Manihot* in the long term, coupled with its evaluation and utilization.

In September 1994, a test of a dynamic conservation of wild Brazilian species of *Manihot* (Mendes *et al.*, 1998; Second *et al.*, 1998) was initiated in the fields of CENARGEN (Centro Nacional de Pesquisa de Recursos Genéticos e Biotecnologia), with focus on the wild species most closely related to cassava (Allem, 1999) and/or to the most threatened species of the Cerrado area. The success of the chosen scheme will be evaluated in the long term. The monitoring of genetic changes occurring in the artificial populations during dynamic conservation, as well as in farmers' participatory breeding, should be largely simplified with the rapid development of new technologies that allow the quantification of the amount of hybridization of a template DNA to a very large number of probes (or oligonucleotides set up in micro-arrays or on a DNA chip). It will become possible to bulk many plants in a single sample for analysis and to obtain the information on allelic frequencies at many loci in a single experiment.

Managing an intraspecific *Manihot esculenta* dynamic conservation

We propose that two aspects of a dynamic conservation of cultivars could be applied: conservation *ex situ* as seeds in partial substitution of *in vitro* conservation and dynamic on-farm conservation of cultivars.

Because we confirmed that the use of sexual reproduction is frequent in the maintenance of traditional cultivars, we propose that most of them could be conserved through seeds. Conservation of seeds represents a dynamic conservation since the original gene combinations of the cultivar are modified. It should be efficient in conserving the useful genetic diversity, if not the genotypes.

Also, since a dynamic management of the diversity of cassava cultivars is at the origin of the present stage of the domestication of cassava, it is natural to think of ways in which this tradition could be maintained in order to contribute significantly to the conservation of cassava genetic diversity.

Dynamic conservation has been approached so far mostly for grain crops (see Enjalbert *et al.*, 1998; Goldringer *et al.*, Chapter 13, this volume) and it should be noted that there is a fundamental difference in a dynamic conservation approach between root and grain crops. In grain crops, the cycle of repeated sowing and reaping can act as a selective drive towards high yield because the propagule is the object of the crop. In the case of root crops, however, it is likely that a repeated cycle of planting and reaping will not preserve most of the attributes of the cultivars. To this aim, it should be necessary that a control of the quantity and the quality of the harvested roots be performed at each cycle and that a selection be imposed. Genotype \times environment interactions would in this way be evaluated in a variety of cases, which is paramount in a crop such as cassava with high levels of morphological plasticity

(Raffaillac and Second, 1997). Then, encouraging farmer-participatory breeding appears as the most appropriate option for the conservation, evaluation and utilization of cassava genetic resources.

This would apply to both the continent of origin of cassava – particularly the Amazon basin and northeast Brazil – and the areas of major present production – humid tropical Africa and Asia.

Acknowledgements

The authors are grateful to two anonymous reviewers and to Dr Jean-Pierre Raffaillac for reading the manuscript and making many valuable suggestions.

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12 The State of the Use of *Musa* Diversity

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Importance of *Musa*

Bananas¹ are cultivated throughout the tropical regions of the world, where they constitute a major staple food crop for many hundreds of millions of people as well as providing a valued source of income through local and international trade. They are grown over a harvested area of approximately 10 million ha, with an annual production of around 88 million tonnes (Mt), of which around one-third is produced in each of the African, Asia-Pacific, and Latin America and Caribbean regions. In terms of gross value of production, they are the fourth most important food crop in developing countries after rice, wheat and maize. The vast majority of producers are small-scale farmers growing the crop either for home consumption or for local markets. As well as being a cheap and easily produced source of energy, they are also rich in vitamins A, C and B6. Furthermore, with growing urbanization, bananas and plantains are becoming increasingly important as cash crops, often providing the main source of income for rural populations, thus playing an important role in poverty alleviation.

In Africa, bananas and plantains provide more than 25% of food energy requirements for around 70 million people. In the East African Highlands region alone, around 15 Mt are produced annually and it is here that bananas reach their greatest importance as a staple food crop. In countries such as Uganda, Burundi and Rwanda, annual *per capita* consumption of bananas has been estimated at more than 250 kg; the highest in the world. The largest producer of bananas in the world is Uganda, which produces over 10 Mt of the crop annually.

Bananas for export account for little more than 10% of global production. They are grown predominantly in Latin America and the Caribbean where the cultivation of banana and plantain is of importance to the food and income security of nearly 200 million people. Even in this region, however, bananas produced for export constitute only around 30% of total production.

¹ The term banana is used throughout the text to refer to all types of bananas including cooking bananas and plantains.

Musa Genetic Resources

Wild species

The family Musaceae consists of two genera: *Musa* and *Ensete*. The genus *Ensete* is distributed from Africa to New Guinea, and no more than eight species have been reported (Stover and Simmonds, 1987). The genus is not of economic importance on a global scale, although *Ensete ventricosum* is locally very important as a staple food crop in parts of southern Ethiopia. Edible starch is extracted from the corm and pseudostem and fermented to make 'kocho', an important food source for several million people in the region (Demeke, 1986).

The genus *Musa* is divided into four sections, the members of which include both sexual (seeded) and asexual types. Two of the sections contain species with a basic chromosome number of 10 ($2n = 20$) (*Callimusa* and *Australimusa*), while the species in the other two sections (*Eumusa* and *Rhodochlamys*) have a basic chromosome number of 11 ($2n = 22$). The species in the sections *Callimusa* and *Rhodochlamys* are of ornamental interest only and do not produce edible fruit. The section *Australimusa* contains *Musa textilis* (Abaca) from which Manila hemp is produced, and it is within this section that the seedless, and therefore edible, Fe'i bananas, found mainly in the Pacific islands, have been selected and propagated by humans.

Virtually all banana cultivars arose from the *Eumusa* group of species. This section is the biggest in the genus and the most geographically widespread, with species being found throughout Southeast Asia from India to the Pacific Islands. The section contains some 11 species (Horry *et al.*, 1997). Most cultivars are derived from two species, *Musa acuminata* (A genome) and *Musa balbisiana* (B genome). However, Shepherd and Ferreira (1982) identified cultivars derived from hybridizations with *M. schizocarpa* (S genome) in the *Musa* germplasm collection in Papua New Guinea, and this was subsequently confirmed by Carreel *et al.* (1993). In addition, a Philippine clone (Butuhan) is considered to be the result of an ancient hybrid between *M. balbisiana* and *M. textilis* (T genome), and landraces containing the three genomes *acuminata*, *balbisiana* and *textilis* have been found in Papua New Guinea (Carreel, 1995).

Musa acuminata is the most widespread of the *Eumusa* species, being found throughout the range of the section as a whole. Chromosome structural changes, which have occurred spontaneously, or as a result of recombination events, have resulted in the development of natural reproductive barriers within the species, causing sub-species divergence and genetic diversity in the species as a whole. Nine sub-species have been recognized (Horry *et al.*, 1997). The centre of diversity of the species is thought to be either Malaysia (Simmonds, 1962) or Indonesia (Nasution, 1991; Horry *et al.*, 1997).

The majority of species in the section *Eumusa* produce separate male and female flowers on the same inflorescence. These flowers are produced asynchronously and pollination occurs exogenously. In a few cases (*M. schizocarpa*, *M. acuminata* ssp. *banksii*, *M. acuminata* ssp. *errans*), hermaphrodite flowers are produced and in these species the level of heterozygosity is low – less than 10%. Even in the non-hermaphrodite sub-species, the heterozygosity rate averages only 25% (Horry *et al.*, 1997).

M. balbisiana is distributed through the seasonally dry, northern and eastern fringes of the *Eumusa* area. Although originally thought to be a genetically homoge-

nous species, recent work using PCR-based techniques indicates that the species may in fact be more heterozygous than previously suggested (Jarret and Gawel, 1995).

Cultivars

The export banana trade is almost completely dependent on only one variety: Cavendish. On the other hand, a great deal of morphological variation exists within the cultivated, non-export bananas, and at least 500 varieties are thought to exist worldwide (Purseglove, 1988). The great amount of genetic variation in cultivated bananas has arisen from three sources: sexual recombination within and between the original parents (*M. acuminata* and *M. balbisiana*), ploidy-level differences and somatic mutations.

Although details of the early cultivation and spread of banana cultivation remain a matter for conjecture, bananas are considered to have been among the first plants to be domesticated by humans. In Oceania, the earliest agriculture has been dated at around 8000 BC, and it is in this region that the Fe'i bananas are of some importance. Their early cultivation has been described as 'proto-agriculture': that is, they were gathered from the wild rather than planted (Price, 1995). The domestication of *Eumusa* bananas is thought to have occurred at around the same time in Southeast Asia (Simmonds, 1962) and it has been suggested that the earliest uses of these plants may have been non-food, or at least not involving the fruit. The plants would have produced a fibre, which could be used in fishing nets, and leaves for constructing shelters. In addition, various parts of the plant apart from the fruit are edible, and the male bud is still widely used in parts of Asia as a vegetable.

Edibility of mature fruits of diploid *Musa acuminata* (AA) came about as a result of two mutation events, resulting in female sterility and parthenocarpy, and such edible types would no doubt have been selected and maintained by humans. Triploid AAA cultivars arose from these diploids, perhaps as a result of crosses between edible diploids and wild *M. acuminata* sub-species, resulting in a wide range of AAA genotypes. In most parts of Southeast Asia these triploids, which are more vigorous and have larger fruit, have replaced the original AA diploids. However, in New Guinea, AA diploids remain agriculturally significant and a wide range of diversity is still found in cultivation. This last remaining area of AA diploid diversity is, however, now under threat due to the increasing cultivation of high-yielding triploid varieties. Many of Papua New Guinea's primitive diploids were collected in the late 1980s during a series of collecting missions funded by the then International Board for Plant Genetic Resources (IBPGR). The material collected is now established in germplasm collections and is available to the *Musa* research community.

The diploid and triploid *acuminata* cultivars were taken by humans to areas where *M. balbisiana* is native, and natural hybridizations resulted in the formation of hybrid progeny with the genomes AB, AAB and ABB. The Indian subcontinent is thought to have been the major centre for hybridization of *acuminata* types with the indigenous *M. balbisiana*, and the region is noted for the wide variety of AAB and ABB cultivars. *M. balbisiana* is considered to be more drought and disease resistant than *M. acuminata*, and such characteristics are often found in cultivars containing a 'B' genome. Hybridization would have given rise to a wide range of edible types of banana, some of which would have survived and been multiplied under domestication. Consequently, a

diverse selection of cultivars of *Musa* is thought to have arisen in Southeast Asia along with the earliest development of agriculture many thousands of years ago (Price, 1995).

It is thought that the subsequent dispersal of edible bananas outside Asia was brought about solely by humans (Simmonds, 1962) and the history of banana cultivation is therefore closely linked to the early movement of human populations. This early dispersal of banana cultivars resulted in the development of distinct sub-groups of varieties in different geographic locations. Secondary diversification within the major groups of cultivated bananas is thought to have been the result of somatic mutations rather than sexual reproduction. Mutations affecting traits of economic or horticultural interest have been selected by farmers over the years and multiplied by vegetative propagation to produce morphotypes.

Movement eastwards resulted in the development of a distinct group of AAB bananas cultivated throughout the Pacific Islands. These are known as the Maia Maoli/Popoulu group, and the progenitors of these bananas are thought to have been carried eastwards by proto-Polynesians from an area in or near the Philippines more than 4000 years ago (De Langhe, 1996). It is argued by some that bananas existed in South America in pre-Columbian times, and this is taken as evidence for early Polynesian contact with America (Langdon, 1993).

A very distinct type of cooking banana (plantain) is found growing in the wet tropical zones of West Africa. Plantains are rare in most of Asia as well in other parts of Africa, and their origin in West Africa is shrouded in mystery. It is thought that they have been cultivated in this region for more than 3000 years, but the identity of the people responsible for such cultivation is unknown (De Langhe *et al.*, 1996). It is possible that the same proto-Polynesians that carried the banana east to the Pacific islands also carried it west to Africa. As dry suckers can survive storage for several months, long sea voyages would not have been a problem. Such a hypothesis fits with the finding that plantains must have reached Africa more than 3000 years ago, but archaeological evidence for such voyages is unlikely to be found.

Recent research suggests that tetraploid *Musa* hybrids, which evolved through sexual polyploidization, may have been the progenitor of the original plantains, rather than diploids as previously believed (Ortiz and Crouch, 1997). Molecular analysis of a large number of plantain landraces using random amplified polymorphic DNA (RAPD) indicates that most plantains have a very high level of genetic similarity to one another (Crouch *et al.*, 1998). This supports the suggestion that somatic mutations are responsible for the diversity of 'morphotypes' of plantains now found in West Africa.

Another distinct group of bananas are found in the East African Highlands. These are thought to have been introduced between the 5th and 10th centuries, and a wide range of unique varieties now exists here. This area of secondary diversity is clearly the work of East Bantu-speaking people (De Langhe, 1996), but the origins of these bananas remain unknown.

The occurrence of distinct sub-groups of cultivars in particular geographic locations is significant in relation to accessing and using diversity. For example, plantain diversity is mainly found naturally in West Africa, although diversity in the Indian plantains ('Nendran' varieties) has been reported recently. Therefore, although it might be possible to introduce 'new' diversity of this type of banana from other regions, the main way to produce new diversity in the plantain subgroup in West and Central Africa is through breeding. The same is true for the East African Highland bananas.

A review of the history of banana cultivation is provided by Price (1995) and further information on the number of varieties found within each of the major subgroups of bananas is given in Table 12.1.

Studies on diversity in *Musa* germplasm have been carried out by several researchers. Isozyme analysis of banana and plantain cultivars has identified a large amount of variation in the AAB group. This is apparently due to the genetic heterogeneity of the progenitor species, particularly *M. acuminata*, over the wide geographic range in which the hybridizations took place (Lebot *et al.*, 1993). These results support the evidence of Horry and Jay (1990) that suggested two independent centres of domestication for *M. acuminata*: one in Southeast Asia and the other in Papua New Guinea. Further details of studies on genetic diversity of wild and cultivated *Musa* are given by Careel (1995), Jarret and Gawel (1995), Jarret *et al.* (1992) and Lebot *et al.* (1993).

Opportunities and Constraints to Accessing Diversity for Breeding/Use

Availability of genetic resources

The Asia Pacific region is the centre of diversity of the genus *Musa*, and activities related to the collecting and conservation of banana germplasm have historically been given priority by countries in the region. Collecting missions have already covered much of the region, and representative diversity of the material collected is being conserved in genebanks both within and outside the region. Widespread general collecting is therefore no longer considered necessary. However, targeted collecting in specific locations is still ongoing by national programmes in the region. At present, these include China, northeastern India, Indonesia, Pemba and Zanzibar. Other areas that have been identified as priority areas for germplasm collecting include the Andaman Islands and Sabah and Sarawak states in eastern Malaysia. Prospection in Malaysia would complement the efforts of Indonesia to collect, characterize and conserve the *Musa* germplasm from Kalimantan, the Indonesian part of Borneo where forest fires annually destroy large areas of biodiversity, including *Musa* germplasm.

In recent years, germplasm collecting in Papua New Guinea, Vietnam and China has been carried out in collaboration with the International Network for the Improvement of Banana and Plantain (INIBAP). As a result, duplicates of all distinct accessions collected have been, or will be, provided to INIBAP for inclusion in the INIBAP *Musa* germplasm collection. This collection is now the largest *in vitro* collection of *Musa* germplasm in the world and, following an agreement with the Food and Agriculture Organization (FAO), is held in trust and is freely available to *bona fide* users worldwide. Guidelines for the Safe Movement of *Musa* Germplasm have been developed and published by FAO/IPGRI (Diekmann and Putter, 1996), and INIBAP has put in place the necessary virus-indexing capability to ensure that all germplasm distributed from the INIBAP Transit Centre (ITC) is in accordance with these guidelines. Breeding programmes thus have unlimited access to a wide range of *Musa* genetic resources for use in improvement programmes. This is particularly important in view of the fact that none of the major *Musa* breeding programmes is located in Southeast Asia, the centre of diversity of the genus.

Table 12.1. Review of available information on the extent and centre of diversity of the main sub-groups of bananas and plantains.^a

Genome	Subgroup	Centre of diversity	No. of clones/morphotypes ^b	Additional references
Fe'i		Pacific Islands	2 main clones 10–20 morphotypes	MacDaniels, 1947
AA		PNG	80+	Sharrock, 1995
		Malaysia	10	
		Philippines	18	Pascua, 1988
		East Africa	10	
AAA	Gros Michel Cavendish	China	3 8 main clones 30+ morphotypes	Houbin and Zehuai, 1997; Daniells, 1990
	Red/Green Red Lujugira-Mutika	East Africa	2 9 main clones 140+ cooking morphotypes 80+ beer morphotypes ^c	Karamura and Karamura, 1994
AB	Ney Poovan	India	2–3	
AAB	Pisang Raja		3	Valmayor <i>et al.</i> , 1981
	Pisang Kelat		1	
	Mysore	India	4–5	
	Silk	India	1–2	
	Pome	India	2–3	
	Laknao	Philippines	?	
	Maia Maoli/ Popoulu	Pacific	2 main clones 60+ morphotypes	Lebot, 1994
	Iholena	Hawaii	1 main clone 10+ morphotypes	Lebot, 1994
	Plantain ^d	West and Central Africa	4 main clones 110+ morphotypes	Swennen, 1990

ABB	Bluggoe	India	5–7	Valmayor <i>et al.</i> , 1981
	Pisang Awak	Thailand	4–5	
	Monthan	India	4–5	Sharrock, 1990 Singh and Uma, 1996
	Kalapua	Papua New Guinea	5–6?	
		India	10	
	Philippines	?		
BBB	Saba	Philippines	10–12	Valmayor <i>et al.</i> , 1981 Singh and Uma, 1996
		N.E. India	2	
AAAB,		S.E. Asia/PNG	10–15	
AABB,				
ABBB ^e				

^a The information provided in this table is taken exclusively from the available literature and it should not be regarded as definitive. It is merely an attempt to present, in one place, existing information. The table is derived mainly from Stover and Simmonds (1987); additional references are given in the table.

^b The terminology used by different authors in describing ‘types’ of bananas is confusing. The terms ‘cultivar’, ‘variety’, ‘clone’, ‘morphotype’, ‘type’ are used interchangeably. In this table we use the term ‘clone’ to describe a main cultivar type and the term ‘morphotype’ for the mutations derived from the main clone. The number of clones/morphotypes given in each subgroup is based on the best available information. The widespread occurrence of synonyms and duplications from country to country, as well as the high level of mutations in *Musa*, makes it extremely difficult to give accurate figures. In some cases, the different varieties described have not been divided into clones and morphotypes.

^c It is a common phenomenon for cooking cultivars to change to beer cultivars, especially in highland regions above 1400 m above sea level.

^d Although plantains are generally rare in Asia, several varieties, ‘Nendran’, are widely grown in India.

^e Naturally occurring tetraploid varieties are generally uncommon.

Movement of germplasm

Musa germplasm is also maintained in field genebanks in many countries where it is readily available for characterization and evaluation studies (Horry, 1999). Such germplasm is also available for direct use by farmers within the country, but in many cases the lack of evaluation data on accessions in collections means that potentially useful cultivars have not been identified. Germplasm maintained in field collections is not readily accessible to potential users outside the country due to the strict quarantine measures imposed by most producing countries. It is generally required that all germplasm introductions should be in accordance with the FAO/IPGRI Guidelines for the Safe Movement of *Musa* Germplasm to prevent the inadvertent introduction of pests and diseases, especially virus diseases. The guidelines require all material to be distributed *in vitro*, and only after completing virus indexing according to the recommended tests. Three virus-indexing centres are presently in operation. These are located in France at the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD); Australia, at the Queensland Department of Primary Industry (QDPI); and South Africa, at the Plant Protection Research Institute (PPRI). The time required for virus indexing is around 10–12 months per accession. Virus indexing is a major bottleneck in the distribution of material from the ITC, with some 38% of accessions at present unavailable for distribution as they still have not completed indexation or are infected with viruses. Effective virus therapy techniques remain under development and, until such techniques have been perfected, accessions that are currently virus infected cannot be made available.

Use of genetic resources in breeding

Banana breeding first started in the 1920s at the Imperial College of Tropical Agriculture (ICTA) in Trinidad, and soon after this a parallel programme was developed in Jamaica. Initial efforts were directed towards breeding for resistance to Panama disease (*Fusarium* wilt), already present in the Caribbean and to which the principle export clone, Gros Michel, was susceptible. The continuing spread of Panama disease and the ensuing destruction of Gros Michel plantations led to the initiation of a breeding programme in Honduras in 1959 by the United Fruit Company. Efforts to produce a *Fusarium*-resistant Gros Michel-type cultivar proved unsuccessful, and the naturally selected Cavendish variety replaced Gros Michel as the main export variety. The United Fruit Company decided to withdraw from genetic improvement research in 1984 and donated its programme to the Honduran Government. Nevertheless, *Musa* breeding continued and the programme is now maintained by the Fundación Hondureña de Investigación Agrícola (FHIA).

A major constraint for *Musa* breeding programmes is the breeding behaviour of the crop. Most important cultivars, both for export and local consumption, are triploid, and triploidy leads to problems during meiosis due to uneven numbers of chromosomes. Consequently, *Musa* cultivars exhibit low seed set and poor seed germination. Indeed, some cultivars, such as the important export variety Cavendish, are almost completely sterile and can only be used with difficulty in breeding. The complicated nature of breeding bananas, together with a lack of appreciation of its importance

as a staple food crop, has meant that relatively few funds have been directed by either the private or public sector to banana breeding. Indeed, until the 1980s there were effectively only two banana breeding programmes in existence (Honduras and Jamaica), both of which focused on improving bananas for the export market.

The basic breeding procedure developed in the late 1920s in Trinidad and Jamaica (ICTA) relied on the use of natural diploids and later on the production of improved 'elite' diploids, which were then used as male parents for crossing onto the desired triploid as the female parent in the production of improved tetraploid progeny. One limitation to this strategy is the low level of female fertility in desirable triploids. Cavendish, for example, being highly sterile, is a very poor female parent. While the quest to develop a dessert-type variety able to replace Cavendish continues, the advanced diploids are now also being used to great effect in the improvement of other types of bananas and plantains. Breeding work in Honduras now has a global focus and efforts are being made to produce plantains and other types of cooking bananas suitable for smallholder production in Africa and Asia as well as in Latin America.

The basic breeding scheme developed by ICTA has been adopted by several new breeding programmes that have emerged, including those of the International Institute for Tropical Agriculture (IITA) in Nigeria and Uganda; CIRAD, France; Centre Régional de Recherches sur Bananiers et Plantains (CRBP), Cameroon; and Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Brazil. All these programmes use breeding schemes involving either natural diploids (wild seeded species or edible landraces) or improved diploids for the production of improved tetraploid hybrids. In addition, CIRAD has developed a new breeding scheme that has resulted in the synthesis of triploid varieties solely from natural or improved diploid varieties (Horry *et al.*, 1997). Breeding using genetic transformation technology is also being carried out at a number of institutes, including the Katholieke Universiteit Leuven (KUL), Belgium; Queensland University of Technology (QUT), Australia; CIRAD-FLHOR, France; the Boyce Thompson Institute (BTI), USA; and the University of Hawaii, USA. Most of the main sub-groups of bananas are now being addressed by one or more of the breeding programmes (see Table 12.2).

Despite the efforts of the various *Musa* improvement programmes, production for both the export market and local consumption still depends essentially on farmers' varieties selected from naturally occurring germplasm. The absence, until very recently, of improved cultivars has been attributed to the difficulties of breeding *Musa* at the genetic and practical levels (Ortiz *et al.*, 1995). Genetic improvement has been severely hampered by the lack of useful genetic variability (i.e. in cultivars that are either male or female fertile) and low levels of female fertility (for crossing with improved diploids developed as male parents).

Applications of biotechnology in breeding

Musa improvement programmes are making increasing use of a wide range of biotechnological tools in order to improve breeding efficiency in bananas. A comprehensive review of this is provided by Crouch *et al.* (1998). Techniques such as embryo rescue are now used routinely to overcome some of the barriers to hybridization. Indeed, embryo rescue has increased seed germination rates by a factor of 3–10 at IITA, and

Table 12.2. Focus and aims of the main *Musa* breeding programmes (information obtained from Frison *et al.*, 1997a).

Breeding programme	Focus	Aims	Production area
FHIA Honduras	Export bananas	Sigatoka resistance	LAC, Asia, Australia
	Plantains	Dwarf, disease resistance	West and Central Africa, LAC, India
	Cooking bananas	Dwarf, disease resistance	Asia, East Africa
IITA Nigeria	Plantains	Disease resistance (Sigatoka), high stable yield, wide adaptability, fruit quality, disease resistance	West and Central Africa
IITA Uganda	AAA–EA Highland bananas	(Fusarium), high stable- yield fruit quality	East Africa
CIRAD, France	AAA export bananas	Disease and pest resistance	ACP countries, French West Indies West Africa, LAC, East Africa, Pacific
	AAA/AAB cooking/ dessert bananas	Disease and pest resistance	
CRBP, Cameroon	Plantains	Disease and pest resistance	West and Central Africa
EMBRAPA, Brazil	AAB dessert bananas	Disease resistance (Sigatoka, Fusarium, Moko)	South America, Asia
Banana Board, Jamaica	AAA export bananas	Disease resistance (Sigatoka, Fusarium)	LAC, Australia
IAEA, Vienna	AAA–Cavendish	Dwarf, disease resistance	LAC/Asia
TBRI, Taiwan	AAA–Cavendish	Fusarium resistance, dwarf, short cycle	Asia

ACP: Africa, Caribbean, Pacific; CIRAD: Centre de Coopération Internationale en Recherche Agronomique pour le Développement; CRBP: Centre Régionale de Recherches sur Bananiers et plantains; EA: East African; EMBRAPA: Empresa Brasileira de Pesquisa Agropecuária; FHIA: Fundación Hondureña de Investigación Agrícola; IAEA: International Atomic Energy Agency; IITA: International Institute for Tropical Agriculture; LAC: Latin America and Caribbean; TBRI: Taiwan Banana Research Institute.

micropropagation has played a key role in the rapid propagation of large numbers of male and female parents for crossing blocks (Ortiz *et al.*, 1995). Colchicine treatment has also been used extensively to double the chromosome number of selected diploid clones, and this forms part of the breeding strategy adopted by the CIRAD breeding programme (Horry *et al.*, 1997).

A number of research groups are also working on *Musa* molecular genetics with the aim of developing marker-assisted breeding strategies.

Genetic transformation

Most banana breeding, both for export and local cultivars, is focused on the introduction of pest and disease resistance. Although sources of resistance to the major pests and diseases (Sigatoka diseases, Fusarium wilt and nematodes) have been identified, the introduction of such useful genes into sterile cultivars may only be possible through the use of genetic transformation techniques. Research in this area has progressed rapidly in recent years, and stable, genetically transformed banana plants have been produced (May *et al.*, 1995; Sági *et al.*, 1995, 1999).

Extent of Diversity Utilized by *Musa* Breeding Programmes

Conventional breeding

Diploids, both wild and cultivated, are widely used in breeding programmes as sources of resistance to diseases and pests. The wild species *M. acuminata* and *M. balbisiana* are generally used as male parents in crosses, particularly in the development of 'elite' diploid hybrids for further crossing on to triploid cultivars as female parents. While resistance traits may be transferred from wild species, often these are transferred together with unfavourable agronomic features, such as poor bunch size and long fruiting cycles. Other wild *Musa* species have not been used by breeding programmes, although interspecific fertility is not necessarily a problem. It is known, for example, that *M. schizocarpa* hybridizes readily with *M. acuminata* in the wild, and this species has proved to be involved in the ancestry of some cultivars (Careel *et al.*, 1993). Other species, such as *M. textilis*, have also been implicated in the domestication of bananas (Careel, 1995) but are not presently being used by breeding programmes. Cultivars are used in breeding mainly for their favourable agronomic characteristics.

Breeding for resistance

Pests and diseases are the main constraints to banana production at the global level. Resistant varieties are the base upon which sustainable systems of production at the smallholder level can be developed. Genetic improvement is therefore aimed at the introduction of resistance. Black Sigatoka leaf spot disease caused by *Mycosphaerella fijiensis* is considered to be the most serious constraint to banana production globally. This pathogen, to which many important and widely grown cultivars are susceptible, can cause severe leaf necrosis reducing yields by 30–50% and losses of up to 100% of marketable quality fruit. The cost of controlling the disease in Costa Rica alone is estimated at \$50 million annually and involves some 38–50 fungicide-spraying operations. Such control measures are obviously beyond the means of the majority of small-scale producers.

Fusarium wilt is a soil-borne disease which affects many important cultivars of banana and plantain. This disease has a long and destructive history. Caused by the fungus, *Fusarium oxysporum* f. sp. *cubense*, it almost destroyed the export trade, which was exclusively based on the susceptible cultivar Gros Michel, during the first half of the 20th century. Gros Michel plantations were then replaced by Cavendish, a resistant dessert-type cultivar. Cavendish varieties are, however, susceptible to race 4 of the pathogen, which causes losses in subtropical areas such as Taiwan, Australia and South Africa, and a tropical race 4 has recently been reported in Southeast Asia.

In addition, a complex of plant parasitic nematodes (*Radopholus similis*, *Pratylenchus* spp. and *Helicotylenchus multicinctus*) cause serious crop losses in all regions. Nematode infestations interfere with nutrient uptake and transport, resulting in slow growth, reduced fruit filling and susceptibility to wind lodging.

Sources of resistance to these major pests and diseases have been identified, together with genes controlling a number of other traits. Genetic studies at IITA, for example, have resulted in the identification of genes controlling resistance to black Sigatoka and weevil borer, virus susceptibility, dwarfism, albinism, suckering behaviour, parthenocarpy and male/female fertility (Horry *et al.*, 1997). However, identified genes for resistance are still generally considered to be from too narrow a base, and greater efforts are required in identifying further sources of resistance (INIBAP, 1998).

The main source of black Sigatoka resistance originally utilized in breeding was Calcutta 4, a wild, non-edible diploid banana. A model to explain the inheritance of this resistance to black Sigatoka has been developed by Ortiz and Vuylsteke (1994a). The resistance in plantain–Calcutta 4 hybrids appears to involve one major recessive gene and two additive minor genes with dosage effects (Craenen and Ortiz, 1997). However, the high level of resistance shown by Calcutta 4, although thought to have a polygenic basis, has already been overcome by the pathogen in the Pacific (Fullerton and Olsen, 1993). Alternative sources of resistance are obviously required and IITA have now identified more than 30 sources of resistance in their germplasm collection, most of them diploid *M. acuminata*, (AA) both wild and cultivated types (Vuylsteke *et al.*, 1997). Different sources of resistance are now being incorporated in a single genotype by crossing tetraploid hybrids of Calcutta 4 parentage with other resistant diploids with the hope of generating durable host plant resistance.

In relation to Fusarium wilt, although natural sources of resistance do occur in wild and cultivated *Musa*, different resistances are required for the different races of the pathogen. Segregation in progenies derived from crosses between three susceptible *Musa* spp. and the resistant cultivated diploid banana Pisang Lilin suggested in the latter the presence of a single dominant gene for resistance to *Fusarium* race 1. However, resistance to race 4 seems to be under polygenic control (Rowe and Rosales, 1993). Further sources of resistance to tropical race 4 are particularly required in view of the fact that the widely grown Cavendish cultivars are susceptible to this race of the pathogen, and no chemical control measures are available.

Resistance to the nematode species *R. similis* has been identified in the cultivar Pisang Jari Buaya, and this has been used extensively by banana breeders. It appears that one or more dominant alleles control this resistance (Rowe and Rosales, 1993). Further sources of resistance to this pathogen as well as to the other nematode species affecting *Musa* are still required.

In all cases, the identification of sources of resistance requires time and money. The development of early screening tests, whereby seedlings or *in vitro* plantlets can be tested for resistance under laboratory or nursery conditions, will go a long way towards facilitating this work. This, along with increased characterization of existing collections, will assist breeding programmes in identifying germplasm with useful traits with which they can enlarge the number of cultivars or wild species utilized in the breeding of improved varieties.

Recent reviews of *Musa* breeding activities are given by Ortiz *et al.* (1995), Bakry *et al.* (1997) and Ortiz and Vuylsteke (1994b)

Mutation breeding and somaclonal variation

Spontaneous mutations have contributed to the genetic diversification of the *Musa* gene pool, and the induction of mutations through the irradiation of *in vitro* cultures of banana is currently performed by several teams, including the International Atomic Energy Agency (IAEA; Austria), the Queensland Department of Primary Industry (QDPI; Australia) and Instituto de Biotecnología de las Plantas (IBP; Cuba). Although few clones of interest have so far been produced, an early flowering Cavendish clone has been selected in Malaysia from a mutant Cavendish clone produced through irradiation by the IAEA (Ortiz *et al.*, 1995), while a *Fusarium*-resistant Gros Michel has been identified in Cuba (INIBAP, 1997a).

Somaclonal variation, or genetic variation resulting from the *in vitro* process, can also be exploited in *Musa* breeding. Somaclonal variation, however, closely parallels natural variability (Israeli *et al.*, 1995) and thus should not be considered as a source of new diversity. Nevertheless, a *Fusarium* race 4-resistant Cavendish clone has been selected by the Taiwan Banana Research Institute (TBRI) in Taiwan (Horry *et al.*, 1997). Other examples of useful somaclonal variants are a Mons Mari (AAA) variant with long fruit (Smith and Drew, 1990) and a female fertile variant in plantain (Vuylsteke, 1991).

Possibilities for decentralized breeding

The possibilities for developing decentralized breeding in plantains are presently being explored by IITA (Ortiz, 1997). Plantain-derived tetraploid hybrids are routinely crossed with diploid accessions for the production of triploid hybrids for evaluation. However, natural open pollination of the same tetraploid hybrids also produces viable seed, and the elite performance of certain hybrids generated in this way offers possibilities for breeding. Under the proposed programme, primary tetraploid germplasm would be crossed with selected diploids using controlled artificial hand-pollination, or through polycrosses among selected parents. Synthetic populations derived from these crosses could then be released to other improvement programmes for evaluation and selection of promising clones. Such a programme would allow breeding programmes and national agricultural research systems (NARSs) early access to potentially elite material and, importantly, allow selection of promising lines under local agroenvironmental conditions.

Diversity and the Smallholder Farmer

At the beginning of the 21st century, smallholder farmers throughout the tropics continue to cultivate a wide diversity of *Musa* germplasm. Up to very recently, there has been virtually no replacement of local cultivars by improved material from breeding programmes. Thus, throughout Africa and Asia a wide range of landraces is still being cultivated by farmers (Sharrock and Engels, 1997). Despite more than 70 years of banana breeding, it is only in the last few years of the 20th century that breeding programmes produced material that is considered to be superior to naturally occurring clones. Wide-scale, multilocational testing of improved varieties from breeding programmes first started in 1991 with the establishment of the International *Musa* Testing Programme, coordinated by INIBAP and funded by the UN Development Programme. As a result of this programme, three improved hybrids from FHIA were identified as performing well over a range of environments and showing significant levels of disease resistance. These were therefore recommended for further evaluation and testing at the national level, and since 1993 they have been distributed to more than 50 countries.

In most countries, evaluation is carried out by the public sector, although in some instances non-governmental organizations (NGOs), universities and private companies may also be involved. One of the main constraints to the rapid distribution of new varieties to farmers is the slow rate of propagation of bananas under field conditions. In addition, the cycling period of the crop means that evaluation over two to three cropping cycles takes a period of more than 2 years. In most countries, therefore, improved varieties are still undergoing evaluation and are not yet widely available to farmers. One exception to this is Cuba, where the necessary infrastructure has been put in place to allow the rapid mass-propagation of banana planting material using 'bio-factories'. The Cuban government has put much effort into identifying new, disease-resistant varieties, introducing these into the country, mass propagating them and distributing them to farmers. By early 1998, around 8000 ha had been planted with a range of improved varieties: this represents some 7.6% of the total banana production area. These resistant cultivars are increasingly replacing black-Sigatoka-susceptible banana and plantain clones on the island.

Despite the lack of introduced improved varieties, losses of diversity in farmers' fields are undoubtedly occurring. Increasing trends towards commercialization, particularly for sale in expanding local and regional markets, in India and other Asian countries favour the establishment of single-cultivar plantations over mixed farming. In addition, the spread of diseases such as black Sigatoka into areas of smallholder production where chemical control measures are unavailable may result in the loss of the most susceptible cultivars.

However, even in areas where farmers still cultivate a range of different varieties, there is a continuing need for diversity to be made available. The spread of pests and diseases into new areas results in a need for resistant germplasm. Likewise, increasing urbanization means that there is a growing demand for varieties suitable for sale in local markets. In many countries the lack of systems for the mass propagation and distribution of germplasm is a major bottleneck to the availability of new cultivars. Many countries possess germplasm collections, but incomplete characterization and evaluation of accessions in the collections means that potentially useful accessions have not been identified. Finally, the acquisition of germplasm from other countries is con-

strained by quarantine requirements, which usually makes the introduction of new varieties a costly and time-consuming exercise.

An important consideration in the introduction of 'new' diversity to farmers is the very specific needs of both producers and consumers in both pre- and post-harvest qualities of the crop. Needs vary considerably from place to place and these may not easily be addressed by acquiring improved germplasm from breeding programmes that operate at the global, or even regional level. A similar constraint exists with traditional varieties acquired from other areas. It is clear that the level of resources required for breeding *Musa* precludes the development of breeding programmes in every country. Furthermore, the reproductive nature of the crop means that farmer-participatory breeding schemes are much more difficult than with seed-propagated crops. One possible solution to these problems, however, could lie in the adoption of the type of decentralized breeding scheme described on page 235. Above all, mechanisms to allow the feedback of information from farmers to breeding programmes are essential, and farmer-participatory evaluation of germplasm can play an important role in this regard.

The Role of Networks

Networks at the global level

The number of *Musa* improvement programmes in existence today is very small considering the scale of the problems to be addressed. In an effort to maximize the output and accelerate the impact of these limited *Musa* improvement efforts, PROMUSA, the Global Programme for *Musa* Improvement, was established in 1997 as a joint initiative of INIBAP and the World Bank. This programme was developed as an innovative mechanism to bring together research carried out both within and outside the CGIAR, creating new partnerships between NARSs and research institutes in both developing and developed countries. The programme specifically aims to bring together, at the global level, all the major players in *Musa* improvement research.

Within the framework of PROMUSA, a *Musa* genetic improvement working group has been established, bringing together all the major *Musa* breeding programmes, including those focusing on breeding using conventional hybridization techniques and those using mutation breeding and genetic engineering approaches.

At the first meeting of the Genetic Improvement Working Group, priority research needs were identified, which included the need for enhanced utilization of plant genetic resources by breeding programmes. It was noted that breeders need better access to existing collections for increased availability of *Musa* germplasm. Where gaps are identified in these collections, targeted exploration and collection of germplasm should be considered, with a particular focus on wild species. It was recognized that attention should be given to the whole range of *Musa* species, not just *M. acuminata* and *M. balbisiana*. To improve access to existing collections, it was recommended that more effort should be put into characterization and evaluation of the germplasm and that the ensuing databases/information should be exchanged between collections and breeders (Frison *et al.*, 1997a).

INIBAP is presently addressing this issue with the development of the *Musa* Germplasm Information System (MGIS). The software for this system has recently

been completed, and curators of collections are now able to input data on the accessions in their collections. The aim is to collect together in a single format characterization and evaluation data for *Musa* germplasm in existing collections worldwide and make these available to interested parties.

During the first meeting of the Genetic Improvement Working Group, it was also agreed that molecular knowledge of the complex genome structure of bananas and plantains is essential in order to better understand *Musa* genetics. It was recognized that the lack of segregating populations is a major obstacle to rapid progress in the identification of molecular markers and their use in *Musa* breeding, and that molecular markers are necessary to increase the efficiency and effectiveness of banana improvement efforts. Within the framework of PROMUSA, INIBAP has therefore recently initiated a project for the production of additional segregating populations and the identification of molecular markers using these.

The various working groups that have been established within the framework of PROMUSA (Sigatoka, Fusarium, Nematodes, Viruses and Genetic Improvement) operate as networks, within which the exchange of information, germplasm (such as parental material from breeding programmes), etc., is facilitated. The networking approach encourages the development of collaborative projects and the creation of synergies. All network members participate in the identification of priorities for the group as a whole and are fully involved in the decision-making process.

INIBAP's International *Musa* Testing Programme, which now operates within the framework of PROMUSA, also adopts a networking approach for the evaluation of germplasm. In this programme, NARS partners use a common evaluation format developed through a participative process to evaluate germplasm provided by a number of *Musa* breeding programmes. Improved material as well as potential breeding parents may be evaluated within this programme. The multilocal nature of the programme allows genotype \times environment effects to be studied in improved varieties. The inclusion of an evaluation mechanism in PROMUSA also provides the necessary opportunity for the feedback of information to the breeding programmes.

The advantages of bringing interested parties together in a global programme such as PROMUSA to address specific research issues are many (Frison *et al.*, 1997b). They include:

- Development of new and innovative partnerships between programme participants, who may be advanced research institutes (ARIs), international agricultural research centres (IARCs), Universities, NARSs, NGOs, private sector.
- Global prioritization of research needs.
- Improved possibilities for funding for programme participants.
- Improved access to information and resources.
- Opportunities for interdependent research projects.

Networks at the regional level

Regional banana research networks have been established in Latin America and the Caribbean (INIBAP-LACNET), Asia and the Pacific (INIBAP-ASPNET), eastern and southern Africa (BARNESA), and West and Central Africa (MUSACO). INIBAP provides the coordination and secretariat function for these networks, which have

proved to be powerful tools in priority setting and in the development of regional collaborative activities. Results and information are exchanged between members of the networks, thus facilitating the creation of synergies and minimizing the duplication of efforts within the region. Regional networks are also responsible for organizing meetings, training courses, workshops and seminars as appropriate for network members.

In relation to the use of *Musa* diversity, the regional networks have an important role to play. They provide a forum for the exchange of information on *Musa* germplasm available within the region and outside. Collaborative projects and scientific exchange visits between network members allow national scientists to become familiar with varieties being cultivated in other countries in the region. INIBAP provides a global dimension, keeping each region in touch with developments in other regions. INIBAP also plays a service role in germplasm conservation and distribution. Through the regional networks, INIBAP is able to maintain close contact with national research activities and provide them with appropriate germplasm.

Networking is an important means of ensuring efficiency and effectiveness in germplasm evaluation and distribution activities. At the regional level, both IITA and CRBP collaborate with NARSs for the evaluation of germplasm. A key feature in the success of this type of collaboration is the development of horizontal relationships between the network partners (Ortiz and Vuylesteke, 1994b).

Networks at the national level

Within the support of the regional networks, national partners are now beginning to develop national *Musa* research networks. In addition to research institutes and universities, countries are encouraged to include NGOs, farmers' organizations and extension agencies in such networks, thus providing an important link with the ultimate end-user of germplasm, the farmer. The bringing together of users and extension agencies is a particularly important step in facilitating and encouraging the use of diversity. National *Musa* networks of varying levels of formality have now been established in a number of countries, in several cases as a direct result of encouragement and support from the regional network.

Thailand provides a useful example of the development and benefits of networking at the national level. A functioning national *Musa* network has been established and a coordinated National Banana Programme developed. Twelve institutes, with approximately 80 scientists, participate in banana research activities coordinated by the network. A Banana Working Group set up under the supervision of the Horticultural Research Institute complements the network. An example of the resulting increased activity is national funding for selection and improvement of two of Thailand's most important banana cultivars for domestic consumption and trade (Kluai Kai and Kluai Namwa) (INIBAP, 1997b).

Conclusions and Recommendations

Although locally important in several countries, the use of diversity is still at an early stage in global banana and plantain production. This is true as much for the direct use

of existing diversity by farmers as it is for attempts at genetic base-broadening in *Musa* improvement programmes. There has been relatively little movement of germplasm from country to country or region to region, and few varieties have had any impact outside their traditional areas of production. It is only in recent years that a system has been put in place for the safe movement of *Musa* germplasm and the necessary virus-indexing capabilities established. In the past, the international movement of *Musa* germplasm was severely restricted by the high risks involved.

Increased efforts in the following areas are required in order to facilitate and enhance the use of *Musa* germplasm:

- Further evaluation of existing cultivars, particularly in relation to disease resistance, in order to identify material that may have potential for direct use by farmers.
- Increased characterization of material in collections and use of the MGIS in order to allow the rapid dissemination of information to potential users (breeders, extensionists, etc.).
- Greater knowledge of the resources available in the wild species is needed before breeders will be prepared to make use of them in breeding programmes.
- Tools, such as molecular markers, are required in order to reduce the time taken to breed new varieties.
- Virus indexing remains a bottleneck. More efficient indexing techniques, together with increased capacity, are required to speed up virus-indexing procedures.
- Virus therapy techniques are required in order to make accessions presently infected with virus available for international distribution.
- Increased, sustainable support to breeding programmes is essential to ensure the continued production of a diverse range of new hybrids for evaluation.

Finally, and perhaps more importantly, is public awareness. There is a continuing need to raise the awareness amongst scientists, policy makers and indeed the general public of the importance of bananas and plantains as a staple food crop. In the last few years of the 20th century, some of the barriers to hybridization in *Musa* were overcome and the first improved varieties ever produced by breeding programmes have been released for widespread testing. However, many research needs remain and, particularly in this time of scarcity of resources, it is important that a crop with the global significance of bananas and plantains does not continue to be neglected by researchers and donors alike.

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13 Dynamic Management of Genetic Resources: a 13-year Experiment on Wheat

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Introduction

Dynamic management (DM) of genetic resources was described by Henry *et al.* (1991) as a complementary strategy to genebanks for conserving genetic resources. The principle of DM is to maintain the evolutionary mechanisms in subdivided populations grown in different environments. Whereas there is an obvious risk of losing some individuals or some alleles, new alleles and genotypes are expected to appear in this system by means of recombination, mutation and migration. Such a DM approach has been experimentally tested in France since 1984 using wheat composite populations (Henry *et al.*, 1991). More recently, it was proposed that DM could also be used as a kind of pre-breeding strategy (Goldringer *et al.*, 1994). The idea was to obtain a gradual increase in the specific adaptation of the different populations to the local conditions of their multiplication sites in order to select interesting parents. In fact, developing these aspects brings DM very close to approaches earlier described as 'mass reservoirs' or 'base-broadening' (Simmonds, 1962). Still earlier, Suneson (1956) had proposed the use of composite cross populations as a base for a new breeding approach, which he called an 'evolutionary plant breeding method'. To support this idea, the author demonstrated the continuous increase in yield of four barley populations growing under competitive natural selection for 12–29 generations. Hence, we think that any kind of DM programme can be conducted with the objective of either variability conservation or germplasm enhancement, or maybe both at the same time.

Great advantages of these methods are that they do not need high-technology equipment, they are easy to decentralize, and hence they may be carried out by farmers, breeders and local technical centres. Moreover, they allow farmers to be involved in developing the parents of new varieties. The positive aspects of farmer-participatory

breeding, particularly in the developing countries, have now been acknowledged (Ceccarelli *et al.*, 2000) where the specific needs of many farmers are often not considered by the breeders.

The purpose of this chapter is, first, review the available results concerning the wheat DM experiment and, secondly, to discuss the possible use of the DM approach as a conservation strategy as well as a pre-breeding or base-broadening method.

The Wheat Experiment of Dynamic Management: Principle and Experimental Protocol

Principle of the dynamic management of genetic resources

The aim of a DM approach is to maintain or mimic natural processes responsible for the diversification and conservation of genetic diversity. Rather than choosing and protecting one or several sites significant for the diversity of a species (for example, in the gene centres) as in the case of 'classical' *in situ* conservation, polymorphic composite cross populations are introduced into contrasting environments so that the different sub-populations evolve under the effects of natural selection, genetic drift and mutation. While each sub-population is expected to lose some of its initial variability due to drift and selection in a particular environment, diversity is expected to be maintained at the level of the metapopulation due to genetic differentiation. As random losses of alleles are expected to be different in each sub-population, the conservation of 'neutral' allelic diversity will depend on the total number of sites. On the other hand, selected variability will be maintained only if the sites differ sufficiently in respect of the selective pressures. In such conditions, the network of populations will also allow new favourable mutations to be captured in the individual sub-populations.

If there is no migration between populations, evolution of the sub-populations and their adaptation to the environmental conditions will depend on the initial genetic variability in the population, on the size of the sub-populations combined with the strength of the selection pressures, and on the mating system. For the latter, theoretical studies showed that, in a finite population under directional selection, the optimal adaptive response (accumulation of positive alleles) was obtained with a low outcrossing rate (David *et al.*, 1993). Such a mixed mating system combines rapid fixation of the good genotypes due to a high level of selfing, and mid- to long-term adaptation due to recombination between these genotypes. Moreover, it allows efficient purging of the mutational load, which might accumulate in populations of pure selfers that had a relatively low effective size.

In a sub-population, the relative effect of selection compared with genetic drift will be all the lower as the population size is small. Even for medium-sized populations, useful variability might be lost within a population through genetic drift and hitch-hiking effects of selection. Hence, it is necessary to maintain some migration between populations so as to renew the variability within each population. The amount of gene flow between populations has to be determined taking account of the effective size of the populations and the degree of differentiation between populations that is desirable.

Arguments in favour of migration between populations also come from the 'shifting balance theory' of Wright (1931, 1982). This predicts that populations will evolve

until they reach the nearest adaptive peak of the fitness surface (known as 'adaptive landscape') and then will not be able to evolve to a better combination of favourable genes since this would involve crossing a maladaptive valley. Such crosses would be possible owing to changes in allele frequencies in the population after a bottleneck event or with migration from other populations.

Dynamic management has been proposed for woody species (Eriksson *et al.*, 1993). For crop species, the pioneering study is that conducted on barley populations in the United States since 1928 (Harlan and Martini, 1929; Allard, 1988, 1990), despite the fact that only two environments were used initially. This experiment on barley inspired the experiment on dynamic conservation of genetic resources of wheat described below.

The dynamic management experiment

Institutional framework

A pilot programme for the DM of genetic resources of winter wheat (*Triticum aestivum* L.) has been conducted by the Direction Générale de l'Enseignement et de la Recherche of the Ministry of Agriculture (DGER, France) and by the Institut National de la Recherche Agronomique (INRA, France) since 1984 (Henry *et al.*, 1991). The experiment relies on the willingness of agricultural teachers who manage many of the populations. One important aim of this programme is to increase the awareness, in future farmers and agricultural technicians, of genetic diversity and the necessity of conserving genetic resources. In the French agricultural context, specific equipment adapted to experimental cultivation and labour with the required technical skill are mostly to be found at agricultural schools or research stations. It seems difficult to involve farmers who are trained and equipped for large-scale field work. However, this may not be the case in areas where a more traditional agriculture still exists.

Plant material

Three initial composite populations (PA, PB and PS) were created by crossing 16 parental lines pyramidally for PA and PB populations (Thomas *et al.*, 1991; David *et al.*, 1997) and by two successive random crosses of 62 lines for PS population. Whereas PA and PB were predominantly selfing, outcrossing was forced in PS in each generation using the recessive male-sterility nuclear gene *ms1b* (McIntosh, 1988). The genetic base of PB was wider than that of PA due to the presence in the former of more exotic lines among the parents. Dwarfism genes were present in disjunction in all three initial populations.

Network and protocol

In 1984, after 3 years of bulk multiplication, seed samples of the three initial populations were distributed to the sites of the multilocational experimental network (Fig. 13.1). The populations were not represented in each locality but there were seven locations for PA, nine for PB and 12 for PS (for more details, see Henry *et al.*, 1991). Two methods of cultivation were used in each site: an intensive farming method, which corresponded to the method usually used for wheat in the area, and an extensive farming method, with one-third of the nitrogen fertilizer used in the intensive method

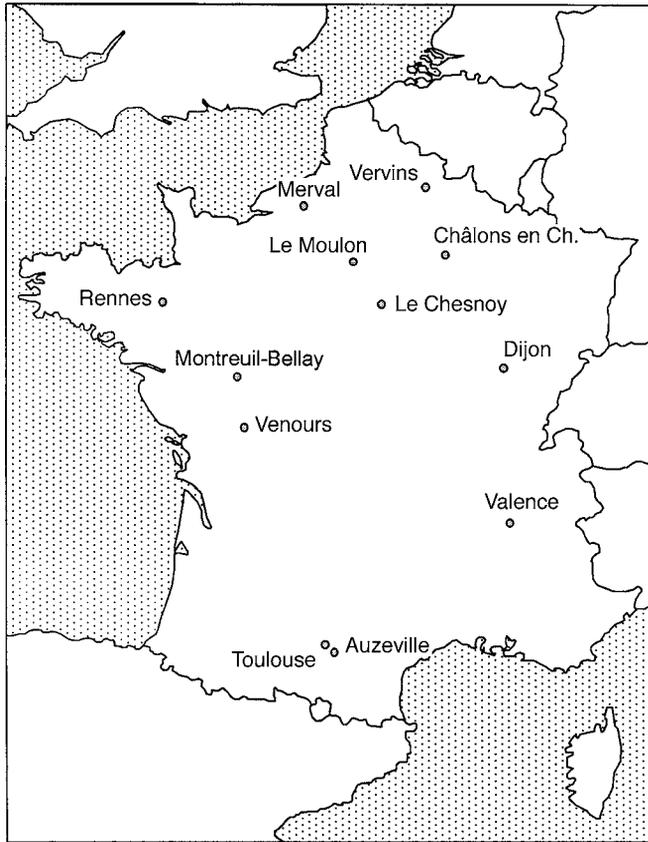


Fig. 13.1. Network for the dynamic management of the wheat genetic resources programme (DGER of the French Agriculture Ministry, INRA, INA-PG and BRG).

and no fungicide treatments. Since 1984, each of the local populations has been cultivated every year without any conscious human selection, using seeds of the same population harvested the previous year in the same location under the same culture condition. The allogamous mating system in PS is maintained because only seeds from the male-sterile plants are harvested each year. A 100 m² cultivated area was generally used so as to obtain around 10,000–15,000 plants per population. For PS populations, male-sterile plants were identified at flowering time and around 2000 plants were harvested. For the self-pollinating populations, PA and PB, 10,000 individuals corresponded to about 5000 individuals of a panmictic population. A demographic size of a few thousand individuals was chosen since it was expected that the genetic drift would be very limited. The outcrossing PS populations were sometimes preferred by the teachers participating in the work because they gave the opportunity of doing practical work with the students and because no specific equipment was required for the harvest. All the populations were isolated from each other and from neighbouring crops to avoid unwanted cross-pollination.

Results

Each year, a sample of the seeds harvested for each population is stored in a centralized cold room. These have been used for comparative studies in different experiments: seeds from some of the samples have been grown in order to evaluate plants from different populations in the same location. Six years of multiplication were sufficient for the first significant changes to appear.

Evolution of agromorphological traits

The mean plant height of all the populations of the autogamous PA and PB pools increased compared with the initial situation (David *et al.*, 1992; Le Boulc'h *et al.*, 1994). This increase was interpreted as the result of the competition for light between plants of a local population. Because the founding populations contained both dwarf and non-dwarf alleles at two major loci (*Rht1* and *Rht2*), there was large phenotypic variability. Competition for light therefore led to rapid evolution in the populations (Pontis, 1992). Plants taller than the tallest plants of the initial populations were also found, indicating that recombination and selection of quantitative polymorphic loci had occurred. Populations PA and PB cultivated in intensive conditions became taller than the populations grown extensively. This may well have been due to a more severe competition between plants in intensive conditions, since the higher nitrogen input amplified height differences (Le Boulc'h *et al.*, 1994).

A north–south gradient of earliness was found among the PA and PB populations (David *et al.*, 1992). The populations cultivated in the south of France became earlier than those cultivated in the north (Fig. 13.2). This was interpreted as an adaptation to climatic constraints. In the south of France, heat and water stress appear early during plant development, and seed filling of late maturing plants may be hindered, whereas in the north these stresses seldom happen and late-maturing plants can accumulate more dry matter (Le Boulc'h *et al.*, 1994).

Besides selection pressures due to climate and soil (physical environment), the response of the populations to biotic selection pressures was studied. The resistance to powdery mildew (*Erysiphe graminis* f. sp. *tritici*) was selected for investigation, since the disease is widespread and can lead to yield reductions in wheat monoculture. Le Boulc'h *et al.* (1994) found significant changes in the frequencies of some specific resistance genes to powdery mildew in the PA and PS populations after 8 years of multiplication. Although these changes differed with multiplication site and initial population, they were not related to the spectrum of virulence genes of the pathogen populations in the different sites. In each genetic pool, individuals were found that accumulated more resistance genes than any individual analysed in the initial population (three genes versus two genes in PA; four genes versus one in PB; more than four genes versus three in PS). Adult field resistance results from the combined expression of specific resistance genes and other quantitative factors that control partial resistance. In the DM populations, adult resistance also differed with multiplication site and initial population (PA, PB or PS). Comparing mean adult resistance of all the populations with the resistance of the corresponding initial population showed no significant difference for pool PA, a slight decrease in pool PB, and an increase in pool PS. These results differ markedly

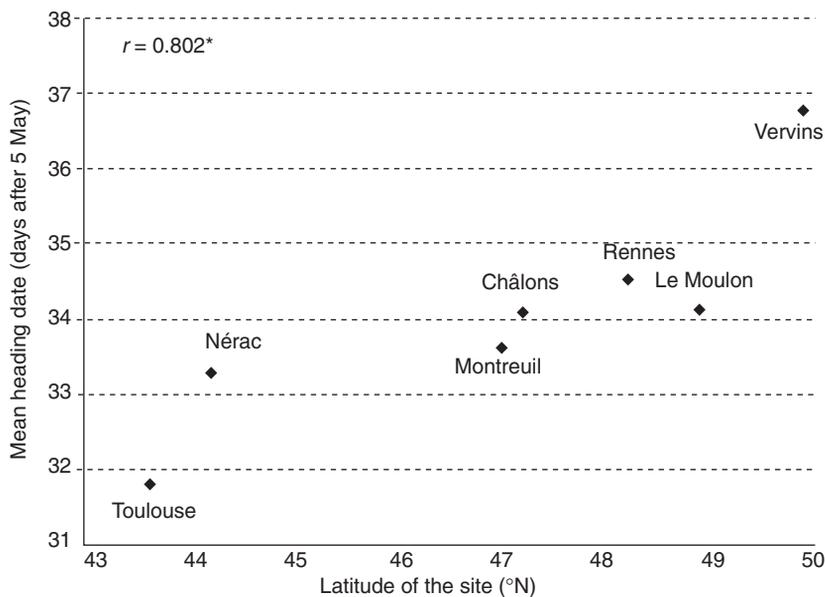


Fig. 13.2. North–south earliness gradient in pool A populations (sixth generation) evaluated at Le Moulon in 1991.

Source: Le Boulc'h *et al.*, 1994.

from those obtained for barley populations in which Allard (1990) and Ibrahim and Barrett (1991), respectively, found an increase of resistance to *Rhynchosporium secalis* (after about 40 generations) and to *Erysiphe graminis* f. sp. *hordei* (after nine generations). In the wheat–powdery mildew interaction, the rapid evolution of the pathogen due to its sexual mating system and its high dissemination level leads to a rapid rotation of its avirulence genes at any given site. This may explain a response that consisted of the accumulation of different resistance genes rather than a general increase in the frequency of one gene. It also underlines the recombination which allowed the pyramiding of genes involved in adaptation to changing environments.

Resistance to *eyespot* was also studied on a sub-set of the short lines extracted from six PA and six PB populations after ten generations. A major resistance gene (*Pch1*) derived from the interspecific crosses with *Aegilops ventricosa* was polymorphic in the initial populations. This gene can be easily identified with seedling tests. Fifty inbred lines per population were tested at INRA Le Rheu in 1996 and 1997. The results showed significant differences in the frequency of the gene according to the multiplication site (Table 13.1). Differences were much greater in PA than in PB. In PA, *Pch1* frequency increased in the sites where the pathogen was more likely to be found, i.e. Vervins, Rennes Châlons, in the north of France. In both pools, the mean frequency over the populations was not different from the initial one, giving evidence of the maintenance of the gene at the metapopulation level.

Some important traits such as grain yield proved to have evolved in each population according to local conditions, although it was not possible to identify the specific physical or biotic characteristic of the environment to which these evolutions were

Table 13.1. Frequency of the phenotype 'resistant' for *Pch1* locus (homozygous + heterozygous lines) in 11 PA and 15 PB populations (after ten generations) and in the initial populations PA0 and PB0.

Populations	Frequency of resistant phenotype at <i>Pch1</i>			
	PA		PB	
	Intensive	Extensive	Intensive	Extensive
<i>Initial population</i>	0.24		0.27	
<i>Final populations:</i>				
Châlons	0.25		0.25	
Le Chesnoy	—	—	0.10	0.21
Le Moulon	0.09	0.17	0.47	0.24
Montreuil	0.08	0.00	0.09	0.12
Rennes	0.35	0.37	0.50	0.15
Toulouse	0.11	0.30	0.07	0.08
Venours	—	—	0.00	0.14
Vervins	0.81	0.23	0.37	0.07
Mean of the final populations (Int. + Ext.)	0.25 ^a		0.19 ^a	

^a Means were not significantly different from the frequencies of the initial populations.

related. This is illustrated by the correlation found ($r = 0.78$, Fig. 13.3) between yields evaluated at Le Moulon and Clermont-Ferrand in 1991 of PA and PB populations originating from the same site and the same cultural condition (David, 1992). Such positive and significant correlations were found for other traits, although correlations between PA or PB populations and the corresponding PS populations were never significant, again indicating that the outcrossing populations showed specific behaviour.

The outcrossing populations (PS) behaved quite differently from the predominantly self-pollinating ones. Though the PS populations have been less studied than the others, it seems that, as expected, for the first ten generations within-population variability was maintained at a higher level, whereas evolution and adaptation to local conditions were slower.

Evolution of biochemical and molecular markers

Two-dimensional electrophoresis of proteins was used to investigate the differentiation between populations at the biochemical level (David *et al.*, 1997). The study was restricted to PB populations cultivated for eight generations in six different sites with two agronomic practices. For each population, extracts of several plants were pooled together and six replications (different extracts and gels) were tested. Spot intensity was measured by automatic image analysis. Analysis of variance revealed that 39 spots out of the 162 reproducible ones were quantitatively polymorphic between populations. The site effect was the predominant contribution to the observed differentiation (60% of the between-population variance), whereas the agronomic practices accounted for

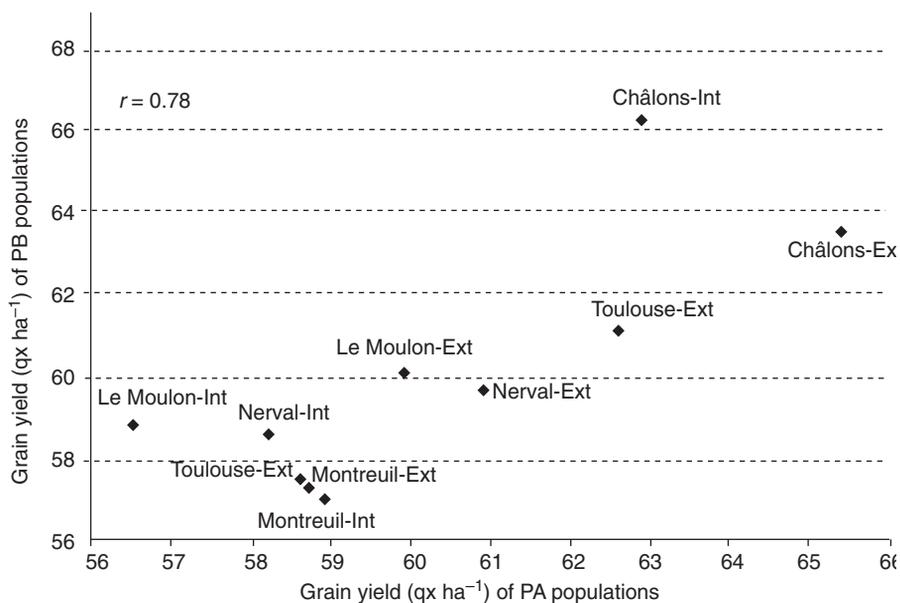


Fig. 13.3. Relationship between the mean over two locations (Clermont-Ferrand and Le Moulon) of grain yield evaluated in 1991 of PA and PB populations (sixth generation).

only 10% and the condition–site interaction accounted for 30% of the variance. This was also confirmed by the multivariate analysis. This convergent evolution of populations cultivated at the same site suggested that natural selection for local adaptation contributed to the differentiation of the protein patterns of the populations. Indeed, hitch-hiking effects amplified by the preferential selfing in the PB pool may have led to convergent evolution of populations submitted to the same selection pressures even for neutral traits, and we can not conclude whether these 39 proteins have any selective value or not.

The diversity of RFLP markers maintained after ten generations of multiplication was studied on three extensive PA populations (Le Moulon, Rennes, Toulouse), three extensive PB populations (Le Moulon, Rennes, Venours) and the two initial populations (PA0 and PB0). The 14 restriction fragment length polymorphism (RFLP) markers that were polymorphic in the 32 parental lines (see Enjalbert *et al.*, 1999a, for more details) produced 38 polymorphic loci (reflecting the hexaploid genome of wheat). The mean number of alleles lost in one population was 3.5 of the 72 initially present for PA, and 2.5 of 75 for PB, but taking the three populations as a whole, no allele was lost in PA whereas only one was lost in PB (Fig. 13.4). This suggests that if we had analysed all the populations of each pool, we would certainly have found all the initial alleles. Estimates of the effective size of the six populations (from 42 to 208) were much lower than expected under genetic drift only (>5000) considering the number plants cultivated for each population (~10,000). Moreover, significant differentiation (estimated with the Wright *F_{st}* parameter) was found within both PA and PB pools (Enjalbert *et al.*, 1999b). These large variations of the allelic frequencies of RFLP markers can be

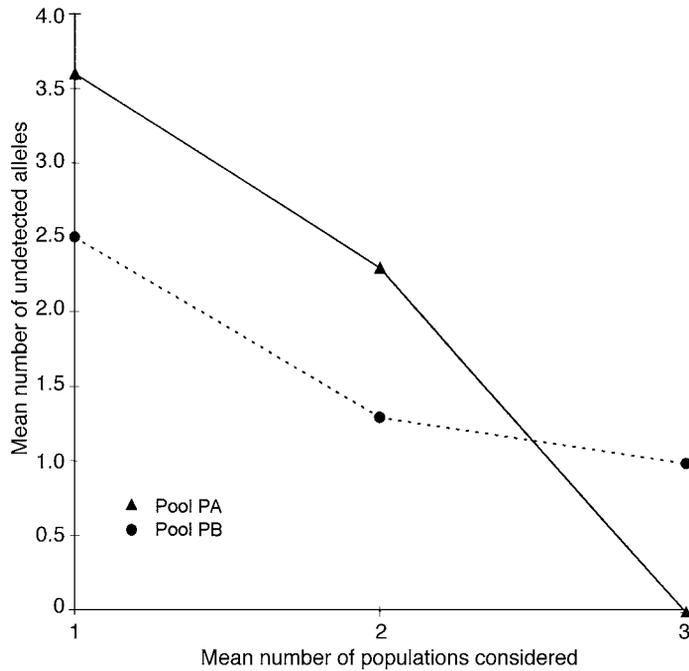


Fig. 13.4. Mean number of missing alleles in dynamic management population samples (number of RFLP alleles initially present = 75).

explained either by hitch-hiking due to linkage with loci subject to selection or by more indirect effects, since strong selection on some loci leads to a high variance of the reproductive contribution of each individual to the next generation and hence to an increase of genetic drift over the whole genome. Yet, we found no convergence between the PA and PB populations cultivated in the same sites (Enjalbert *et al.*, 1999b). We suggest that the difference in evolution found for protein patterns was due to the fact that proteins were studied in populations derived from the same initial pool (PB) and hence the populations had the same initial linkage disequilibriums between markers and selected genes. However, for the molecular markers, completely different linkage disequilibriums may have been present in the initial PA and PB populations. Even though allelic frequencies of biochemical and molecular markers change under genetic drift combined with direct selection or selection by hitch-hiking, the metapopulation appeared to maintain the diversity of such loci overall.

The mating system

Mid- to long-term evolution of the traits involved in individual fitness in the different populations will depend upon the recombination level within each sub-population. Indeed, PS populations appeared to behave in a completely different way to the populations of the two self-pollinated pools. As previously noted, the optimal adaptive

response would be obtained with a low (but not zero) outcrossing rate. Thus a knowledge of the outcrossing rate of the different self-pollinated populations is important for understanding the evolution of traits within each sub-population, and for determining gene flow between populations. For this, we used the data from an RFLP codominant locus on the six PA and PB populations previously described. Outcrossing rates were estimated in each population from the multilocus heterozygote deficiency. Estimations ranged from 2.4% to 10.1%, depending on the population (Enjalbert *et al.*, 1998). The corresponding proportions of heterozygous individuals were significantly higher than expected under strict self-pollination. Outcrossing rate did not differ from one pool to the other but it appeared to be affected by the multiplication site. Populations from Rennes had a higher level of outcrossing than populations from Le Moulon. The interaction between the genetic pool and the cultivation site was also significant since differences were found between the estimation of PA and PB populations grown in the same site. These results indicated that the self-pollinated populations did not evolve towards strict self-pollination but rather towards a mixed mating system. Such a mating system seems to have a genetic basis even though it is probably influenced by climate. Recombination within sub-populations appears to be sufficient for future evolution. We think that the residual outcrossing rate can also be used for geneflows between populations.

Discussion

Assessment of the dynamic management programme

Efficiency of the network for maintaining genetic diversity

Because of the diversity of the environments in the network, the DM system proved to be able to maintain the initial variability for all the agronomic traits studied except for genes poorly adapted to interindividual competition (such as dwarfism genes). The loss of variability within each local population is compensated by the differentiation between populations. Competition between plants seems to be the only selection pressure that leads to unidirectional evolution. However, a high competitive ability (tall plants) is often antagonistic to the agronomic value (low harvest index). In order to limit inter-plant competition effects, we propose to reduce seed sowing density and nitrogen fertilizer supply, i.e. switching to very extensive conditions. Such cultivation conditions seem convenient for developing countries since agricultural systems may be closer to these 'low-input' conditions. In European countries, more limited operations such as cutting the tallest plants before harvest should be preferred since 'low-input' conditions are not generally applied. In any event, we think that both solutions are able to circumvent the specific problem of increase in height.

The DM system also proved to be efficient for the conservation of most of the neutral diversity assessed on the basis of biochemical and RFLP markers.

Adaptation of the populations to local conditions

Most of the evolution observed for agronomic traits could be related to local selection pressures. This was especially obvious when some convergence was found for evolution of different populations in the same site (e.g. between PA and PB for yield, or between

extensive and intensive farming conditions for the proteins revealed by two-dimensional electrophoresis). Disease resistance, earliness and grain production have evolved under the physical and biotic selection pressures of the different multiplication sites. Note that the biotic constraints are expected to fluctuate more than physical ones. Increases in the frequencies of some resistance genes to powdery mildew were found to be independent of the virulence spectrum of the parasite of that site. This means that evolution of this type can not be easily predicted from the characterization of the pathogen populations of each site. This might be different for other pathogens such as yellow rust or leaf rust, the races of which are more stable from one year to the next. In any case, the characterization of the intensity of the parasitic pressure of a given site may provide some elements for predicting the evolution of the adult stage resistance of a population cultivated in this site.

Though the increase in earliness in the populations cultivated in the south of France was believed to be related to selection for heat and drought tolerance, we did not determine whether these populations had developed other mechanisms for drought resistance. We think that such adaptations are likely to happen provided that the initial genetic variability for the trait was sufficient.

Assessment of the agronomic value of the dynamic management material

It should be noted that whatever the material we evaluated and the experiment undertaken, the genotypes from extensive farming methods were never poorer in agronomic performance than genotypes from the intensive farming method. For example, we selected lines from the different populations after 10 years of multiplication mainly on the basis of their height. In 1996/97, 201 were evaluated for grain yield at Le Moulon without replication and 46 at Montpellier with two replications (data not published). In neither of the experiments were intensive lines found to be significantly superior to the extensive ones for yield and kernel weight. In another experiment (Goldringer *et al.*, 1998), when comparing the extensive and intensive populations from Rennes and Le Moulon, the extensive populations were found to be more resistant to leaf rust (*Puccinia recondita*) and powdery mildew (*Erysiphe graminis*) than the intensive ones. Moreover, extensive populations proved to be shorter than intensive ones. Generally speaking, the populations that have been cultivated under extensive farming methods show an equivalent or greater agronomic potential than the intensive populations.

A particular issue with these experiments remains the management of plant height. Unlike the barley composite cross populations (Harlan and Martini, 1929; Suneson, 1956; Allard, 1988), in our wheat populations pure natural selection and between-plant competition did not lead to lines close to varieties adapted to 'classical' cultural conditions. While increase of plant height would not be such a negative property in some developing countries where low-input agriculture is applied (Ceccarelli *et al.*, 1996), in the European agricultural context there was a substantial difference between mean height of the populations and that of cultivated varieties or of improved lines derived from recurrent selection programmes. To use DM populations as a source of variability in a breeding scheme or recurrent selection programme, we have suggested that artificial selection should be introduced in some DM populations in order to preserve their 'cultivated' pattern. We would like to emphasize this point because the selection of new combinations of genes might depend on the genetic context of the *Rht* loci. Dwarfing genes are known to display strong pleiotropic effects (Pinthus and Gale,

1990) on other traits, and the selection of gene combinations in the dwarf genetic background would be much more advisable.

The preliminary agronomic evaluation of lines selected from the different ten-generation populations showed that the very best lines had a good grain production level compared with lines extracted from a recurrent selection programme and the current varieties (Fig. 13.5). Hence, this indicates that interesting parents may be found after one or two steps of intensive selection within the populations. This stage of selection would be reduced if plant height of the populations was under control.

Some propositions for dynamic management programmes

We can identify two different levels of dynamic management more or less connected to each other and open to use in supporting variety breeding:

1. One DM system, oriented towards **genetic resources conservation** with frequent introduction of interspecific crosses, that is more likely to be used by the national and international research institutes.
2. One DM system (could also be termed low-intensity recurrent selection) oriented towards **pre-breeding** with some degree of artificial selection to maintain the cultivated pattern and to improve some economically important traits. This system should be used by experimental stations of research institutes as well as by agricultural or agronomic schools, and, in developing countries, it could also be used by farmers interested in selection.

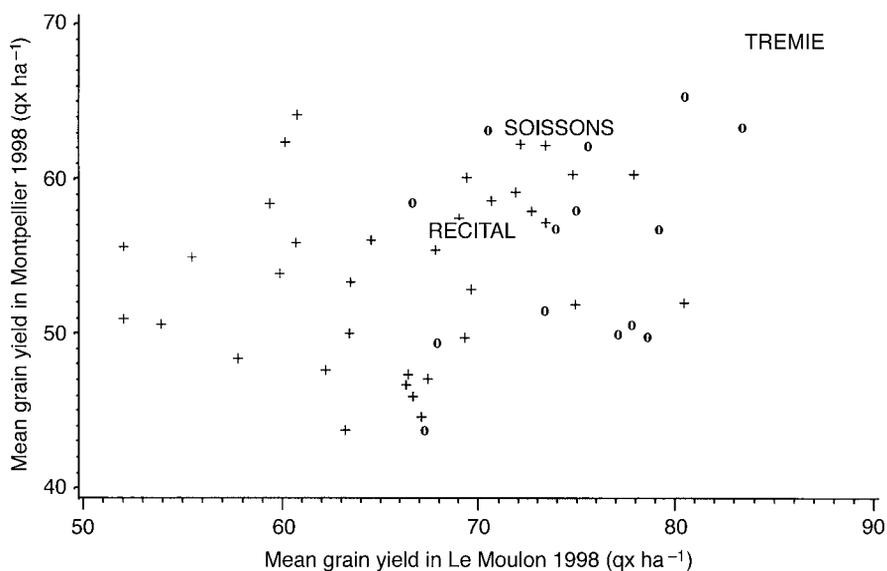


Fig. 13.5. Grain yield of lines derived from the dynamic management populations of PA and PB pools compared with lines derived from recurrent selection and with commercial varieties.

o, lines derived from recurrent selection; +, lines derived from dynamic management.

The idea of this second approach is to recreate types of traditional landraces for species and areas where these have been replaced by a small number of commercial varieties or to structure such a system so as to renew the genetic variability and improve its use for breeding.

The two systems might differ mainly in the amount of genetic variability that is accepted by the people managing the populations, by the emphasis that is put on the conservation of the initial variability, and by the amount of migration that could be set between populations. It is clear that there is no absolute dichotomy between the two systems but it is rather a continuum in which the different programmes may find their place depending on the species, breeding context, country and economic level.

Choosing the sites

The benefit of using sites with high and contrasting parasitic pressures has already been emphasized. The quantitative knowledge of the intensity of parasitic pressure for a given disease seems useful to predict response at the adult stage and hence could be a first indicator. Characterization of the climate, among which latitude can be a good predictor of the response for earliness, provides a second set of criteria. Though the genetic correlation between grain yield of PA and PB populations cultivated in the same site suggested that some sites were more favourable for high yield, the *a priori* characterization of the sites for their ability to select high-yielding genotypes needs further investigations.

Choosing the sites should not be very different depending on whether DM is oriented towards genetic resources conservation or pre-breeding. However, in the first case, environments may be numerous, contrasting or even extreme, while, in the second case, sites should be chosen to maximize the possibility of adaptation to the local conditions and should represent the cultural conditions of the area.

Maintaining the desirable crop characteristics

This should be easy in pre-breeding-oriented DM since artificial selection would be applied. For the populations managed by farmers in developing countries, selection towards an ideotype adapted to the local conditions and also corresponding to the traditional phenotype cultivated by the farmers can be applied, except that selection intensity should not be too strong. The phenotype of the populations has also to be under control in the DM programme oriented towards genetic resources conservation. If part of the aim is to be able to provide new variability to the local farmers or breeders, the material should not be too distant from the cultivated type. Hence, exotic or interspecific variability should be introduced at given generations, and a few generations of adaptation of the populations should interspace the introduction. Material should be distributed to farmers or breeders only after the adaptation period.

What initial variability and how to make the composite population

The amount of initial variability depends much on the aims of a given programme (short-, mid- or long-term) and on the problem that is to be addressed: is there a lack of variability for a given trait such as a resistance, or is there a general need to renew the variability? Sometimes, interspecific crossing will be the only way to find resistance to a pathogen. However, the more interspecific variability is introduced, the longer will be the time needed to return to a cultivated pattern adapted to local conditions.

Populations directly derived from the crossing of interspecific parents should only be distributed in the genetic resources conservation-oriented DM programme. Manual crosses (pyramidal or circular) between a limited number of parental lines (~20) – chosen according to agronomic traits, geographical origins or pedigrees to maximize genetic variability – appear to be a good solution for pre-breeding programmes. For DM oriented towards genetic resources conservation, the number of parental lines of a population can be considerably increased using male sterility systems in self-pollinating species or natural open-pollination in out-crossing species.

Mating system, population size and number of populations

Our study was performed on a preferentially self-pollinating species and it seems difficult to generalize the conclusions to true out-crossing species, even though we had turned the mating system of one of the populations into allogamy. Yet, for self-pollinated species, increasing recombinations with a male sterility gene appears interesting especially for DM oriented towards genetic resources conservation. Elimination of the gene (recessive or dominant) is easy when the material is to be used in the context of the pure line breeding of self-pollinating species. For pre-breeding DM, a more limited level of recombination should be recommended to maximize the medium-term selection response. Indeed, this is what is often found in so-called self-pollinated species.

Our results showed that the size of the populations should be relatively large since the selection due to the adaptation of the populations to their new environments leads to a drastic reduction in the effective population size. At least 10,000 individuals should be cultivated in each population. Yet, even with the low effective sizes we found for the wheat populations, genetic variability was maintained at the level of the metapopulation. Hence, we would emphasize the importance of maintaining sufficient numbers of different populations at a time. Based on our experience, we would propose at least ten populations for a given genetic pool in order to ensure a safe maintenance of the variability in the medium term.

Geneflows between populations

Some theoretical developments are available concerning the modalities of the geneflow that it is desirable to establish between populations, but there is a need for further developments to provide more precise indications. The general idea is that a small amount (small enough so as not to break the adaptation processes) of pollen exchange between the sub-populations would be favourable (see pages 246–247). In the case of the pre-breeding DM populations, geneflows could be based on occasional seed exchange between farmers.

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14 Genetic Base-broadening of Barley (*Hordeum vulgare* L.) in the Nordic Countries

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Introduction

The genetic base of cultivated barley has been narrowed since the beginning of modern plant breeding (Linde-Laursen *et al.*, 1987; Martin *et al.*, 1991; Fischbeck, 1992; Melchinger *et al.*, 1994). A lack of useful genetic variation, decreasing or even imperilling long-term genetic gain, can be especially encountered in breeding programmes targeted to specific environments such as marginal areas or specialized products (malting barley for example) (Wych and Rasmusson, 1983; Melchinger *et al.*, 1994; Saghai-Marooif *et al.*, 1994; Manninen and Nissilä, 1997). The primary gene pool of barley includes cultivated barleys, *Hordeum vulgare* L., and wild barley, *Hordeum vulgare* L. ssp. *spontaneum*. It still contains a very wide range of genetic variation. Since wild barley is cross-compatible with modern cultivated forms, it is available for incorporation into germplasm used in breeding programmes (Brown *et al.*, 1978; Nevo, 1979, 1992; Nevo *et al.*, 1986; Jana and Pietrzak, 1988; Chalmers *et al.*, 1992; Zhang *et al.*, 1993). Wild barley and other exotic, i.e. unadapted (Hallauer and Miranda, 1981), barleys such as landraces are attractive for breeding since they may be a source of novel genetic variation. One difficulty in utilization and selection of exotic sources for breeding is that the favourable genes may be hidden in this non-adapted material. This applies especially to quantitative genes. Thus, how the novel variation can be included in breeding populations in the most effective and sustainable way is an important issue not merely from the breeding point of view, but also for continued evolution in the primary gene pool of barley.

Genetic enhancement of unadapted germplasm whether by introgression (back-crossing programmes) or incorporation (large-scale development of locally adapted populations) is one of the most costly and time-consuming components of any breeding programme. Consequently, plant breeders may not always have enough resources to work with exotic germplasm requiring extensive pre-breeding. In the Nordic countries an incorporation project was initiated by scientists at the Swedish University of Agricultural Sciences, Department of Plant Breeding in Svalöv to link the efforts of

researchers and breeders. The first aim of the programme was to form two dynamic barley gene pools which possessed a high level of resistance to various barley diseases since there was a general lack of resistance sources in Nordic barley breeding material. The second aim was to recombine genes from unadapted exotic germplasm with locally adapted varieties and breeding lines in order to broaden the overall genetic variation in Nordic barley breeding materials and to avoid future problems associated with a narrow genetic base. The establishment of 'Dynamic Gene pools of Nordic Barley' was carried out separately for germplasm adapted to southern (Sweden) and northern parts of Fennoscandia (Finland). The crossing programmes to develop the dynamic gene pools for barley began in both Finland and Sweden during 1991/92.

Materials and Methods

The same unadapted material was included in both Finnish and Swedish gene pools, i.e. five *Hordeum vulgare* L. ssp. *spontaneum* (hereafter called *H. spontaneum*, or wild barley) accessions from Syria and Jordan and ten landraces from different parts of China, Tibet and Pakistan. The adapted material (25 genotypes) for the Swedish gene pool originates from the southern part of Sweden, while the Finnish material (25 genotypes) is adapted to more northern conditions (Fig. 14.1). Both exotic and adapted founder lines possessed resistance to at least one major pathogen and were selected to ensure that there was wide phenotypic diversity among them.

The development of the dynamic gene pools was based on a controlled crossing programme in order to maintain the pedigree information on each line. All of the founder lines contributed to the gene pool with equal frequency. The material was intercrossed for six generations using both pairwise crosses and half-diallel designs so that new multiples were obtained (Fig. 14.1) and were used (Table 14.1). Crosses were made in a glasshouse in order to avoid natural selection during the establishment phase, and no conscious selection was carried out during the establishment. Selected F₂ progeny were used for further studies.

Results and Discussion

Exotic germplasm as sources of novel genetic variation for Nordic barley

In order to verify that the selection of the material for genetic diversity was successful, the parental lines were tested for variation at 11 allozyme loci, of which nine showed polymorphism. Nei's (1975) gene diversities within parental lines used in both the Swedish and Finnish gene pool were 0.13 (adapted parents), 0.16 (landraces) and 0.25 (*H. spontaneum*). Cluster analysis revealed that adapted parents, landraces and *H. spontaneum* were genetically divergent (Fig. 14.2). Thus the genetic studies showed that exotic germplasm possessed greatest diversity and that genetic variation was structured within the germplasm used. It also confirmed the potential utility of exotic germplasm as a source of new genetic variation for Nordic barley.

It was also essential to check that the exotic alleles from unadapted material were incorporated in the gene pools and maintained through all the stages of the crossing

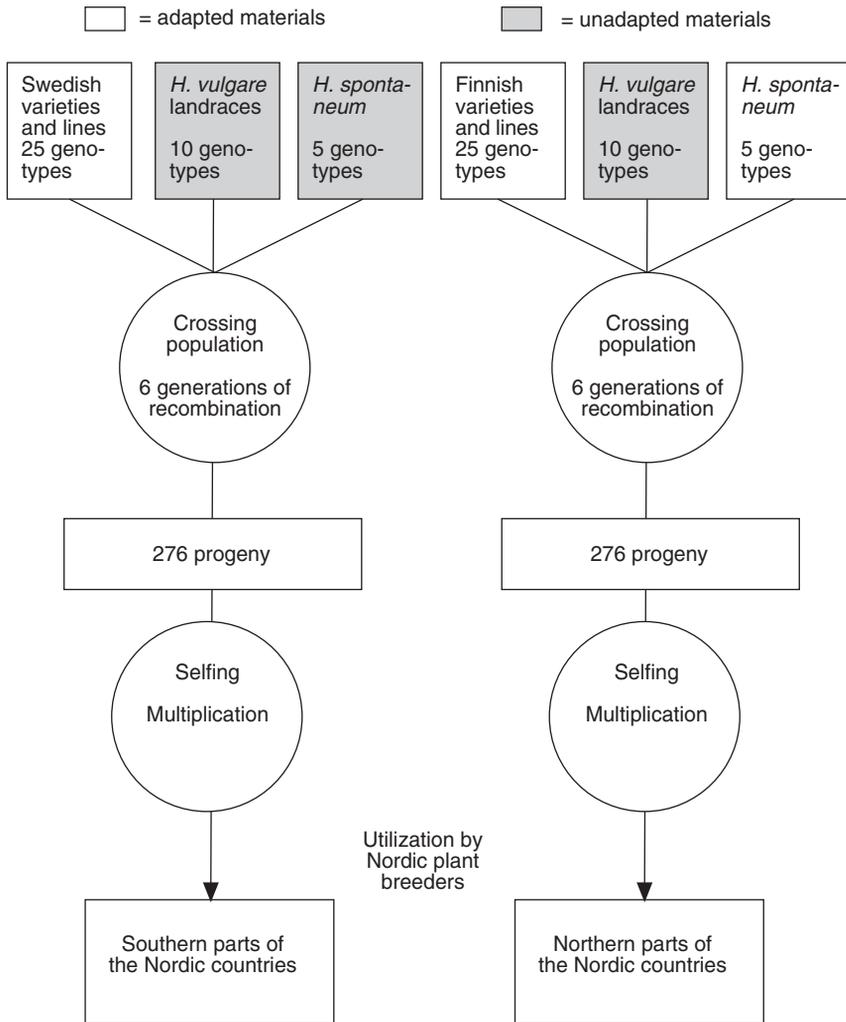


Fig. 14.1. Development of dynamic gene pools for Nordic barley breeding.

programme. In the Swedish gene pool, tests on the third crossing generation showed that exotic marker genes were preserved. Novel recombinants were also observed (Veteläinen, unpublished data).

Agronomic performance and adaptive traits

Modern varieties have been developed during decades under strong directional selection for adaptation, high-quality standards and yield. This leads to difficulties in introducing new sources of genetic diversity into the breeding programmes. The introduction of unadapted germplasm usually lowers agronomic performance due to the disruption of

Table 14.1. Crossing scheme for the establishment of the dynamic genepools.

Generation	No. of progeny produced	Crossing design	Studies
0	40	—	Genetic and quantitative analysis of parent material
1	20	Pairwise	
2	190	Half diallel	
3	95	Pairwise	Effects of exotic germplasm on agronomic traits
4	48	Pairwise	
5	24	Pairwise	Effects of exotic germplasm on agronomic traits
6	276	Half diallel	Test on multiple resistance, allele frequencies and variability in important agronomic traits

inter-loci interactions or by expression of inferior alleles. However, it may also be useful to break up existing gene complexes and increase the likelihood of new valuable recombinants. Agronomic performance of selected progeny drawn from the different crossing generations was tested and compared with their adapted parents/grandparents (Veteläinen, 1994; Veteläinen *et al.*, 1996, 1997). Ten progeny taken from both Finnish and Swedish genepools were evaluated together with their adapted parents for agronomic performance. The results showed that transgressive segregants, tested against the best adapted parent mean, were already produced in the early phase of the base-broadening programme (Table 14.2).

Progeny from the different types of exotic sources were also compared, and progeny from unadapted landraces performed better than those from *H. spontaneum* parents. However, even progeny with wild parents produced transgressive segregants for overall agronomic performance. However, with wild gene sources, the need for longer-term pre-breeding is likely to be an unavoidable consequence of the simultaneous introduction of undesirable wild-traits, such as seed shattering and non-synchronous tillering habit (Veteläinen, 1994; Veteläinen *et al.*, 1996).

In the northern parts of the Nordic countries, the utilization of exotic materials is especially difficult due to marginal environmental conditions demanding a very specific combination of adaptive traits (Tigerstedt, 1994). Cultivation in this area is possible even north of the Arctic Circle due to effects of the Gulf Stream. However, low temperatures, specific light conditions and early frosts create unique circumstances during the short but intensive growing season. Since in northern marginal conditions several traits can limit adaptation, it was necessary to consider in which type of genetic base and in which kind of specific genotypes exotic material should be incorpo-

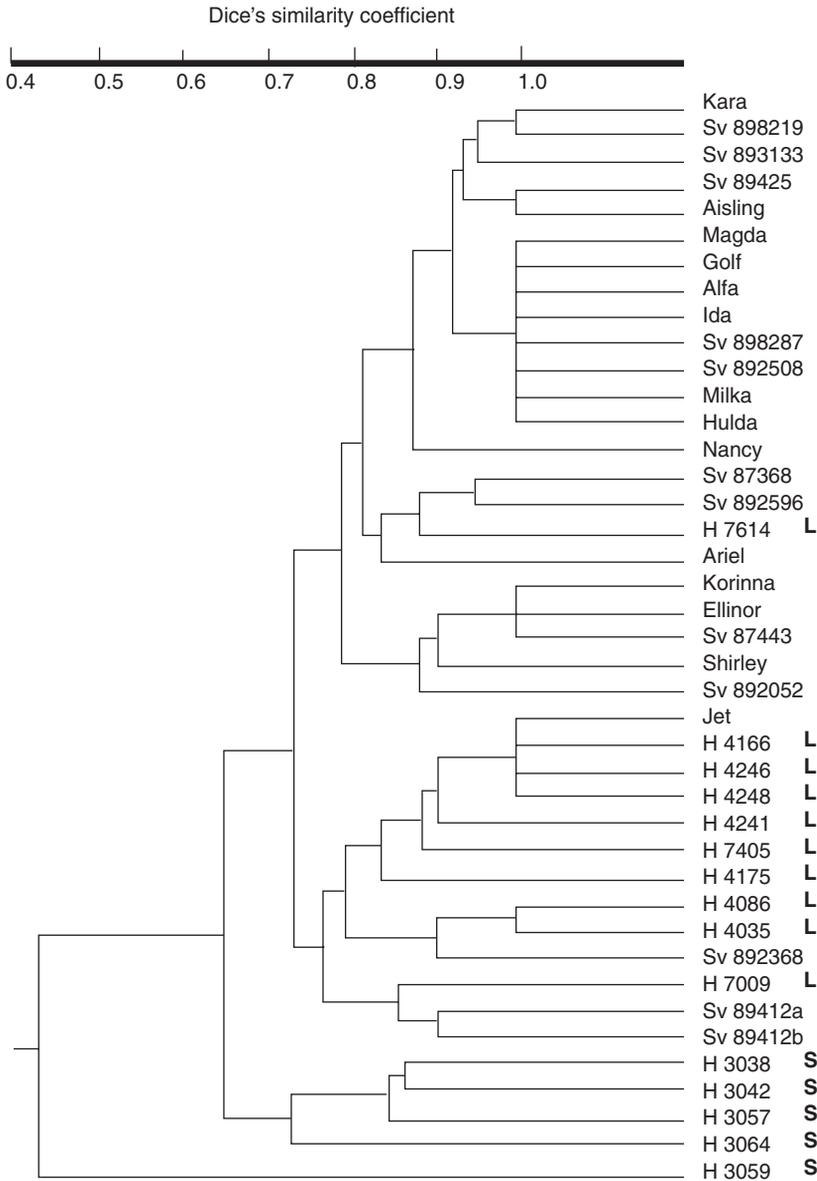


Fig. 14.2. Dendrogram of 41 parent lines in the Swedish dynamic gene pool revealed by UPGMA cluster analysis based on Dice's coefficient. L: landrace; S: *Hordeum spontaneum*.

rated. With both the dynamic gene pools, the majority of parents were adapted to the different northern environments, and two different incorporation schemes were tested: (i) progeny in which the same exotic material was introduced into a genetic background adapted to the agroecological conditions of the extreme Fennoscandian north; or (ii) introduction in the background adapted to the conditions of the southern part

Table 14.2. Percentages of plants from five Finnish (Fi) and five Swedish (Sw) progeny with an index^a above the best adapted parent mean. Unadapted parental lines.

Progeny	Adapted parent 1	Unadapted parent 1	Adapted parent 2	Unadapted parent 2	Index	
					2-row	6-row
Fi 1	Jo 1621	H 4241 (L)	Hja 80138	H 7614 (L)	—	27
Fi 2	Kalle	H 4248 (L)	Meltan	H 7405 (L)	58	11
Fi 3	Kinnan	H 4035 (L)	Pohto	H 3064 (S)	38	8
Fi 4	Hja 83054	Ob 264	Mette	H 3042 (S)	10	—
Fi 5	Arttu	H 4175 (L)	Jo 1545	H 4246 (L)	27	13
Sw 1	Alfa	H 4241 (L)	Aisling	H 7614 (L)	50	—
Sw 2	Korinna	H 4248 (L)	Sv 892052	H 7405 (L)	24	—
Sw 3	Golf	H 4035 (L)	Jet	H 3064 (S)	36	—
Sw 4	Nancy	Sv 89412	Sv 898219	H 3042 (S)	11	—
Sw 5	Ida	H 4175 (L)	Milka	H 4246 (L)	45	—

^a Index = $i_{\text{ear emergence per days}} + i_{\text{straw length cm}} + i_{\text{no. of ears per plant}} + i_{\text{heading synchrony}} + i_{\text{yield per plant}} + i_{\text{seed shattering}} + i_{\text{persistence of awns in threshing}}$

L: unadapted landrace; S: *Hordeum vulgare* ssp. *spontaneum* line.

of this geographical region. The field experiments to study these two incorporation schemes were conducted in the northern conditions of Finland using early maturity as the evaluation criterion of the progeny. It was realized that crosses having a parent specifically adapted to the northern conditions had a higher frequency of transgressive segregants for early heading than those in which adapted parents originated from the more southern part of the region (Fig. 14.3). Exotic sources affected transgression for earliness (Veteläinen *et al.*, 1996), but the main conclusion was that incorporation of exotic material was most successful in the local genetic background. The selection and inclusion of adapted genotypes in base-broadening is also important to the success of such programmes, especially those targeted to harsh marginal areas.

Evaluation of exotic × adapted progeny

The evaluation strategy used for the exotic × adapted progeny is of special importance when the aim is to renew the genetic base of the crop. Strict evaluation of exotic × adapted progeny can hinder the success of pre-breeding and prevent new plant types from entering breeding populations.

In this study, evaluation based on an index composed of several agronomic traits (including traits indicating 'wild status') was compared with breeders' phenotypic evaluation of a sample of the third-generation progenies. Correlation between the two measures was only moderate (Table 14.3). This indicated deficiency of the index composed and/or the conservatism of the breeders' phenotypic evaluation (for example, plants with 'unusual' outlooks were discarded). In the latter case, breeders may have to reconsider their evaluation methods in the early phase of parent development when working with exotics in order to allow new plant types to enter breeding populations.

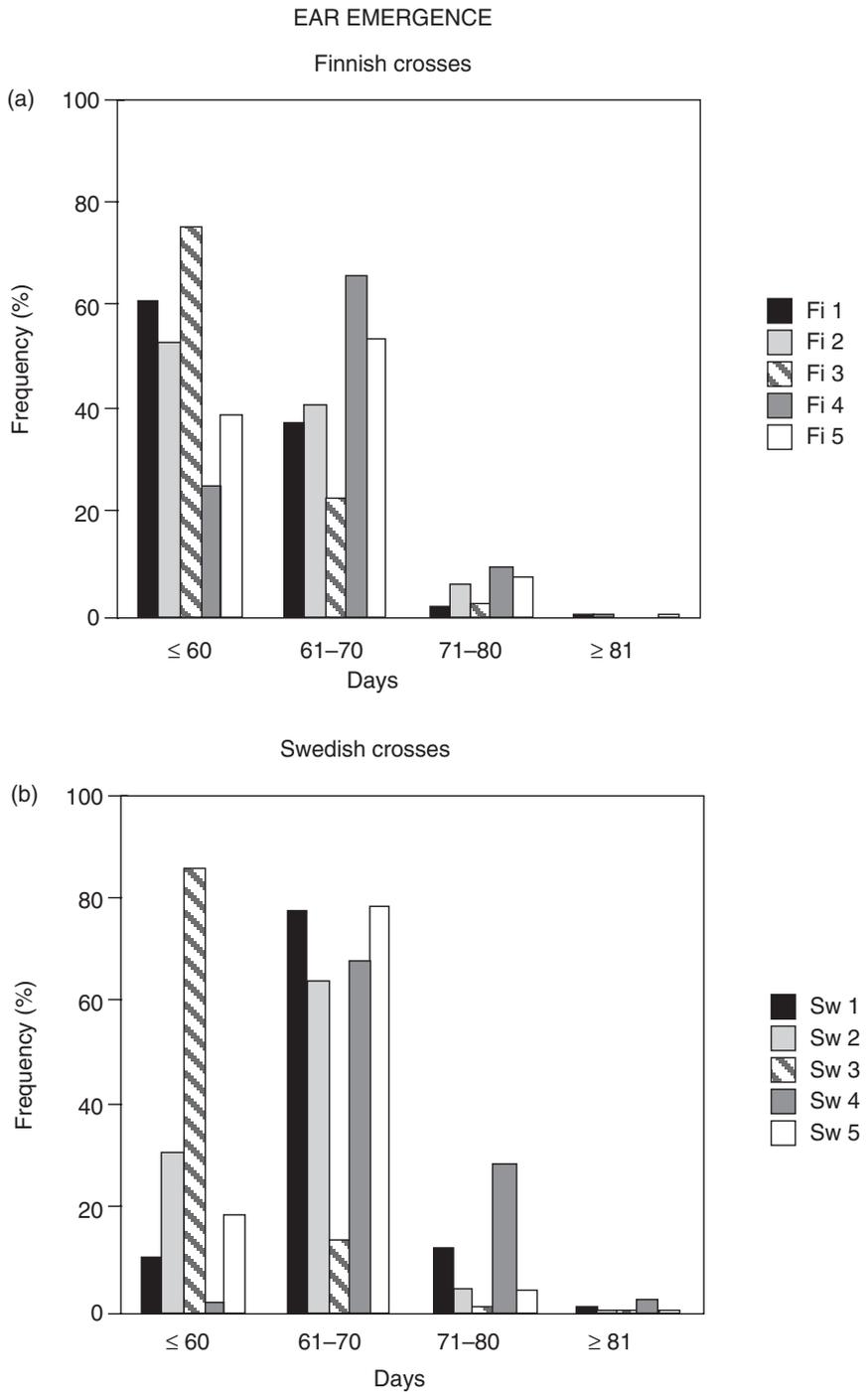


Fig. 14.3. Frequency distribution for ear emergence (days from planting to heading) in (a) Finnish (Fi 1–Fi 5) and (b) Swedish (Sw 1–Sw 5) progeny.

Table 14.3. Spearman correlation coefficients between index (7^a = composed of seven traits, 4^b = four traits and 3^c = three traits) and breeders' evaluation.

Trait	Index	2-row	6-row
Breeders' evaluation	7	0.44**	0.55**
	4	0.26**	0.23**
	3	0.21**	0.12*

^a Traits included: ear emergence, days; straw length, cm; number of ears per plant; heading synchrony; yield, g per plant; seed shattering; persistence of awns in threshing.

^b Ear emergence, days; straw length, cm; number of ears per plant; heading synchrony.

^c Ear emergence, days; straw length, cm; number of ears per plant.

*, **: significant at 5% and 1% levels respectively.

It was noted that parent–progeny regressions for several traits were low, which indicated that the parents were poor predictors of their progeny's performance and supported the hypothesis that inter-loci interactions were important in agronomic performance of barley. Consequently, the overall genetic potential of exotic barleys should only be tested after incorporation in an appropriate genetic background (Veteläinen *et al.*, 1997).

Utility of the programme to breeders

The dynamic genepools were basically established to develop three different types of sources of genetic diversity currently important in Nordic barley breeding programmes. The development of genotypes with multiple resistance to several barley diseases through extensive recombination was the aim in the development of both dynamic genepools. For this purpose exotic genotypes were used which possessed resistance to at least one major pathogen, and 15 phenotypically diverse genotypes were selected for the dynamic genepools. The adapted parents were also selected with a specific focus on the differences in disease resistance. It was planned to screen the progeny from the sixth generation for multiple resistance and to incorporate them into resistance breeding programmes. With the Finnish genepool a special aim was to develop novel variation for adaptive traits critical in breeding for the northern marginal areas. Current six-row breeding material originates from the Nordic landraces and the genetic base of this material is narrow (Manninen and Nissilä, 1997). The most critical adaptive traits for which useful new variation is needed are lodging resistance + drought resistance + early maturity and netblotch resistance + early maturity. The emphasis with the Finnish genepool was also to develop wider variation for the critical yield components and new plant types to enhance yield potential of early maturing six-row barley. In the short-season conditions of the north, the number of tillers per plant is more or less fixed and likely to be only one to three tillers per plant to ensure early maturity. In addition, all the current high-yielding and early-maturing six-row barleys tend to have relatively small seed size. Therefore, the aim was also to produce new desirable recombinants expressing good yielding potential, yield stability and larger seed size.

The evaluation of the gene pools for multiple resistance and adaptive quantitative traits has not yet been extensively started, although in the establishment phase some very promising new recombinants were taken into the six-row barley breeding programme. A genome map for mapping of quantitative trait loci (QTLs) based on the cross between two highly adapted six-row barley lines was developed concurrently with the dynamic gene pools. It is planned to use this for identifying desirable wild QTLs from the dynamic gene pool and for testing gene pools in divergent and directional selection sites.

Resource use

The development phase of the dynamic gene pools was carried out as a collaborative project between research and breeding sectors. Plant breeders benefited with new parental materials, while the research sector could provide education in the fields of applied plant breeding research and pre-breeding. The human resources used in the establishment were one technical assistant per site for crossing work and management of the plant material from planting to harvesting; one PhD student who carried out the research activities including laboratory and field work; and a consultative group including academic supervisors and a plant breeder. The time taken for the establishment of the gene pools was 3 years per site.

Conclusions

The studies carried out in the establishment phase of the dynamic gene pools of Nordic barley showed the following:

1. Exotic germplasm used in the establishment of dynamic gene pools provided new genetic and agronomic variation for Nordic barley. In order to determine the genetic potential of the exotic germplasm, these lines were tested in progeny derived from complex adapted \times exotic crosses.
2. Phenotypes of exotic lines were poor predictors of progeny performance. Thus, exotic germplasm should be tested when incorporated in an appropriate genetic background. A crossing scheme that enhanced extensive recombination was useful for recovering new desirable genotypes.
3. Exotic sources can be used in improving overall agronomic performance. If short-term progress is desired, unadapted cultivated sources are preferred to wild ones.
4. Reconsideration of evaluation methods for progeny after exotic \times adapted crosses may be needed in order to allow new plant types to enter breeding populations. This is of special importance if a breeder wishes to renew the genetic base of the breeding material.
5. Incorporation was most successful when done in the local genetic base.
6. The adaptive value of a genotype can depend on several traits and their interaction with the environment. Therefore, further testing of transgressive segregants in different environments is needed to verify their value as parental material.

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15 Evolutionary Changes in Cambridge Composite Cross Five of Barley

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Introduction

The breeding methods commonly used in barley, *Hordeum vulgare*, rely on selecting desirable genotypes from genetically heterogeneous landraces (pure-line breeding) or from the segregating progeny of crosses between lines with superior traits (pedigree breeding). Another method that can be used is the bulk-population method, where the segregating progeny of multiple crosses between superior lines are harvested and propagated in bulk. Nilsson-Ehle is believed to have been the first breeder to use the bulk-population method (Allard, 1960). He adopted it in handling the segregating generations of hybrids made to combine winter hardness and high yield in wheat. The action of natural selection was assisted by discarding plants that had suffered winter damage during successive generations. Growing a large population increased the chances of high-yielding types appearing among the favoured winter-hardy selections and also disposed of the need for keeping detailed pedigree records. After a few generations of bulking, homozygosity among the selfed plants would be at a level such that selected plants could be expected to breed true.

In 1929, Harlan and Martini proposed the composite cross method (CC method) of breeding barley. This method is essentially similar to the bulk-population method except that the hybridization stage involves crossing a large number of varieties of diverse origin, and genetic make-up, in order to create a heterogeneous population of recombinant genotypes, as well as the parental types. This population would then be grown under normal agricultural conditions in the areas where locally adapted varieties were needed. Natural selection acts on the available variation during the successive generation, leading to an increase in the frequency of locally adapted genotypes without creating a genetically uniform population. Mak and Harvey (1982) state that this method not only produces new genetic variation during the hybridization and segregation stages but also preserves the variation in an exploitable form. Suneson (1956) referred to the technique as an 'evolutionary' plant breeding method.

Composite cross populations can be created in a number of ways. Hybridization may be carried out either by hand-crossing or using genetically controlled male-sterility to facilitate out-crossing. The majority of the early composite crosses of barley were synthesized by hand-crossing diverse accessions and mixing the F_2 seeds in known proportions or by using bridge crosses in a hierarchical way to produce a final stock of hybrid seed. An example of the former is composite cross two (CCII) which was created by mixing equal numbers of F_4 seeds from 378 hybrids obtained from pairwise crosses among 28 varieties of barley (Harlan and Martini, 1929). Composite cross five (CCV), on the other hand, was created by crossing 30 diverse varieties in pairs followed by pairwise crosses with the F_1 hybrids for three generations.

Composite crosses can be used as:

1. Dynamic reservoirs of genetic variation in projects of germplasm conservation especially when maintenance of locally adapted diversity in an exploitable form is required.
2. Experimental populations for use in studies of the effects of natural selection on heterogeneous populations of cultivated crops that are maintained under natural conditions.
3. Sources of locally adapted new varieties by single plant, or progeny selection once the composite cross populations attain high levels of homozygosity.
4. As animal feed.
5. As food crops where legislation does not preclude the marketing of heterogeneous varieties and where performance under adverse conditions, and not maximum yield under optimal input, is the main objective.

These and other uses of the composite crosses of barley have been reviewed by Allard (1988) and Simmonds (1993). Suneson (1956) showed that the yields of four composite crosses was lower than that of a commercial variety of barley, Atlas, for the first eight to 15 generations, but all exceeded Atlas after between ten and 15 generations. Similar trends of rapid increase in yield to the levels of commercial pure-line varieties, followed by slower but steady increase have been observed in CCII, CCV and CCXXI (Allard, 1988).

The major drawback of the CC method is the length of time required to produce new varieties. While 5–6 years is normal for the development of cereal varieties using standard breeding methods, successful barley varieties derived from CCs have all been selected from well-advanced generations, all beyond F_{15} . This led Simmonds (1962) to argue that the CC method should not be seen as a breeding technique *per se*, but rather as an adjunct to breeding where reservoirs of locally adapted variability can be maintained permanently. This is, however, only valid to the extent that the adaptive phenotypes are also agronomically desirable. Various studies of metrical characters in CCs have confirmed that the populations become fitter and more adapted to local environments (Jain and Marshall, 1967; Luckett and Sharif, 1987; Allard, 1988; Ibrahim and Barrett, 1991). Among the selected phenotypes were longer straw, late flowering, prostrate growth habit and smaller seed, which are, in the main, agronomically undesirable (see also Goldringer *et al.*, Chapter 13, this volume). However, Ibrahim (1990) has argued that the ease of implementation of the CC method, when compared with pedigree breeding, has many advantages for crop improvement in developing countries, for example in Eritrea.

The Origin of Cambridge CCV

CCV was developed by the late H.V. Harlan of the United States Department of Agriculture from intercrosses among 30 varieties of barley chosen to represent the major barley-growing regions of the world (Suneson, 1956). The hierarchical crossing scheme was started in 1938 when 15 lots of hybrid seeds were produced from paired crosses between the selected varieties. In the following 2 years, two cycles of pairwise crossings generated four lots of hybrid seed. Lastly, in 1940, these were crossed in all six possible combinations (no reciprocals) and the harvest was bulked to form the F_1 generation of CCV. Subsequent generations were propagated in Davis, California, under normal agricultural practices, growing 10,000–15,000 plants every season (Jain and Allard, 1960).

In 1974, seed samples from the F_{10} , F_{20} and F_{30} generations were brought to Cambridge, England, and have been maintained ever since as parallel populations designated populations 1, 2 and 3 of CCV. Successive generations are produced by sowing about 10,000 seeds from the previous harvest as spring barley with no conscious selection and no application of fungicides or pesticides. Thus populations 1, 2 and 3 of Cambridge CCV, although from the same initial segregating population, had undergone 10, 20 and 30 generations of selfing and selection, respectively, under Californian conditions, when they were established in Cambridge. Maintaining the populations in parallel enables the detection of selection-induced evolutionary changes such as directional changes in allele frequencies or changes in the phenotypic traits of the three populations. It may also be possible to attribute significant changes that are not consistent in the parallel populations, either in magnitude or direction, to the differences in the genetic composition of the initial samples of seed transferred to Cambridge.

The Usefulness of Cambridge CCV

By the beginning of the 21st century, the three populations of Cambridge CCV had been maintained under the same environmental conditions and agricultural practices in a major barley-growing region of the UK for almost a quarter of a century. They offer a unique opportunity to evolutionary and population geneticists as well as to applied breeders who want to assess the potential agronomic value of composite cross populations. In the following sections, we describe briefly some studies conducted so far using Cambridge CCV material.

Host–pathogen interaction in Cambridge CCV

Powdery mildew caused by *Erysiphe graminis* f. sp. *hordei* is an economically important fungal disease of barley. Ibrahim and Barrett (1991) derived inbred lines from selected generations of the three populations of Cambridge CCV and screened them for variation in mildew resistance. Host reaction to open-air infection as well as to selected isolates of known virulence genotype was scored. Increased resistance to both was observed in the advanced generations of all three populations. There were significant differences between the populations in the rate of change towards higher resistance.

Population 1 had the highest proportion of resistant plants (Fig. 15.1). Mildew attack, which is known to cause yield losses of up to 20% in untreated commercial varieties, appears to have conferred selective advantage to the individual plants that carry resistance genes.

This work also identified specific mildew resistance loci where strong directional changes in allele frequencies over successive generations were apparent. A comparison of inbred lines extracted from population 1 and the 30 parental lines (Fig. 15.2) using a number of mildew isolates of known virulence genotypes identified the resistance genes in the host plants which increased in frequency in response to mildew attack (Ibrahim and Barrett, 1991).

The predominantly selfing Cambridge CCV populations consist of a mixture of lines that are highly homozygous. With regard to the evolution of disease resistance, these lines are expected to be affected by epidemic development in the same manner as variety mixtures (Barrett, 1978). In general, when their composition with respect to a known trait is observed to change in a particular direction over time, that trait is usually identified as a target of natural selection. Such directional change can also be brought about by the hitch-hiking of the genes which control that trait with other genes that are the target of selection. However, comparative studies have identified mildew resistance as a strong candidate target of natural selection (Ibrahim *et al.*, 1996). Of course, overall, directional selection targets the combination of genes that produce the best phenotype.

Variation in discrete and metrical characters

The three Cambridge CCV populations have also been studied extensively for variation in many discrete morphological characters for which the mode of inheritance is known. These include: growth habit (prostrate, erect), chaff colour, aleurone colour, awn type (smooth, rough), ear type (brittle, tough) and rachilla hair (long, short). Metrical characters such as flowering time, plant height, seed number, seed weight and other measurements on the inflorescence have also been investigated. Luckett and Sharif (1987) reported that within 6 years of their introduction to Cambridge, the CCV populations

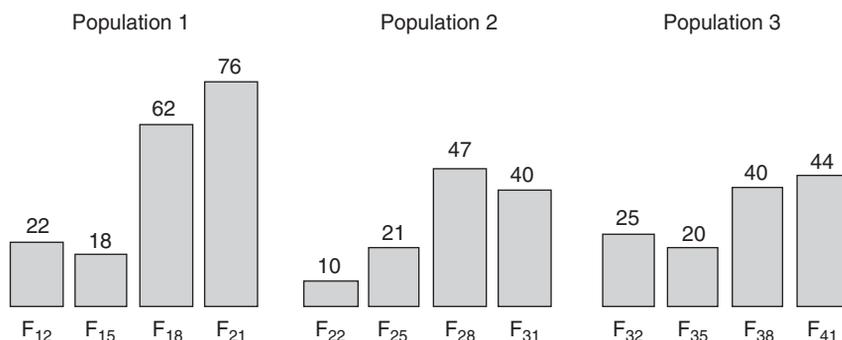


Fig. 15.1. Frequency (%) of plants resistant to open-air spores of powdery mildew in the three parallel-grown populations of Cambridge CCV.

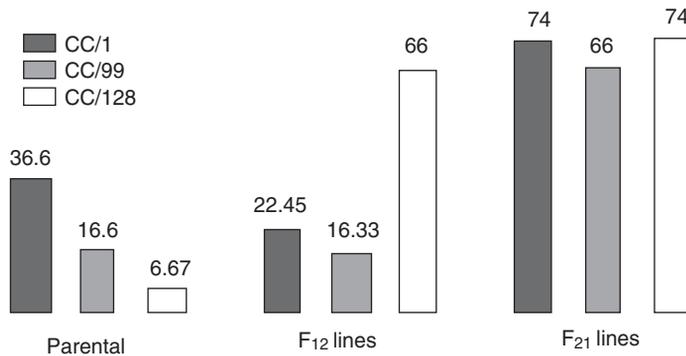


Fig. 15.2. Frequency (%) of resistance to three mildew isolates in the CCV parental lines ($n = 30$) and inbred lines from F_{12} ($n = 49$) and F_{21} ($n = 50$) of population 1. Isolate CC/1 has the *Va8* and *Va12* mildew virulence genes. CC/99 and CC/128 are more complex. See Ibrahim and Barrett (1991) for their virulence genotypes.

evolved towards later flowering, increased height at maturity and higher yield compared with the original introductions.

Ibrahim (1989) observed similar trends in comparisons between generations from all three populations spanning 10 years' propagation under Cambridge conditions. In the case of flowering time, it was apparent that an increase in the frequency of few genes with major effect was the cause of the shift towards later flowering. A bi-modal distribution of flowering time was observed and, in the advanced generations, more lines fell in the late-flowering class compared with the early generations, as shown in Fig. 15.3 for the samples from population 1. A similar shift towards later flowering was also observed when CCXLII was grown over several generations in Cambridge (Knight, 1991).

The concurrent generations from populations 2 and 3 also showed similar trends. A nested experimental design using 50 inbred lines from each of five population 1 generations spanning 10 years showed that mean flowering time had increased by 1 day per generation, on average. The mean number of days from sowing to the first appearance of awns from the flag leaf were 42, 45, 52 and 52 for generations F_{12} , F_{15} , F_{18} and F_{21} , respectively. Comparisons of means were statistically significant except for that between F_{18} and F_{21} . Furthermore, there was significant variation in the mean flowering time of each of the lines within each generation. Lines extracted from the Californian CCV generation concurrent to F_{21} of Cambridge CCV flowered on average 42 days after sowing.

The most striking change in the discrete morphological characters was the marked increase in the number of plants with prostrate growth habit (Table 15.1). The single recessive gene responsible for prostrate growth habit, *sh*, is known to cause the pleiotropic effect of late flowering compared with the dominant allele (Whitehouse *et al.*, 1972). The shifts observed in the frequencies of the *sh* allele could therefore be the result of selection acting on either phenotype. A χ^2 test of the association between early or late flowering and growth habit in the four generations is shown in Table 15.2, which also gives the frequencies of the four phenotypic combinations. The partitioning

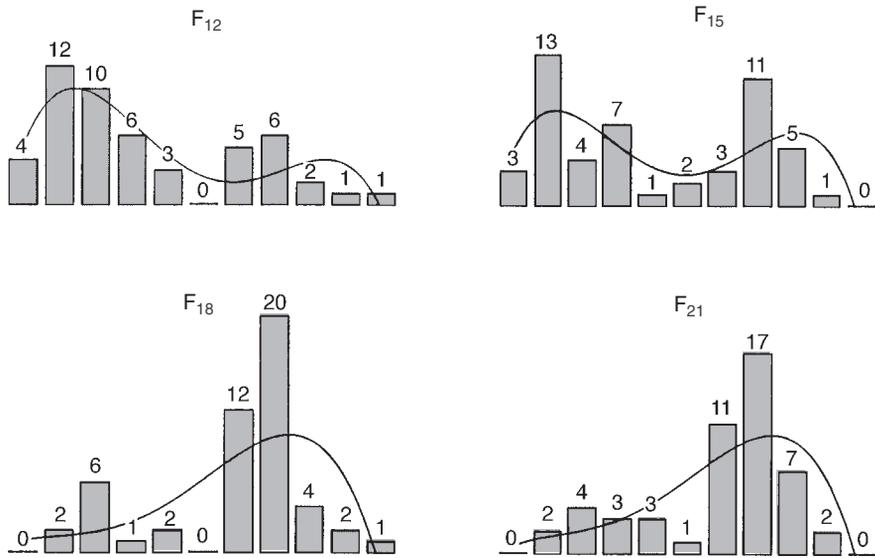


Fig. 15.3. Distribution of the average time to flowering (days from sowing date) in lines derived from four generations of population 1, Cambridge CCV. The bars represent 3-day intervals starting at 30–33 days and ending with flowering time of more than 69 days from sowing.

of the total variation in this three-dimensional contingency table reveals that the frequency of growth habit and flowering time variants varied significantly across generations. The significant interaction between the two is the expected outcome of pleiotropy. The marginally significant triple interaction, which is problematic to interpret when the two-way interactions are significant (Everitt, 1977), implies that the association between any pair of the three variables may differ in degree or in direction in the different categories of the third. It is clear that early-flowering erect lines have declined considerably in the advanced generations. Neither could, however, individually account for the shift in the other, contrary to the findings of a previous study (Luckett, 1980) where prostrate growth habit was proposed as the selected phenotype.

In the case of the morphological characters that showed frequency fluctuations across generations, a number of causes can be hypothesized. The chance association of different alleles with alleles at loci that are targets of selection could bring about this effect. Changes in the environment that result in fluctuations in the optimal phenotype selected may also lead to significant non-directional phenotype shifts. For those characters in which directional trends were apparent, it is again difficult to ascertain that the characters are the actual targets of selection but it is possible to use frequency shifts in these loci to demonstrate the effect of selection on the CCV populations. If the characters studied are just markers for other selected alleles, the strongly inbreeding nature of barley makes them effectively targets of selection, because when recombination is restricted due to inbreeding the whole genome is effectively 'linked' (Jain and Allard, 1960; Jain, 1961a,b).

Table 15.1. Morphological variation of 50 inbred lines in each of four generations of population 1, Cambridge CCV.

Character	Phenotype	F ₁₂	F ₁₅	F ₁₈	F ₂₁	χ^2
Chaff colour	Black	4	12	3	1	15.56**
	White	46	38	47	49	
Aleurone colour	Blue	25	24	34	36	9.36*
	White	25	26	16	14	
Anthocyanins	Present	10	11	2	4	10.06*
	Absent	40	39	48	46	
Awn type	Smooth	31	25	35	42	13.09**
	Rough	16	24	13	8	
Rachilla length	Long	1	4	2	4	8.37*
	Medium	26	36	31	29	
	Short	20	9	15	17	
Rachilla hair	Long	8	2	1	1	12.78*
	Short	39	47	47	49	
Ear type	Brittle	11	9	7	10	9.41*
	Tough	36	40	41	40	
Neck type	Long	11	13	13	9	1.24
	Short	39	37	37	41	
Growth habit	Erect	28	29	10	7	34.75**
	Prostrate	22	21	40	43	

* = $P < 5\%$; ** = $P < 1\%$.**Table 15.2.** Percentage of different phenotypic combinations in 50 inbred lines in each of four generations of population 1, Cambridge CCV and χ^2 tests of associations.

Phenotype	F ₁₂	F ₁₅	F ₁₈	F ₂₁
Erect and early	28	20	5	4
Erect and late	0	9	5	3
Prostrate and early	8	8	5	7
Prostrate and late	14	13	35	36
Source	df			χ^2
Total	10			141.10
Two-way interactions				
Generation \times flowering time	3			40.49
Generation \times growth habit	3			34.74
Flowering time \times growth habit	1			57.30
Three-way interaction				
Generation \times flowering time \times growth habit	3			8.57

Variation in biochemical markers

Edwards (1975) investigated the isozyme variation of the first seeds of CCV harvested in Cambridge and, in a subsequent study, Luckett and Edwards (1986) reported that polymorphism at four esterase loci changed significantly in successive generations grown in Cambridge but the trends were not similar in the three populations. They concluded that the esterase genes were hitch-hiking through chance initial associations with other selected genes, when CCV was introduced into Cambridge.

An extensive survey of polymorphism at three storage protein loci (hordeins) was carried out by Ibrahim *et al.* (1996). The B hordeins are encoded by a single structural gene, *Hor2*, located on the short arm of chromosome 5, 7–8 cM distal to the *Hor1* locus which codes for the C hordeins (Jensen *et al.*, 1980; Shewry *et al.*, 1981). The *Hor3* locus of the D hordeins is located on the long arm of chromosome 5 (Shewry *et al.*, 1983). The estimated map distance between *Hor1* and *Hor3* is 65 cM and the gene order is *Hr2–Hor1–Hor3* (Shewry *et al.*, 1984).

Hordein polypeptides of the three classes separated using SDS-PAGE revealed extensive band pattern variation in the three populations of Cambridge CCV. The frequencies of single locus banding patterns as well as pattern combination for *Hor1* and *Hor2* showed marked directional changes in successive generations. This trend was highly correlated to the observed increase in resistance to powdery mildew (Ibrahim *et al.*, 1996). Because the genes that encode the hordeins *Hor1* and *Hor2* are linked to major mildew and yellow rust loci, *Mla*, *Mlat*, *MlGa*, *Mlk*, *Mlmm*, *Mlra* and *Yr4* (Shewry *et al.*, 1981; Kreis *et al.*, 1985; Jorgensen, 1994), it was concluded that the observed shifts in hordein banding patterns were the combined result of this linkage, the selective advantage of resistance to mildew and the inbreeding nature of barley.

The association between mildew resistance and specific B hordein and C hordein polypeptide variants makes the latter good markers for selecting for mildew resistance. For example, the overall probability of randomly selecting a resistant line in the sample of 400 lines screened (P_1) was 0.45. If lines are first selected on the basis of the Hor B and Hor C patterns most commonly associated with mildew resistance, the probability (P_2) is 0.81 and 0.77, respectively. When Hor B and Hor C band combinations are used, the probability of an otherwise randomly chosen line being resistant to mildew is 0.84. Thus, gains in selection efficiency, $((P_2 - P_1)/P_1)$, of 75–85% could have been attained by using these markers when screening for resistance to infection by the prevailing mildew population in the field.

Maintenance of genetic diversity in Cambridge CCV

The dynamics of the genetic make-up of the three populations of Cambridge CCV observed in the various studies described above is complex, but there is strong evidence to support the conclusion that resistance to powdery mildew has been selectively advantageous. Other phenotypic variants such as prostrate growth habit, tallness and early flowering also appear to have been favoured. However, in spite of the detectable effect of natural selection favouring particular phenotypes, the surveys of variation in morphological, quantitative, disease resistance and biochemical characters in Cambridge CCV have clearly shown that a substantial amount of genetic variation still

exists in the populations. Most of the individual variants, be they morphological phenotypes or biochemical markers, were still present in the advanced generations, albeit in frequencies significantly different from the early generations and the parental lines. However, the number of phenotypic combinations was significantly reduced. For example, in the five dimorphic morphological characters (chaff colour, rachilla hair, ear type, awn type and growth habit) shown in Table 15.1, the total number of possible phenotypic combinations is $2^5 = 32$. The actual numbers detected in F_{12} , F_{15} , F_{18} and F_{21} were 16, 15, 9 and 9, respectively, clearly indicating some loss of diversity over time. The same trend was also apparent in quantitative characters. The variance between inbred lines within generation declined with time, showing reductions of 24.9%, 39.6% and 47.9% for flowering time, height and number of seeds, respectively (Ibrahim, 1989).

In a further study, using both SDS-PAGE of hordeins and restriction fragment length polymorphism (RFLP) analysis using a probe for the *Hor2* locus, Danquah (1993) showed not only the same association of hordein variation and mildew resistance, but also that the most frequent B hordein variant was the same as that for the parental line cv. Algerian, which is known to carry the mildew resistance genes *ML-a1* and *ML-at*.

The hordein loci showed the greatest amount of genetic diversity of the markers studied in Cambridge CCV so far. Ibrahim *et al.* (1996) compared two samples of 100 seeds seven generations apart (F_{12} and F_{21}) and were able to detect in the advanced generation (F_{21}) all but the four rarest *Hor2* alleles of the 19 present in the early generation (F_{12}). The mean expected panmictic heterozygosity averaged over the three hordein loci was 0.55, 0.64, 0.44 and 0.40 in F_{12} , F_{15} , F_{18} and F_{21} , respectively. This indicates that genetic diversity at the hordein loci has not been seriously eroded when measured on a per locus basis. However, there was a significant decline in the diversity of multilocus pattern combinations from 26 in the F_{12} samples to 15 in F_{21} .

Conclusion

The usefulness of composite cross populations depends on how their genetic make-up is affected by natural selection. Their use as mass reservoirs of genetic diversity was first proposed by Simmonds (1962). Marshall and Brown (1974), however, have argued that mass reservoirs are of little value in preserving variation because they retain only a small proportion of the parental diversity. The Cambridge CCV studies outlined above have clearly shown that while a substantial amount of single locus diversity is still retained in CCV some 40 generations after the initial hybridization, multilocus genotypic diversity has declined demonstrably. Because this decline in the overall heterogeneity of CC populations is correlated with adaptedness to local environment (Ibrahim, 1989; Allard, 1990, 1996), it can be seen as an effective method of retaining locally useful diversity. On the other hand, the magnitude of the reduction in multi-locus genotypic combinations observed within the relatively short period of the propagation of Cambridge CCV clearly precludes the use of CCs for conservation purposes *per se*.

The use of CC populations as food, or feed, crops can only be considered under two conditions: (i) where variety release and seed regulatory legislation do not preclude their use and plant breeders' rights are not sought; and (ii) where emphasis is on

breeding for reliability of yield in less than optimum management conditions. Both conditions are characteristic of the agricultural systems of many developing countries. Apart from the initial crossing phase, no highly skilled labour or detailed record keeping is required, and the combination of natural selection to local conditions, combined with selection by local growers to their own needs in the later generations, can make this approach very cost-effective.

Ibrahim (1990) has argued that for the example for Eritrea, adoption of the CC method could be beneficial particularly in barley. In the traditional barley cultivation in Eritrea, genetically diverse landraces are grown for a variety of uses and in proximity to the wild relatives of barley. The potential free movement of genes, even with limited outcrossing, the possibility of coevolution of the crop with its pests and diseases, and the diversity arising from selection by growers for different uses of the grain as well as straw produce has created these landraces. However, the long liberation war in Eritrea and the famines of the 1980s have forced farmers to consume their traditional seed stocks and thereby break the chain that maintains the locally adapted diversity. The unavoidable encroachment of 'modern agriculture' which uses uniform varieties is yet another potential cause of the irretrievable loss of diversity that appeared after the end of the war. We argue that the creation of composite crosses from the most desirable surviving landraces, perhaps combined with some introgression of elite material from other areas, could form the basis of a national barley improvement programme for Eritrea, without the risk of loss of genetic diversity and vulnerability to diseases and pests.

Several questions need to be addressed in order to assess the potential use of CCs for this purpose.

- How many parental lines to use and how diverse do they need to be both genetically and in terms of their geographic origin?
- Should the choice aim at providing maximum diversity in specific characters such as drought tolerance or disease resistance?
- Should the method of maintenance simulate the traditional farming systems or the recommended practices?
- Should limited artificial selection be allowed in order to direct the evolution of the population?
- How many generations of propagation are required before the population can be used by the local growers?

Furthermore, conditions of seed storage and schemes for rejuvenation of stored seeds would also need to be developed. Yield trials at different locations, different seasons and possibly different management practices would need to be conducted. Finally, on utilization, should the farmers maintain their own seed stocks of the CC populations?

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16 Genetic Base-broadening in the West Indies Sugar Cane Breeding Programme by the Incorporation of Wild Species

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Introduction

Sugar cane is a large perennial grass. In agriculture, it is propagated vegetatively as stem cuttings, each node having a bud and a ring of root initials. Varieties of cane are therefore clones and once selected are fixed genetically. Although sugar canes are tropical in origin, through breeding and selection the geographical range of their production has been extended to sub-tropical areas such as South Africa, Louisiana and Texas in the USA and São Paulo in Brazil.

Modern sugar cane varieties are complex interspecific hybrids and are highly polyploid with a degree of aneuploidy. Their possible evolution is shown in Fig. 16.1, which is simplified from Roach (1995). Sugar cane is a crop of ancient cultivation, the history of which is summarized by Roach (1995). As a crop, it has been subject to improvement through breeding since the late 19th century. Although progress was initially good, by the 1960s it was realized that the exceedingly narrow genetic base of the existing clones was beginning to impede further progress. Walker (1962) noted direct evidence of this in the West Indies. The need for the introduction of new genetic material into breeding programmes was generally accepted. Several new collections of wild relatives of sugar cane were made, particularly of *Saccharum spontaneum*. A wider collection of the cultivated forms of *Saccharum officinarum* was also accumulated. This chapter describes a genetic base-broadening programme in the West Indies that utilizes this wide diversity of genetic material. Essentially, the programme repeats the nobilization stage of the crop's evolution, on a wider genetic base.

Origin of sugar cane

The basic genome of $x = 10$ is generally accepted for the *Saccharum* genus. There are five main species recognized as being involved in the sugar cane complex, and the tax-

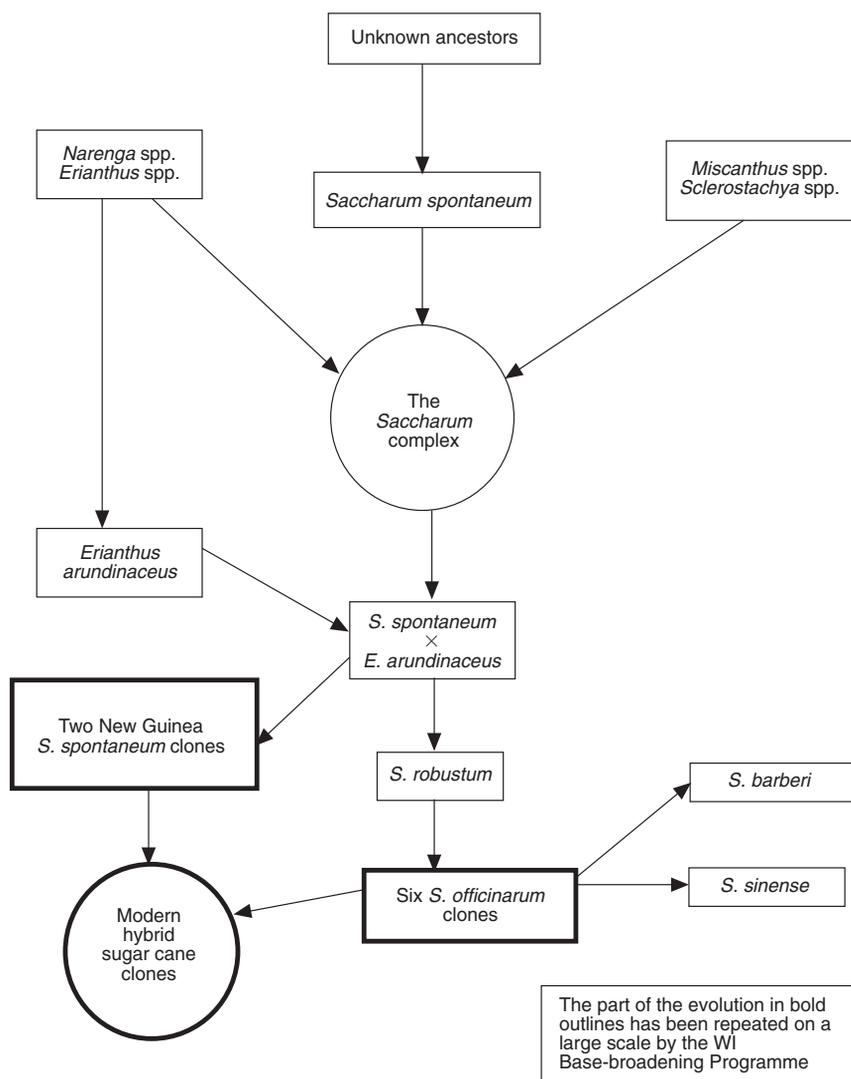


Fig. 16.1. A simplified evolution of sugar cane. From Roach (1995).

onomy and evolution of these are reviewed in detail by Daniels and Roach (1987) and summarized by Roach (1995). A brief description of these species is given here.

1. *Saccharum spontaneum* L. ($2n = 40-128$): this is a highly polymorphic species with a wide ecological range in the tropics and sub-tropics from 8°N to 40°S . Its centre of origin and of diversity is in India, but it is widely distributed from Africa to the Solomon Islands and even Japan.

2. *Saccharum robustum* Brandes and Jeswiet (ex Grassl) ($2n = 60$ or 80): this species is a name given to a wide variety of populations that probably arose through hybridiza-

tion and introgression between *S. spontaneum* and other genera, such as *Erianthus* and *Miscanthus* in New Guinea.

3. *Saccharum barberi* Jesw. ($2n = 81-124$): Daniels *et al.* (1991) describe the taxonomy of this species and separate it into six different horticultural groups. It is native to northern India where it was cultivated for sugar production. It is thought to be a natural hybrid between *S. officinarum* and *S. spontaneum*.

4. *Saccharum sinense* Roxb. ($2n = 115-120$): this species is very similar to *S. barberi* and is described by Daniels *et al.* (1991). It too is a hybrid between *S. officinarum* and *S. spontaneum*. It was cultivated in India and China.

5. *Saccharum officinarum* L. ($2n = 80$): this species is found only in cultivation, with centres of both origin and diversity in New Guinea. Selected clones of *S. officinarum* formed the original basis of sugar cane plantation cultivation and are known as the 'noble' canes.

6. Modern commercial cultivars.

As can be seen from the above descriptions, sugar canes are very complex in their genetic make-up, often being the product of both interspecific and intergeneric hybridization. It is now accepted that modern sugar canes as we know them have arisen from what is termed the *Saccharum* complex, which comprises the interbreeding genera *Saccharum*, *Erianthus*, *Sclerostachya*, *Narenga* and *Miscanthus*. However, the two major contributors are *S. officinarum* and *S. spontaneum*.

History of breeding and variety development

During the 16th century sugar cane cultivation shifted from *S. sinense* and *S. barberi* to a more extensive cultivation of *S. officinarum*, the noble canes. These were cultivated successfully for over 300 years. However, they were unthrifty, requiring frequent replanting, and were susceptible to many diseases. The noble canes spread throughout the tropics wherever sugar was produced. In 1858 it was recognized for the first time that sugar cane could produce fertile true seed. This was reported in the Barbados Liberal newspaper in February 1859 (Parris, 1954). A worker on Highlands Plantation named Harper spotted the seedlings and reported them to the overseer named Parris. Although 4.5 acres of seedlings were grown on the estate, they appear not to have had favourable characteristics (possibly because they would have been selfs from the original clone, Cheribon, and displayed inbreeding depression) and nothing more was done.

In 1888 Harrison and Bovell in Barbados (Harrison and Bovell, 1888) and Soltwedel in Java (Kobus, 1893) simultaneously rediscovered the fertility of sugar cane and began breeding programmes. The first bred variety in Barbados was named Burke and was selected from seedlings produced in 1888. From 1902 to 1919 Bovell began a series of controlled pollination crosses and seedling selection that gave rise to BH10(12) and Ba11569. All of the breeding in Barbados and Java was initially done using the existing noble varieties.

Between 1910 and 1925 in Java, breeding was to take a new path. Forms of noble canes were crossed with the wild relative *S. spontaneum*, mimicking what had occurred in the speciation process in nature. This combined the sugar-producing characters of nobles with the vigour and disease resistance of the *spontaneum* clones. Similar work was done in India using a local noble called Vellai and Indian forms of *spontaneum*.

Two very important varieties came out of this work. POJ2878 from Java and Co205 from India. These two varieties were soon distributed very widely.

In the Caribbean, noble (*S. officinarum*) breeding continued until interspecific hybrids were imported from Java and India in 1928. From then, hybrids between these and the locally improved nobles formed the basis of the breeding programme. Some very well-known varieties such as B 34104 and B 37161 were produced.

Because of the high degree of heterozygosity and polyploidy, these programmes were initially able to generate a large variability and so were very successful for many years, gradually producing better and better varieties adapted to local conditions. By the 1960s, however, the initial variability had been exploited and progress slowed considerably (Walker, 1972).

Collections and the beginning of genetic base-broadening programmes

During the 1950s and early 1960s, it became apparent that there were limitations on the rate at which improvements could be made because of lack of genetic variability and that gains made from the initial phase of hybridization could not be sustained. All of the breeding then in existence was based on parental material originating from only two forms of *S. spontaneum* and six forms of *S. officinarum* (Arceneaux, 1965). In the West Indies, the results of this narrow base were indicated by diminishing returns from conventional breeding (Walker, 1962). Many cane breeders began then to accumulate collections of wild forms and species to supplement their breeding by the introduction of new genes.

The designated world collections of sugar cane germplasm are maintained by the Governments of India and the USA at centres in Kerala and Florida, respectively. Collections of *S. officinarum*, *S. spontaneum*, *S. robustum*, *Erianthus arundinaceus*, *Miscanthus floridulus* and *M. sinensis* were made from Papua New Guinea in 1957 and 1977, and from the Indonesian Islands in 1976 and 1984 (Warner and Grassl, 1958; Berding and Koike, 1980; Krishnamurthi and Koike, 1982; Tew *et al.*, 1986). Over 400 clones of *S. spontaneum* were collected from the Indian subcontinent (Panje, 1956). Further collections have been made from the Philippines (Medina *et al.*, 1986), northern Thailand (Srinivasan and Sadakorn, 1983) and Taiwan (Lo and Sun, 1969). The world collections, therefore, contain a very wide range of wild materials that may be at the disposal of sugar cane breeders.

The current germplasm collection, held by the West Indies Central Sugar Cane Station, is some 3030 clones from different origins. These are given in Table 16.1. The clones in this germplasm are kept as a live field collection occupying about 15 ha. It must be managed such that fields are replanted frequently to maintain adequate growth for good flowering. The actual numbers in each category are not stable since new hybrids and new selections are added each year while older clones may be discarded as being less desirable. The proportions of each group do stay more or less the same.

The commercial clones in the collection are predominantly of regional origin but there is an ongoing policy to import and exchange breeding varieties with other breeding institutions around the world. There are clones from Australia, Brazil, Cuba, South Africa, Fiji, Taiwan, India, the USA (Louisiana, Hawaii and Florida), Mauritius,

Table 16.1. West Indies Central Sugar Cane Station Collection.

Type of accession	Number of clones
Commercial clones (regional and worldwide origin)	1780
'Near commercial' products of base-broadening (see below)	394
Base-broadening backcrosses – BB ₁ and BB ₂ clones	302
Base-broadening noble × <i>S. spontaneum</i> F ₁	287
<i>S. officinarum</i> (nobles)	110
<i>S. robustum</i>	29
<i>S. spontaneum</i>	114
<i>Erianthus arundinaceus</i>	14

Reunion and Mexico in the collection. The regional varieties are supplemented every year with the latest selections from member countries that comprise the West Indies Sugarcane Breeding and Evaluation Network (WISBEN): that is, Guyana, Trinidad, Barbados, St Kitts, Dominican Republic, Jamaica and Belize.

In the early interspecific crossing programmes it was generally considered that the noble canes would contribute the ability to store sucrose, while the vegetative vigour, good ratooning and disease resistance would come from *S. spontaneum*. More recently it became clear that there was scope for selection for higher sucrose storage capacity among *spontaneum* clones (Brown *et al.*, 1969).

Some degree of genetic base-broadening has been utilized in several sugar cane breeding programmes other than in Barbados, most notably in the USA (Louisiana and Hawaii), Australia, Taiwan, India and South Africa. Berding and Roach (1987) comprehensively review all these efforts. In Louisiana the two aims were to obtain cold resistance and resistance to mosaic. *S. spontaneum* accessions were screened for these characters thus limiting the genotypes that were used in crossing. In Hawaii, base-broadening was used to obtain selections that would tolerate the extremes of environment found in those islands, such as high elevation and low-nutrient, acid soils. In Taiwan, effort was concentrated on using *Miscanthus* spp. as a source for tolerance to drought and soil salinity, and resistance to downy mildew. Thus, in general, these programmes are characterized by having well-defined, but limited, goals using the introgression of specific traits. On the other hand, in the West Indies a more general incorporation approach (Simmonds, 1993) was taken with no prior selection among the large number of *S. spontaneum* clones used and the philosophy was that of incorporation of new germplasm on a population basis. The details of this work will be described later.

Nobilization

The process of crossing *S. spontaneum* on to *S. officinarum* is known as 'nobilization'. The noble parent is usually the seed bearer or female. Although *S. officinarum* ($2n = 80$) in intraspecific crosses shows normal $n + n$ inheritance, when crossed with *S. spontaneum* it displays the unusual pattern of transmission of the somatic chromosome number. The progeny are, therefore, $2n + n$ (Bremer, 1925; Price, 1961; Roach, 1969).

Thus, if a 64 chromosome *spontaneum* is used, the F_1 progeny have 112 (80 + 32) chromosomes, whereas the F_1 from a 112 chromosome *spontaneum* will have 136 (80 + 56) chromosomes. This pattern is also followed in the subsequent generations when the F_1 is 'backcrossed'¹ to noble canes although here the degree of aneuploidy is highly variable and there is usually a loss of *spontaneum* chromosomes. By the second backcross to a noble, only one-quarter, or less, of the *spontaneum* complement remains in the hybrid. Crosses between F_1 s 'backcrossed' populations and commercial varieties all show $n + n$ transmission. Since, with this mode of chromosome transmission, the proportion of *spontaneum* chromosomes is reduced with each generation of backcrossing, it is generally considered that it is unproductive to beyond the first 'backcross' generation before resorting to crossing on to commercial hybrid varieties where $n + n$ inheritance is found. Roach (1978) suggests that $n + n$ chromosome transmission predominates where *spontaneum* chromosomes are present in both parents. Heterosis for vigour and sugar content has been shown in $F_1 \times F_1$ crosses that combine chromosomes from two different *S. spontaneum* clones (WICSCBS, 1975).

Using *in situ* DNA hybridization on chromosomes it has been possible to distinguish the chromosomes coming from *S. officinarum* from those coming from *S. spontaneum* in the commercial sugar cane variety R 570 (D'Hont *et al.*, 1996). This work also showed the new fact that there has been crossing over between the chromosomes of the two species. This has implications for the degree of new variability generated from such crosses. This was previously thought not to occur. If it has happened in hybrid varieties based on the first two *S. spontaneum* clones used in hybrid production, then presumably it may also occur in our base-broadening hybrids using new sources of *spontaneum* chromosomes. Only about 10% of the chromosomes in the hybrid variety came from *S. spontaneum*.

Genetic Base-broadening in the West Indies

The objectives of the base-broadening work in Barbados were very general. The characters of interest were adaptations to various environments within the Caribbean region and better overall vigour and ratooning ability. The range of environments that the breeding programme in Barbados serves spans from Guyana (8°N), on the South American mainland, through the Caribbean island chain as far north as Jamaica (18°N). This represents an enormous diversity of sugar cane environments. Although the crossing is done at the Central Station, selection is distributed across the region. The West Indies Sugar cane Breeding and Evaluation Network (WISBEN) comprises the sugar industries of Guyana, Trinidad, Barbados, St Kitts, Dominican Republic, Jamaica, Belize and the Central Breeding Station.

Different forms of *S. spontaneum* had been used in the programme in Barbados as early as 1935 and had given rise to a very popular variety, B 41211, which was known locally as 'juicy cane' and was popular for chewing. From the 1960s, a concerted effort was made to introduce a wide genetic base from wild species. A deliberate programme

¹In this work, and in the base-broadening programme described later, the generation-wise process is usually termed 'backcrossing', even though the recurrent noble may be a different genotype in each generation.

to broaden the genetic base of our breeding clones was established by 1965 and has been described by Walker (1972), and Berding and Roach (1987).

Base-broadening clones are the products of deliberate crosses using new wild germplasm. The approach was to repeat the evolution of the crop on a very wide genetic base. Alternating clonal (parental) and seedling cycles (selection) with a short generation time were used. Large populations and weak selection pressure carried a large number of potential parents from a wide range of crosses forward to each successive generation. Starting from an original cross between a clone of *S. spontaneum* and a noble cane (*S. officinarum*), the resulting seedlings are selected for the best types. These are termed an F_1 generation. These, in turn, are then crossed to either a different noble variety or to a commercial sugar cane clone to produce the first BB_1 generation selections, which are crossed to a different commercial sugar cane clone to give the second BB_2 generation. This process is repeated until truly commercial-level selections are produced. These we term near-commercial or semi-commercial clones. Seed from the second and later BB generations is sent to the WISBEN countries for selection in their very diverse environments. By starting from many sources of *S. spontaneum* and *S. officinarum*, and by avoiding inbreeding at the various backcross generations, a substantially new genepool has been created from which to select improved, more productive clones. Further, by distributed selection in WISBEN territories, genepools with specific adaptation to each local environment have been developed.

The early generation base-broadening clones are selected in Barbados but the near commercial clones are, as indicated above, selected throughout WISBEN.

The overall breeding programme makes between 800 and 900 crosses every year. On average about 25% of these are of the base-broadening crosses of various generations, although they have at various times taken up between 30% and 40% of the crossing effort. The fertility of interspecific crosses is low and about half of the crosses attempted fail to set any seed (WICSCBS, 1978).

There are two unique aspects of the base-broadening effort in Barbados when compared with other programmes worldwide. First, there was a deliberate attempt to improve the noble population through a generation-wise polycross and selection of resulting progeny. Three generations of selection were performed with the aim of improving sugar content and reducing fibre content (Walker, 1972). The starting point was 80 noble clones selected on their visual appearance from the USDA World Collection combined with 35 noble varieties bred in Barbados (Walker, 1972). These 115 clones were planted in a high rainfall area 300 m above sea level in St Vincent to encourage flowering. Ninety-two clones flowered and were put into a polycross; 57 of them gave viable seed. The seedlings were planted in both Barbados and Trinidad. Selection was for sucrose content, softness (correlated with fibre content), ratooning ability and vigour. The second and third cycles of crossing were made in Barbados. At each generation about 100 selected clones formed the breeding population. Improvement for sugar content was limited, probably because of the lack of variation in the original population. There was, however, significant reduction in fibre content and general improvement of vigour. Such a programme was possible in Barbados because of the large collection of nobles available and the relative ease with which nobles flower in the Caribbean. Nobles hardly flower at all in most other locations that have breeding programmes and elaborate photoperiod facilities are required to induce flowering.

The second distinctive feature of our programme has been its wide scope. In all,

over 70 new *S. spontaneum* clones have been incorporated into the programme and many breeding lines developed with two or more different *spontaneums* in their pedigree. The whole programme may be viewed as population improvement aimed at incorporation of completely new wild germplasm into our existing commercial genetic background.

The breeding programme in the West Indies is largely funded by a levy on the revenues from sugar sales of all the owner member states. It is to the credit of these individually small industries that they were prepared to keep faith with such a long-term project. It was, after all, over 20 years before commercial breeding began to benefit directly from the base-broadening efforts. They not only supported the genetics and breeding work, but also supported and funded essential research on the physiology of flowering that allowed photoperiod treatments to synchronize the flowering of *S. officinarum*, *S. spontaneum* and commercial varieties of sugar cane. The effective networking of distributed selection across WISBEN guaranteed that a wide genetic diversity was maintained, not only in the base parental material, but also in the selected products of base-broadening crosses.

The base-broadening programme in sugar cane is described in the various annual reports of the station (WICSCBS, 1975, 1978, 1984, 1985) and has been summarized by Simmonds (1993).

Synchronization of flowering times

The flowering times of the very diverse sugar cane germplasm in Barbados range from September to the end of December. The noble canes tend to flower from late October to the end of November. The collection of *S. spontaneum* clones, however, has a very wide origin from 9.5°S of the equator to 32°N. They display an equally wide range of flowering times in Barbados (13°N). The natural flowering range is from July or August through to the following January (Walker *et al.*, 1977). These authors point out that generally the flowering time is related to the latitude of their origin. To make many desirable crosses it was necessary to develop photoperiod control systems in order to synchronize the flowering of the genotypes to be crossed. Simple procedures to achieve this were developed by MacColl (1977) and Midmore (1980). We now routinely use night light breaks to delay flowering in early-flowering clones to bring them in line with the mainstream and late-flowering clones.

The use of *Saccharum robustum* and *Erianthus arundinaceus*

Crosses with *S. robustum* have in general proved to be disappointing by comparison with those from *S. spontaneum*. Although the hybrids show potential for sugar content they do not show the same vigour and lack ratooning ability (characters of *S. robustum* itself). The exploitation of *S. robustum* was discontinued for this reason.

Interest in the use of hybrids between commercial sugar cane and *E. arundinaceus* began in 1980, largely as a response to the possibility of producing varieties, not for sugar production but a source of biomass production for other purposes. However, the initial hybrids looked very promising as potential sugar canes (WICSCBS, 1984, 1985). The vigour, appearance and sugar content of the F₁ hybrids were comparable

with those of the BC₂ hybrids derived from *S. spontaneum*. The morphology (D.I.T. Walker, personal communication) and chromosome numbers (P.S. Rao, unpublished) suggested that true hybrids had been achieved. However, the use of PCR markers has so far failed to find *Erianthus* DNA in the putative hybrids (A. D'Hont, personal communication). It is possible that what were thought to be exciting hybrids were in fact the result of self-pollination of the commercial female parent. Both restriction fragment length polymorphism (RFLP) and PCR techniques have been used to confirm pedigrees of crosses involving wild relatives of sugar cane (D'Hont *et al.*, 1997).

Products from the base-broadening programme

There is evidence now that products from the base-broadening programme are regularly reaching late selection stages in all of our member countries. This is illustrated by Table 16.2 showing the accumulated results from crosses made between 1979 and 1994.

As more advanced generations of crosses between commercial varieties and base-broadening clones are made, the distinction between the two programmes becomes more and more blurred. We are at the point now where an increasing number of crosses each year involve parents that can be described as semi-commercial which have been derived from base-broadening programmes. Presently about 20% of WISBEN's crosses each year are of this nature.

In Barbados, two varieties have been released that were derived from new *S. spontaneum* germplasm: B 79474 and B 80251. B 79474 has in its pedigree three 'old' wild sources – SC12/4, a noble; Toledo, a *spontaneum*; and 28NG251, a *robustum* – to which have been added a new noble, 57NG68, and a new *spontaneum*, SES49. B 80251 has one old *spontaneum*, Moentai, to which a new noble, BNS55, and a new *spontaneum*, SES84/58, have been added. To reduce vulnerability to disease, a relatively large number of varieties are grown in each country throughout the West Indies (Rao and Gardiner, 1997). The products of the base-broadening programme are now

Table 16.2. Results of crosses made between 1979 and 1994 in the West Indian Sugarcane Breeding and Evaluation Network (WISBEN).

Country	Number of clones with new germplasm in their pedigree	
	Reaching third selection stage	Reaching final selection stages
Guyana	40	16
Trinidad	*	13
Barbados	**	24
Jamaica	7	6
Dominican Republic	13	3
Belize	19	3
Total	79	65

* Trinidad does not have this selection stage in its programme.

** Large numbers have reached both Stage 2 and Stage 3 selections from the base-broadening crosses for many years and have been incorporated back into the commercial breeding programme.

beginning to contribute to this broad genetic diversity in the field. Although WISBEN's programme has been long term (35 years) and required considerable effort and resources, it is felt that its benefits are now becoming apparent and it was well worth the devotion to it.

The generation of large populations of clones from the West Indies sugar cane genetic base-broadening was directed to the selection of new varieties for the production of sucrose. It is now in the phase where its products are being absorbed into the commercial breeding or combined with clones developed especially for very high sucrose content. The range of genetic diversity in these new clones remains very large. There is potential among the base-broadening selection for the development of canes with alternative uses. The vigour in early generations means that they have potential as producers of biomass for such uses as fibre production to make paper or board. Fibre content of sugar canes is in the range of 10–15% with most being about 13%. In the base-broadening clones, fibre content as high as 20% is encountered, with potential to select even higher types. Similarly, types with high total sugar content, but a relatively low sucrose component, are encountered. Such clones could be developed into varieties suitable for molasses or syrup production or for the production of rum. The impressive genetic variation generated by this kind of base-broadening is such that appropriate selection pressures could generate varieties with a wide range of uses. As such, it is maintained as a resource that may be more widely exploited in the future.

Acknowledgements

I cannot conclude without paying a tribute to Professor N.W. Simmonds, whose help, ideas and enormous encouragement kept the project alive for so many years, and to Mr D.I.T. Walker and Dr P.S. Rao, who carried out much of the early work and whose ideas guided the programme from its inception.

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17 Potential of Genetic Resources and Breeding Strategies for Base-broadening in *Beta*

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Introduction

In Europe, cultivated forms of *Beta* (leaf beet, garden beet, fodder and sugarbeet) are grown on more than 5.6 million ha, to which can be added approximately 550,000 ha in North America; 600,000–670,000 ha in China (with a promising production and market potential for sugarbeet); and a number of smaller areas in Chile, Egypt, Iran, India, Japan, Morocco, Tunisia, Turkey and Syria. Altogether, sugarbeets are grown on about 7.5 million ha worldwide. Breeding efforts are focused on the sugarbeet crop, while leaf, garden and fodder beet breeding is of regional importance only.

The genus *Beta* is native to Europe and adjacent areas. Sections *Nanae* (Greece) and *Procumbentes* (Canary Islands) have a limited distribution area, while wild species of section *Beta* occur along the coastline from the south of Sweden to Morocco and from the Canary Islands to Iran. Section *Corollinae* occurs at altitudes higher than 800 m. It has a large distribution area in Turkey and neighbouring countries. The centre of diversity is probably located where the species distribution of sections *Beta* and *Corollinae* overlap (eastern Turkey and the western part of Transcaucasia). The domestication of beets probably started in the Euphrates and Tigris region and continued in Turkey and Greece, from where cultivated beets were introduced to northern Europe (Boughey, 1981). Cultivated beets have occurred in China since the 5th century (Sun Yi Chu, 1994) and also in Arabic countries.

One of the youngest cultivated forms, the sugarbeet, has become a cash crop of worldwide importance which has been cultivated on a large scale only since 1811, when Napoleon decreed that beet should be grown for sugar. As the sugarbeet was probably selected from one single cultivated population only, the 'White Silesian', the genetic base of the crop is supposed to be very narrow. The 'White Silesian' beet had a rather low sugar content. However, the German scientist Achard considered the good root shape of this fodder-beet-like type as a favourable trait and started to select within this population for higher sugar content and yield. The sugar content increased from 4% to 16.5% between 1784 and 1981 (Winner, 1981).

Before 1960, open-pollinated multigerm varieties were developed using family selection methods and the breeding material had a comparatively broad genetic variation (Desprez and Desprez, 1993). Compared to potato, barley and other economically important crops, sugarbeet did not seriously suffer from pest and disease attacks or adverse environmental conditions in the main production areas (Lewellen, 1992). Though almost all beet pests and diseases were already known, the sugarbeet crop was considered as a relatively healthy crop until the 1960s. However, because of the growing acreage, the sugarbeet was increasingly cultivated in short crop rotation, amplifying disease problems. During the 1960s the rising cost of hand labour became an even more pressing problem. The ordinary sugarbeet seed ball contains three to four seeds; seedlings emerge in clumps and had to be thinned by hand. Savitsky (1950) found in a seed field of about 1.5 ha one monogerm, homozygous plant. This character was essentially inherited by a single recessive gene, which became of great economic importance in sugarbeet breeding and production. Lines derived from that plant, such as SLC101 (Savitsky, 1952), were extensively used in breeding programmes. In 1942 Owen (1954) discovered cytoplasmic male-sterile germplasm. After the Second World War, sugarbeet breeders focused their work on the development of monogerm, cytoplasmic male-sterile hybrid varieties with a high sugar quality, a high yield of recoverable sugar (Oltmann *et al.*, 1984) and a good level of field resistance to diseases. Only one monogerm line (C562) was resistant to bolting and all of the first monogerm varieties from the Hilleshög company, which reached more than 60% of the European market (cv. 'Monohill' and others), were derived from this line. In addition, all hybrid varieties were based on a single source of cytoplasmic male sterility, the Owen cms (Owen, 1948; Bosemark, 1979). After the introduction of cytoplasmic male sterility and monogermness, the female breeding pool went through a genetic bottleneck. Accordingly, breeders have systematically enlarged the female genepool by using their own breeding stock. Even though exotic germplasm was not used, after 30 years of broadening the female genepool, the genepool has sufficient variability. Today, breeders wish to broaden the whole breeding pool as such (female and male pools).

Strikingly, for sugarbeet breeders the crop itself still is the most important genetic resource used for the development of improved varieties today. One could argue that the genetic base of the crop as such is not as narrow as generally assumed. It seems rather that it is a lack of specific traits which hampers breeding progress. Indeed, because commercial plant breeders use a large number of different, heterozygous pollinator populations, hybrid varieties still have much genetic variation.

Additionally, sugarbeet is a wind-pollinated, strongly outcrossing crop. Therefore, plant breeders today may profit from exotic germplasm that was introgressed in the sugarbeet breeding pool, either by chance or deliberately by breeders. The first introductions of wild germplasm into sugarbeet probably occurred at the beginning of the 20th century, in Russia, the USA and Italy. Cultivated \times wild beet crosses were, for example, described by Tjebbes (1933), who used *Beta vulgaris* ssp. *maritima* from the North Sea coast with a sugar content ranging from 15.7% to 17.6%; and Munerati (1932), who crossed a population from the Po estuary with sugarbeets to introduce genetic variation for resistance to *Cercospora beticola*. The Munerati material, at least, has been widely used in sugarbeet breeding.

Probably because of these early experiences with wild beet crosses, in the 1970s and early 1980s there was a great fear that introgression of undesirable genes of wild or

exotic germplasm along with the desired disease resistance trait would destroy the results of costly selection on high sugar quality and bolting resistance. However, the view on potential benefits arising from the utilization of exotic germplasm began to change when soil-borne diseases such as the beet cyst nematode (*Heterodera schachtii*) (Hellings, 1943) or the beet necrotic yellow vein virus (BNYVV) (Grünwald *et al.*, 1983), already identified as very harmful disease agents in sugarbeet fields, began to spread and threaten the sugarbeet production in the whole northern hemisphere. Though many lines were tested, no major disease resistance genes against these important pests and diseases were detected in the crop. In addition, the level of tolerance to the cyst nematode proved to be insufficient in the breeding genepool (Curtis, 1970; Heijbroek, 1977). Interestingly, in some Italian varieties (cv. 'Roxane', 'Java', 'Alba'), there was some resistance or tolerance in an agronomically satisfactory genetic background. It is assumed that Italian varieties still contained some wild genes originating from the Munerati material. These sources have been used to develop the first varieties with Rizomania tolerance/resistance (Desprez and Desprez, 1999).

In 1956 Savitsky (1960) detected strong *Heterodera schachtii* resistance genes in *Beta* section *Procumbentes*. However, due to strong crossing barriers between section *Beta* and section *Procumbentes*, the utilization of this source proved to be very difficult and time-consuming. It is easy to understand that this specific experience did little to promote a broader use of exotic material in breeding programmes (Desprez and Desprez, 1996).

In the 1980s, the continued collecting and evaluation efforts of the USDA/ARS programme yielded more and more exciting results on new sources of resistances, for example to the Rizomania disease (Doney and Whitney, 1990) in *B. vulgaris* ssp. *maritima*, which crosses easily with sugarbeet. Since then, the interest in utilization of *Beta* genetic resource collections has been increasing worldwide. Breeders are mainly searching for disease resistance genes in exotic germplasm to supplement their breeding pool. The introduction of additional genetic variation for sugar content and yield genes from exotic germplasm is thereby welcomed as a positive side effect that can benefit breeding progress in the long run.

The Sugarbeet Breeding Research Community

Because of the small number of remaining large sugarbeet seed companies, collaboration between experts is no longer restricted to national projects. In the non-competitive sector particularly, there is a strong willingness to cooperate at international level. Knowledge as well as germplasm is exchanged across the northern hemisphere where sugarbeets are mainly produced. Pre-selected wild material from Europe can be found in Chinese breeding gardens, and Chinese leaf beets in European evaluation programmes. Due to the exchange of scientists between universities and the fusion of breeding companies at international level, national projects are becoming more and more an integral part of international activities. The different partners can be grouped as follows:

- Institutes and companies in Europe and the USA, with a strong interest in novel genetic variation for pest and disease resistance, drought and salt tolerance, which are

required to develop varieties meeting the demand for an ecologically sound sugarbeet production.

- Governmental institutes developing varieties (China, India, Iran, Poland, Ukraine, Bulgaria), with interest in access to high-yielding, high-quality breeding material, resistant germplasm and high-temperature tolerance.

Sugarbeet breeders and researchers from the commercial and public sector convene in different associations. The Study Group 'Genetics and Breeding' of the International Institute of Sugarbeet Research (IIRB) meets once a year and organizes joint research projects at international level that interest all breeding companies. Another international forum with a wide coverage of nationalities and scientific disciplines is provided by the World *Beta* Network (WBN). WBN meetings take place every 3 years and deal with joint activities for genetic resources conservation, documentation and utilization. Smaller, but nevertheless very important groups are the USDA/ARS Sugarbeet Crop Advisory Committee (annual meetings), other similar national associations and the French *Beta* Network which can also cooperate with partners outside the country. Discussion on the utilization of *Beta* genetic resources collections has become a permanent topic on the agenda of all these groups.

The Genus *Beta* and its Useful Characters

The genus, which is the raw material for breeders, consists of four sections, which can be grouped into three gene pools (Table 17.1).

Breeders have successfully tapped the primary and tertiary gene pools, while only a few attempts were made to use the secondary gene pool. There are a number of reasons for this. Although stronger crossing barriers exist between section *Corollinae* and section *Beta* than between species within section *Beta*, interspecific hybrids can be produced. First attempts to introgress yellowing virus resistance from the *Corollinae* section into the sugarbeet (Dalke cited in Jassem, 1985) failed probably because of lack of sufficient chromosome homology between the *Corollinae* and the sugarbeet chromosomes, which is a prerequisite for crossing-over and recombination. In addition, while breeders were still engaged in the introgression of the nematode resistance genes from section *Procumbentes* into the sugarbeet, large-scale screening of the *B. vulgaris* ssp. *vulgaris* and ssp. *maritima* germplasm yielded donors of interest to breeders. For the time being there is therefore no real pressure for an urgent utilization of the secondary gene pool. A third reason is lack of evaluation of the *Corollinae* section due to a practical problem arising from the fact that all *Corollinae* species are hard seeded. Thus, the pericarp cap has to be removed manually to facilitate germination, which is very time-consuming and has deterred investigators from large-scale screening. Section *Nanae* (*B. nana*) has never been taken into consideration for base-broadening projects. As a species adapted to high altitudes it is very difficult to handle at locations where sugarbeet breeding work is generally conducted. It is not known whether this species has ever been successfully multiplied *ex situ*, not to mention successfully grown for evaluation purposes.

All three gene pools contain useful as well as undesirable wild characters (Dale *et al.*, 1985; Van Geyt *et al.*, 1990; Lewellen, 1992; Paul *et al.*, 1992; Stanescu, 1994; Büttner *et al.*, 1997; Mesbah *et al.*, 1997; Yu, 1997; Bosemark, 1998; Michalik *et al.*, 1998; Panella, 1998). Examples are provided in Table 17.2.

Table 17.1. Taxonomy of the genus *Beta*.

Primary genepool	Section <i>Beta</i> syn. <i>Vulgares</i> Ulbrich <i>B. vulgaris</i> L. ssp. <i>vulgaris</i> (cultivated beets) Leaf beet group Garden beet group Fodder beet group Sugarbeet group ssp. <i>maritima</i> (L.) Arcang. ssp. <i>adanensis</i> (Pamuk.) Ford-Lloyd & Will. <i>B. macrocarpa</i> Guss. <i>B. patula</i> Ait.
Secondary genepool	Section <i>Corollinae</i> Ulbrich Base species <i>B. corolliflora</i> Zosimovich <i>B. macrorrhiza</i> Steven <i>B. lomatogona</i> Fisch & Meyer Hybrid species <i>B. intermedia</i> Bunge <i>B. trigyna</i> Wald. & Kid. Section <i>Nanae</i> Ulbrich <i>B. nana</i> Boiss. & Heldr.
Tertiary genepool	Section <i>Procumbentes</i> Ulbrich syn. <i>Patellares</i> <i>B. procumbens</i> Smith <i>B. webbiana</i> Moq. <i>B. patellaris</i> Moq.

Bottlenecks to the Utilization of *Beta* Genetic Resources

The utilization of *Beta* genetic resources is confronted by several different kinds of problems. Accordingly, different strategies and methods have been developed for the introduction of new genetic material into the sugarbeet breeding pool.

The first problem is the fear of breeders that introgression of wild beet germplasm would require excessively high investments to recover the root shape, root yield, sugar yield and sugar quality of the cultivated parents. Hence, breeders tend to search in the sugarbeet breeding genepool first – sometimes in vain as in the case of resistance to *Heterodera schachtii*. O. Bosemark, head breeder of a Swedish company, was the first to say that this fear had no rational basis (Bosemark, 1989). In fact, the discussion initiated by Bosemark helped to promote the breeding approaches of researchers like Munerati (1932). Bosemark demonstrated in selection experiments that after crossing exotic material with sugarbeet, only a few selection cycles are required to regain a reasonable yield and root shape. In view of the narrow genetic base of the crop, he considered the potential profit for a breeder higher than the loss of funds arising from selection against wild characters in cross progenies of cultivated × exotic crosses.

Annual, quick-bolting wild types of section *Beta* form the second problem. The

Table 17.2. Characters relevant to beet breeding and their distribution over species.

Trait	Taxon code																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Annual life cycle																		
Monogerm seed balls																		
Hard seededness																		
Seed shattering																		
CMS																		
Genic male sterility																		
Salt tolerance																		
Frost tolerance																		
Curly top																		
Yellowing viruses																		
Beet mosaic virus																		
BNYV virus																		
Yellow wilt																		
<i>Peronospora farinosa</i>																		
<i>Erysiphe betae</i>																		
<i>Rhizoctonia solani</i>																		
<i>Cercospora beticola</i>																		
<i>Polymyxa betae</i>																		
Black leg disease																		
<i>Erwinia</i> ssp.																		
<i>Heterodera schachtii</i>																		
<i>Heterodera trifolii</i>																		
<i>Meloidogyne hapla</i>																		
<i>Myzus persicae</i>																		
<i>Pegomya</i> ssp.																		

Taxon codes used: (1) *B. vulgaris* ssp. *vulgaris*; (2) *B. vulgaris* ssp. *vulgaris* leaf beet group; (3) garden beet group; (4) fodder beet group; (5) sugarbeet group; (6) *B. vulgaris* ssp. *maritima*; (7) ssp. *adanensis*; (8) *B. macrocarpa*; (9) *B. patula*; (10) *B. corolliflora*; (11) *B. macrorrhiza*; (12) *B. lomatogona*; (13) *B. intermedia*; (14) *B. trigyna*; (15) *B. nana*; (16) *B. procumbens*; (17) *B. webbiana*; (18) *B. patellaris*. ■ = variation detected.

evaluation for disease resistance is sometimes difficult to realize directly on such annual types and even if a useful trait is detected it is not always transferable to the crop as it may not be expressed in the genetic background of cultivated material. Because of these difficulties it has been suggested that annual wild types are first crossed with cultivated germplasm and the resulting biennial material is then screened. In the case of the leaf spot disease, for example, early-bolting plants cannot be evaluated precisely in the field test, while greenhouse and laboratory tests have a low correlation with field results (W. Mechelke, KWS, personal communication). Screening in the field is equally difficult because plants are already senescent when the disease develops. In the case of the *Cercospora beticola* leaf spot disease, it is then very difficult or even impossible to score. Similar difficulties are known for various other diseases. In addition, annual types when

tested in the field may contaminate the soil with seeds and contribute thereby to the weed beet problem.

The third problem arises from crossing barriers between section *Beta* and sections *Corollinae*, *Nanae* and *Procumbentes*, respectively (Jassem, 1992). They are particularly strong in the case of *Procumbentes* species. However, section *Corollinae* and *Procumbentes* contain characters that have not yet been detected in section *Beta*, such as insect resistance. Stanescu (1994) noted that *B. corolliflora* may be resistant to attack by *Mamestra brassicae* L. and *Noctuide loxostege stricticalis* L. larvae. Only few accessions of these hard-seeded species have been evaluated today. Breeders will perhaps one day find strong resistance genes acting against *C. beticola* in the secondary gene pool.

Breeding Approaches to Broaden the Genetic Base of *Beta*

The different breeding programmes which have been developed to overcome these difficulties can be grouped in two categories:

1. In previous years, breeders only concentrated on the introgression (Simmonds, 1993; Spoor and Simmonds, Chapter 3, this volume) of desirable traits into the sugar-beet crop as fast as possible. 'Fast' can mean a few years as in the case of the primary gene pool or more than a decade, as in the case of the tertiary gene pool (see examples below).
2. Today, breeders have also started programmes that do not concentrate on a specific character but aim at broadening the genetic base of the crop in general. This type of approach has been described by Simmonds (1993; see also Spoor and Simmonds, Chapter 3, this volume) as 'incorporation'. Two examples are given below for incorporation from the primary gene pool.

Introgression from the primary gene pool

Examples of conventional breeding approaches are described by Desprez and Desprez (1999) and in more detail by Büttner *et al.* (1997). The BGRC 54817 (RNR 870909) held by the BAZ Genebank and collected in Normandy, France by Dutch scientists in 1970 showed variation for Rizomania resistance. Through selection of resistant single plants, followed by selfing and selection of resistant plants in the S_1 -line, the character 'Rizomania resistance' could be fixed. A parallel backcross programme was started for inheritance studies and for broadening the genetic base of Rizomania resistance in sugarbeets. Büttner *et al.* (1997) applied a well-known breeding method, which is very successful if the donor parent crosses easily with the sugarbeet and if the character is simply inherited.

Introgression from the tertiary gene pool

Strong crossing barriers exist between the *Procumbentes* species (*B. procumbens*, *B. webbiana* and *B. patellaris*) and the section *Beta*. Phylogenetic research using DNA

fingerprinting (Jung *et al.*, 1993) even suggests that the section *Procumbentes* could be considered as a separate genus. Recent results presented by Shen *et al.* (1997) also suggest that the section *Procumbentes* diverged from the other *Beta* species at a rather early evolutionary stage. This explains why introgression of resistance genes against the cyst nematode *Heterodera schachtii* into sugarbeet has been so difficult and time-consuming. Savitsky (1960) was the first who crossed *B. vulgaris* with nematode-resistant *B. procumbens*. In Germany, crosses between cultivated forms and the wild species *B. procumbens*, *B. webbiana* and *B. patellaris* were done by Löptien (1984) at the University of Hanover. Today, the resulting varieties are mainly used to decrease the nematode population density in infested fields. The first steps were production of alien monosomic resistant addition lines; the second step was production of diploid sugarbeet translocation lines carrying a small fragment of the wild chromosome with the resistance gene; the third step was genetic localization of the gene(s), cloning and sequencing of the nematode resistance gene *Hs1^{pro-1}*, and testing of the function of *Hs1^{pro-1}* in transformation experiments (Cai *et al.*, 1997; Jung, 1997). By means of genetically transformed sugarbeet an important disadvantage of the conventionally developed nematode-resistant varieties – insufficient agronomic performance – may be overcome.

The nematode resistance gene originating from *B. procumbens* encodes a 282-amino acid protein, which has features quite similar to disease resistance genes previously cloned from other higher plants. This gene is not only useful for sugarbeet resistance breeding, but may also be of interest to breeding programmes outside the genus *Beta*, such as rapeseed (Jung, 1997).

Incorporation from the primary gene pool

Colleagues from the USDA/ARS started a systematic sugarbeet enhancement programme in 1986. Crosses with wild *B. vulgaris* germplasm were made in 1986, 1990 and 1994. In 1990, male-sterile sugarbeet plants were chosen as the female parent to obtain F₁ plants. F₁ plants of each cross were intercrossed to produce F₂-families, which were then bulked to produce F₃ families. At least two recombination cycles were allowed before mild selection on root shape and bolting resistance was started. After five cycles of mass selection some of the progenies started to resemble sugarbeet. In this case no prior selection on useful characters was done. Testing on disease resistance followed later. Our USDA colleagues are very satisfied with this programme, which has steadily started to produce USDA germplasm releases (Doney, 1998; Panella, 1998). When officially registered by the *Journal of Crop Science*, the releases can be used by any breeder and fed into elite breeding programmes.

French colleagues have recently started a similar but more sophisticated breeding programme. It was launched by the company Florimond Desprez at the request of the Bureau des Ressources Génétiques (BRG). Almost all European breeding companies actively participate in this programme, which uses wild material of French origin. One of the interesting features is that the 'value' of the wild sources is only partly known. Wild material from Corsica, for example, contains variation for Rizomania resistance. Yet, no selection on this specific character is done before crossing. The difference compared with the introgression work done by Büttner *et al.* (1997) is the long-term

strategy behind it. It is a declared aim of the project: (i) to allow maximum recombination between the cultivated and wild sources; and (ii) to keep a half-and-half 'equilibrium' of the wild and cultivated genome (Doggett and Eberhard, 1968). For that purpose, so-called Doggett populations containing the alleles 'MM' for multigermicity, 'aa' for genetic male sterility, and the S_f allele for self-fertility are used as female parents (Owen, 1942, 1954). Crosses between $MMaaS_fS_f$ and wild *Beta vulgaris* ssp. *maritima* populations were made in 1996. The presence of the *aa*-allele allows the identification of male sterile plants in the population. Seeds are harvested on male-sterile plants only, which ensures maximum outcrossing and recombination. The programme is designed in such a way that each participant receives two French wild beet populations and produces two 'buffer' populations. It was agreed to exchange seed samples of the two progenies amongst the 11 participants in 1999 when the pre-competitive character of the programme ended. At that stage each partner owned pools originating from 22 different French wild beet populations. Subsequently, selection started for agronomic characters (especially root shape) and with the introduction of selfing cycles to produce inbred lines and crossing cycles to recombine the different sub-populations. Though sugarbeets are self-incompatible, the production of inbred lines is possible because of the presence of the S_f allele in each population. How to exploit this genetically broad material, which will get adapted to the environmental conditions prevailing at each selection site, is now at the discretion of each partner. This differentiation process will also contribute to a diversification of the elite breeding pool amongst companies and breeding institutions. A simplified description of the base-broadening programme is given in Scheme 17.1.

The activities of the French *Beta* Network follow similar principles as described by Mitteau (1997) for bread wheat and barley. The *Beta* programme allows collaborative projects on genetic resources management since the common material has no property rights on it. This is also an open programme so that any new participant can enter by contributing two new populations which can then be shared with the already participating partners without much disturbance. New participants, however, need to contribute actively to the network programme before they can profit from the work done by the others. In the long run it will produce material that could become useful for many international cooperative studies.

Incorporation from the secondary gene pool

A fraction of the *Corollinae* material that is used in a research programme at the University of Kiel (Germany) was collected by a German scientist in Turkey in the 1970s. The Genebank of the Federal Centre for Breeding Research on Cultivated Plants (BAZ) maintains this material and has provided the Chinese University at Harbin in northeast China with *Corollinae* accessions. The aim of the project is the establishment of a set of alien monosomic addition lines, which were developed by the Chinese counterpart using *Corollinae* accessions.¹ The actual value of the *Corollinae* sources is not known, and it will be determined only after all theoretically possible alien

¹ See <http://www.plantbreeding.uni-kiel.de> July 1998; personal communication of Professor C. Jung.

Scheme 17.1. Production of a buffer population using wild *Beta* from France.Step 1: Production of F_1 seeds.

Year	Generation	Doggett population (DP) genotypes	Female parent (DP)	Wild population (WP) genotypes	Male parent (WP)	Explanation of the breeding step
1	F_0	1/2 <i>Aa</i> ; 1/2 <i>aa</i> 1 <i>MM</i> 1 S_1S_1 1 <i>bb</i>	Sugarbeet	1 <i>AA</i> 1 <i>MM</i> 1 <i>S</i> / ? 1 <i>B</i> / ?	Seabeet	Production of sugarbeet and seabeet stecklings (= small beets cultivated for seed production, only)
2	F_0	1 <i>aa</i>	Sugarbeet	1 <i>AA</i>	Seabeet	Before flowering <i>Aa</i> sugarbeet genotypes are discarded. Seabeet plants pollinate male-sterile sugarbeet plants. Seeds are harvested on <i>aa</i> sugarbeet genotypes separately (half-sibs). Seeds of the seabeet population are harvested as a bulk to maintain the original accession.

Explanations of genotypes: *AA* = genic male-fertile; *aa* = genic male-sterile type; *MM* = multigerm; *mm* = monogerm type; S_1S_1 = self-fertile type; $S_{1-n}/?$ segregating self-incompatible, sterile type, S_1 is dominant to all alleles of the S-series; *BB* = annual, *bb* = biennial type, *B*/? = segregating annual type.

Step 2: Production of the F_3 generation starting from F_1 seeds.

Year	Generation	Male-fertile (<i>AA</i> , <i>Aa</i>) /sterile (<i>aa</i>) genotypes	Explanation of the breeding step
2	F_1	1 <i>Aa</i>	Sowing of separately harvested half-sib families. The genome consists of 50% sugarbeet and 50% seabeet genes.
3	F_1	1 <i>Aa</i>	Singling of F_1 plants to an equal field stand per half-sib family to ensure about equal genetic contributions of each of half-sib family to the F_2 . The F_2 seed sample is harvested on each half-sib family separately.
3	F_2	1/4 <i>AA</i> , 1/2 <i>Aa</i> , 1/4 <i>aa</i>	Sowing of half-sib families to produce F_2 stecklings.
4	F_2	1/4 <i>AA</i> , 1/2 <i>Aa</i> , 1/4 <i>aa</i>	All <i>aa</i> genotypes are earmarked at flowering and seeds are harvested only on <i>aa</i> genotypes.
4	F_3	2/3 <i>Aa</i> , 1/3 <i>aa</i>	Mailing of F_3 seed samples to each participant. Mutual exchange of F_3 seed material.

Step 3: Production of the buffer population.

Year	Generation	Male-fertile (<i>AA</i> , <i>Aa</i>) /sterile (<i>aa</i>) genotypes	Explanation of the breeding step
4	F ₃	2/3 <i>Aa</i> , 1/3 <i>aa</i>	Sowing of the separately harvested half-sib families derived from an individual sugarbeet × seabeet accession cross $DP \times WP_{1\dots n}$ to produce <i>aa</i> genotypes of this specific F ₃ . Other F ₃ families produced by programme partners are sown accordingly.
5	F ₃	2/3 <i>Aa</i> , 1/3 <i>aa</i>	Depending on the number (<i>k</i>) of F ₃ s within a particular $DP \times WP$ cross exchanged between participants, a maximum of $n \times k$ half-sib families will jointly flower and intercross. Seeds are again harvested on <i>aa</i> genotypes, only. Within each $DP \times WP_{1\dots n}$ family, <i>aa</i> genotypes can be harvested as a bulk.
5	F ₄	1/2 <i>Aa</i> , 1/2 <i>aa</i>	The Doggett population is at gene equilibrium. The individual $DP \times WP_{1\dots n}$ should be kept separately during the next generations of intercrossing. Plants still contain about 50% sugarbeet and 50% seabeet genome.
6	F ₄	1/2 <i>Aa</i> , 1/2 <i>aa</i>	Sowing of $n \times (DP \times WP)$ families for mild mass selection on agronomic characters such as root shape and bolting resistance. Production of inbred lines, if considered to be already useful, is possible through the segregating <i>S</i> ₁ allele.

WP_1 = wild population no. 1; WP_2 = wild population no. 2; etc.

■ = generative phase.

monosomic addition lines have been established. By testing these addition lines for disease resistance, the researchers will try to localize resistance genes on the wild beet chromosomes. After backcrossing with sugarbeet, diploid, resistant recombinants can perhaps be selected as basic material for breeding. This approach has a basic similarity to the French Doggett population concept: the specific value of the wild *Corollinae* parent is not known precisely.

Future Role of Genebanks in Germplasm Enhancement Programme

As a consequence of the long-term base-broadening programmes initiated in the USA and France, considerable fractions of genetic diversity will be maintained in buffer populations. Genebank accessions which were used to create these buffer populations are further maintained as individual accessions in genebanks. Hence, genetic diversity stored in genebanks will become duplicated in base-broadening programmes. Today, our *Beta* collections are static. Genebank managers keep nicely classified and documented seed samples in their stores. In future, at least in the case of outcrossing species, genebanks could assume new functions. Besides the maintenance of rationalized static collections, genebanks could become responsible for the maintenance of more dynamically managed genepools resulting from different kinds of programmes. In an outcrossing crop, the role of a genebank manager may become more that of a genepool manager, coordinating and linking: (i) *in situ* maintenance of natural populations; and (ii) sampling and *ex situ* conservation of populations; with (iii) base-broadening work.

Base-broadening work can last for a long period aiming at the creation of new diversity through continued recombination and evolution. Since genebanks already have long-term responsibilities, these institutions may be in a good position to follow long-term germplasm maintenance and breeding strategies.

In France, native *B. vulgaris* ssp. *maritima* populations are already managed *in situ* in their natural environment, which enables seed harvest on request for evaluation purposes, and helps to avoid multiplication and storage of accessions in an *ex situ* collection. In addition, by grouping a number of wild populations of similar origin, the French base-broadening programme decreases the number of accessions that need to be manipulated. Furthermore, better adapted, dynamically managed material is of higher interest to breeders.

In the field of base-broadening, genebanks could:

- Run simple selection projects that are required to adapt wild germplasm to routine screening methods, as in the case of annual wild *Beta vulgaris*.
- Maintain buffer populations in the deep-freeze store if there is a temporary lack of funds required for continuation of the work, or if populations have fulfilled their current purpose.
- Maintain information on the purpose and breeding history of buffer populations for future users.
- Maintain donor lines with high frequencies of useful genes, as has already been briefly described by Büttner *et al.* (1997).

Natural evolution, as well as breeding, is a dynamic process. An integrated germplasm conservation and utilization programme linking *in situ* maintenance, *ex situ*

conservation and base-broadening can therefore better mediate between evolution and breeding than static genebank collections. It is at least our impression that the integration of these three elements of germplasm conservation and utilization has made considerable progress in sugarbeet in recent years.

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18 HOPE, a Hierarchical, Open-ended System for Broadening the Breeding Base of Maize

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Rationale and Objectives

The hierarchical, open-ended population enrichment (HOPE) breeding system was designed to broaden significantly the genetic base presently deployed in commercial maize breeding programmes in Canada and similar short-season maturity areas. This base is extremely narrow and relies heavily on the earlier maturing derivatives of the six inbred pedigrees (Goodman, 1990) that dominate the US hybrid maize industry. Some potential consequences of a constricted breeding base are an eventual reduction in the rate of breeding progress, greater vulnerability to biotic and abiotic stresses, and the lack of alternative or additional gene complexes which may exist in untapped germplasm. As Frankel (1977) points out, the use of such germplasm may result in breeding material with new developmental pathways or ecological adaptations. The latter may, for example, be important as agricultural practices change to reduced or no tillage, lower inputs, increased use of marginal lands, etc. The objective of the HOPE breeding system is to develop a breeding source for inbred lines that have markedly different genetic backgrounds from lines presently used in commercial breeding and that have the agronomic qualities and combining ability to serve as a parent or parents of commercially successful hybrids, thereby enhancing the genetic diversity available to the maize grower.

Methods and Strategy

The HOPE breeding system

The HOPE breeding system is presently undergoing its second revision. The original design, described in Cramer and Kannenberg (1992), was employed from 1977 to 1985. From 1986, the system was modified to the one described in detail by Kannenberg and Falk (1995). Following a recent evaluation (Popi, 1997), the

HOPE system is now undergoing a radical alteration, resulting in considerable simplification.

The version of the HOPE system described by Kannenberg and Falk (1995) involves A and B heterotic sets, each consisting of four genepools, arranged in a hierarchy of performance levels: low (L), intermediate (I), high (H) and elite (E) (Fig. 18.1). The performance hierarchy is to separate materials with poorer agronomic characteristics from immediately more useful germplasm. The A and B heterotic sets are meant to provide sources at the E level for, respectively, A and B inbred lines that have good combining ability, i.e. the hybrid formed by crossing the two inbreds will exhibit good heterosis (hybrid vigour). The genepools are open-ended: thus, new germplasm (introductions) can be continually introduced into the system based upon level of performance and heterotic pattern, and improved germplasm can be moved stepwise up the hierarchy of performance levels. Increasingly stringent selection procedures are employed at each successively higher hierarchical level: this allows shaping of the extensive variability at the lower levels into diverse, but potentially more useful, germplasm at the E level, the level from which inbred lines are developed.

The newest version of HOPE, as proposed by Popi (1997), maintains the same overall concept but in a considerably simplified form. Genetic analysis of the system has shown that only three hierarchical levels are necessary and that the A and B sets are useful only at the E level (Fig. 18.2). Essentially, Popi found that the various recurrent selection procedures employed in the HOPE breeding system increased agronomic performance at all levels of the hierarchy. In the most recent cycles of selection, the L genepools had similar grain yields to the I and H level genepools for the respective A and B sets; however, grain moisture at harvest (an indicator of maturity) and stalk breakage were higher for the L level genepools, thus distinguishing performance of the L level germplasm from the I and H level genepools for these important traits in short-

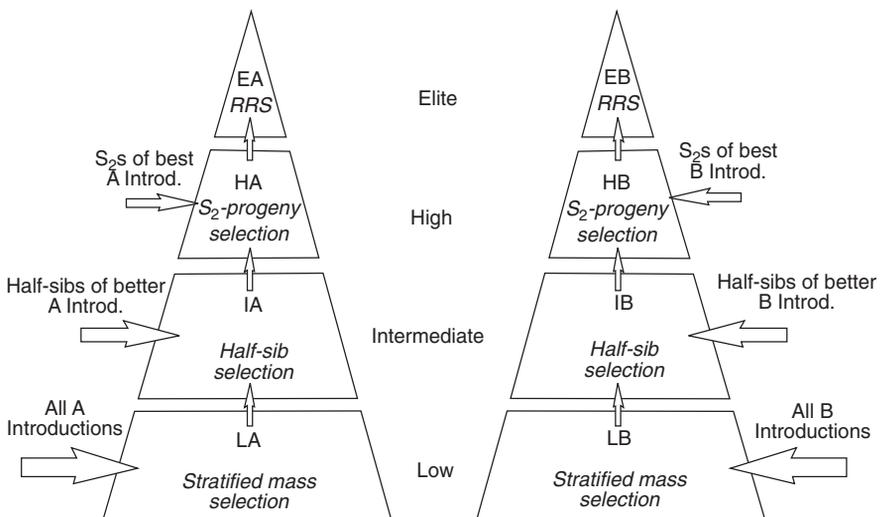


Fig. 18.1. The version of the HOPE breeding system that was used from 1986 to 1997. The A and B sets represent complementary heterotic groups.

season corn. Agronomic performance of the I- and H-level genepools in the most recent cycles was similar within each set. Further, the degree of heterosis of the cross between genepools at the L, I and H levels, respectively, remained low (less than 10%) for grain yield even after several cycles of selection. Consequently, it was decided to combine LA and LB into a single L genepool and, as well, the four genepools (IA, IB, HA and HB) into a single H-level genepool. At the E level, heterosis of the EA \times EB cross increased from 9% in the original cycle to about 21% in the current cycle, indicating that the reciprocal selection practised at the E level has been effective; consequently, both the EA and EB genepools are being kept in the newest version of HOPE. Relative to the breeding procedures, stratified mass selection will continue to be employed at the L level, and selfed progeny recurrent selection (Hallauer and Miranda, 1988) at the H level, but the number of families tested at the H level will be approximately doubled to 196. The number of families selected per cycle will also be increased to 30–40 to reduce random drift effects. Selfed progeny selection has been chosen because selfing unmasks deleterious recessive genes, which is an especially important consideration when working with highly variable germplasm. However, at the E level, instead of reciprocal selection (RRS), reciprocal full-sib selection (RFS), as described in Hallauer and Miranda (1988), will be employed. Compared with RRS, RFS doubles the number of families tested without changing the number of test plots. This is because each RFS plot is a cross of an A family with a B family, whereas with RRS each A family and each B family is crossed to a different tester. In the newest revision of HOPE, the number of families tested at the E level will also be approximately doubled to 196 and the number of families selected increased to 20–25 in order to reduce random drift effects. The system will remain open-ended with new introductions included into the L level and, when performance is sufficient, into the H level as well. However, no testing of heterotic pattern will be required. Germplasm will also be moved upward in the hierarchy as before, except that in each cycle at least one entry will be advanced to each genepool of the E level: this will ensure some geneflow from the H to the E level in each cycle. The procedures to initiate this revision of the HOPE system were begun in 1997.

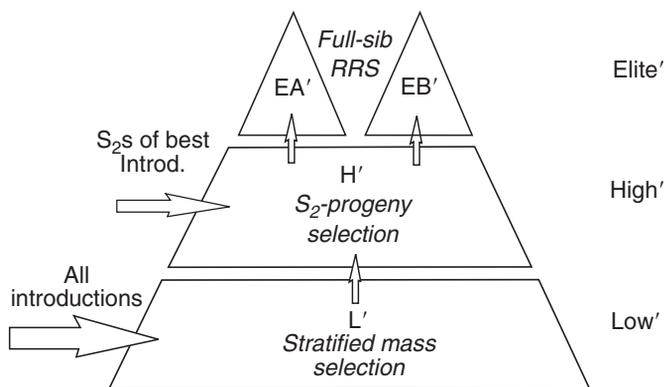


Fig. 18.2. The newest version of the HOPE breeding system.

This newest version of HOPE will substantially reduce the complexity, human resources, field requirements and costs relative to the previous HOPE systems.

The synthesis of HOPE and subsequent germplasm introductions

The initial synthesis of each of the H, I and L gene pools involved a total of 43 components, consisting of adapted open-pollinated varieties, synthetics, composites and four double-cross hybrids of foreign origin. Six to eight of the 43 components were assigned to each of the six gene pools based on agronomic performance and heterotic pattern as deduced from historical information from the Guelph breeding programme. These six to eight components were then extensively intercrossed to form the original cycle of that gene pool. Subsequently, the E-level gene pools were developed by intercrossing within each set S_2 lines of the best entries from the first cycle of selection in the H-level gene pools.

Introductions have continually been added to the HOPE system. During the first 5 years of HOPE, 408 introductions were made. In the following 11 years (to 1992), an additional 448 introductions were added. To date (2000), approximately 1000 introductions have been included in the HOPE system. All introductions are incorporated into the L-level gene pools, but some (less than 3%) have also been introgressed into the I or H levels, depending on their relative performance. No introductions are put directly into the E-level gene pools.

Most introductions have been of short-season maturity suitable for Guelph and are worldwide in origin. The majority of introductions during the first years of HOPE were accessions from the North Central Regional Plant Introduction Station in Ames, Iowa. Subsequently, germplasm has been received from short-season breeding programmes in many parts of the world. The only criterion for incorporating such germplasm into the HOPE system is that it can produce mature grain in the Guelph environment. Even germplasm with poor agronomic performance is included in HOPE on the assumption that desirable attributes may be hidden by obvious faults. About 5% of introductions have been so-called exotics, i.e. germplasm requiring a longer growing season than available at Guelph. In the case of exotic materials, only elite improved sources, such as improved populations from the International Maize and Wheat Improvement Centre (CIMMYT), are chosen for inclusion in the HOPE system because of the time and cost of adapting such germplasm to the necessary maturity. For these reasons, no efforts have been made to introgress germplasm of wild progenitors of maize, such as teosinte or *Tripsacum* ssp., into HOPE.

Results

Utility of HOPE germplasm

Popi (1997) used random amplified polymorphic DNA (RAPD) analyses to determine the genetic distances among the HOPE gene pools and also relative to 11 short-season commercial hybrids. Principal component analysis indicated that the HOPE populations vary considerably among themselves and represent markedly different germplasm

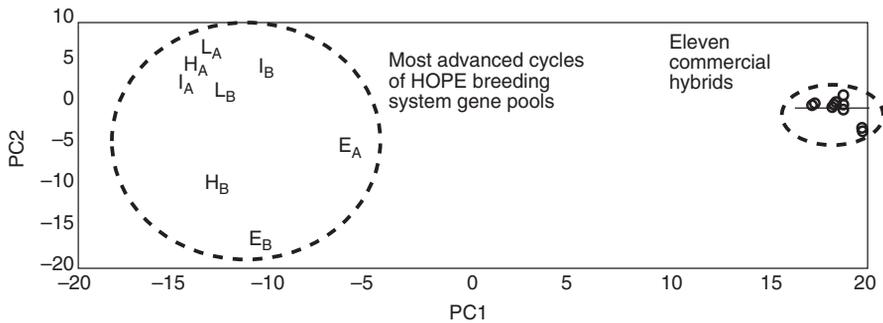


Fig. 18.3. Principal component analysis* of HOPE populations compared with 11 commercial hybrids.

E_A, H_A, I_A, L_A are, respectively, elite, high, intermediate and low levels of the A set of HOPE populations. E_B, H_B, I_B, L_B are, respectively, elite, high, intermediate and low levels of the B set of HOPE populations. The number of selection cycles represented are four at the E level, 11 at the H level, and 15 at the I and L levels.

*Note that the vertical axis of the graph has been reduced relative to the horizontal axis.

from that deployed commercially (Fig. 18.3). Thus, HOPE germplasm has the potential to contribute to the genetic diversity of commercial germplasm. We have some evidence that this potential may be realized: two University of Guelph inbreds (CG91 and CG96, released in 1997), contain HOPE germplasm. They were derived from a cross of a selected HOPE family to a commercial hybrid. We have found that HOPE germplasm, as with many improved populations, although competitive in yield performance, is typically lacking in such agronomic traits as stalk quality, resulting in more stalk breakage than acceptable. Crossing population germplasm to commercial hybrids with their long history of intensive selection for agronomic qualities provides a breeding source that combines agronomic eliteness with the unique and selected germplasm from the populations. Our testcross data indicate that CG91 and CG96 can produce hybrids competitive in performance with current commercial materials. Whether CG91, CG96 and subsequent HOPE inbred releases will be used commercially will be dependent on their capacity in hybrid combinations to perform under the intensive and extensive testing to which commercial materials are subjected.

Stalk quality is being intensively selected for in the HOPE gene pools and, if experience with other Guelph populations is any indication, future inbred releases from the HOPE programme may be derived solely from a HOPE background rather than the cross of HOPE material to a commercial hybrid. In any event, we are optimistic that HOPE-based inbreds will ultimately be used in commercial breeding programmes, directly as a parent in a hybrid and/or indirectly as a component in a company breeding programme. In either case, the HOPE breeding system will meet its goal of diversifying the commercially deployed genetic base.

Lessons from the HOPE experience

Popi's (1997) evaluation of the HOPE breeding system showed little heterosis in $A \times B$ crosses at the L, I and H levels, respectively, while at the E level, which was subjected to

reciprocal recurrent selection, heterosis was satisfactory (over 20% for grain yield). This indicated that the A and B heterotic grouping was desirable only at the E level. Further, little difference in performance was observed among the L, I and H levels of each set. Therefore, these levels could be combined. However, we believe it is still important to separate the L-level materials from the E germplasm; in particular, selfing at the H level helps to decrease inbreeding depression because of unmasking of deleterious recessives before these materials are elevated to the E level. Thus, the H level functions as a buffer between the L- and E-level gene pools. These changes (depicted in Fig. 18.2) have greatly simplified the logistics of the previous HOPE scheme.

The relatively good performance of the L-level germplasm has been surprising, especially considering that about 1000 accessions have been introduced into the L level over the past 20 years. The fact that introductions were crossed to the E level before inclusion probably helped, but stratified mass selection would also appear to be an effective selection tool in broad-based germplasm.

Requirements for HOPE

In general, breeding systems such as HOPE require personnel trained in plant breeding, especially population improvement methods. One exception is the stratified mass selection procedure used at the L level: farmers, village teachers or other interested peoples could easily be taught this procedure as a means for systematic improvement of local varieties. The technologies and costs of the HOPE breeding system are equivalent to those of other maize breeding programmes. The L-level requirements are for an isolation area of about 1 ha and one cycle of stratified mass selection can be completed each season. The selfed progeny selection at the H level and reciprocal full-sib selection at the E level both require 3 years per cycle with a winter nursery. Of the 3 years, one is for replicated field trials at two or more locations and the other 2 years include summer and winter breeding nursery activities. Details of the above procedures can be found in Hallauer and Miranda (1988) and, specific to HOPE (except for RFS selection), in Kannenberg and Falk (1995).

Conclusion and recommendations

The HOPE breeding system has two goals. The first is to provide a source of inbred lines that are genetically very different from those currently used in commercial breeding programmes. The second goal is that HOPE inbreds must be at least comparable in performance with current commercial inbreds both in *per se* performance and in hybrid combinations. Popi's (1997) molecular analyses showed that the first goal has been achieved. Whether or not HOPE germplasm will be used commercially depends on the success of meeting the second goal. The hybrid maize industry is highly competitive and our experience has been that commercial breeders will not expend time and resources working unproven breeding germplasm. Commercial breeders, however, will evaluate inbred lines from other than their own programme if these inbreds are considered to have potential. In the approximately 20-year history of the HOPE programme, only four inbreds have been released to the industry. The first two HOPE inbreds did

not have adequate performance to serve directly as parent lines in a hybrid programme, but were released because we thought they might have potential as genetically different germplasm in a breeding programme. Although several commercial companies obtained this germplasm, to our knowledge, no commercial inbreds have been developed from it. The two 1997 inbred releases, which are a combination of HOPE and commercial germplasm, have, according to our data (which are not extensive because of our limited resources), the potential for direct commercial exploitation as a parent line of a hybrid and/or a source of new and different germplasm in a breeding programme. Future HOPE inbred releases should be more frequent, based more or less on the 3 years per cycle of selection required at the E level, and should be incrementally improved, perhaps to the point where the HOPE selections can be inbred without first crossing to commercial germplasm. Regardless, the ultimate measure of the success or failure of the HOPE breeding system will be whether inbred lines with HOPE germplasm are used in commercial hybrids. Only then will the HOPE breeding system have contributed to diversification of the commercially deployed genetic base of maize.

The HOPE breeding system is in effect a continuing experiment. The two evaluations (Cramer, 1986; Popi, 1997) to date have resulted in substantial modifications to the HOPE system, especially from Popi's study. A number of questions remain. For example, although we are inclined to favour reciprocal full-sib selection at the E level, primarily because of the increased testing efficiency (2:1) relative to other procedures, a half-sib programme using two commercially recognized inbred testers of opposite heterotic pattern might be a desirable alternative. Also, the kind and extent of genetic diversity within the system need to be characterized, especially at the E level and especially relative to the genetic diversity available from other more traditional and simpler population breeding projects, such as the eight other broad-based populations undergoing recurrent selection in the Guelph breeding programme.¹ Essentially, we need to know how unique and how useful HOPE germplasm is. Another question is whether we should continue to add new introductions regardless of their agronomic quality or should only accessions with superior performance to existing HOPE germplasm be used? For that matter, are introductions adding to desirable genetic diversity, or should the HOPE breeding system be closed to introductions so that selection within the existing HOPE germplasm might be more effective in developing desirable gene combinations? Modern molecular technologies may be helpful in the analyses required to resolve these and other questions relevant to the HOPE breeding system.

Although the HOPE breeding system has been used to date only for developing breeding germplasm suitable for the short-season maturity of Guelph, there is of course no reason why HOPE or breeding systems of similar intent cannot be developed on a wider scale. Indeed, we have devised a scheme in which interfacing HOPE-like systems were developed for the northern, central and southern maize-growing areas of Ontario. Commercial companies agreed to contribute evaluation trials and breeding nursery space. However, external funding was necessary to support the programme and we were not successful in obtaining this. Nevertheless, breeders recognize the critical need to diversify the breeding base of maize and they are prepared to apportion a share of their physical resources in collaborative ventures to accomplish this endeavour.

¹ A description of these and other Guelph population can be found at: http://131.104.232.5/research/corn_breeding/populations2.htm

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19 The Germplasm Enhancement of Maize (GEM) Project: Private and Public Sector Collaboration

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Rationale and Objectives of LAMP and GEM

GEM could not exist if the Latin American Maize Project (LAMP) (Salhuana *et al.*, 1991; Pollak, 1993; Sevilla and Salhuana, 1997) had not come first. LAMP provided the information necessary to efficiently select germplasm bank accessions for enhancement. In this regard, LAMP served as the first step to sharing promising maize materials from the germplasm banks with breeders. GEM completes the process by returning to the germplasm bank enhanced materials developed from the accessions, which can be directly used in breeding programmes.

The primary objective of LAMP was to evaluate accessions found in Latin American and US germplasm banks so they could be used in breeding programmes. This project was the first coordinated international effort to deal with the evaluation of the genetic resources of a major world crop. LAMP was based on the cooperative effort of 12 countries: Argentina, Bolivia, Brazil, Colombia, Chile, Guatemala, Mexico, Paraguay, Peru, United States, Uruguay and Venezuela. The results of LAMP indicate that there are accessions (native and foreign) that show good yield potential on which enhancement can be initiated in order to improve yield, agronomic characteristics and adaptability before being incorporated into breeding programmes.

In 1991, a catalogue and CD-ROM of data of 12,113 accessions evaluated in LAMP's first stage, and 2794 selected (primarily on yield) accessions evaluated in the second stage, in 59 different locations of 32 regions of the 12 countries, was published (LAMP, 1991). Based on those data, the principal investigators in each country selected a total of 268 elite accessions that were crossed with the best testers of each region. Thirty-one testers were used for crossing with the elite accessions. Within similar homologous areas, principal investigators exchanged testcrosses among other principal investigators in the same homologous area, so that testcross evaluations were done in more than one country. Data from the testcross evaluations were published in a catalogue and updated CD-ROM in 1995 (Salhuana and Sevilla, 1995), and a final report published in 1997 (Salhuana *et al.*, 1997). In the fifth stage of LAMP, each principal

investigator was to enhance selected germplasm to meet his or her country's breeding objectives, yet funding for only a year of small-scale enhancement was available.

In the USA, the seed source for virtually all maize grown commercially is the seed industry. For any of the LAMP accessions to be useful in maize improvement, some mechanism had to be established to enhance them so they could enter commercial maize breeding channels. The competitive nature of the seed industry made it unlikely that any one company would support an enhancement effort. Public breeders are poorly funded, and there are few if any grant sources for germplasm enhancement, so it was unlikely that public breeders could find the financial resources to support an enhancement effort. It was clear that a coordinated and cooperative effort among public and private sectors was needed before the LAMP materials would be used in US breeding programmes.

US Maize Diversity Prior to GEM

Maize is the USA's major crop, where over 30 million ha are planted each year, and is extremely important to the US economy due to the amount produced, its value to industry and its export value. Through feeding livestock that is processed into meat and dairy products, maize affects nearly everyone in American society. The USA is also the world leader in maize production.

Genetic variability is essential in plant breeding programmes (Michelini and Hallauer, 1993), but improvements in crops by plant breeding are usually followed by decreased genetic diversity, particularly in materials that reach commercial production. Thus farmers' hybrids face increased genetic vulnerability while farmers face increased economic risk. Since the early 1960s, there have been frequent and urgent warnings about maize's genetic vulnerability and the potential of exotic germplasm to decrease this vulnerability (Anon., 1972; Brown, 1975; Walsh, 1981; Wilkes, 1989; Goodman, 1990). Concerns increased after a southern maize leaf blight (incited by *Bipolaris maydis* (Nisikado) Shoemaker, race T) epidemic in 1970, which was due to the widespread genetic uniformity of the crop speeding development of the disease to epidemic proportions.

The concerns regarding maize's genetic vulnerability have been reinforced by studies documenting a reduction in genetic variability among domestic lines and hybrids. The most recent survey of germplasm sources for the maize crop (Darrah and Zuber, 1985) found that 88% of 1984 US maize seed produced for 1985 planting included germplasm derived from one variety of the Corn Belt Dent race: Reid Yellow Dent. From a biochemical data perspective, US maize cultivation and breeding remain dependent upon the inbred lines B73, A632, Oh43 and Mo17, or closely related derivatives (Smith, 1988). In the US Corn Belt, exotic germplasm includes unimproved domestic as well as foreign populations (Stuber, 1986). A comprehensive survey conducted in 1983 on the use of exotic germplasm in commercial maize revealed that less than 1% of the US germplasm base consisted of exotic germplasm (Goodman, 1985).

In spite of the above concerns, maize breeders have continued to focus on short-term breeding goals largely because of the predominance of the private sector in maize breeding and its need for short-term results. This results in a very narrow genetic base of maize produced on the farm, with many companies selling closely related hybrids (Smith, 1988). This may lead to a yield plateau, greatly increases vulnerability to pests,

and makes it difficult to meet new market demands. Jenkins (1978) found the genetic base of maize breeding programmes reduced because greater emphasis was given to developing recycled lines instead of lines developed from improved populations or synthetics. Private companies are, however, growing increasingly concerned about their narrow germplasm pools, although tough competition in the industry results in the tendency to increase diversity by focusing on elite proprietary exotics from branch stations within a company. Although breeders are still making 1.5–2.0% per year of genetic gain for yield in adapted materials, it is not known how long these gains will continue. Geadelmann (1984) suggested that incorporation of exotic strains into adapted germplasm would increase the available genetic variability and give rise to additional heterotic vigour, lessening chances for a yield plateau.

Objectives and Goals of GEM

GEM's objective is to provide to the maize industry materials developed using germplasm enhancement of useful exotic germplasm, with the ultimate aim of improving and broadening the germplasm base of maize hybrids grown by American farmers. Because proprietary germplasm is used to make breeding crosses, access to breeding materials is limited to GEM cooperators, but the opportunity to become a cooperator is available to all. Data collected on GEM materials are freely available, and GEM-enhanced lines and synthetics will be freely available through the US North Central Regional Plant Introduction Station (NCRPIS) after their public release. Traits targeted for improvement are agronomic productivity, disease and insect resistance, and value-added characteristics.

Methods and Strategy Used in GEM

Development and organization of the project

GEM began in 1993 when several public and private maize breeders, with support from the American Seed Trade Association (ASTA), developed a proposal for a public/private collaborative effort to enhance the accessions identified as useful by LAMP. In addition to enhancement, the proposal also addressed other concerns of ASTA member companies including the diminishing role of the public sector in maize breeding, federal and state budgetary constraints causing decreased financial support of public programmes, and relative lack of public support for maize research compared with other crops despite the greater economic importance of maize to the nation.

In 1994 the proposal and a breeding protocol (modified pedigree breeding procedure) was sent to all ASTA membership with maize breeding programmes asking for their willingness to become a member of GEM. Participation as a private-sector collaborator in GEM involved signing an agreement and following the protocol. The protocol required them to:

- Cross exotic accessions assigned by the coordinator to their proprietary inbred lines and return the crosses to the coordinator.

- Contribute in-kind support for the breeding effort (winter and summer nursery rows, yield trial plots and disease observation rows).
- Not distribute proprietary \times exotic germplasm outside the company.

In-kind support by industry was considered important for lobbying the US Congress, for providing the necessary number of testing environments, for ensuring that the enhanced materials have commercial relevance, and for providing public programmes with routine cooperation and guidance. In return, a participating company received early access to GEM materials. The following points addressed proprietary concerns.

- It is extremely difficult to extract an inbred line once it has been hybridized, especially with an accession.
- Pedigrees are coded so that only the coordinator knows which company made a proprietary cross.
- A company's S_2 lines are considered proprietary.
- Publicly released material from company breeding efforts are S_2 synthetics, as opposed to S_3 lines from public breeders.

The proposal also was sent to public-sector maize breeders giving them the opportunity to become collaborators, although they were not required to make breeding crosses. Signing an agreement allowed them access to GEM materials, potential financial or in-kind support to participate, and signalled to the US Congress and the US Department of Agriculture (USDA) their belief in the value of the project.

A sub-committee from ASTA lobbied key legislators of the US Congress for permanent base funding to the Agricultural Research Service (ARS) to support the public effort at ARS and university locations. Besides recognizing the value of the work, Congress was impressed by the \$1.5 million contribution Pioneer Hi-Bred International made to LAMP, and the in-kind support from companies for GEM that was estimated to be worth approximately \$450,000 per year. This amount underestimated the actual value of the contributions because it ignored the value of the proprietary germplasm, overhead costs, and advice and service of the private breeders. In 1995, \$500,000 of permanent yearly funding was appropriated by Congress to fund GEM.

In 2000, there were 38 companies, 42 public scientists and one international agency (Empresa Brasileira de Pesquisa Agropecuária – EMBRAPA) serving as GEM cooperators. A cooperators' meeting is held once a year at the Corn & Sorghum ASTA meetings to discuss progress. A Technical Steering Group (TSG) meets three times a year to discuss policies, protocol and results. The TSG is presently composed of eight members from industry, two from USDA-ARS (members are limited to the GEM coordinator and North Carolina project leader and are *ex officio* due to conflict of interest) and one from a university. Members from companies and universities serve a staggered 3-year term.

The GEM coordinator in Ames manages seed curation, line evaluations and release, cooperative nurseries and yield tests using in-kind support, data analysis and management, public cooperator research plans and finances, and public relations. In addition, the Ames location conducts value-added trait research and develops enhanced lines for improved yield and value-added traits. The Raleigh project leader manages enhancement of the 50% tropical breeding crosses for the southern USA, enhancement

of the 50% tropical breeding crosses for moving to the Corn Belt, and public cooperator projects in the southern USA. From the US Congress's appropriated funds, some public cooperators receive partial financial support for conducting GEM-related research. In-kind support from private cooperators each year provides over 6500 summer and 2000 winter nursery rows. Over 7000 rows of yield test plots throughout the eastern, southern and Corn Belt sections of the USA provide a wide diversity of environments. Additional GEM-related nursery rows and yield test plots are grown in the Ames and Raleigh locations.

Starting materials used for breeding

GEM is an ongoing project, but to initiate enhancement 51 elite tropical and temperate LAMP accessions were chosen on the basis of yield performance in LAMP, and seven commercial tropical hybrids were provided by DeKalb Genetics. The enhancement protocol is for one of the private cooperating companies to cross an exotic material by a proprietary inbred line to make a 50% exotic breeding cross, then for another private cooperator to cross the 50% cross with their proprietary line of the same heterotic pattern to make a 25% exotic breeding cross. All 50% and 25% breeding crosses are evaluated for yield as testcrosses, and the best used to develop breeding lines by cooperators.

Breeding activities and results to date

In 1994 the coordinator assigned four accessions or tropical hybrids (from the 51 accessions/seven tropical hybrids initial starting materials) to each private cooperator to cross to a proprietary inbred line in the 1994/95 winter nursery. The coordinator specified the heterotic pattern – Stiff Stalk (SS) or non-Stiff Stalk (nSS) – to use, based on information from LAMP testcrosses. If the heterotic pattern of the exotic material was unknown, both crosses were made. Private cooperators returned exotic \times private inbred breeding crosses to the coordinator, then balanced samples of the two-way breeding crosses were sent to two different companies for making three-way SS or nSS breeding crosses in 1995 summer nurseries or day-neutral locations. Each private cooperator was assigned eight crosses.

In the 1995/96 winter nurseries, two companies (Golden Harvest and Pioneer) made nSS testcrosses with all available SS breeding crosses, and two companies (Cargill and Holdens) made SS testcrosses with nSS breeding crosses. Cooperative yield testing during 1996 involved 16 experiments grown in more than six locations, evaluating 564 testcrossed 50% and 25% exotic breeding crosses. From these results, breeding crosses were selected for advancement to line development. Results for the best topcrosses of Stiff Stalk breeding crosses and non-Stiff Stalk breeding crosses are shown in Table 19.1, expressed as a percentage over the five check hybrids (Holden's Foundation Seeds Single Cross LH195/LH212, Holden's Foundation Seeds Single Cross LH195/LH59, Pioneer Brand Hybrid 3489, Pioneer Brand Hybrid 3525 and Pioneer Brand Hybrid 3163).

Some results are similar to the mean of the checks or better; thus we expect the testcrosses of the best lines developed from these breeding crosses to be superior to the

Table 19.1. Relative yields and moisture values of some testcrossed GEM breeding crosses evaluated in 1996.

Experiment	Locations	GEM breeding cross	Percentage of five check hybrids	
			Yield (%)	Grain moisture (%)
<i>Pioneer nSS tester</i>				
50% tropical breeding crosses	5	DKB844:S16	98	116
		CUBA117:S15	98	108
25% tropical breeding crosses	4	CUBA164:S52008a	103	93
50% temperate breeding crosses	5	FS8A(S):S09	93	103
		UR10001:S18	92	105
<i>Golden Harvest nSS tester</i>				
50% tropical breeding crosses	9	CUBA164:S15	97	100
		CHIS775:S19	96	102
25% tropical breeding crosses	8	CHIS740:S1411a	101	91
		CHIS740:S1415	96	98
50% temperate breeding crosses	8	AR16035:S19	100	104
		FS8B(S):S03	96	105
25% temperate breeding crosses	7	AR16021:S0908b	106	92
		FS8A(S):S0915	99	91
<i>Cargill SS tester</i>				
50% tropical breeding crosses	6	ANTIG03:N12	96	110
		CHIS775:N19	92	105
25% tropical breeding crosses	8	DKXL370:N11a20	101	109
		CHIS775:N1920	101	105
<i>Holden's SS tester</i>				
50% tropical breeding crosses	6	DKB844:N11b	96	107
		DREP150:N20	94	117
25% tropical breeding crosses	9	BR51501:N11a08d	101	103
		BR51501:N11a12	99	108
25% temperate breeding crosses	5	FS8B(T):N11a08a	103	98
		UR13085:N0215	102	105

check hybrids. Because any line selected through this procedure will probably need agronomic improvement, they are best used as breeding lines.

Line development was started in a few breeding crosses based on LAMP and grown as S_2 testcrosses in yield tests in 1997. Results for testcrosses are shown in Table 19.2.

After the initial seasons of developing and evaluating breeding crosses, GEM's seasonal breeding programme has developed into a balance of the above elements

Table 19.2. Results from experiments evaluating topcrosses (Holden's SS tester) of lines developed from two breeding crosses using the Chilean temperate accession CH05015, grown in 1997 in Corn Belt locations.

Pedigree	Moisture			
	Yield (kg ha ⁻¹)	Moisture (%)	Lodged (%)	
			Stalk	Root
CH05015:N15-98-1	9,041	20.7	3.7	4.7
CH05015:N15-76-1	8,493	18.5	5.4	4.7
<i>Check hybrids</i>				
LH195/LH212	10,262	20.0	4.3	0.9
LH195/LH59	8,644	18.7	2.7	2.5
Pioneer 3163	10,175	22.4	9.6	6.4
Pioneer 3489	8,981	17.8	5.5	0.5
Pioneer 3525	9,210	16.4	14.2	0.0
Checks mean	9,454	19.0	7.2	2.1
LSD _{0.05}	20.3			
CH05015:N12-183	10,670	20.4	4.8	0.0
CH05015:N12-186	10,638	19.8	6.8	0.0
<i>Check hybrids</i>				
LH195/LH212	10,518	19.3	6.5	0.0
LH195/LH59	8,607	18.5	6.2	0.0
Pioneer 3163	10,774	20.4	17.9	0.0
Pioneer 3489	10,309	17.6	15.2	0.0
Pioneer 3525	10,684	16.4	8.6	1.2
Checks mean	10,178	18.5	10.9	0.2
LSD _{0.05}	32			

(developing and evaluating new breeding crosses) plus ongoing line development at various stages. To date, we have developed over 350 breeding crosses, and instituted pedigree breeding for line development in over 46 breeding crosses. Over 3200 topcrossed lines were in Corn Belt and southern US yield tests in 1998. Results indicate that these lines have true yield potential. In experiments grown by Pioneer Hi-Bred International, Inc. to test S₂ lines from CUBA164 breeding crosses topcrossed with a Pioneer non-Stiff Stalk tester, a CUBA164 topcross was the second-highest-yielding entry behind Pioneer 3525, in six replications. Seven other lines yielded more than Pioneer 3163, ranking five to eleven after Pioneer checks 3489 and 34G81. In another experiment with seven replications, eight CUBA164 topcrosses yielded more than Pioneer 3163, ranking two to nine after Pioneer 33A14. In an experiment with three replications, seven CUBA164 topcrosses yielded more than the first check, LH195/LH212, two with yields over 200 bushels per acre. Twenty-five topcrosses yielded more than the first Pioneer check, 34E79.

Another experiment of four replications grown by DeKalb Genetics evaluated lines from a 50% exotic breeding cross with an accession from Argentina, AR01150, test-

crossed with a DeKalb Stiff Stalk line. Six AR0150 topcrosses were the highest-yielding entries, beating the highest-yielding check, Pioneer 3163. Four more AR01150 topcrosses beat the next highest-yielding check, DK621.

Based on previous experience with LAMP germplasm, GEM cooperators are confident of finding many economically important traits in this germplasm, which will lead to inbred lines improved for a wide variety of characteristics as well as productivity. For example, 691 Peruvian maize accessions were evaluated for resistance to European maize borer leaf feeding (Abel *et al.*, 1995). Eleven resistant varieties were identified, with all 11 commonly grown in coastal valleys of Peru's northern coast. Further analysis indicated that the resistance factor was unrelated to that found in Corn Belt-adapted maize, DIMBOA concentration. Lines developed from breeding crosses of the resistant accessions with Corn Belt lines also show resistance. None of the 11 accessions were included in the top 5% of LAMP accessions, representing the highest-yielding accessions, indicating the importance of screening a wide variety of germplasm for non-yield-related traits.

Social and Economic Impact of LAMP and GEM

Overall utility to breeders

This is the first coordinated public/private effort that addresses the need to reduce genetic vulnerability by diversifying the germplasm base and providing enhanced, improved germplasm to help private industry meet changing markets in a major crop. In spite of industry consolidation, the number of private cooperators has increased since the project's inception, cooperating companies have increased their donation of in-kind support, and end-users are starting to participate. There is increasing interest in participating by foreign companies. As the unique germplasm is publicized, new public cooperators come from a diversity of backgrounds, such as animal nutrition and food science. The impact on US farmers and agriculture in general will be enormous as the germplasm diversifies and extends the use of the maize crop.

Opportunities and constraints – demonstrating the importance of genetic resources

The importance of genetic resources will be easier to demonstrate when economic pay-offs ensue from safeguarding those resources, which are the product of several thousands of years of evolution and human experimentation. This is very difficult to demonstrate since precise information about the use of genetic resources does not exist. However, the impact of the utilization of new germplasm can be examined through the examples of LAMP and GEM.

The success of the LAMP project was founded upon the cooperative efforts of the principal investigators, who believed that it was necessary to collaborate with strategies focused on success without being daunted by the limitations that would inevitably occur. The results of the LAMP project (Salhuana and Sevilla, 1995) show that for each country there exists germplasm from other countries that performs better than native

germplasm. It is imperative to exchange germplasm among countries without restrictions since experiences from several countries have shown that the best germplasm is often derived from foreign accessions. The utilization of selected germplasm for the tropics, temperate and highland areas will bring to other regions the increase in yield and other agronomic characteristics for which the germplasm was selected in the native environment, resulting in a higher quality grain supply for human and animal consumption.

Another cooperative project is GEM, in which private industry is participating by contributing the proprietary inbred lines in crosses with the best LAMP accessions as well as with in-kind support in the form of nursery rows, yield test plots and isolation rows. Alliances among countries and collaboration of private industry will help ensure the success of present and future projects in genetic resources, especially in this period of scarce financial resources, because genetic resource activities must compete for funds from other investments that can yield more immediate, but fewer long-term benefits. Collaboration helps additional important traits to be identified in exotic germplasm since some cooperators have the facilities and expertise that others do not have. The results obtained in GEM shows that the contribution of exotic germplasm for disease and insect resistance and value-added traits accompanied with yield will have a large impact on maize productivity.

Opportunities and constraints – use of biotechnology

New capabilities to introduce exotic genes are becoming increasingly available from biotechnology. Transformation technologies make it easier to transfer genes into maize from other genera than it is to transfer useful genetics from related species through crossing and repeated backcrossing. Conventional procedures impose 3–7 years of additional time and effort to segregate and recombine genes and break up linkage blocks that would otherwise render the genotype poorly adapted to agriculture. It is critical to realize that the most important traits in agriculture are controlled by groups of genes, which by themselves have a small effect. For the foreseeable future, the most useful genetic diversity will be found in the crop species itself. Advances in biotechnology can help to utilize more effectively a wider variety of diversity.

Biotechnology can contribute in at least two broad areas in plant breeding. Genetic markers can identify important genes or chromosome regions, and genetic transformation can move potentially useful exotic genes into inbred lines. Unfortunately, considering the large numbers of accessions in germplasm banks, limited resources do not permit using biotechnology methods to establish variability and genetic distances among exotic and elite that will permit utilization of exotic germplasm in the most efficient way.

The results from tomato and rice indicate that exotic germplasm does contain useful genes that can significantly enhance agricultural production. The preliminary results of GEM also demonstrate the same results for yield, disease and insect resistance, and value added-traits. After identifying the regions of DNA of the trait that we would like to transfer from the exotic material it will possible to transfer this to the elite material by using transformation or by a backcross technique, identifying and selecting the offspring that contain the favourable genes from both parents.

Challenges and Future Tasks

The immediate challenges must therefore be:

1. To conserve genetic diversity securely.
2. To characterize genetic diversity.
3. To evaluate genetic diversity more completely in pre-breeding and enhancement programmes.
4. To provide resources to accomplish these tasks.
5. To develop and apply new biotechnologies to improve the effectiveness of germplasm conservation, evaluation and utilization.
6. To continue to improve the efficiency of agriculture and its degree of harmony with the environment by successful plant breeding.

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20 A French Cooperative Programme for Management and Utilization of Maize Genetic Resources

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Introduction

It has been observed in several countries, particularly in the USA and France, that there are very few effective genitors of commercial maize hybrids, in spite of a great number of hybrid varieties. This is due to the fact that few elite inbred lines can yield very good hybrids and that, when such a good line is developed, it is used in several combinations, as well as in pedigree selection to develop new lines. The consequence is relatedness among hybrids because they share a same parent or related parents. In France the situation for early maize was particularly alarming around 1985. At this time, the famous flint line F2, derived from the Lacaune population, was involved in about 85% of early maturing hybrids.

Such a situation may present a risk for agriculture due to the lack of diversity among varieties used by farmers. The risk can be a susceptibility to environmental conditions and in particular to disease, as illustrated by the *Helminthosporium* epidemic in 1970 in the USA, following a large-scale use of a cytoplasm allowing male sterility for the production of hybrids. Another risk for the breeder of early maize was a limit in the genetic advance due to a narrow base in breeding material, particularly for flint material.

To stimulate and prepare long-term genetic advance through the broadening of the genetic base of the breeding material, mainly in early maturing maize, a cooperative programme was developed, in a first phase from 1983 to 1993, between INRA and PROMAIS (an association grouping 13 private breeding companies). The technical objectives were:

- To collect, multiply and conserve a large number of populations adapted to French conditions, with particular emphasis on early-maturing material.
- To study the performance of the populations and their combining abilities, for grain and also for silage yield because silage production is important in northern Europe and the combining ability groups of lines are not necessarily the same for grain and silage productions.
- To develop a restricted number of pools with good 'usefulness for selection', i.e. with a good average performance and a large genetic variance for traits of agronomic interest.

Two other important objectives were: (i) to develop methodology for the management of populations as genetic resources in maize; and (ii) to develop a permanent organization to maintain maize genetic resources in France.

In a second phase, developed since 1993, studies with restriction fragment length polymorphism (RFLP) molecular markers were initiated: (i) for classifying the populations in groups; (ii) for predicting the genetic variance within each population; and (iii) for studying the origin of flint material to have better management and use of this type of material in breeding programmes. As this phase was a continuation of studies begun in the first phase, it was integrated into the whole programme.

Material and Methods

Collecting and multiplication

A total of 1236 adapted accessions were involved in this programme. Most of them were landraces or open-pollinated varieties. They originated from Europe, Asia, North and South America (see Table 20.1). Special emphasis was put on European landraces. In addition to 267 French populations, many populations were obtained from Eastern European countries. One hundred and twelve accessions were obtained by collecting missions to Chile and Argentina during 1984. Synthetic accessions (323) from bred material were also gathered, mainly from the USA.

Although not considered in the present report, about 200 exotic accessions were also obtained from CIMMYT (Centro Internacional de Mejoramiento de Maiz y Trigo) and CIRAD (Centre de Coopération Internationale en Recherches Agronomiques pour le Développement). These accessions, which originated from tropical countries (South America or Africa), were used by INRA to develop tropical \times temperate pools, and to study the introgression of exotic material within the temperate material (Gouesnard *et al.*, 1996).

All adapted accessions were multiplied, with controlled pollination, in 1983, 1984 and 1985, on the basis of 200 full-sib progeny for each population, i.e. 400 plants. They were maintained at Mauguio INRA Station under long-term storage conditions with safety duplication.

Table 20.1. Geographic origin of the accessions.

Country	Landraces	Synthetics	Total
Asia	55	27	82
North America	45	157	202
USA	38	137	175
Canada	4	13	17
Mexico	3	7	10
South America	131	13	144
Europe	676	125	801
France	267	64	331
Iberian peninsula	68	0	68
Italy	22	15	37
Bulgaria	85	13	98
Hungary	87	10	97
Romania	57	17	74
Former Yugoslavia	35	3	38
Poland	18	3	21
Czechoslovakia	21	0	21
Other European	16	0	16
Others	6	1	7
Total	913	323	1236

Evaluation of the populations

Per se and testcross values

All accessions have been evaluated for their *per se* and testcross value. For maize, as hybrids are developed, it is important to classify the accessions according to their behaviour in combination with testers representative of different heterotic groups.

Accession performance was tested at two locations with two replicates per location. Data were recorded for silking, plant and ear heights, length and width of ear leaf, ear characteristics (length, diameter, etc., for a subset of populations), kernel texture and for qualitative traits such as lodging resistance, prolificacy, protandry and health of ear. Based on maturity, the populations were distributed into six groups. In a second step, 262 populations originating from France were evaluated simultaneously for the previous morphological and ear traits including kernel size and weight (Gouesnard *et al.*, 1997).

The evaluation of testcross performances was carried out according to maturity-based groups for grain and silage production. Each population was evaluated in combination with three testers for grain, and with two testers for silage at two locations and three replicates. Grain yield, grain moisture, lodging resistance, and plant and ear height were observed in the grain trials whereas dry-matter yield, dry-matter content, lodging resistance and some morphological traits were recorded in the silage trials.

The overall analysis of all data was made difficult by the distribution of earliness groups across different locations. Some locations were common to different groups. Data of two locations were grouped only when the residual variance-covariance matrices were homogeneous. Analysis of interactions was only studied in these situations of homogeneity (Miclo and Desselle, 1991).

Polymorphism of molecular markers

ENZYMATIC LOCI (STUDIES IN THE FIRST PHASE) Enzymatic polymorphism were studied on 204 populations (Lavergne, 1988; Lefort-Buson *et al.*, 1991; Garnier, 1992). The results were used for the classification of accessions into groups and for the prediction of within-population variability for quantitative traits. Each population was represented by 10–60 individuals and characterized up to 27 polymorphic loci.

RFLP (STUDIES IN THE SECOND PHASE) RFLP studies were undertaken to take into account the limitations of enzymatic markers, and to examine further genetic polymorphism and classification in groups. In a first step, 117 inbred lines were characterized for 63 probe \times enzyme combinations (Dubreuil, 1996). This study showed that RFLP markers are very efficient for classifying inbred lines in heterotic groups. Thus, they were used in a second step to characterize ten populations, each represented by 30 individuals, with 35 probe \times enzyme combinations (Dubreuil and Charcosset, 1998). To apply this technique for the classification of a great number of populations at a reasonable cost, RFLP analyses were subsequently done using bulks of ten individuals and three bulks per population (Rebourg, 1996). These methods are now being applied to about 200 European populations to study their origin and their polymorphism. A study was also undertaken to see whether the within-population RFLP polymorphism could give some information on the genetic variability for quantitative traits.

Development of pools

To facilitate the management of the variability and to prepare the material for breeders, it was necessary to create a small number of operational pools of germplasm accessions. Several approaches, such as principal component analysis (Desselle, 1991), illustrated that the variability among populations had a continuous distribution. No clear relationship between the geographical origin of the populations and their agromorphological characteristics could be established in test-cross trials (Lavergne, 1988). Thus, geographical origin of the populations was not considered as a classification criterion for the development of pools. Instead, they were created using utilization criteria.

Using an index that combined *per se* and testcross traits (grain yield, grain moisture, lodging resistance for grain pools, and dry-matter yield, dry-matter content and lodging resistance for silage pools), the poorer populations were not selected for inclusion in germplasm pools (but always maintained in a coldroom). For grain and silage and for a given earliness, two types of pools were developed: (i) pools with populations exhibiting a good average value in crosses with the different testers (good combining ability – GCA); and (ii) pools developed from the best populations in combination with a given tester (GCA + SCA – specific combining ability). In all cases, emphasis was put on early-maturing germplasm.

For each year of population evaluation, a series of pools was developed. Using previous criteria for definition of groups, populations can be present in several pools. Populations with a good general combining value can also be present within a pool having good combining value with a given tester. Also, many populations are present both in grain and silage pools. About half of the populations (630) were included in pools. A total of 31 broad-based pools were developed (Table 20.2).

Nine additional restricted-based pools were developed by intermating about ten populations for each pool, chosen on the basis of their combining ability with a given tester. They were expected to have a better performance and a lower level of genetic variability than broad-based pools.

After a generation of intercrossing in isolation, all developed pools were evaluated for their *per se* and testcross value with three testers in a multisite experiment.

Genepool enhancement

In spite of selection for lodging resistance among populations to form the pools, they were still very susceptible to lodging and therefore difficult to use in classical breeding programmes. To improve adaptation traits, and particularly lodging resistance, 24 of the 31 pools were crossed to six elite inbred lines or three single-crosses of the same heterotic group. Two generations of random mating were developed, and then the derived 'improved broad-based pools' were evaluated for their *per se* and testcross value.

Breeding potential of developed pools

The breeding potential of four grain and four forage improved broad-based pools was assessed by one cycle of recurrent selection for combining ability with a tester

Table 20.2. Number and characteristics of developed pools.

Heterotic group	Good GCA ^a	Good SCA ^a with flint tester F2 × F257	Good SCA with early dent tester F250 × F252	Good SCA with dent tester A632 × F742 or MBS847 ^b
Grain early pools				
broad-based	4	4	4	4
improved broad-based	4	4	4	
restricted-based		1	2	2
selected improved broad-based		2	2	
Silage early pools				
broad-based		4	4	
improved broad-based		4	4	
restricted-based		2	2	
selected improved broad-based		2	2	
Grain half-late pools				
broad-based		4		
improved broad-based		4		
Grain late pools				
broad-based		3		

^aGCA: general combining ability (average of crosses with three testers); SCA: specific combining ability.

^bIn 1985 and 1986.

(Table 20.2). The tester was chosen for its combining ability with the pool. For each pool, 400 plants were selfed, and 200 were selected on their S_1 -value basis and then crossed to the tester. The progeny were evaluated in several locations in comparison with the best commercial hybrid check. According to an index combining agronomic traits for grain or silage production, 40 S_1 families were finally selected and intercrossed.

Results

Evaluation of populations

At the level of *per se* value, for all measured traits, a large variation was observed among populations. A part of the observed variation for morphological traits was explained by variability in flowering earliness. However, variability was still present when the flowering earliness differences among populations were taken into account in the analysis (Miclo and Desselle, 1991). Variability for ear morphology traits among populations appeared to be particularly large (Duval *et al.*, 1994). Recently, the study of all French populations by Gouesnard *et al.* (1997) has shown a relationship between their morphological traits and their geographical origin; studies are in progress for the development of a core collection applied to this set of populations.

Population × location interactions of the testcrosses were significant in most situa-

Table 20.3. Yield (q ha^{-1}) and lodging (%) for *per se* value of grain pools.

Heterotic group	Good GCA		Good SCA on flint tester F2 × F257		Good SCA on early dent T. F250 × F252	
	Yield	Lodging	Yield	Lodging	Yield	Lodging
Broad-based pools	53	34	46	43	52	31
Improved broad-based pools	62	26	64	34	57	28
Restricted-based pools			56	29	54	20

GCA: good combining ability; SCA: specific combining ability.

tions studied; however, they had a smaller magnitude than the population effects. The population × tester interactions were also lower in magnitude than those of the tester effects and the population effects. This interaction was greater for grain yield than for grain moisture (Miclo and Desselle, 1991).

Lavergne *et al.* (1991) and Miclo and Desselle (1991) found positive correlations between *per se* and combining ability values in crosses with different testers. This suggests the predominance of additive gene effects for traits of interest. This also emphasizes the value of preliminary selection on *per se* value for these materials.

Value of the pools

For *per se* value, yield increase of improved broad-based pools relative to unimproved broad-based pools was significant, mainly for grain pools (Table 20.3). Grain moisture and lodging resistance were also improved (−1% and −1 to −6%). Nevertheless, improvement depended on combining ability group: the increase in yield was about 30% for dent pools, and about 10% for the flint pools. The improvement for the restricted pools was lower than for improved pools. The improvement according to an agronomic index for silage pools was lower than the improvement for grain pools.

The progress in testcross value was lower, because the tester buffers the genetic variance (Table 20.4, for dent pools). Yield of dent pools increased by about 20%, and that of flint pools by 10%. In reference to hybrid checks (100%), flint material progressed from 84% to 92%, and dent material progressed from 80% to 93%. Progress on grain moisture was about −1.3% obtained both on improved and

Table 20.4. Grain yield (q ha^{-1}) and grain moisture (%) of grain dent pools in crosses with flint tester.

Pools	Grain yield	Grain moisture
Broad-based pools	54.2	29.8
Improved broad-based pools	64.0	29.1
Restricted-based pools	57.3	28.7
F250 × F252	69.4	27.5

restricted pools.

This study shows that the improvement of agronomic traits of broad-based pools is possible using these two methods, either by crossing with elite hybrids, or by using restricted pools. Although the first one appears more efficient, the choice of material is very important. In this study, it appears that the flint elite inbreds used for improvement had a lower agronomic value than the dent inbreds. Flint inbreds are generally first-generation lines, and so their value is expected to be close to that of flint populations, relative to the difference in value between dent populations and dent inbreds, which have been selected for several cycles. In addition, crossing with elite inbreds makes the pools closer to a specific combining ability group, which orients its further utilization.

Breeding potential for recurrent selection

The results show a great variability among S_1 families for yield, lodging resistance and earliness, on both *per se* and topcross evaluations. The expected gain from selection in one cycle was calculated, using the actual selection rate (from 10% to 20%). On grain pools, the expected genetic gain was about 0.4 t ha^{-1} for yield and 1% for grain moisture. On silage pools, it was about 0.7 t ha^{-1} , which allows a yield of about 90% of that of the commercial check.

Polymorphism at marker loci and relationship with genetic variation

Enzymatic polymorphism

Most loci displayed two or three alleles. It appears that within-population variability was important relative to the differentiation among populations. On average, the within-population diversity represented 75% of the total allozyme diversity (Lefort-Buson *et al.*, 1991; Gallais *et al.*, 1992). It appeared that two groups of populations which were clearly differentiated for their specific combining ability with two testers displayed similar allelic frequencies. From this result, isozymes appeared to be of limited value to define relevant heterotic groups. This may be due to a low number of loci and alleles per locus and indicates the value of alternative marker techniques such as RFLP.

RFLP

The study showed, on average, six alleles per locus, which is clearly superior to isozymic polymorphism for similar studies (Dubreuil *et al.*, 1996). Furthermore, it showed that classifications of inbred lines, established based on RFLP information, are highly consistent with the origin of these lines and their known combining ability (heterotic groups).

The study of populations for their RFLP and enzymatic polymorphism showed that within-population diversity represents about 75% of the total diversity for both techniques. However, unlike isozymes, groups of populations defined by using 25–35 RFLP probe \times enzyme combinations share common origins (Dubreuil and Charcosset, 1998) or specific combining abilities (Rebourg, 1996). This result can be explained both by the greater polymorphism that was observed at RFLPs and by the larger number of loci that were considered.

Relationship between genetic diversity and genetic variation

Besides the establishment of genetic groups, another potential interest of the markers could be the prediction of the variance of a population for agronomical traits through the amount of genetic diversity. Isozyme data (Garnier, 1992; Gallais *et al.*, 1992) showed that populations that had the lowest isozyme diversity also displayed the lowest variance. Thus, populations that display a low diversity should be considered for direct selection only if their average value is high. Complementary investigations on another set of populations and using RFLP markers (Dubreuil, 1996) confirmed such a relationship within populations from the same origin.

Conclusion

This comprehensive genetic resource conservation and utilization programme depended upon the long-term cooperation between French public and private breeders. Important results included the following:

- The collection of a large number of populations of maize and their evaluation for agronomic molecular traits.
- The development of a restricted number of broad-based genetic pools, which facilitates the management and use of broad diversity.
- The improvement of some pools to stimulate their use and to broaden the genetic base of material used by breeders.

All participants in the programme were supplied with all pools and have, to some extent, exploited them for their breeding proposes. Today, breeders are aware of the value of these genetic resources and willingly share the tasks associated with the long-term conservation of the populations.

The programme was also very informative concerning the methodology for the management and use of genetic resources. First, with the use of different types of data, it was possible to classify the populations into groups, and to develop 'pools' useful for the breeders. RFLPs appear to have a greater potential value than isozymes for the classification into groups and the prediction of within-population variability for quantitative traits; they can allow populations without sufficient potential to be discarded. Finally, the strategy that was used to prepare new material useful in the relatively short term for the plant breeder, i.e. development of pools after low selection intensity between populations and 'introgressing' these pools by elite material, seems very efficient. However, it is clear that to make the maximum use of the genetic variability of such promising pools, several cycles of recurrent selection are necessary. This kind of strategy should be all the more important as the difference in performance between elite germplasm and genetic resources of the collection increases.

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21 Broadening the Genetic Base of Lentil in South Asia

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Introduction

Lentil (*Lens culinaris* Medikus) was developed from *Lens culinaris* ssp. *orientalis* (Boiss.) Ponert in the eastern Mediterranean region as one of the first domesticated plants (Zohary and Hopf, 1988). Evidence of the spread of lentil eastward into the Indo-Gangetic Plain dates to around 2000 BC, but previous contacts between Mohenjo-Daro and the Sumerians and Akkadians of Mesopotamia are well documented, and it may have been introduced into the Indus valley earlier (Cubero, 1981). De Candolle (1882) wrote that on linguistic evidence 'It may be supposed that the lentil was unknown in this country [India] before the invasion of the Sanskrit-speaking race'.

Today, approximately half of the world's area (46.3%) of lentil is in South Asia (FAO, 1996) (Table 21.1), where indigenous lentils are of a specific ecotype (*pilosae*) and exhibit a marked lack of variability. This lack of variability has limited breeding progress. This chapter describes the genetic bottleneck in lentil in South Asia and the introduction of new genetic diversity into the region.

Genetic and Phenotypic Variation in South Asian Lentils

Qualitative morphological characters

In a monograph on lentil in 1930, Barulina described a special endemic group of cultivated lentil in South Asia, characterized by strong pubescence on the vegetative canopy. The foliage of this group, named *grex pilosae*, is grey-green because of the presence of soft hairs, and it contrasts with the green colour common for lentil.

Table 21.1. Average area (ha) sown with lentil in selected lentil-producing countries in 1996 (FAO, 1996), together with the mean coefficient of variation (CV%) over nine agro-morphological characters measured on accessions (acc.) in the evaluation of a world germplasm collection. The number of accessions in each country sample is also given.

Country	Area (1000 ha)	No. of accessions	CV ^a (%)
Afghanistan	n.a.	32	19.6
Bangladesh	206	n.a.	n.a.
India	1124	100	15.7
Iran	175	100	19.0
Lebanon	7	25	21.2
Nepal	175	n.a.	n.a.
Pakistan	63	14	16.6
Syria	128	31	19.0
Turkey	630	77	19.1
SED ^b	—	—	2.6
World	3389		

n.a.: data not available

^a Coefficients of variation (%) calculated for each trait in each country. The mean CV over traits is presented. Data from Erskine *et al.* (1989).

^b SED from a one-way analysis of variance of CV over countries for nine traits.

Additionally, *pilosae* lentils either lack tendrils or have only short or rudimentary tendrils. These two qualitative characters differentiate the lentil of South Asia from other cultivated lentils.

Quantitative morphological characters

Regional groups were revealed in a study of the quantitative agro-morphological variation in germplasm from 13 major lentil-producing countries (Erskine *et al.*, 1989). Landrace accessions from India and Ethiopia were strikingly similar for the nine quantitative traits surveyed, and clustered together in one group. The group was characterized by early flowering and maturity, low biological yield, short stature and lowest pod height, and small seeds. This similarity for quantitative traits was previously noted by Barulina (1930), but she indicated that germplasm from these countries differed markedly for qualitative characters, with the Ethiopian material characterized by an elongated pod apex and the Indian material characterized by the *pilosae* traits.

Using data of Erskine and Witcombe (1984) and Erskine *et al.* (1989), it is possible to assess if germplasm from various countries differs in phenotypic variability. To this end, the coefficient of variation among accessions from a country for each trait was subjected to a one-way analysis of variance on the basis of country of origin undertaken over characters (Table 21.1). India and Pakistan have the lowest CV despite the fact that India is the world's largest lentil producer (Table 21.1) and has considerable heterogeneity among its growing environments.

Adaptation

When lentil was first introduced into the Indo-Gangetic Plain, it was exposed to environmental conditions very different from those at its origin in the Fertile Crescent of West Asia. A possible reconstruction of the phenological problems associated with the initial spread of the crop into the Indo-Gangetic Plain was inadvertently made when lentil selections from West Asia were introduced there through early International Center for Agricultural Research in Dry Areas (ICARDA) international nurseries. When lentils selected in West Asia were sown in India and Pakistan, most came to flower when the indigenous lentils were maturing (Ceccarelli *et al.*, 1994). This finding prompted research on environmental factors that control flowering in lentil and it is now known that temperature and photoperiod modulate flowering (Summerfield *et al.*, 1985). In a study of a broad spectrum of germplasm under a range of temperatures and photoperiods, Indian germplasm was more sensitive to temperature and less responsive to photoperiod than germplasm from West Asia (Erskine *et al.*, 1990, 1994). This suggests that selection for local adaptation during the spread of lentil into the Indo-Gangetic Plain at least 4000 years ago has greatly affected phenology and the genetic response to environmental factors. Thus, *pilosae* germplasm is also strikingly more susceptible to cold damage than germplasm from West Asia (Erskine *et al.*, 1981).

There is also evidence for the specific adaptation of *pilosae* germplasm to the edaphic factors of iron (Fe) and boron (B) deficiencies, providing a further contrast to genetic material from the Middle East. Fe-deficiency symptoms are observable on some accessions of lentil grown in calcareous soil with pH >8.0, as is common in the Middle East (Erskine *et al.*, 1993). In a germplasm collection, originating from 18 countries, very few landraces from Syria and Turkey exhibited Fe-deficiency symptoms. Those landraces exhibiting symptoms of Fe-deficiency mostly originated from relatively warm climates, such as India and Ethiopia. This resulted from either the chance introduction to these regions of susceptible to low levels of iron in the soil, or unconscious selection pressure in favour of such types.

Recently, a sample of the world lentil germplasm collection was screened for boron (B)-deficiency tolerance in a soil with low boron content at Rampur, Nepal. All accessions showed severe B-deficiency symptoms except *pilosae* accessions from Bangladesh, India, Nepal and Pakistan (W. Erskine, personal observation).

Recent evidence from seven isozyme loci and 22 random amplified polymorphic DNA (RAPD) loci show that germplasm from South Asia (Bangladesh, India, Nepal and Pakistan) and Afghanistan differs markedly from that from the rest of the world. Additionally, South Asian and Afghanistan germplasm was found to have low levels of genetic diversity (Ferguson *et al.*, 1998). These data confirm the morphological and physiological distinctiveness of *pilosae* germplasm. However, Afghan germplasm is not of the *pilosae* type. One explanation for the similarity of *pilosae* lentils and Afghan material at the isozyme and DNA level is that Afghanistan was the route of entry into the Indian sub-continent. On average, Afghan germplasm is among the latest to flower in the world, flowering on average 3 weeks later than Indian material (Erskine *et al.*, 1989). Afghan (highland) lentils are now reproductively isolated from the lowland *pilosae* type because of the mismatch in flowering time. A detailed study of germplasm from Pakistan including material from highland areas adjacent to Afghanistan and from the lowland Indo-Gangetic Plain may provide the key to further understanding of

the introduction of lentil into South Asia. However, the evidence from isozyme and DNA studies clearly indicates that lentil was not introduced into India from Ethiopia along the same route as crops such as sorghum (*Sorghum bicolor* (L.) Moench.) and cowpea (*Vigna unguiculata* (L.) Walp.), despite the similarity in quantitative morphological characters between Ethiopian and the *pilosae* lentil of South Asia (Simmonds, 1976).

In summary, by comparison with other Asian lentils, the *pilosae* group of South Asia is characterized by two endemic qualitative morphological traits, precocity in flowering and maturity, low biomass, increased sensitivity of the temperature control of flowering, and high frequency of boron efficiency and of iron inefficiency. Furthermore, lentil germplasm from India is the least variable among lentil-producing countries, despite India being the largest producer in the world. It further seems likely that the asynchrony in flowering between exotic material from West Asia and the indigenous germplasm in South Asia enforced reproductive isolation of *pilosae* lentil. A genetic bottleneck occurred which was maintained by differing flowering times and resulted in germplasm with reduced genetic diversity for agro-morphological, isozyme and molecular traits.

Broadening the Genetic Base in South Asia

Plant introduction

A narrow genetic diversity limits the scope for new recombinations, and the simplest approach to widening the variation available to breeders in South Asia is plant introduction. As noted above, the introduction of material from West Asia into the Indo-Gangetic Plain is difficult because of non-overlapping flowering. The introduction of some exotic, earlier-flowering material, however, has been more fruitful. For example, 'Precoz' (ILL 4605) was the first early-flowering, large-seeded (*macrosperma*) (4.5 g per 100 seeds) lentil introduced into South Asia, where endemic germplasm has a seed weight <3.0 g per 100 seeds. Precoz thrives in the wetter areas of Pakistan, such as the National Capital Territory and parts of Northwest Frontier Province, where it has been released for cultivation as 'Manserha 89'. Its early flowering synchronizes with the flowering of indigenous germplasm, allowing artificial crossing without the need for extended photoperiod (Tyagi and Sharma, 1981). 'Precoz' and/or its derivatives have been included in every crossing block in India.

For the upland areas fringing the Indo-Gangetic Plain, the introduction of germplasm and breeding material from West Asia is important because of the specific needs for cold tolerance and a medium-duration crop. For example, in Baluchistan, Pakistan, the medium-maturing accession ILL 5865 was released as ShirAZ-96 in 1996 (ICARDA, 1997).

Hybridization

The genetic variation in a region may also be increased through hybridization within the primary gene pool. The use of the early-flowering 'Precoz' in South Asia is one

example of this. However, a major systematic effort to widen the genetic diversity available to breeders in South Asia has been made at ICARDA by extensive crossing of *pilosae* lentils with primary genepool germplasm from other origins since 1981. An extended photoperiod (18 h) has been used in the crossing block to improve synchrony in flowering between diverse parents. The F₁ generation was grown in a high-elevation (890 m above sea level) summer nursery at Terbol, Lebanon, for rapid generation advancement, allowing two generations per year. Segregating populations were then either distributed to national programmes as part of the International Legume Testing Network in an international F₃ or F₄ nursery or sent to specific national programmes. Selections were made locally for adaptation and disease resistance. This system exploited the comparative advantage at ICARDA in crossing and rapid generation advancement with selection in the target production area.

In this manner, targeted crosses for Bangladesh were made at ICARDA, Syria, to incorporate resistance to rust, a major production problem. Selections were then made in Bangladesh of adapted rust-resistant plants from the segregating populations. As a result, Bangladesh released its first rust-resistant lentil 'Barimasur-2' (selected from cross ILL 4353 × ILL 353) in 1993. Barimasur-2 has yield advantage of *c.* 20% over the standard check (Table 21.2) with wide adaptation. A further selection 'Barimasur-4' (selected from L5 × FLIP 84-112L) was released in 1995 for high yield (53% increased yield over the check) with combined resistance to rust and stemphylium blight (Table 21.2). In a pilot production project, the results of 12 farmer-managed on-farm trials (1996/97) showed that the new cultivars were superior to the local cultivar by 23–110% in Bangladesh. With an erect plant stature the variety Barimasur-4 is suitable for inter-cropping with sugar cane and mixed-cropping with mustard and linseed.

In Pakistan the variety 'Masoor 93' was released for cultivation in the Punjab province of Pakistan with a 31% increased yield over the check and improved disease resistance and seed size (Tufail *et al.*, 1995) (Table 21.2). It comes from the cross 18-12 (local) × ILL 4400 (from Syria) made at Faisalabad, Pakistan, using hybridization techniques learned at ICARDA. The cultivar Masoor 93 is now grown on about 20–25% of the lentil area in Pakistan.

In India, the intensive use of Precoz and its derivatives in hybridization by local lentil improvement programmes has resulted in the development of extra-bold and extra-early lines. The All-India coordinated lentil trial programme has recently started

Table 21.2. Varieties released in South Asia from crosses between *pilosae* lentils from South Asia and representatives of other genepools.

Country	Variety	Year of release	Parentage	Yield (t ha ⁻¹)	% increase over check	Other important traits
Bangladesh	Barimasur-2	1993	ILL4353 × ILL353	1.8	20	Resistant to rust
	Barimasur-4	1995	L5 × FLIP84-112L	2.3	53	Erect, resistant to rust and Stemphylium blight
Pakistan	Masoor-93	1995	18-12 × ILL4400	1.7	31	Resistant to rust, Botrytis and Ascochyta blights and sclerotinia stem rot

two new categories of trial, as a result of the broadening of the genetic diversity of lentil in South Asia: (i) extra-bold seeds (>35 g per 1000 seeds); and (ii) extra-early (maturity <115 days). In the 1996/97 cropping season there were a total of 93 lines in the All-India Coordinated Trials, of which 44% (predominantly in the extra-bold seeded and extra-early nurseries) had exotic ICARDA parentage. In India, the extra-early nursery is particularly important because it opens up a large new potential cropping niche for lentil in India, namely late-sown lentil (using an early-maturing cultivar) following the harvest of a long-season rice crop. At present, there are 4 million ha left fallow in winter after the harvest of long-season rice in India annually. With intensive cropping, the newly developed early lines can be fitted in late planting conditions. These lentil lines mature in <115 days compared with 135–145 days for landraces from North India.

Evolution of the ICARDA Breeding Programme

The above is illustrative of a changing approach by ICARDA and national programmes as national capacities for lentil breeding have risen and the need for specific adaptation has been recognized (Ceccarelli *et al.*, 1994). The lentil breeding programme at ICARDA is built upon the foundation of the germplasm collection, as the source of variation for breeding. Additionally, the germplasm collection has contributed philosophically to breeding because the strategy of the improvement programme flows from an understanding of the evolutionary patterns of variability of landraces and their adaptation. ICARDA's lentil breeding programme aims to produce genetic material for a series of separate, but finely geographically targeted streams, linked closely to national breeding programmes (Robertson and Erskine, 1997).

The breeding strategies used for this annual, diploid, self-pollinated food legume have changed with time. In Stage 1, the variation in the world lentil germplasm collection was directly exploited. Selection was made among and within locally adapted landraces. These selections were distributed to national programmes through the International Nursery Network to test for local adaptation. As a result, many cultivars released by national programmes are actually selections from landraces in the ICARDA germplasm collection (Fig. 21.1) (Robertson *et al.*, 1996). These Stage-1 registrations emphasize firstly the value of direct exploitation of landraces and secondly the under-exploited nature of lentil germplasm.

The particular combinations of characters required for specific regions were often not found 'on the shelf' in the germplasm collection. Consequently, ICARDA started hybridization, and selections from segregating populations made at ICARDA in Syria to produce Stage 2 material. Such selections were then distributed after multiplication to the national programmes to select in their respective agroclimatic conditions. This has resulted in the release of a number of cultivars in different regions (Fig. 21.1).

However, lentil lines developed from selection at ICARDA in West Asia are mostly limited to adaptation to the home region. As a result, the breeding programme has decentralized to work closely with national programmes. For the other regions, at Stage 3, crosses are agreed upon with national-level cooperators and then made at ICARDA, Syria. Country-specific segregating populations are then shipped to national cooperators for local selection. Approximately 200 such crosses are made annually at ICARDA.

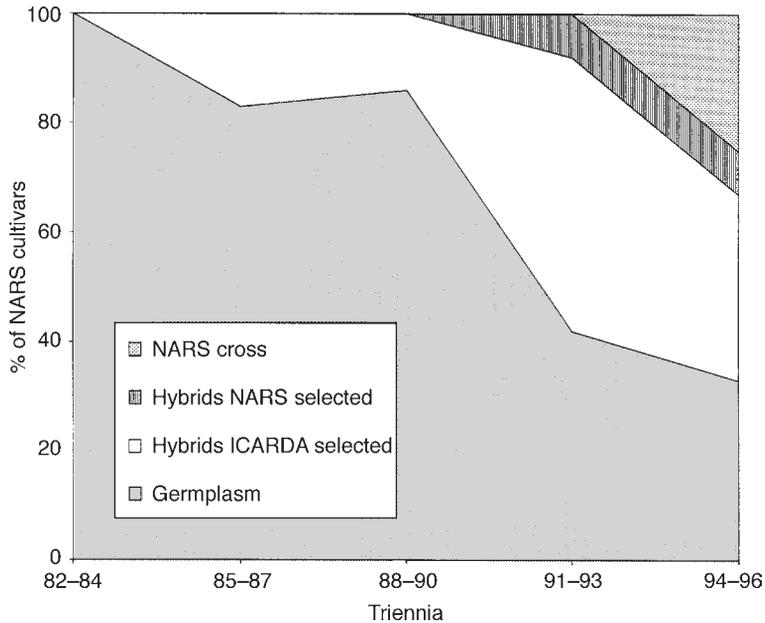


Fig. 21.1. Lentil varieties released by NARS (1982–1996). Germplasm: Stage 1 – selections among and within accessions in ICARDA germplasm collection. Hybrids ICARDA selected: Stage 2 – selections made at ICARDA, Syria in segregating populations from ICARDA crosses. Hybrids NARS selected: Stage 3 – selections made by NARS from segregating populations from ICARDA crosses. NARS crosses: Stage 4 – selections made by NARS from segregating populations from NARS crosses with parents from ICARDA.

Selections made by national programmes are then fed back into the International Nursery Network for wider distribution. In Stage 4, the national programmes use ICARDA-derived material in their own crossing programmes and selections are made locally.

Future Prospects

In addition to broadening the genetic base of lentil production in South Asia, the hybridization of *pilosae* lentils with germplasm from other origins is producing spin-offs for regions outside South Asia. In particular, the early flowering of the *pilosae* type is useful in drought escape through the avoidance of terminal drought in dry areas of the Mediterranean region (Silim *et al.*, 1993). Furthermore, shifting from spring to winter planting of lentil in the highlands requires winter-hardy varieties. Winter-hardy germplasm is available to exploit this niche to boost lentil production in these regions. These lines are also being used in hybridization by ICARDA to generate high-yielding lines with improved cold tolerance.

These examples illustrate the progress made in increasing the genetic variation of lentil in South Asia and the removal of an ancient genetic bottleneck. Plant introduction is of immediate value for lowland areas only for early flowering and maturing germplasm; it is of greater value in the highland edges of South Asia, where the

cropping season is longer. Hybridization has introduced resistance to rust, and Stemphylium and Ascochyta blights, increased seed size together with extra-early flowering into South Asia; it may also be useful in introducing a rapid early growth rate for the late-planting crop. Mutation breeding or gene transformation technology may be useful to incorporate resistance currently unavailable in the primary gene pool to grey mould (caused by *Botrytis cinerea*), broomrape (*Orobancha* sp.) and pea leaf weevil (*Sitona* sp.).

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22 Genetic Diversity of Barley: Use of Locally Adapted Germplasm to Enhance Yield and Yield Stability of Barley in Dry Areas

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Introduction

The area of the Near East that includes parts of Jordan, Lebanon, Palestine, Syria, southeast Turkey, Iraq and western Iran is known as the 'Fertile Crescent' (Fig. 22.1). The domestication of several of our main crops, including wheat and barley, took place in this area some 10,000 years ago (Zohary and Hopf, 1993) and this made it possible for man to move from hunting and food collecting to farming. Probably the most important of the early cereals was barley, and archaeobotanical material from the region clearly shows that the first barleys were two-rowed (Harlan and Zohary, 1966). The wild progenitor of cultivated barley, *Hordeum spontaneum*, is still widely distributed along the Fertile Crescent where, particularly in the driest areas, it can be easily identified at a distance because of its height.

Over the course of time since early domestication, barley has spread, together with agriculture, to new environments first in close proximity to the primary area of domestication and then east and west to other areas in Europe, Asia and North Africa. Due to the exposure to new environments and repeated conscious selection by man for different purposes, new gene complexes for adaptation, resistance, quality and other traits have been developed. Natural selection gave rise to locally adapted landraces. Barley thus developed into a crop with high genetic diversity over the temperate areas of the old world. Like *H. spontaneum*, landraces constitute a major gene pool of importance for breeding programmes.

Barley is still one of the most important cereal crops in the Fertile Crescent, covering an area of approximately 5 million hectares. It is a typical crop of marginal, low-input, drought-stressed environments (Ceccarelli, 1984) except for few pockets where it is also grown in favourable conditions. Barley grain and straw are the most important source of feed for small ruminants, mostly sheep. Conventional breeding and high-yielding (HY) varieties had virtually no success in this area. But this lack of success has

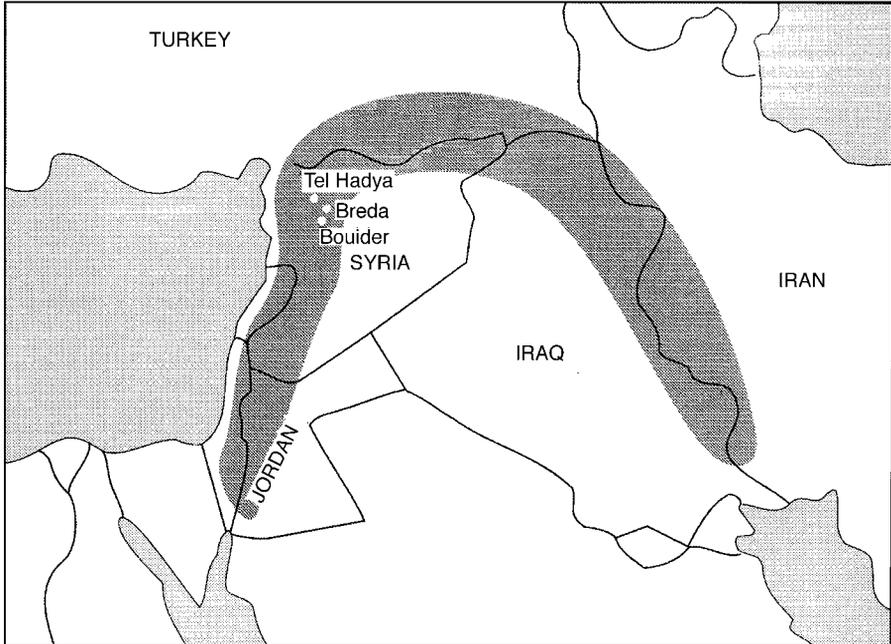


Fig. 22.1. The 'Fertile Crescent', where crops such as barley, wheat, lentil, stone fruits and olives were domesticated (modified from Harlan and Zohary, 1966). Experimental sites used by ICARDA's barley project are shown.

had a positive effect in preserving biodiversity because in these environments all the barleys grown are landraces (Weltzien, 1988) that have evolved directly from the wild progenitor in hostile environments; they are very popular among farmers for their good feeding quality as both grain and straw.

In Syria, farmers distinguish two major groups of landraces, largely on the basis of seed colour, namely Arabi Abiad (white seed) and Arabi Aswad (black seed). The first is common in environments receiving between 250 and 400 mm annual rainfall; the second is cultivated in harsher environments with less than 250 mm annual rainfall. Although collected as early as 1950 by Vavilov, little is known about these two groups. A few accessions were included in the world's genebank collections but, as in many other crops, little use has been made of these valuable genetic resources.

Generally, in both developing and developed countries, the use in barley breeding of exotic or primitive germplasm, such as *H. spontaneum* and landraces, is not common. Elite breeding based on modern lines and newly released varieties prevails. Though these modern lines were originally based on material extracted from previous landraces of a particular area, modern breeding, private or public, concentrates its breeding efforts on a narrow gene pool. This is a vulnerable strategy and base-broadening needs to receive higher priority from genebank curators, practical plant breeders and society in general.

Pre-breeding efforts, mainly in the shape of testing of exotic material for disease resistance and backcrossing to highly bred varieties, have been carried out (Lehmann and Bothmer, 1988), but programmes where base-broadening is the major concern

have only recently been initiated in some countries and should be further encouraged. So, for example, particular composite cross populations – dynamic genepools – composed of both landraces and *H. spontaneum* have been made separately for Swedish and for Finnish conditions (Veteläinen, 1997; Veteläinen and Nissilä, Chapter 14, this volume).

In the early 1980s it was postulated that because barley landraces have been grown continuously since domestication in unfavourable and stress environments and without inputs, their evaluation could teach a barley breeder a few lessons on adaptation to low-input, stressful environments (Ceccarelli, 1984). It was also postulated that the lesson(s) could be useful to other breeders in countries where barley landraces are still predominant, as well as to breeders of crops grown prevalently in stress environments.

This chapter illustrates the contribution that landraces and the wild progenitor of cultivated barley, *H. spontaneum*, can make to increase agricultural production, particularly in areas with severe climatic and nutritional stresses such as the Syrian steppe.

Experimental Conditions

From 1984, all breeding material was tested under typical northern-Syrian growing conditions, i.e. strictly rainfed, predominantly in areas with low and erratic rainfall, and without fertilizers, pesticides or herbicides.

Three experiment sites (Fig. 22.1), representing three distinct agricultural systems, were used: Tel Hadya, where ICARDA's headquarters are located, is a typical high-input favourable environment with a wide choice of different crops; Bouider, rented from a farmer, is the opposite extreme, with a typical low-input highly risky environment and barley being the only possible rainfed crop; Breda, an ICARDA field station, is intermediate between the two. The three sites are geographically close, being located at 35 (Tel Hadya), 60 (Breda) and 80 km (Bouider) south-southeast of Aleppo, respectively, and this is an enormous advantage in terms of field operations. Table 22.1 shows the total rainfall at the three sites since the work on landraces began. Although rainfall does not convey all the information about climate, rainfall distribution and winter temperatures also play a determinant role; it is evident that there is a consistent rainfall gradient between the three sites, which makes the area unique in providing large climatic contrasts within short distances.

Source of Material

Wild barley

The wild progenitor of cultivated barley was earlier treated as a separate species (*Hordeum spontaneum* C. Koch) but – due to the full compatibility in crosses, no postzygotic sterility barriers and morphological close resemblance to cultivated barley – it is now treated as a subspecies, *Hordeum vulgare* ssp. *spontaneum* (C. Koch) Thell. (Asfaw and Bothmer, 1990; Bothmer *et al.*, 1995). For simplicity, however, the taxon is called *H. spontaneum* in this chapter.

H. spontaneum is an annual, brittle, two-rowed, diploid ($2n = 14$), predominantly

Table 22.1. Total rainfall (mm) in the three experimental sites used by the barley breeding programme in northern Syria.

Year	Tel Hadya	Breda	Bouider
1984/85	372.6	276.6	—
1985/86	316.4	218.3	203.0
1986/87	357.9	244.6	176.2
1987/88	504.2	414.0	385.7
1988/89	234.4	194.8	189.0
1989/90	233.4	183.2	148.7
1990/91	293.5	241.3	213.4
1991/92	352.6	263.2	249.6
1992/93	290.1	283.0	224.2
1993/94	373.3	291.2	245.6
1994/95	312.9	244.2	203.1
1995/96	404.5	359.8	316.0
Long-term average	337.2	267.8	232.2

self-pollinated and colonizing species. There is considerable morphological similarity between *H. spontaneum* and cultivated two-rowed varieties, the major difference being in their modes of seed dispersal. In *H. spontaneum*, ears are brittle and fragment at maturity into individual arrow-like triplets, each containing one seed and two sterile lateral spikelets. Following dispersal, the seeds insert themselves into the ground driven by the movement of twisting awns due to changes in temperature and/or humidity. Under cultivation, this specialization, which ensures the survival of the plant in nature, is undesirable, and was replaced by non-brittle mutants, which were selected by man for reaping, threshing and sowing. The difference is controlled by one or two very closely associated genes (*Bt* and *Bt₁*) on chromosome 3. Brittle rachis is dominant over non-brittle. *H. spontaneum* is also characterized by an extremely long period of seed dormancy, very long and rough awns, and densely haired empty glumes.

The wild form occupies primary habitats such as dry mountain slopes, steppes and semideserts or more ephemeral biotopes. It is more open pollinated than modern types of cultivated barley; up to 10% outcrossing has been reported (Brown *et al.*, 1978). It has thus a higher degree of heterozygosity and heterogeneity than cultivated barley in its populations. The high degree of genetic variation in *H. spontaneum* is visualized by the fact that there is a strong effect of natural selection for microhabitats (shady, exposed, dry, moist, etc.) leading to development of sub-population systems within very small areas (Nevo, 1992). In areas where *H. spontaneum* grows in contact with the barley crop, crosses and gene introgression are fairly common. This has certainly contributed to gene flow between the two taxa over the entire period of cultivation in the Middle East, giving rise to a very versatile genetic system favouring the adaptive radiation of barley over the years. Most probably *H. spontaneum* still contributes to the evolutionary processes of barley landraces through a continuous introgression of genes.

There is ample evidence in the literature that *H. spontaneum* can contribute useful genes for several characters. Resistance to powdery mildew (Moseman *et al.*, 1983; Gustafsson and Claesson, 1988; Nevo, 1992; Lehmann *et al.*, 1998), leaf rust

(Moseman *et al.*, 1990; Nevo, 1992) and other diseases (Nevo, 1992) has been identified in *H. spontaneum*, and its use in breeding for disease resistance has been reported by several authors. The species showed variation for important agronomic traits such as earliness, biomass, grain yield, grain protein, and tolerance to salinity and drought. This vast potential store of genetic resources is as yet largely unexploited. *H. spontaneum* is thus expected to have a potential in contributing useful genes in barley breeding as a donor of adaptive traits to extreme stress conditions, as suggested by its distribution in the driest areas of the region.

In general, *H. spontaneum* is less vigorous in early growth than cultivated barley, although lines with good vigour are present. The level of cold tolerance is similar to that of *H. vulgare* but within the wild genepool accessions much earlier than *H. vulgare* are available. It was interesting to find a large number of lines with a long peduncle as well as with the ability to extrude the spike above the flag leaf. High straw protein content may offer additional justification for the use of *H. spontaneum* (Table 22.2).

The decisive year for including *H. spontaneum* in the breeding activities for stress environments was 1987 when a group of lines were evaluated at Bouider. That year, rainfall was only 176.2 mm and there was a crop failure (Ceccarelli, 1994) with virtually no lines able to produce grain. The only lines able to head and to produce some grains were two accessions of *H. spontaneum*. In these, some photosynthetic activity was found between 0700 and 0800 hours, the average net photosynthesis was $2.7 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and stomatal conductance was $0.060 \pm 0.003 \text{ mol m}^{-2} \text{ s}^{-1}$. At the same time the stomata of the locally adapted landrace, Arabi Aswad, were closed. By midday the stomatal conductance of the *H. spontaneum* accessions decreased to $0.025 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at a leaf water potential of -4.6 MPa while the leaf water potential of Arabi Aswad was -3.5 MPa and the stomatal conductance was zero. These lines combined earliness with an acceptable level of cold resistance, they were able to maintain good plant height under drought conditions and, despite the very dry conditions, they were also able to extrude part of the last internode outside the flag leaf.

From the preliminary evaluation it was concluded that the most useful traits that *H. spontaneum* could contribute in relation to adaptation to stress environments are earliness combined with adequate level of cold tolerance and plant height under drought. The importance of plant height under drought is associated with the fact that one of the most evident effects of drought is a reduction in plant height. In environments where both grain and straw have a value to the farmers as animal feed, plant height is an important trait as it is related to biological yield. Also in dry years the crop is too short to be harvested by combine and farmers either leave it for grazing or harvest it by hand at much higher cost.

Barley landraces

In 1981 a large collection of barley landraces was made by E. Weltzien in Syria and Jordan: from the fields of 70 farmers (60 in Syria and 10 in Jordan), who had been using their own seed for generations, 100 spikes were collected at random (Weltzien, 1988). The spikes were kept separate, unlike what most conventional collectors, such as germplasm specialists, often do. This was a key in the subsequent utilization of the collection.

Table 22.2. Mean and range of seven characters measured in 55 accessions of *H. spontaneum* and in nine cultivars of *H. vulgare*.

Character ^a	<i>H. spontaneum</i>		<i>H. vulgare</i>	
	Mean	Range	Mean	Range
Cold damage	3.0	1.0–5.0	3.7	1.5–5.0
Early growth vigour	2.9	1.0–5.0	1.6	1.0–2.5
Days to heading	141.8	131.5–152.5	141.1	138.5–145.5
Peduncle length	44.2	32.8–50.3	23.5	20.3–32.1
Peduncle extrusion	18.4	8.2–26.3	4.4	1.0–10.5
Straw yield (t ha ⁻¹)	4.4	2.8–6.5	5.1	4.1–6.1
Straw protein (%)	5.1	2.7–7.0	3.5	2.8–4.7

^aCold damage (1 = resistant, 5 = susceptible); early growth vigour (1 = good, 5 = poor); days to heading (days from emergence to awn appearance); peduncle length (distance from last node to base of spike, in cm); peduncle extrusion (distance from collar of flag leaf to base of spike, in cm).

When the seed collected was multiplied off-season (planting in summer) as head-rows, two main characteristics were noted: first, a high degree of seed dormancy was observed, with the material collected from the south showing a higher percentage of germination; secondly, few of the rows were able to head and produce seed, with differences in the material collected at the same sites (Weltzien, 1982). These were the first lessons the landraces were teaching, both by indicating traits of adaptive significance (such as vernalization requirement and seed dormancy), and by expressing the variability that these populations harbour.

Additional information on the structure of the variation between and within collection sites was obtained when the material was evaluated under field conditions as individual rows (Weltzien, 1988, 1989) or as plots (Weltzien and Fischbeck, 1990). Significant genetic variation was found for seed colour, growth habit, awn barbing, days to heading, culm length, leaf width, awn length, early growth vigour, lodging and powdery mildew resistance.

Three important indications, which were confirmed later, emerged from these studies. Firstly, that the genetic variability within the landraces was also expressed in stress sites, where the heritability was even higher than in a non-stress site; secondly, in a stress site the majority of landraces outyielded the check (improved) cultivars; thirdly, in the non-stress site the checks outyielded the landraces but not always significantly.

Arabi Abiad and Arabi Aswad – the two barley landraces widely grown in Syria – show a large and significant variability for virtually all characters (growth habit, early growth vigour, cold damage, plant height, days to heading, days to maturity, grain-filling duration, grain yield, spike length, peduncle extrusion, 1000 kernel weight, protein content and lysine content).

This is based on the evaluation in 1984/85 of 420 single-head progenies (lines) in three trials at Breda (Ceccarelli *et al.*, 1987). In each of the first two trials, 140 lines were evaluated (10 for each of 14 collection sites) together with four checks (Arabi Abiad and Arabi Aswad, and two improved cultivars Harmal and Rihane-03). In the third trial, 70 lines for each of two collection sites were evaluated.

The data quantified some of the differences between the white-seeded and the black-seeded landraces. These are of particular interest to plant breeders to verify the

firm belief of Syrian farmers that the black-seeded landrace is better adapted to dry areas and it is a better feed for sheep than the white-seeded landrace. The use of lines with the required seed colour could be important to ensure quick adoption.

The differences between the two landraces are summarized in Table 22.3 using the data of the third experiment where number and length of seminal roots – these are the only roots produced in very dry conditions – and coleoptile length were measured. The black-seeded landrace usually has less-vigorous early growth, is more cold tolerant, matures slightly earlier, has a shorter grain-filling period, is taller under drought, is more productive under stress, has smaller kernels, a shorter coleoptile length, and shorter and fewer seminal roots. Some of these differences – such as those related to phenology, and cold tolerance, growth vigour, kernel size and plant height – are easily interpretable as related to adaptation to dry and cold areas where the black-seeded landrace is predominantly cultivated. The advantage of plant height under drought is often quoted by farmers in Syria as one of the main reasons for preferring Arabi Aswad to Arabi Abiad in the drier areas.

The most interesting aspect of this early work was the extraordinary amount of variability found within landraces as shown by the intervals of variation in Table 22.3. The fact that landraces are composed of several genotypes is neither new nor original. In fact this has been reported for several crops, such as lentil (Erskine and Choudhary, 1986), sorghum (Blum *et al.*, 1991), bread and durum wheat (Damania and Porceddu, 1983; Porceddu and Scarascia Mugnozza, 1984; Spagnoletti-Zeuli *et al.*, 1984; Damania *et al.*, 1985; Lagudah *et al.*, 1987; Blum *et al.*, 1989; Elings and Nachit, 1991), beans (Martin and Adams, 1987a, b), both cultivated and wild barley (Brown, 1978, 1979; Asfaw, 1989) and others.

In addition to grain yield and other agronomic, morphological and physiological characters, an unexpected amount of variability was found for resistance to yellow rust,

Table 22.3. Differences between the black-seeded (Arabi Aswad) and the white-seeded (Arabi Abiad) barley landraces commonly grown in Syria.

Character ^a	Arabi Aswad (black)		Arabi Abiad (white)	
	Mean ± SE	Range	Mean ± SE	Range
Cold damage	2.10 ± 0.06	3.08–1.02	3.26 ± 0.08	4.68–1.58
Early growth vigour	2.99 ± 0.09	4.65–1.52	2.31 ± 0.10	5.00–1.06
Days to heading	147.4 ± 0.22	153.0–141.5	147.7 ± 0.14	150.4–145.3
Days to maturity	171.9 ± 0.30	177.6–168.8	173.8 ± 0.28	178.5–168.8
Grain-filling duration	24.5 ± 0.26	30.5–19.50	26.1 ± 0.25	30.5–20.5
Plant height (cm)	52.1 ± 0.47	61.8–40.9	43.1 ± 0.46	53.4–33.4
Grain yield (kg ha ⁻¹)	1769 ± 36	2480–944	1542 ± 40	2324–920
Grain protein content (%)	10.5 ± 0.05	11.6–9.7	10.6 ± 0.06	11.9–9.9
Grain lysine content (%)	0.43 ± 0.00	0.45–0.41	0.43 ± 0.00	0.46–0.40
1000 kernel weight (g)	35.7 ± 0.29	43.5–31.1	41.9 ± 0.35	47.9–34.6
Seminal root number	5.7 ± 0.06	7.1–4.4	6.2 ± 0.05	7.4–5.0
Seminal root length (mm)	55.8 ± 1.23	86.3–37.16	69.1 ± 1.11	99.3–43.3
Coleoptile length (mm)	47.5 ± 0.44	55.4–39.4	52.4 ± 0.55	61.4–41.4

^aCold damage (1 = resistant; 5 = susceptible); early growth vigour (1 = good; 5 = poor); days to heading (days from emergence to awn appearance); days to maturity (days from emergence to yellowing of entire plant); grain-filling duration (days between heading and maturity); plant height (measured at maturity, distance from base of plant to top of spike, excluding awns).

powdery mildew, scald and covered smut (van Leur *et al.*, 1989). With the exception of covered smut, there was a significant variation both between and within collection sites.

The reaction to diseases varied from absolutely or partially resistant types to highly susceptible lines. This was of particular interest because the common belief is that landraces are disease susceptible, and therefore not worth the attention of modern plant breeders. The data indicated, however, that although landraces look disease susceptible because the majority of plants are susceptible, they contain a small amount of resistant individuals which are an important source of genes for disease resistance within an adapted genetic background.

In the case of Syrian landraces, the presence of such a high level of heterogeneity is not as obvious at first sight as it is, for example, in Ethiopian or Nepalese barley landraces. This might explain why Syrian farmers do not select within landraces either before or after harvesting. One might have hypothesized that thousand of years of natural and human selection in a stress environment could have reduced the amount of heterogeneity by continuously selecting for the most adapted genotypes. However, this does not seem to be the case and the variation available within populations appears to be large and of great value to a breeding programme for stress environments and low-input conditions.

This is evident by looking at the yield advantage of some of the pure lines extracted from landraces over the original landraces and some improved (modern) cultivars (Table 22.4) in low rainfall conditions and with little or no use of inputs. These data have been confirmed in many comparisons between different types of germplasm in that type of environment and explain the failure of introducing modern cultivars

Table 22.4. The highest-yielding pure lines extracted from landraces in 1984/85 in Breda (277 mm rainfall), compared with the two commonly grown landraces and two improved cultivars.

Entry	Seed colour	Plant height (cm)	Grain yield (kg ha ⁻¹)	% increase over Arabi Abiad
SLB 45-48	Black	50.8	2480	149
SLB 39-31	White	42.4	2324	139
SLB 39-58 (Arta)	White	45.1	2287	137
SLB 45-83	Black	55.9	2232	134
SLB 45-95	Black	53.7	2227	134
SLB 45-40	Black	61.5	2216	133
SLB 39-05	White	45.3	2189	131
SLB 45-04	Black	55.2	2180	131
SLB 39-10	White	45.0	2162	130
SLB 45-90	Black	61.8	2153	129
SLB 45-34	Black	53.1	2146	129
SLB 45-76	Black	53.6	2122	127
<i>Checks</i>				
Arabi Abiad (landrace)		45.4	1666	
Arabi Aswad (landrace)		47.7	1547	
Rihane-03 (modern)		49.4	1013	
Harmal (modern)		45.9	1017	
LSD _{0.05}		5.4	453	

LSD, least significant difference.

into the area. The most important information from a breeding point of view is about the amount of improvement it is possible to achieve by simply utilizing the variability available within landraces.

The presence of large genetic diversity within populations adapted to an environment where conventional breeding has failed suggested that, in addition to the need for continuous collection and both *ex situ* and *in situ* conservation, there was the almost unexplored possibility of using this large reservoir of useful genetic variation in these landraces for plant improvement. There were four ways to do that:

1. Develop highest-yielding pure lines extracted from landraces into pure line varieties.
2. Utilize pure lines extracted from landraces that are superior for yield, as well as for other characters including resistance to pests and diseases and quality characteristics, as parents in the crossing programme to introduce additional desirable characters in an adapted genetic background.
3. Develop mixtures or multi-line varieties, constructed with a variable number of pure lines properly characterized for a set of agronomic characters. This permits exploitation of the buffering capacity of genetically heterogeneous populations in relation to stability and will conserve a certain amount of the evolutionary process within populations.
4. Evaluate lines with contrasting expressions of specific attributes to quantify the adaptive role of specific morphological traits in stress environments, and to identify, localize and tag gene complexes or quantitative trait loci (QTLs) associated with adaptation with molecular techniques.

The four avenues were initiated within a few years of each other, with the exception of the molecular approach, which has started only recently. The remainder of this chapter describes the results for the first three approaches. These activities had two main objectives. On one hand, they had the objective of generating new cultivars for the dry areas of Syria; on the other hand, they were intended to generate a methodology of utilization of landraces to be used in those countries where landraces, even of other crops, are still available. With this second objective in mind, the methods of exploiting the genetic variation between and within landraces were kept as simple as possible in view of their utilization by breeders in developing countries with limited resources. Another key aspect of the methodology was to employ the level of inputs used by farmers to make sure that the products (pure lines and mixtures) would be beneficial to poor farmers and that the yield increases could be sustained.

Landraces and *H. spontaneum* as Breeding Material

Pure line selection within landraces

Since 1984/85 the collection of 7000 spikes described earlier has been systematically evaluated. This has been done by testing between 300 and 400 lines each year, with a classical pure-line selection method (the oldest and simplest of breeding methods), under typical farmers' conditions. Farmers were invited to visit the plots and to make their own selection: their selection criteria (tall plants under drought and soft straw) were subsequently used as routine.

After 10 years, and with about half of the collection evaluated, three pure lines (two with black seed, named Tadmor and Zambaka, and one with white seed, named Arta – the only one officially released) are already grown in farmers' fields each on an area estimated as between 500 and 2000 ha. Before 1981, Tadmor, Zambaka and Arta were three spikes, among millions, in three farmers' fields. In 2000, the progeny of these three spikes grow in farmers' fields and outyield the local landraces by between 10 and 25% without additional inputs.

Figure 22.2 shows an example of the yield advantage that can be obtained in farmers' fields with this strategy. Arta was compared with the local landrace (either Arabi Abiad or Arabi Aswad, depending on the location) in 69 farmers' fields in five provinces of Syria. The locations have been ranked in ascending order using the yield of the local landrace. The superiority of Arta is larger at low-yield levels than at higher-yield levels: in all the 23 lowest-yielding locations Arta always outyielded the local landrace (only in one case were the yields similar), and therefore Arta is mostly beneficial to farmers in difficult environments. Interestingly enough, as one of the first few lines to be yield tested, Arta was already showing its superiority in 1984/85 (see Table 22.4; the collection number of Arta was SLB 39-58).

The evaluation of the collection of landraces has not only produced three varieties rapidly spreading from farmer to farmer. During the past 10 years we also identified, within the landraces, sources of resistance to most of the major barley diseases such as powdery mildew, scald, yellow rust, covered smut, barley stripe and root rot, which have been selected to be used as parental stocks.

The collection of pure lines is evaluated within the context of the breeding programme. Therefore, it has been possible during the years to make several comparisons between the landraces of Syria and Jordan and modern cultivars.

A typical example of this type of comparison is given in Table 22.5, where 77 lines

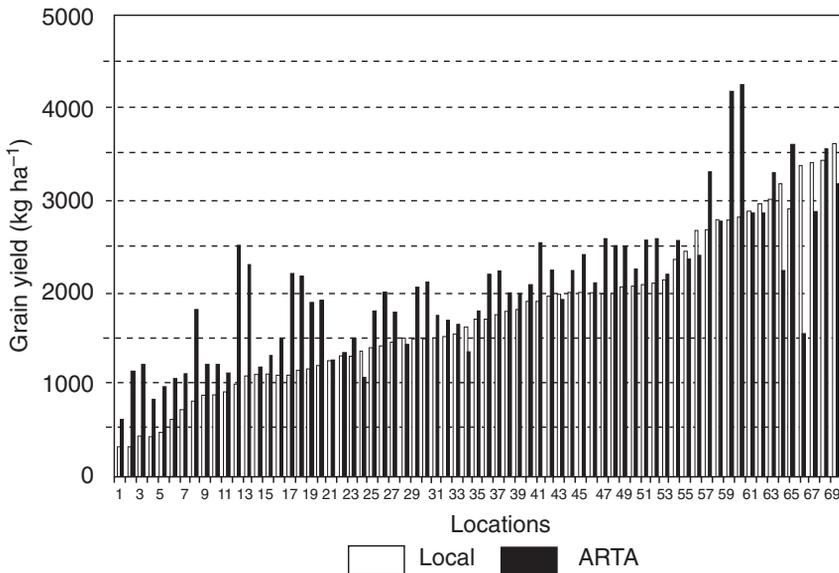


Fig. 22.2. Grain yield of Arta compared with local barley in 69 farmer's fields in five provinces of Syria in 1996. Each cultivar was grown on plots of 1 ha.

Table 22.5. Grain yield (kg ha⁻¹) under stress and under non-stress of barley landraces and modern cultivars in Syria.

Type of germplasm	Stress ^a		Non-stress ^b	
	Yield	Range	Yield	Range
Modern (<i>n</i> = 155)	488	0–893	3901	2310–4981
Landraces ^c (<i>n</i> = 77)	788	486–1076	3413	2398–4610
Best check	717		4147	

^aAverage of two stress sites.

^bAverage of three non-stress sites.

^cPure lines obtained by pure-line selection within landraces.

from landraces were compared with modern cultivars using the average grain yield of two stress sites and the average grain yield of three non-stress sites. The landraces have an average yield advantage of 60% under stress while the modern cultivars have an average yield advantage of 14% under non-stress. Besides the mean performance of the two types of germplasm, the interval of variation is also very informative. All 77 lines yielded something under stress, while some of the modern failed even though the best modern yielded almost much as the best landraces. Under non-stress it was interesting to find that the yield of some landraces was not much less than that of the best modern cultivars.

The lower yield potential of the lines from landraces, specifically selected for stress conditions, is not a serious problem because in the dry areas of Syria, the probability of yields exceeding 3 t ha⁻¹ is about six times lower than the probability of yields less than 1.5 t ha⁻¹ (Ceccarelli, 1996).

One of the most important messages of Table 22.5 is about the choice of the selection environment. It is clear from the two examples that, had the selection been done only under the high-yielding conditions of a typically high-input experiment station, the landraces would have had a short life as breeding material (see Ceccarelli *et al.*, Chapter 6, this volume).

Today, a similar approach has begun in Ethiopia and Eritrea with barley, work on barley landraces is very active in Tunisia, and some work is being done in Iraq. New collections of barley landraces have recently been made in Nepal to begin a similar type of programme.

Crosses: building on adaptation

The identification of agronomically superior pure lines within landraces, and of sources of disease resistance, opened a second avenue in exploiting adapted germplasm, i.e. their use as parental material in a breeding programme. This started about 3 years after the systematic evaluation of pure lines began (the first crosses with *H. spontaneum* were made in 1987).

One example of the value of using landraces in a crossing programme for dry areas is given in Table 22.6, where 514 breeding lines unrelated to landraces (improved) and 525 pure lines extracted from landraces are compared with lines derived from three

Table 22.6. Grain yield (kg ha⁻¹), biological yield (kg ha⁻¹), plant height (cm) and harvest index in Breda and grain yield (kg ha⁻¹) in Tel Hadya (both in 1995) of different types of breeding material.

Breeding material	Grain yield (TH95)	Grain yield (BR95)	Biological yield (BR95)	Plant height (BR95)	Harvest index (BR95)
Improved (<i>n</i> = 514)					
Mean	4125 ± 27	591 ± 8	2559 ± 17	23.2 ± 0.2	22.8 ± 0.3
Max	5812	1201	4504	40.3	41.3
Min	1375	69	1559	14.8	3.24
Improved × landraces (<i>n</i> = 214)					
Mean	3883 ± 33	775 ± 10	2678 ± 24	25.1 ± 0.3	29.1 ± 0.3
Max	5206	1252	3658	38	37.9
Min	2630	259	1930	16.9	11
Landraces (<i>n</i> = 525)					
Mean	3657 ± 23	752 ± 7	2549 ± 16	21.4 ± 0.1	29.8 ± 0.2
Max	5455	1232	4027	30.5	39.9
Min	2250	320	1529	13.1	16.5
Landraces × <i>Hordeum spontaneum</i> (<i>n</i> = 133)					
Mean	2797 ± 49	724 ± 11	2829 ± 32	29.1 ± 0.4	25.9 ± 0.3
Max	4489	1077	4007	43.6	35.6
Min	1515	369	2060	20.5	11.5
Improved × <i>Hordeum spontaneum</i> (<i>n</i> = 17)					
Mean	2814 ± 118	537 ± 37	2362 ± 111	27.1 ± 1.7	20.6 ± 1.2
Max	3995	907	3681	44.1	30
Min	1780	306	1842	19.2	11.4

BR95 = Breda 1995; TH95 = Tel Hadya 1995.

types of crosses. The comparison was done in a very dry site and year (Breda in received 244 mm rainfall 1995) where grain yield, total biological yield, plant height and harvest index were measured, and in a relatively wet site (Tel Hadya with 313 mm rainfall) yield potential was measured. The landraces yielded, on average, more than the improved lines under stress but had a lower average yield potential. Under stress, landraces and improved lines had a similar biological yield, but the landraces were much shorter and had a higher harvest index – two characteristics usually associated with high-yielding varieties.

Crosses between landraces and improved germplasm generated breeding material that was as good as landraces for grain yield and total biological yield under stress, and superior for plant height while maintaining a relatively high harvest index. However, crosses between landraces and *H. spontaneum* generated breeding material which is almost as good as that derived from crosses between landraces and improved germplasm. The total biological yield and plant height are higher than in any other material, and both grain yield under stress and harvest index are probably underestimated because of the presence of some brittle-rachis genotypes. The last type of cross –

improved varieties \times *H. spontaneum* – generated the least promising type of breeding material, except perhaps for plant height (Table 22.6).

The superiority of the crosses with landraces suggests that the strategy of using adapted germplasm in a breeding programme is to capitalize on their specific adaptation to drought and low-input conditions rather than to consider them as sources of a few useful genes as done in most plant breeding programmes. Therefore, in breeding for stress environments, landraces should be regarded as the recipient of a few useful genes to be added to their adapted genetic background, rather than as donors of traits not available in ‘elite germplasm’. This is conceptually similar to what breeders in favourable environments do: once they have found genotypes with high yield potential and good adaptation to high-yielding conditions, they continue to build on them. The strategy is strengthened by the availability of genes for disease resistance within landraces. If a line extracted from landraces is agronomically superior but susceptible to a disease, the source of resistance is first sought among lines from the same collection site to preserve as much adaptation as possible, and secondly sought among lines from neighbouring collection sites. Sources of disease resistance from germplasm adapted to different environments are the last resource. It is for these reasons that the best germplasm pool for the Fertile Crescent is now derived from crosses involving lines extracted from landraces.

One type of cross – landraces \times *H. spontaneum* – has been the most promising avenue to improve plant height under drought: this characteristic, together with straw softness, is very often indicated by farmers as one of the most desirable traits, particularly in dry areas. As mentioned earlier, a crop that remains tall even in very dry years is important to farmers, because it reduces their dependence on costly hand-harvesting, while soft straw is considered important in relation to palatability. Table 22.7 shows the tallest of 1532 most recently developed breeding lines tested in 1994/95 at Breda.

Table 22.7. Plant height at Breda (244 mm rainfall) in 1995 of barley lines derived from crosses with *Hordeum spontaneum*, compared with the barley landrace most common in dry areas (Arabi Aswad) and with a cultivar selected specifically for plant height under drought (Zanbaka).

Cross/name	Plant height (cm)
<i>Hordeum spontaneum</i> 20-4/Arar 28//W12291/Bgs	43.5
SLB 45-40/ <i>Hordeum spontaneum</i> 41-1	43.0
Zanbaka/ <i>Hordeum spontaneum</i> 41-2	42.5
Zanbaka/ <i>Hordeum spontaneum</i> 41-2	41.5
Moroc 9-75/Arabi Aswad// <i>Hordeum spontaneum</i> 41-3	41.0
Arabi Aswad	24.8
Zanbaka	26.0
Mean of all breeding lines	23.5
Maximum	43.5
Minimum	12.5
LSD _{0.05}	5.6

While the mean plant height of all the lines was 23.5 cm, the shortest lines were only 12.5 cm tall, and the most widely cultivated landrace (Arabi Aswad) was about 25 cm, some of the lines derived from crosses with *H. spontaneum* were taller than 40 cm. They were also significantly taller than Zambaka, a pure line selected from Arabi Aswad and already grown by some farmers for its plant height.

It is obvious that these two characteristics – tall plants and soft straw – represent a drastic departure from the typical selection criteria used in breeding high-yielding cereal crops – short plants with stiff straw and high harvest index. Cultivars possessing the two characteristics considered important by farmers in dry areas would be unsuitable for high-yielding environments because of their lodging susceptibility, and in a traditional breeding programme will not be made available to farmers – a further indication of the importance of specific adaptation.

Mixtures

Although successful, pure-line selection within landraces is potentially dangerous because it tends to replace genetically heterogeneous populations with genetically pure lines. The adoption by Syrian farmers of three different pure lines almost at the same time and in a relatively small geographical area – some farmers even adopted two different cultivars at the same time – suggests that the danger may be less dramatic than what happened with the spreading of single genotypes over very large areas as in the case of HY varieties. There is also evidence that in marginal environments replacement of landraces is often only partial (Brush, 1995). But, in principle, genetic uniformity is in contrast with the genetic diversity that characterizes the agricultural systems of difficult environments and poor farmers. In these systems diversity is preserved at one or more levels by using different crops in the same farm, by using different cultivars of the same crop, and by using heterogeneous cultivars. Diversity reduces the risk of crop failures due to abiotic and biotic stresses, while monoculture of a single genotype maximizes it.

One wonders why millennia of natural selection operating in harsh environments on a crop such as barley in the Fertile Crescent have left us with heterogeneous populations rather than with a single or few genotypes with superior adaptation. Is it perhaps yet another lesson landraces are imparting: that it is the structure of the population, in addition to the genetic constitution of the components it harbours, which is the secret of adaptation to difficult and unpredictable environments.

Therefore, constructing mixtures with a number of superior yet genetically different pure lines selected from landraces is the long-term objective of using landraces in the breeding programme. This would add the advantage of a population-buffering mechanism to the adaptation of the individual components (Simmonds, 1962; Grando and McGee, 1990; Lenné and Smithson, 1994). This is an additional way, perhaps more time-consuming and experimentally more complex than the first two, to respond to the need of poor farmers for stable yields.

Therefore, in the last 10 years of the 20th century we conducted trials with mixtures of variable numbers of superior, yet genetically different, pure lines selected from landraces to compare yield and yield stability of pure lines and of mixtures. The results have shown the superiority of some specific mixtures but also that some pure lines have similar yield and stability to mixtures.

In the most recent of these trials, mixtures and pure lines within the two barley landraces, Arabi Abiad and Arabi Aswad, were compared. Mixtures with 72, 34, 17 and 5 components in the black-seeded group and 75, 34, 15 and 5 components in the white-seeded group were used. The constituent lines were either unselected (the more complex mixture) or derived from one, two or three cycles of selection. The material was evaluated from 1990/91 to 1994/95 in 22 environments with mean yields ranging from 614 to 4385 kg ha⁻¹.

Black-seeded material tends to have lower average grain yield, lower response and higher frequency of positive intercepts than white-seeded material. In both groups the mixtures with five components had an advantage over the more complex mixtures. In the black-seeded group (Table 22.8), the mixture of five lines did not have a clear advantage over the components. In particular, SLB 5-96 had a high average yield (2164 kg ha⁻¹), combined with a relatively good response ($b = 0.97$) and a positive intercept ($a = 99.9$).

In the white-seeded group (Table 22.9) the mixture of five components had an advantage over the single lines, combining a high average grain yield (2263 kg ha⁻¹), with a good response ($b = 1.05$) and positive intercept ($a = 32.9$). The only other line with a positive intercept (SLB 9-98) had a very low average grain yield (1833 kg ha⁻¹) and low response ($b = 0.79$).

The results indicate the possibility that the two Syrian barley landraces possess different buffering mechanisms. The advantage of both five-component mixtures over the more heterogeneous mixtures would suggest that yield stability may be achieved with a modest degree of heterogeneity.

Table 22.8 Average grain yield (kg ha⁻¹), regression coefficient (b) and intercept (a) of four black-seeded mixtures, five lines and three checks.

Material	Grain yield	b	a
Mixtures			
MIX 72	2017	0.88	147.4
MIX 34	2060	0.96	10.2
MIX 17	2076	0.97	11.8
MIX 5	2131	0.93	150.1
Pure lines			
SLB 5-96	2164	0.97	99.9
SLB 5-07	2179	0.98	97.6
SLB 5-86	1950	0.84	167.0
SLB 5-31	2266	1.05	35.7
SLB 5-30	1982	0.86	144.2
Checks			
Arabi Aswad	1896	0.83	116.7
Tadmor	1971	0.86	140.0
Zanbaka	1946	0.84	154.9
LSD _{0.05}	164		

Table 22.9. Average grain yield (kg ha^{-1}), regression coefficient (b) and intercept (a) of four white-seeded mixtures, five lines, and three checks.

Material	Grain yield	b	a
Mixtures			
MIX 75	2237	1.15	-226.7
MIX 34	2209	1.17	-277.1
MIX 15	2174	1.08	-139.1
MIX 5	2263	1.05	32.9
Pure lines			
SLB 9-63	2288	1.14	-144.4
SLB 9-71	2302	1.15	-152.3
SLB 9-76	2388	1.24	-248.5
SLB 9-09	2328	1.13	-86.8
SLB 9-98	1833	0.79	146.1
Checks			
Arabi Abiad	2202	1.14	-222.9
Arta	2414	1.19	-117.9
Harmal	2204	1.15	-248.8
LSD _{0.05}	164		

Understanding adaptation to stress

Landraces have also been extremely useful for understanding the adaptive role of given traits. For example, barley lines extracted from landraces collected from five sites in the Syrian steppe (Table 22.10), when compared with barley lines extracted from landraces collected in Jordan and with a wide range of modern barley genotypes, showed a higher frequency of genotypes with prostrate or semi-prostrate growth habit, cold tolerance and short grain-filling period, and a lower frequency of genotypes with good growth vigour and early heading. Their average grain yield in unfavourable conditions (Bouider, 1989) was 984 kg ha^{-1} (ranging from 581 to 1394 kg ha^{-1}), more than twice the average grain yield of modern genotypes (483 kg ha^{-1} ranging from crop failure to 1193 kg ha^{-1}). The average yield in favourable conditions of the Syrian landraces (3293 kg ha^{-1}) was 75% of the average yield in favourable conditions of the modern germplasm (4398 kg ha^{-1}).

Although this particular set of data is based on one environment only, it confirms the existence of a trade-off between yield in unfavourable conditions and yield in favourable conditions (Ceccarelli, 1989) found in other sets of data based on more environments. Landraces collected in Jordan, from sites with milder winters than the Syrian steppe, have a higher frequency of genotypes with better growth vigour, more erect habit, less cold tolerance, slightly longer grain-filling period and earlier heading than Syrian landraces. Their average grain yield in unfavourable conditions was only slightly lower (835 kg ha^{-1}) than Syrian landraces, while their average yield in favourable conditions (3947 kg ha^{-1}) was in between that of the Syrian landraces and

Table 22.10. Mean of morphological and developmental traits in 1041 modern (unrelated to Syrian or Jordanian landraces) barley genotypes compared with 322 pure lines extracted from Syrian landraces and 232 pure lines from Jordanian landraces.

Traits ¹	Landraces		
	Modern (<i>n</i> = 1041)	Syria (<i>n</i> = 322)	Jordan (<i>n</i> = 232)
Early growth vigour	2.5 b ²	3.2 a	2.4 b
Growth habit	2.8 c	4.0 a	3.1 b
Cold damage	3.0 a	1.3 c	2.3 b
Days to heading	117.9 b	121.2 a	116.9 c
Grain-filling duration	39.3 a	35.5 c	37.4 b
Grain yield under non-stress	4398.0 a	3293.0 c	3947.0 b
Grain yield under stress	483.1 c	984.0 a	834.7 b

¹Early growth vigour (1 = good, 5=poor); growth habit (1 = erect, 5 = prostrate); days to heading (days from emergence to awn appearance); grain-filling duration (days between heading and maturity) and grain yield under non-stress (kg ha⁻¹) were scored or measured at Tel Hadya in 1987/88 (504.2 mm rainfall); cold damage (1 = resistant, 5 = susceptible) was scored at Bouider in 1987/88 (385.7 mm rainfall); grain yield under stress (kg ha⁻¹) was measured at Bouider in 1988/89 (189 mm rainfall) on 521 modern lines, 92 Syrian landraces and 86 Jordanian landraces.

² Means followed by the same letter are not significantly ($P < 0.05$) different based on *t*-test for samples of unequal size.

the modern germplasm. The highest yield under stress of Syrian landraces is not due to an escape mechanism, as they are the latest group in heading, and therefore could be a combination of resistance (or tolerance) and avoidance (prostrate habit and cold tolerance result in good ground cover) mechanisms.

Landraces are not only variable for above-ground characteristics. A recent study (Table 22.11) shows that considerable variation exists for both the number and the length of seminal roots (Grando and Ceccarelli, 1995) between different germplasm types. Seminal roots are very important because in dry years they represent the only roots the plant produces. It appears that during the domestication of barley the number of seminal roots has evolved from about three in *H. spontaneum* to five to seven in

Table 22.11. Mean and range of variation for number of seminal roots and their maximum length at Zadoks stage 10 in three groups of barley germplasm.

Germplasm group	Number		Length	
	Mean	Range	Mean	Range
Modern	5.5	4.6 – 6.1	96.5	70.8 – 115.3
Landraces	5.1	4.4 – 5.9	118.8	107.4 – 131.6
<i>Hordeum spontaneum</i>	3.3	3.0 – 3.8	107.3	97.2 – 118.1
LSD _{0.05}	0.7 ^a	0.4 ^b	14.9	11.6

^aLSD_{0.05} for group means comparison.

^bLSD_{0.05} for entry means comparison.

cultivated forms, while there has been a reduction in early root growth (root length) in modern varieties. In addition, the data show that also for below-ground characteristics – probably important in relation to the use of water: one of the most limiting resources – there is considerable variability within landraces. Therefore, the advantages of heterogeneity are probably also valid underground.

The genetic structure of landraces then, may be considered as an evolutionary approach to survival and performance under arid and semi-arid conditions (Schulze, 1988). It follows that, during millennia of cultivation under adverse conditions, natural and artificial selection have not been able to identify either an individual genotype possessing a key trait associated with its superior performance, or an individual genotype with a specific architecture of different traits. On the contrary, the combined effects of natural and artificial selection have led to an architecture of genotypes representing different combinations of traits.

This is shown more clearly in Table 22.12 where 321 lines derived from Syrian landraces collected in the steppe were classified according to the score for early growth vigour in three classes: good vigour (score <2.5), intermediate (score = 2.5–3.5) and poor vigour (score >3.5). Each class was then classified according to the score for growth habit (erect <2.5; semiprostrate = 2.5–3.5; prostrate >3.5).

No genotypes were found in the good vigour–erect, intermediate vigour–erect, poor vigour–erect, and poor vigour–semiprostrate classes. The groups were compared not only for the two traits used in their classification, but also for days to heading, cold tolerance and length of the grain-filling period. Lines with good early growth vigour tend to be less cold tolerant, earlier and with a longer grain-filling period. This small percentage of genotypes presumably will have a yield advantage in years with slightly milder winter temperatures, absence of late frosts and less severe terminal stress. The highest frequency of genotypes (71.3%) combines an intermediate early growth vigour with semiprostrate or prostrate growth habit. These genotypes are slightly more cold tolerant than the first group, but are slightly later in heading. However, they are better

Table 22.12. Frequency of different combinations of early growth vigour (GV) and growth habit (GH), and mean values of cold tolerance (CT), days to heading (DH) and length of the grain-filling period (GF) in a sample of 322 lines of barley collected in the dry areas of Syria^a (traits as indicated in footnote of Table 22.10).

Groups	%	GV	GH	CT	DH	GF
Good vigour – erect	0	—	—	—	—	—
Good vigour – semiprostrate	1.2	2.2	3.3	1.6	118.8	37.4
Good vigour – prostrate	5.3	2.4	3.9	1.4	119.8	36.6
Intermediate vigour – erect	0	—	—	—	—	—
Intermediate vigour – semiprostrate	6.2	2.9	3.4	1.5	119.7	35.8
Intermediate vigour – prostrate	65.1	3.1	4	1.4	121.2	35.4
Poor vigour – erect	0	—	—	—	—	—
Poor vigour – semiprostrate	0	—	—	—	—	—
Poor vigour – prostrate	22.1	3.9	4.2	1.3	121.9	35.4
LSD _{0.05}		0.2	0.1	0.1	0.6	0.7

^aCollection sites are all included in the Palmyra region as defined by Weltzien (1988).

LSD, least significant difference.

equipped to escape terminal drought because of the shorter grain-filling period. About one-quarter of the genotypes (22.1%) have a poor early growth vigour but a very prostrate growth habit ($GH = 4.2$) and a high level of cold tolerance (1.3). Their slightly (although significant) later heading is not necessarily a negative attribute, mostly because it is compensated by a very short grain-filling period. In the reference environment, a population with such an architecture of genotypes is probably the best solution to long-term stability.

Conclusions

The use of barley landraces from a section of the Fertile Crescent in the barley breeding programme at ICARDA contains a number of messages, potentially of general relevance. Landraces should be considered not only as genetic resources to conserve for the needs of tomorrow, but as breeding material to be used today, particularly in breeding programmes for stress environments and for poor farmers. Landraces are adapted to levels of inputs farmers can afford, yet are variable. So, they can be improved without requiring additional inputs. Landraces are adapted to their environment; they fit in the farming systems of their area of adaptation; they are often essential in the diet; in many cases they are the only food or feed available: the welfare of people depending on landraces should and can be improved not by replacing landraces but by improving them.

We have shown that this is possible provided that a number of conventional concepts in plant breeding are challenged, not least the concept of wide adaptation in a broad sense. The advantage of selecting for specific adaptation in space is the production of different varieties in different countries as well as different varieties, not necessarily homogenous, in different environments within a country, thus contributing to conserving biodiversity.

Eventually, testing and evaluating landraces under the conditions of poor farmers will ensure that no additional inputs are required to benefit from the new varieties. The participation of farmers during selection is essential to identify meaningful selection criteria and, later, to maximize the probability of adoption.

The story of utilizing the genetic variability within a collection of landraces made in 1981 in Syria and Jordan is a success story. Yet the variability used is only what was sampled at a given moment of the evolutionary processes taking place within the landraces; the benefits that variability has generated give a measure of the importance of keeping those processes alive through *in situ* conservation. Keeping the genes of landraces alive in breeding programmes is a moral obligation towards those many farmers who maintained landraces available for future generations.

Acknowledgements

The Government of Italy has supported the work on barley landraces and on *H. spontaneum* in Syria conducted after 1987.

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23 Breeding *Phaseolus* for Intercrop Combinations in Andean Highlands

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Rationale or Impetus for Undertaking the Breeding Strategy

The common bean, *Phaseolus vulgaris* L., is by far the most important pulse crop in Latin America, its centre of origin and diversity. The species is the most valuable source of dietary protein, particularly among the low-income populations. Small farmers are the principal producers of beans, often as a secondary crop in association with cereals, root and tuber plants, and vegetables (Francis, 1986; Woolley *et al.*, 1991). A high proportion of the seeds is directly consumed on the farm or traded only in local markets. Despite their nutritional importance, production growth rates have been declining in Latin America, with dry seed yields averaging less than 600 kg ha⁻¹ (Woolley *et al.*, 1991; Lobo, 1994). This is particularly true for the low-input intercropping systems of the Andean highlands, where beans are suffering from several constraints: high incidence of diseases and insect pests, soil mineral deficiencies, cold or drought stresses, poor crop management, competition with associated crops and lack of improved seeds. Most of the landraces and improved varieties of the common bean are susceptible to one or more of these production constraints, preventing the realization of their full yield potential and causing production instability from one year to the next.

One way to increase seed production of common bean in the Andean highlands is to develop a breeding process well adapted to the traditional multiple-cropping systems. In the small-scale subsistence farms of the regions, *P. vulgaris* and other *Phaseolus* cultigens are very often associated with maize, in small dispersed plots, mainly on sloping land of limited fertility and prone to soil erosion. In such marginal conditions, the association ensures reduced variability in total biomass and yield, arising mainly from compensatory effects among the crops, lower weed and erosion problems due to better soil cover, and reduced incidence of pests and diseases. Intercropping also gives a greater diversity of diet and a more stable source of income, particularly for farmers with limited land resources (Francis, 1986; Baudoin and Marechal, 1987; Baudoin and Camarena, 1994). However, when considering the benefits of the association, we

should not underestimate one major obstacle: the substantial interspecific competition of the associated components in environments sometimes limited in natural resources (water, nutrients and light). This competition affects particularly understorey crops, such as the *Phaseolus* beans.

In this study, we consider breeding *Phaseolus* beans for intercrop combinations in Andean regions, ranging from 2000 to 3600 m altitude. The data and discussions come mainly from collaborative projects at Gembloux Agricultural University (Belgium) developed with the Centro Internacional de Agricultura Tropical (CIAT), Colombia, the Corporación Colombiana de Investigación Agropecuaria (CORPOICA), Colombia, and the Universidad Nacional Agraria La Molina (UNALM), Peru. In the target regions of Colombia and Peru, two main cropping patterns prevail. In the first pattern, found in areas with a single rainy season (Ancash, Cajamarca and Cusco in Peru; Cauca, Nariño and Putumayo in Colombia), maize and beans are mainly planted simultaneously under mixed, row or hill intercropping, with beans climbing on the maize stems. In the second pattern, found in eastern Antioquia of Colombia under bimodal rainfall distribution, maize is planted in the first rainy season while beans are broadcast into the maize during the second season at a period corresponding to the physiological maturity of the cereal. This system is called relay cropping, with 1–2 months' overlap of maize and bean cycles. The stems of the strong-stalked highland maize offer a good support for the long and twisted branches of climbing beans.

In the two patterns, bean genotypes are always of indeterminate growth habit, with a strong climbing ability and a long growth duration, requiring usually 7–10 months to reach the fruit ripening stage. This slow-maturing trait is very frequent in highland areas affected by low temperatures during the cultural season. The length of the bean growth cycle is similar to that found in local traditional maize varieties. In the cultural associations of the target regions, the cultivated *P. vulgaris* genotypes belong to a rather limited number of large-seeded classes, i.e. in Colombia: mainly Cargamento (with cream-beige speckled seed colour) and Mortiño (with purple seed colour); in Peru: mainly Panamito and Caballero (with white seed colour), Canario and Bayo (with yellow seed colour) and Nuñas (popping beans with striking colours and patterns).

Whatever the type of cultivated genotypes and cropping systems, beans are very often considered as a high-risk crop, prone to many diseases and not receiving a good crop husbandry management by small farmers (such as use of improved seeds, regular weeding, organic matter application, chemical treatment against pest, etc.). We decided therefore to rank our objectives according to this situation. First priority was given to multiple disease resistance, a prerequisite for better response of beans to improved crop husbandry and food marketing. Secondly, priority was given to fitting plant architecture and yield components into the frame of traditional intercrop combinations.

To achieve these objectives, one key factor of our breeding strategy consisted of exploiting fully the interspecific diversity available in *Phaseolus*. Indeed, within the common bean primary gene pool, insufficient genetic variation has been found to overcome several major production constraints (Baudoin *et al.*, 1995). Past experiments conducted mainly in Colombia demonstrated the excellent potential of two *Phaseolus* species, of Mesoamerican and north Andean origin: *P. coccineus* L. and *P. polyanthus* Greenm. Both species are well adapted to Andean highlands (above 2000 m) and belong to the secondary gene pool of *P. vulgaris* (Baudoin *et al.*, 1992). The species

show several desirable agronomic attributes, such as pest, insect and disease resistance, cold tolerance, lodging resistance due to thick stem bases, presence of tuberous or fibrous root systems allowing a perennial cycle, long epicotyls and racemes, and a large number of pods per inflorescence (Schmit and Baudoin, 1987). The base germplasm collection is maintained at CIAT and represents genetically broad unimproved germplasm, found as a garden or backyard crop in small farms or as a weedy vine climbing on trees at the border of montane rain forest (Schmit and Debouck, 1991). In the genetic improvement of beans for multiple cropping systems, these two food legumes have a value in their own right and could be bred as distinct crop, particularly for higher and colder Andean regions. They can also be utilized in interspecific crosses with *P. vulgaris*, to introgress genes controlling useful traits not commonly present in the primary common bean gene pool.

Methods and Strategy Used

Breeding approach

The best way of achieving significant progress in breeding for multiple cropping systems is to adopt a farming systems approach, involving diagnosis, on-farm experimentations and active farmer participation at an early stage (Steiner, 1990; Woolley and Davis, 1991; Sperling *et al.*, 1993). Evaluation and breeding are carried out under cultural conditions representative of the traditional cropping systems but in conditions sufficiently uniform to allow reasonably reliable selection. In this case, the experimental design should mimic the two prevailing cultural associations (relay cropping and simultaneous intercropping) at some stages of the breeding process.

Although any genetic modification of one crop will have an effect on the other associated crop, it is more efficient to breed each species separately, the other partner being represented by a locally well-adapted cultivar. Indeed, Davis and Garcia (1983) demonstrated that when indeterminate climbing beans are intercropped with different maize cultivars, the interaction between the two associated crops is usually not significant. It is therefore not worthwhile selecting both cereal and food legume simultaneously. In these investigations, priority was given to the understorey crop, the *Phaseolus* beans. Segregating hybrids or unimproved populations of both *P. coccineus* and *P. polyanthus* were selected in association with one or two representative maize cultivars for each of the two cropping systems prevailing in the target regions. These maize cultivars are well adapted in the Andean highlands, have strong stalks to provide support to long and twisted branches of beans with indeterminate growth and are relatively resistant to lodging.

Although the desirability of selecting under the target intercrop combinations is obvious, the cost and complexity of such investigations often compel the breeder to carry out part of the field trials under single cropping. This is usually advised for early hybrid generations and qualitative traits. Quantitative traits or traits of specific adaptation are evaluated in more advanced generations, in relevant multiple cropping situations (Francis, 1985, 1986).

As the objectives of the breeding programme are not to introduce selectively a few genes in some elite cultivars but rather to broaden the genetic base of locally adapted

varieties, a population improvement scheme was adopted. The aims were to break up unfavourable linkage blocks and to incorporate a wider diversity of genetic resources into forms that can be further exploited by small farmers or integrated in more conventional varietal improvement (Poehlman, 1987).

Description of the breeding method

The breeding methodology relied mainly upon the genetic wealth available in the two species: *P. coccineus* and *P. polyanthus*. At the onset of the research project (1986), the CIAT base collection contained 1570 populations, divided as follows: 1013 and 496 cultivated forms of, respectively, *P. coccineus* and *P. polyanthus*, and 61 wild forms closely related to *P. coccineus*. Most populations (73%) came from Mexico and Guatemala; the other important countries of origin were Puerto Rico, Costa Rica, Colombia, Venezuela and Bolivia (Schmit and Baudoin, 1987). The genetic improvement of *Phaseolus* beans using this germplasm collection followed a gradual process involving several activities.

Seed increase of the collection

The two species are characterized by an outcrossing breeding system ascribed chiefly to the extrorse stigma and its position relative to the anthers. An appropriate seed-increase method was therefore used which maintained genetic integrity and total variability of the separate populations. Multiplication was carried out in two research stations of Colombia: Popayan (altitude 1750 m, Cauca) and Rionegro (altitude 2200 m, Antioquia). For each population grown in mesh cages, daily manual pollinations on several plants were made with a pollen mixture from all the flowering individuals (Vanderborght, 1983). This was a tedious and costly method but was worthwhile to prevent a dilution of useful genes, which would have occurred in a more open system of mass reservoir maintenance. Seed samples from about 800 populations were produced from this seed increase operation and were available for evaluation trials.

Evaluation of the collection

Trials were first conducted in the two Colombian stations of Popayan and Rionegro. Priority was given to plant architecture and yield component characters (such as stout main stems, moderate branching, long racemes, high pod setting rates and large seed size), earliness in maturity, adaptation to poor soil, cold tolerance and, more especially, resistance to the major diseases prevailing in Andean highlands: *Ascochyta* leaf blight (due to *Phoma exigua* var. *diversispora* (Bubak) Boerema), anthracnosis (due to *Colletotrichum lindemuthianum* (Sacc. and Magn.) Scribner) and angular leaf spot (due to *Phaeisariopsis griseola* Sacc.). Among the three, *Ascochyta* leaf blight appeared the most destructive enemy of beans in the target regions. On local *P. vulgaris* varieties, early attack of *Phoma exigua* var. *diversispora* can completely destroy leaves and pods and cause 74% yield losses in the Andean highlands. For this reason disease nurseries were established in Rionegro and Popayan for the years 1987 and 1988. The nurseries included 285 populations selected on the basis of their geographical distribution, using a randomized complete block design with three replications, and three locally adapted large-seeded varieties of *P. vulgaris* as control. The bean genotypes were single cropped

or intercropped with maize (Schmit and Baudoin, 1992). Disease evaluation of *Ascochyta* leaf blight relied either on natural or artificial inoculation, and scores, based on a 1–9 severity scale (van Schoonhoven and Pastor-Corrales, 1987), were taken at three different stages: flowering, pod filling and seed physiological maturity.

Creation of interspecific hybrids

The objectives were to increase the genetic diversity of the locally adapted Andean cultivars of *P. vulgaris*, adding useful genes from *P. coccineus* or *P. polyanthus* populations identified mainly for their high disease resistance (particularly to *Phoma*). Crosses were made in the greenhouses of the University of Gembloux, using two systems: direct hybrids between *P. vulgaris* and one of the two donor species (with the help of embryo culture for some specific combinations) or indirect hybrids involving three or four parents with a wild *P. coccineus* form as a first maternal parent. Several genotypes of the latter were identified for their high combining ability with *P. vulgaris* in previous experiments (Baudoin *et al.*, 1992). The presence of wild *P. coccineus* cytoplasm favours interspecific gene exchange between the recurrent *P. vulgaris* parent and the donor parent (either *P. coccineus* or *P. polyanthus*). Such complex crosses, with *P. coccineus* cytoplasm, avoid a quick reversal towards the recurrent *P. vulgaris* parent and consequently the loss of useful genes from the donor parent (Baudoin and Maréchal, 1991).

Field breeding in Colombia and Peru

Breeding work was carried out in several research stations representative of the target Andean regions – in Colombia: Popayan, Rionegro and Pasto (altitude 2710 m, Nariño); in Peru: Chiquian (altitude 3550 m, Ancash) and other sites of Ancash, Cajamarca, Cusco and Lima Departments, at altitudes ranging from 2200 to 2800 m. Trials were carried out separately for the two types of material: *P. coccineus* and *P. polyanthus* bred as a distinct crop and the interspecific combinations created at Gembloux. For the two species, the selection units consisted of tested populations and single plants within the best populations. Open-pollinated seeds from progeny of selected plants or populations formed the next generation. In advanced generations, the most interesting populations were field isolated and selected at within-population level. For the interspecific crosses, hybrid breakdown, zygotic elimination and reduction in heterogenetic recombination impeded the following up of any kind of single plant, mass or bulk selection. The most appropriate breeding methodology adopted was cumulative or recurrent selection, designed to maintain a good state of heterozygosity during several generations and to increase the probability of crossing over in between linked genes (Baudoin and Maréchal, 1991). The breeding scheme included reselection at each generation with intermating of selected plants to provide genetic combination and breakage of unfavourable linkage. Another similar methodology adopted for such interspecific hybrids was congruity backcrossing. This method consisted of recurrent backcrossing to each parent (both the recurrent *P. vulgaris* and the donor species) alternately at each generation. This procedure gave an increased fertility level of hybrid genotypes and maintained a balanced set of genes from the two species over several generations (Baudoin *et al.*, 1995). In these two breeding schemes, intermating was carried on during several seasons, with a constant flow of new interspecific hybrids added to the recombination nursery. The purpose was to develop mixed-genotype populations, with a high frequency of favourable genes and enough variability for

adaptation to a wide range of microenvironments (representing the small-scale Andean farms).

Field breeding of *P. coccineus*, *P. polyanthus* and interspecific combinations was conducted during the first generations at on-station level, in single cropping. The emphasis was on traits of interest whatever the cropping system involved, e.g. disease resistance, seed coat colour, seed size or earliness in flowering. For advanced generations, breeding trials were conducted at both on-station and on-farm levels, in relay or intercropping systems. Selection, at this stage, concerned traits with specific interest for multiple cropping systems and were mostly of a quantitative nature: for example, competitive ability with the associated maize crop, tolerance to shade, rapid seedling growth, vegetative vigour, harvest index and dry seed yield (Baudoin *et al.*, 1997).

Figure 23.1 illustrates the outline of the breeding scheme

Results to Date

Evaluation of *P. coccineus* and *P. polyanthus* germplasm collections

The disease nursery trials in the two highland stations of Rionegro and Popayan demonstrated the high resistance levels of the two donor species to *Ascochyta* leaf blight, compared with the susceptibility of the control *P. vulgaris* variety (Table 23.1).

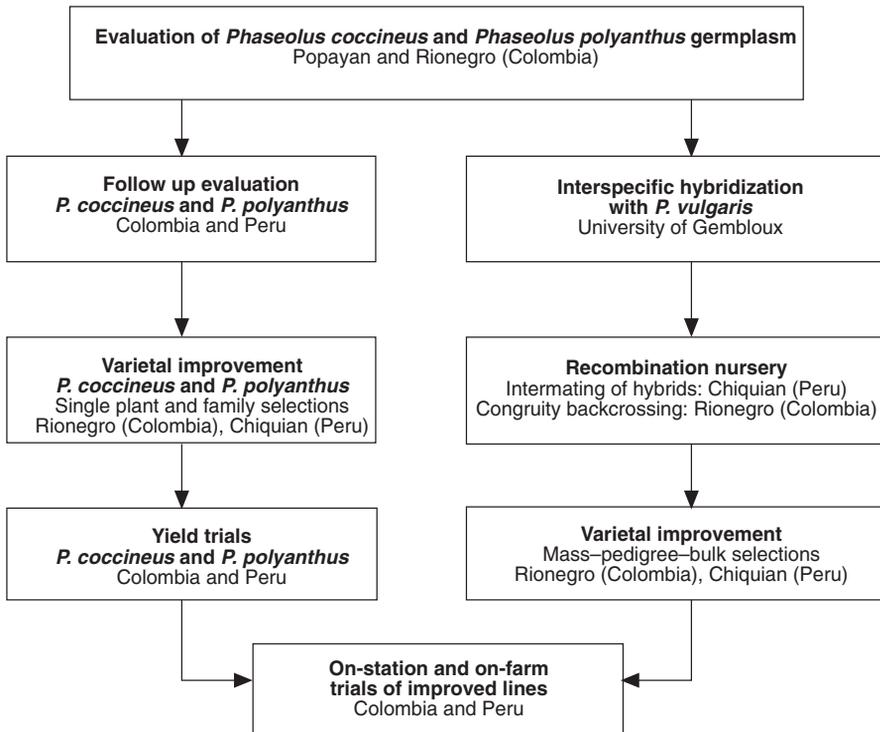


Fig. 23.1. Outline of the breeding scheme.

Table 23.1. Field reaction of *P. coccineus* and *P. polyanthus* populations to *Ascochyta* leaf blight at Popayan and Rionegro (Colombia).

Species and site	No. of populations in the three reaction classes ^a		
	Resistant (score 1–3)	Intermediate (score 4–6)	Susceptible (score 7–9)
<i>Phaseolus coccineus</i>			
Rionegro	76	19	—
Popayan	7	12	1
<i>Phaseolus polyanthus</i>			
Rionegro	110	—	—
Popayan	60	—	—

^aScores recorded at the stage of seed physiological maturity.

The 170 *P. polyanthus* populations showed outstanding resistance, with most accessions (64%) exhibiting no symptoms in the two stations. The best ones originated from Colombia, Venezuela and Mexico. The reaction of *P. coccineus* was more variable, with 83 populations classified as resistant, 31 classified as intermediate and one classified as very susceptible. The best genotypes originated from Costa Rica, Mexico and Guatemala. We also noticed the highest level of resistance from populations collected from sites above 2000 m, where climatic conditions (high humidity and cool to moderate temperatures) favour infection by the fungus. In the same nurseries, all the *P. coccineus* and *P. polyanthus* populations also showed an excellent reaction to the other two prevailing fungus diseases: anthracnosis and angular leaf spot, while a severe attack of these diseases occurred on *P. vulgaris* controls. According to genotypes and locations, dry seed yield of *P. coccineus* and *P. polyanthus* ranged from 250 to 3500 kg ha⁻¹, with a growing period of 6–7 months. Dry seed yields of *P. vulgaris* ranged from 150 to 1200 kg ha⁻¹, but with a shorter growing period of 4–5 months.

Additional trials were conducted from 1989 in the same Colombian stations and in Pasto (Nariño) and Peru (mainly Chiquian), covering a wider geographical distribution of the germplasm collection (with a total of 400 populations). These observations confirmed the field resistance to *Ascochyta* leaf blight in the two species and revealed high variability in growth duration, plant architecture and yield components.

Creation of interspecific hybrids

Table 23.2 shows the interspecific hybrid types, developed in Gembloux from 1985 to 1989. A total of 360 genotypic combinations of direct crosses and 220 genotypic combinations of complex crosses were obtained. The highest rates of success were obtained in crosses using *P. vulgaris* as female parent and a single donor species. Hybrids with *P. polyanthus* cytoplasm required *in vitro* embryo culture, due to starvation of embryos at a very early developmental stage (Mergeai *et al.*, 1997). In the complex crosses, we identified three wild forms of *P. coccineus*, from Mexico, which showed a good crossing compatibility with *P. vulgaris*. Hybrids with such wild cytoplasm could act as a bridge

Table 23.2. Creation of interspecific hybrids with *Phaseolus* beans.

Direct crosses			No. of genotypic combinations		
Female	Male				
<i>P. vulg.</i> ^a cv ^d	×	<i>P. cocc.</i> ^b cv	120		
<i>P. vulg.</i> cv	×	<i>P. poly.</i> ^c cv	220		
<i>P. poly.</i> cv	×	<i>P. vulg.</i> cv	2		
<i>P. cocc.</i> wld ^e	×	<i>P. vulg.</i> cv	13		
<i>P. cocc.</i> wld	×	<i>P. poly.</i> cv	2		
<i>P. poly.</i> cv	×	<i>P. cocc.</i> cv	3		
Complex crosses			No. of genotypic combinations		
Female		Male			
<i>(P. cocc. wld</i>	×	<i>P. vulg. cv)</i>	×	<i>P. vulg. cv</i>	14
<i>(P. cocc. wld</i>	×	<i>P. vulg. cv)</i>	×	<i>P. cocc. cv</i>	88
<i>(P. cocc. wld</i>	×	<i>P. vulg. cv)</i>	×	<i>P. poly. cv</i>	18
<i>(P. cocc. wld</i>	×	<i>P. poly. cv)</i>	×	<i>P. vulg. cv</i>	92
<i>(P. poly. cv</i>	×	<i>P. cocc. cv)</i>	×	<i>P. vulg. cv</i>	4
<i>(P. poly. cv</i>	×	<i>P. vulg. cv)</i>	×	<i>P. vulg. cv</i>	4

^a*P. vulg.* = *P. vulgaris*; ^b*P. cocc.* = *P. coccineus*; ^c*P. poly.* = *P. polyanthus*;

^dcv = cultivated forms; ^ewld = wild forms.

to combine genes from both the recurrent (*P. vulgaris*) and donor *P. coccineus* or *P. polyanthus*.

Field breeding

At the onset of the breeding programme, selection focused on dry seed yield (above 1500–2000 kg ha⁻¹ according to the sites), earliness in flowering (from 90 to 130 days), seed size (with a preference for large-seeded genotypes with 100-seed weight above 45 g) and disease resistance (mainly to *Ascochyta* leaf blight). By doing so, we retained in each station 80–100 populations from each of the two species, *P. coccineus* and *P. polyanthus*, and around 200 interspecific lines from the crosses developed in Gembloux.

Single plant and family selections were carried out with *P. coccineus* and *P. polyanthus* materials, using different cropping patterns: single cropped, relay and intercropped with maize. The best lines, from 15 to 30 in each of the two species, were tested in multilocational yield trials with locally adapted cultivars of *P. vulgaris*. Table 23.3 shows the performance of promising lines in single and multiple cropping systems in two Colombian stations. No fertilizer treatment and no protection against diseases were practised. In Rionegro, the two improved lines of *P. coccineus* and *P. polyanthus* out-yielded the local common bean variety. This reflects partly their very good disease

Table 23.3. Seed production of improved *Phaseolus* lines in single cropping and association (Colombia).

<i>Phaseolus</i> genotypes	Dry seed yield (kg ha ⁻¹)	
	Single cropping	Association
<i>Rionegro: relay cropping with maize</i> ¹ (August 1993 to January 1994)		
G 35099 (<i>P. coccineus</i>)	875b	1770a
G 35224 (<i>P. polyanthus</i>)	932b	1769a
ICA VIBORAL (<i>P. vulgaris</i>) ²	146c	315c
<i>Pasto: simultaneous intercropping with maize</i> (October 1994 to April 1995)		
G 35544 (<i>P. polyanthus</i>)	6514.3a	3645.7a
G 35522 (<i>P. polyanthus</i>)	5978a	3057.7ab
G 35521 (<i>P. polyanthus</i>)	2981b	2874.7ab
G 35560 (<i>P. polyanthus</i>)	5724a	1840.bc
G 35516 (<i>P. polyanthus</i>)	2772.7b	1269.3a
BOLON ROJO (<i>P. vulgaris</i>) ²	2894.9 b	1534.4c

¹Beans sown at flowering period of maize; ²best local variety used as a control. Means followed by the same letter are not significantly different ($P < 0.05$).

resistance, compared with the heavily attacked control. In the same location, seed production of *P. coccineus* and *P. polyanthus* genotypes was higher in relay cropping than in single cropping. This can be explained by the good complementarity and lack of competition between maize and bean in such cultural conditions. In Pasto, most *P. polyanthus* improved lines outyielded the dry seed production of the *P. vulgaris* control in both single and intercropping. However, we observed a significant yield reduction of intercropped *Phaseolus* beans compared with single cropping. This reflects the strong competition between the two associated crops. However, farmers adopting this cropping pattern are usually more interested in the overall productivity and stability of the intercrop combinations, rather than in the seed production of each crop component. A good parameter to assess this overall productivity is the land equivalency ratio (LER), as described by Willey (1979). Preliminary results from Peru show an LER >1 for some maize-bean associations.

The interspecific lines were integrated in a recombination nursery, under single cropping and with the purpose of developing a large source population combining useful traits of *P. vulgaris*, *P. coccineus* and *P. polyanthus*. This recombination nursery was maintained for at least 4 years at the two stations of Rionegro and Chiquian. At each cultural season, we selected for the crossing block around 20–30 hybrid plants with complementary characters (particularly in terms of disease resistance, earliness in flowering, branching, seed production and harvest index) and a sample of the parental genotypes involved in the initial hybrids. In the case of cyclic recurrent selection (Chiquian), intermating was done each season between the most interesting interspecific individuals. In case of congruity backcrossing (Rionegro), hybrids were backcrossed alternately with the recurrent (*P. vulgaris*) and donor (*P. coccineus* and *P. polyanthus*) parents. In the recombination nursery, two major conditions were required in order to obtain progress in breeding interspecific hybrids. First, disease pressure had to remain high in the crossing block to keep genes of resistance from the donor species

from one generation to the next. Secondly, intermating always had to involve parents having *vulgaris*-like and donor species-like characters. This was a prerequisite to broaden the genetic base of the improved populations, to avoid the rapid reversal toward the recurrent parent and to break undesirable linkage blocks present in either *P. coccineus* or *P. polyanthus*. One major difficulty in breeding interspecific hybrids was rupturing the linkage between high levels of resistance to *Ascochyta* leaf blight and some unfavourable traits, such as lateness in flowering, profuse branching and low harvest index.

Once good interspecific genotypes were identified, they were grouped according to similarity traits (mainly degree of branching, growth duration, seed size and colour, etc.) and submitted to mass, pedigree and bulk selection for 2–3 years. Such trials were first conducted on-station under relay cropping (Rionegro) or simultaneous intercropping (Chiquian). Later hybrid generations were tested in both on-station and on-farm trials, using only traditional intercrop combinations. In Peru, the breeding scheme adopted for the interspecific hybrids generated two improved composite populations from the combination (*P. coccineus* wild form \times *P. vulgaris*) \times *P. coccineus*: Bulk 1H and Bulk 2H. In first experiments made in Ancash and Lima Provinces, these two improved lines outyielded the *P. vulgaris* control (ANC-034 from Canario class), flowering 20 days earlier and giving a higher seed index (70–80 g 100 seeds⁻¹ compared with 45 g 100 seeds⁻¹ in ANC-034). The two lines also showed high field resistance to both anthracnosis and *Ascochyta* leaf blight. Bulk 1H and Bulk 2H are being tested in different small-scale farms of the Province of Ancash. For this purpose, we identified around 20 farmers interested in the improved varieties. As each variety represents a composite material, farmers are encouraged to practise their own selection and to modify their crop husbandry.

Conclusions and Recommendations

Our research on *Phaseolus* breeding is based upon a large genetic reservoir made of local germplasm stocks of two New World species (*P. coccineus* and *P. polyanthus*) and their crosses with *P. vulgaris*. The breeding outline follows the principles of a population improvement programme and leads to bulk varieties keeping sufficient genetic variation to cope with a traditional and heterogeneous agrosystem. The strategy is well fitted to breeding for multiple characters of both quantitative and qualitative inheritance and to developing varieties that combine good seed production, stress tolerance and competitive ability with the companion crops. In this process, small-scale farms can pick up improved populations with a broad genetic base from the breeding nurseries. This material has sufficient plasticity to respond favourably to various environmental constraints.

Success in breeding for intercrop combinations, however, requires several pre-conditions. These include availability of a large body of germplasm collection and hybrid populations, sufficient knowledge of the major agronomic constraints, good understanding of the yield components in relation to competitive ability, resources to breed at both on-station and on-farm levels and to adopt experimental layout mimicking traditional cropping systems. In order to upgrade productivity of intercrop combinations, any genetic changes among the component crops should also be accompanied by

modifications in agronomic practices. The final objective will be not to disturb markedly a traditional cropping system but rather to open it up to other innovations. The ultimate impact of the research efforts will be the farm families themselves, which are faced with a need for food security and better income.

As stated before, the farming system approach will help to develop end-products that outperform existing varieties and are readily acceptable by the local populations. In this approach, on-farm trials are essential to back station-based investigations and to reorient the selection process according to the new constraints observed in a less uniform and more stressful environment. Testing in farmers' fields will also enable the selection of improved materials not only on the basis of yield but also on the basis of economic value, stability, total cropping system production or labour input.

The link between breeders, extension services and farmers is of course essential to achieve the breeding objectives. Such a close collaboration between these three should be financially supported by public agencies involved in agricultural research and integrated rural development.

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24 Improving Potato Resistance to Disease under the Global Initiative on Late Blight

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Introduction

Late blight is the most devastating plant disease, occurring in almost every potato-growing area of the world. The disease affects both foliage and tubers and it can destroy an entire field within a few days. Late blight was responsible for the Irish potato famine in the 1840s, and it causes estimated crop losses of nearly 14 million tons annually, equivalent to nearly \$3 billion (International Potato Centre, 1997). Despite major and expensive use of crop protection chemicals to control potato diseases, more than 20% of the potato crop's potential annual yield is lost (James, 1981).

Whereas in the past late blight was barely known in the potato-growing areas of the South American Andes (Cox and Large, 1960), it is now reported to be the number-one constraint in potato production in Bolivia, Argentina, Peru, Ecuador and Colombia, where potato is a staple food of small-scale farmers. In developing countries, production has soared by nearly 200% in the past 30 years. It now constitutes about one-third of global production and is expected to continue to rise by about 3% a year. Blight is especially serious in tropical regions due to continuous production cycles, year-round persistence of inoculum, and limited access to or frequent misapplication of fungicides. The small-scale, labour-intensive farming systems typical of developing countries provide specific conditions that call for the development and implementation of new integrated crop management procedures. This has prompted a worldwide increase of efforts towards the efficient control of the disease, with a focus on the use of resistant varieties. In 1996, the Global Initiative on Late Blight (GILB)

was inaugurated by breeders and late blight researchers from 30 institutions of 16 countries.

This Initiative unites late-blight researchers from institutions of developing and developed countries in their efforts to collaborate in the development of integrated pathogen management strategies in which new potato varieties with long-lasting resistance to late blight would play the pivotal role. It was recognized that conventional breeding and selection of potato are central to any attempt to enhance durable resistance in new potato varieties (French and Mackay, 1996).

The initiative facilitates the exchange of information and germplasm, to carry out independent and collaborative research on the pathogen's diversity in and among different regions of the world, and to better characterize and understand genetic resistance and its interactions with the environment. The principal focus of the initiative is the development of cultivars with durable resistance to numerous variants of the fungus that are appropriate for use in integrated disease management programmes in developing countries.

This chapter focuses on those activities of the GILB that aim to broaden the genetic base for durable resistance to late blight, and examine genotype \times environment (GE) interactions for such resistance.

Background

The pathogen

The causal agent of late blight is *Phytophthora infestans*. Epidemics result from asexual propagation through the formation of sporangia, and the mycelium can overwinter in plant tissue such as potato tubers and debris. Sporangia either germinate directly or they release infectious zoospores.

Many species of the *Solanaceae* and *Nolanaceae*, including potato and tomato, are natural hosts of *P. infestans*, and inoculation experiments have revealed that it causes disease on more than 130 species of higher plants (Abad *et al.*, 1995).

The sexual form of propagation via oospores has been observed in Mexico for many years (Gallegly and Galindo, 1958), while in other parts of the world it is seldom observed in the field (Goodwin and Drenth, 1997). *P. infestans* is heterothallic and strains can be distinguished by two mating types: A1 and A2. It is generally assumed that because the A2 mating type was not found in Europe or North America until 1980, populations of *P. infestans* outside of Mexico consisted of only the A1 mating type and, therefore, could not propagate sexually (Fry and Goodwin, 1997). The common European strain of *P. infestans* has been shown to be of clonal origin (Goodwin *et al.*, 1994a), and the phenotypes of its limited virulence spectrum correspond to 12 well-studied virulence factors: 11 from *S. demissum* (Malcolmson and Black, 1966) and one from *S. stoloniferum* (Schick and Schick, 1959). This strain, which may have originated in Mexico, was introduced to Europe along potato trading lines (Goodwin *et al.*, 1994a) and was also prevalent in North America, Africa, Asia and South America. Around 1980, migration from Mexico of new, more aggressive strains of the pathogen, comprising both mating types, resulted in a significant increase in the number and severity of epidemics, reduced effectiveness of established fungicides due to resistance of the new strains, and increased the area where epidemics occur (Fry *et al.*, 1993).

Although discussion about the possible occurrence of sexual recombination of the fungus outside of Mexico before 1980 continues (Fry and Goodwin, 1997; Ristaino, 1998), the well-documented migration of two sexually compatible mating types provides the opportunity for even more aggressive genotypes to develop through sexual recombination (Drenth *et al.*, 1994). Many pathogen populations have acquired resistance against xymoxanyl, the active compound of metalaxyl and several other popular fungicides used to control late blight (Goodwin *et al.*, 1994b). As a result of these pathogen dynamics, the incidence of the disease and severity of epidemics have increased significantly since the early 1980s.

Breeding for late blight resistance

Breeding for resistance continued with varying degrees of success with the introduction of resistance from wild and weedy germplasm, such as *S. edinense* and *S. demissum* which started in around 1900 (Müller, 1951). These sources were employed to transfer to potato major resistance (R) genes conferring hypersensitive resistance and immunity. However, the R genes, interacting on a gene-for-gene basis (Flor, 1956) with the pathogen's virulence, did not provide lasting protection in the field because of the frequent and ubiquitous occurrence of pathotypes of *P. infestans* matching all 12 R genes. For the same reason, combining or pyramiding of these R genes into one genotype also did not lead to resistant varieties. Pyramiding of major resistance genes could result in durably resistant genotypes only when genes were employed that were not matched by the virulences of any pathotype occurring in the area where the crop would be grown. The duration of resistance of such a complex genotype also depends on the assumption that a pathotype able to overcome the first acting gene in the pyramid is not able to establish a population on the host sufficiently large to allow selection of mutants that can overcome the second gene, and so on (Wolfe and Gessler, 1992).

In contrast to R-gene resistance, the quantitative expression in the field of the horizontal, rate-limiting type of resistance can be measured as a partial reduction of the amount of disease relative to a susceptible standard. A small number of European potato varieties – namely Robijn, Populair, Libertas, Pimpernel and Surprise – have maintained their comparatively high resistance levels in the field in middle Europe for up to 50 years (Colon *et al.*, 1995). This evidence that these varieties still express unaltered levels of resistance in spite of the changing composition of the pathogen population allows the interpretation of their resistance as the horizontal type and more durable than R-gene resistance. Proof of the genetic nature of this resistance – whether it is polygenic, oligogenic or governed by single genes – can only be obtained through genetic analyses on segregating progeny from a self or cross of these varieties, yet to be carried out.

The genetic nature of race-non-specific resistance to late blight has remained unknown, and diverse hypotheses about its genetic architecture have been put forward. Black (1945) concluded from empirical evidence that horizontal resistance is polygenic. The importance of selecting for partial resistance, in contrast to immunity, has been stressed by Parlevliet (1979) based on the underlying assumption that most combinations of minor resistance factors will not result in perfect, complete resistance or immunity and that, in contrast, extremely high levels of polygenic resistance may be

confounded with single, major gene resistance. Since then, this viewpoint of partial resistance in the field resulting from the additive action of many genes, each one contributing a minor positive effect, has been the basis of successful resistance breeding of potato and other crops by many breeders and pathologists (Simmonds and Malcolmson, 1967; Umaerus, 1970; Ross, 1986; Parlevliet, 1993). The key feature of horizontal resistance is its race-non-specificity, i.e. it is effective against all strains of a pathogen. Race-non-specific, durable major (R) gene resistance is known from several other pathosystems involving wheat (Johnson, 1988; Roelfs, 1988) and barley (Jorgensen, 1994). Whether race-non-specific resistance to potato late blight always depends on the action of additive polygenes or on other mechanisms remains to be elucidated, as does the need for developing more efficient breeding strategies for this characteristic.

Recent efforts to determine on genetic maps the position of quantitative trait loci (QTLs) conferring plant disease resistance have revealed that QTLs are frequently located in the vicinity of major resistance gene loci (Gebhardt, 1994; Veldboom *et al.*, 1994; Mitchellolds, 1996; Steffenson *et al.*, 1996). Resistance genes often are clustered at specific regions of the plant genome (Michelmore, 1995). In an analysis of a large number of potato varieties with and without R genes, Darsow *et al.* (1987) observed an overall increased resistance level of varieties with R genes, which, as they proposed, could be the result of undetected introgression of resistance factors other than the R genes from the wild sources.

Outline of Activities

Breeding and broadening the genetic base for durable resistance to late blight at the International Potato Centre

Evaluation of existing varieties (SIFT)

Plant breeders have developed many potato varieties that are resistant to late blight under local conditions. Comparison of resistance levels in varieties has been problematic because of lack of knowledge about the extent to which different environments influence the expression of resistance, because different pathogenic races have been used, and because local evaluations may use different methods. Therefore, a multilocation standard international field trial (SIFT) was launched in 1998 (French and Mackay, 1996) and its task is to distribute and test the best available late-blight-resistant potato varieties and breeding lines, submitted by breeders from all around the world, for adaptation and acceptance in developing countries. In this way, producers should gain ready access to the best available resistant materials that are adapted to their needs. The trial is being carried out at seven locations in America, Africa and Asia.

Breeding for horizontal resistance to late blight using advanced sources

This activity focuses on developing improved varieties for a wide range of environments that possess high and stable levels of resistance to late blight in combination with resistance to viruses and suitable culinary and processing quality.

Several sources of resistance are used in three groups of materials differing in their genetic base and degree of enhancement. The groups are:

- Group B1, in which native cultivated forms of short-day-adapted *S. tuberosum* ssp. *andigena*, which are assumed not to depend on R-gene resistance, are intercrossed.
- Group B2, in which clones of both subspecies of the common potato, *tuberosum* and *andigena*, are intercrossed. Materials in this group are adapted to short-day and they are gradually improved for resistance and agronomic traits. Group B2 germplasm is being improved for adaptation to long-day at the Instituto Nacional de Tecnología Agropecuaria (INTA), Argentina, as will be explained on page 391.
- Group B3, which represents the agronomically most advanced group of International Potato Centre (CIP) breeding clones that do not rely on race-specific R-gene resistance, developed as described below. This group combines quantitative resistance from *S. tuberosum* spp. *tuberosum* and *andigena*, from Neotuberosum clones (Plaisted, 1987), and from complex hybrids of *S. acaule*, *S. bulbocastanum*, *S. phureja* and *S. tuberosum* ssp. *tuberosum* (Hermesen, 1994). Again, the role of INTA, Argentina, is to select, recombine and adapt for long-day the germplasm of this group.

Recurrent selection is carried out within each of these groups, to increase the frequency of alleles that contribute to quantitative resistance. Extensive testing for resistance and other agronomically important characteristics is carried out in each generation of the recurrent scheme. The procedures employed focus on:

- Selection for quantitative, race-non-specific resistance.
- Selection against race-specific resistance that simplifies testing in the following generations. Clones possessing quantitative resistance can then be detected by using any race of the pathogen, independently of its particular virulence.
- Selection in those geographic areas where the new varieties will be grown. In that way, genotypes adapted to a specific environment can be identified.
- Selection of clones possessing a high general combining ability for resistance and yield. These clones can then be used as parents in local breeding programmes of National Agricultural Research Systems (NARSs).

Description of group B3

To develop the B3 group of late-blight-resistant clones, first crosses were done in 1990. Best-performing individuals were selected from segregating progeny through field testing for quantitative resistance and desired agronomic characteristics. These clones were then screened to eliminate individuals that expressed race-specific quantitative resistance (Landeo and Turkensteen, 1989), by crossing with a tester that does not possess R genes for resistance. Segregating seedling populations resulting from these test crosses are inoculated with an avirulent isolate (0-race) of *P. infestans*, as an additional screen against race-specific resistance. Parents of seedling populations segregating in a way that is expected for R-gene resistance are discarded. Parental clones that produced seedling progeny of non-segregating partial resistance in that test are used for recurrent crosses.

A set of 112 clones possessing race-non-specific resistance was selected from the second cycle of recurrent selection. When used as parents, the potential to obtain, under a wide range of environments, varieties with resistance to late blight and improved agronomic and quality attributes is increased.

Field tests to quantify the resistance levels of a sample of partially resistant clones

were carried out at four locations in Peru (two), Colombia and Mexico, using segregating progeny that had been obtained in a line \times tester mating design during 1992. Narrow-sense heritabilities for resistance were 0.5–0.7 and those for total tuber yield were 0.25–0.5, indicating that further improvement through breeding of these characteristics is possible. The values obtained may, however, overestimate the actual heritability coefficient because the cross progenies tested at each site consisted of unique seedling individuals.

Screening of related germplasm and pre-breeding for resistance at CIP

The gene pool of potato is comprised of six cultivated species and over 200 wild tuber-bearing relatives (see Ortiz, Chapter 10, this volume). Ploidy levels range from diploid ($2n = 2x = 24$) to hexaploid ($2n = 6x = 72$), but 80% are diploid and self-incompatible.

Several thousand accessions of cultivated and wild potato are held at six major and several minor genebanks, and attempts to evaluate the value for late-blight resistance breeding of these sources are as old as the collections themselves (Schick, 1932; Lehmann, 1938).

Most procedures employed in the past to characterize late-blight resistance used only one or a few isolates of *P. infestans* to test a small sample of genotypes drawn from an accession, and could assess only the average resistance of an entire accession. Specific individual plants of an accession found to be resistant were not saved. The efficiency of these methodologies for providing resistant germplasm and information immediately applicable by plant breeders is therefore limited. More recent approaches aim at overcoming these difficulties by providing information about the type of resistance and the genetic structure of an accession. One such example is the fine screening method of germplasm for resistance to Colorado potato beetle proposed by Bamberg *et al.* (1996). An approach taken at CIP illustrates this development for characterizing late blight resistance of genebank accessions.

The collection of wild potatoes held at CIP holds 1500 accessions representing 110 species. Current investigations on this collection are designed to: (i) better characterize the frequency and relative levels of resistance available in the accessions; (ii) characterize the nature of resistance (race-specific, non-specific); (iii) estimate the diversity of resistance genes present; and (iv) provide new genetic sources for resistance breeding. To meet these objectives, a complex procedure involves testing of a comparatively large number of samples of each accession for their response to several *P. infestans* isolates that represent the widest possible range of known contrasting virulences. Simultaneously, resistance sources and hybrid individuals are evaluated for important traits.

Selected genotypes may then be studied further by geneticists, or used by breeders for introgression of their resistance into potato. Because potato varieties are clonal, and high levels of heterozygosity are advantageous, most efficient breeding relies on parental clones of known resistance genotype. Testing and selection of one potato cross generation takes 3–5 years (Ross, 1986), and more than five crossing generations may be needed to breed a variety. Therefore, reduction of the number of generations could considerably reduce the time for variety development. Generations can be saved when the inheritance of resistance is known.

Several populations of wild species selection \times *S. tuberosum* dihaploids are being investigated (Trognitz *et al.*, 1995, 1996). One example is a hybrid population of a cross between a highly resistant genotype of wild *S. verrucosum* and a susceptible geno-

type of cultivated *S. phureja*, designated population VP. Hybrid seeds of this cross were provided by Dr Nelson Estrada, PROINPA, Bolivia. The progeny were tested for resistance in the field in Peru during 3 years and analysed for occurrence and segregation of race-specific R genes (Trognitz *et al.*, 1997).

The high potential value of this population for increasing the resistance to late blight of potato is illustrated by its extremely high resistance level in the field. The entire VP population had a higher average field resistance (measured as the area under the disease progress curve) than the resistant variety Perricholi that was used as a standard. Its frequency distribution deviated, however, from the expected normal distribution typical for a polygenic, quantitative trait. Therefore, detached leaflet tests were performed to study the occurrence of R-gene resistance expressed as a hypersensitive response to infection. Of 99 plants tested with five isolates of *P. infestans*, none was resistant to two isolates, and with the remaining three isolates segregation into resistant and susceptible classes was observed. The ratios of resistant:susceptible individuals obtained with either isolate significantly diverge from ratios expected for a model of single dominant genes. The complementary action of two or more resistance genes, or a resistance gene and a suppressor gene, were more feasible models (Trognitz *et al.*, 1997).

Breeding for durable resistance to late blight under the long-day conditions of Argentina

Testing for both foliar and tuber blight resistance is being performed at two locations in Argentina; Balcarce (38°S) and Tucuman (27°S). The first location is situated in the centre of the main potato growing area of Argentina and the second in a highland valley with excellent natural conditions for seed production, but severe late-blight epidemics.

The objective of the INTA breeding programme is to develop varieties for Argentina that combine resistances to late blight and viruses with early maturity, good tuber characteristics and culinary quality (Mendiburu and Huarte, 1987; Huarte *et al.*, 1994).

Breeding is carried out at both the tetraploid and the diploid level.

The tetraploid breeding programme

To select for resistance to late blight, in each year a minimum of 20,000 seedling plants are inoculated in the field with *P. infestans* isolates that are representative of pathogenic strains occurring in the potato production areas of Argentina. A set of potato R-gene differential genotypes is planted each year in the experimental field to monitor the actual virulence spectrum of *Phytophthora* throughout the growing season.

Because several virus diseases are an important constraint to potato production in Argentina, advanced clones from the late blight programme are tested for virus resistance, using natural and artificial inoculation methods.

In the tetraploid breeding programme, progenitors obtained from the CIP as well as from European and North and South American potato breeders are used as pistillate parents in crosses with local clones. Argentinian clones that produce superior pollen quality are used as pollen parents.

Breeding clones and varieties produced by the INTA programme combine high levels of field resistance to several diseases including late blight (Mendiburu and Huarte, 1987). Tests of these varieties at CIP revealed a wide range of resistance levels (Table 24.1) although many varieties do not express any of the known R genes conferring race-specific resistance (G. Forbes, CIP-Quito, unpublished data). The varieties that are adapted to long-day and have good tuber characteristics and resistance to viruses represent valuable progenitors used in the breeding programmes. Examples of the success achieved in the Argentinian national potato breeding programme are the varieties Serrana INTA and Achirana INTA, both possessing good general combining ability (GCA) for virus resistance, in particular potato leafroll virus (PLRV) (Huarte *et al.*, 1990); and Pampeana INTA with high GCA for late-blight resistance (M. Huarte, unpublished).

Tetraploid breeding for late blight resistance has been intensified since 1994 through the collaboration with CIP when CIP breeding clones were received and selected for several seasons in Balcarce and Tucumán. These materials were late-maturing and they had tuber quality characteristics not accepted by the Argentinian market although they possessed high degrees of resistance to late blight. The performance of the group B clones indicated the possible presence of R genes, as the instability of the resistance was evident.

In 1995, selection work began on 20,000 seedlings from cross progeny of CIP's group B3 that does not express any of the known R genes. In 2000, after 2 years of field trials, 150 clones of superior late-blight resistance in combination with other characteristics of agronomic importance were intercrossed to obtain a second generation of seedling plants for recurrent selection. Seed produced at INTA, of the same group B3 progeny tested at Balcarce, were also distributed for selection for late-blight resistance on seedlings and clonal plants to Toluca, Mexico, and Rionegro, Colombia. Linear correlation of progeny means of resistance rating obtained at Balcarce and the two short-day environments was low ($r < 0.46$), whereas progeny means obtained at Toluca and Rionegro were highly correlated ($r > 0.84$), indicating a significant genotype \times environment interaction of resistance. Pathogen variability, photoperiod and temperature may have significantly contributed to this genotype \times environment interaction. The development of long-day adapted potato varieties with high levels of horizontal resistance to late blight under high disease pressure has been lengthy and not free from con-

Table 24.1. Comparison of late-blight resistance of Argentinian with European potato cultivars in a 2-year field trial.

Cultivar	Origin	Resistance (AUDPC)		Other characters
		1996/97	1997/98	
Pampeana INTA	Argentina	242	878	High dry-matter content
Serrana INTA	Argentina	1075	1147	Resistance to PLRV
Huinkul MAG	Argentina	1157	1259	Resistance to PVY
Pimpernel	Holland	387	929	Horizontal resistance to late blight
Bintje	Holland	1786	2695	Susceptible to late blight
		SE 261	SE 357	

straints, which were imposed by these environmental conditions and the short-day adaptation of the initial genetic material available.

The variety Pampeana INTA may be used to demonstrate the potential of a classical pedigree breeding scheme conducted at INTA. Pampeana INTA is moderately resistant to late blight, it is resistant to several virus diseases and produces round tubers of high dry-matter content and high mashing and baking quality. This variety was released in 1985 and since then it has been used as a progenitor of both resistance and quality traits, and good market acceptance.

The diploid programme at INTA, Argentina

Wild species have been exploited in the breeding programme for several decades. Three species are used at present (Capezio *et al.*, 1997; Huarte *et al.*, 1997): *S. microdontum*, *S. commersonii* and *S. chacoense* have been extensively screened for the presence of R genes and assessed for their level of horizontal, non-R-gene, resistance. Within these sources, intraspecific cross populations segregating for horizontal resistance to late blight have been obtained, and molecular markers are being identified to assess horizontal resistance (Micheletto *et al.*, 1997).

Crosses of selected wild species clones to *S. tuberosum* dihaploids are made and resulting hybrids tested for resistance. Superior diploid hybrids are then used in $4x \times 2x$ interploidy crosses, to select tetraploid progeny for their direct use as cultivars or progenitors in the tetraploid programme.

Diploid segregating hybrid progeny, using Argentinian wild species as sources of resistance, are also developed for experimentation with molecular-marker-assisted selection for late-blight resistance, using random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP) and microsatellite (SSR) markers. The efficiency of the initial markers to detect resistance loci could be diminished, as the markers may not be perfectly associated with the loci determining horizontal resistance. Therefore, markers will be modified through genetic engineering.

Wild species progenitors possessing true quantitative resistance and no R genes conferring race-specific resistance are being selected for further molecular tagging of resistance genes.

Lessons learnt from the Argentinian programmes

The approach chosen to select resistant genotypes to late blight initially depended on field selection under natural infection on favourable environments for the development of the disease (Tucumán and Balcarce). Out of that simple scheme, an outstanding variety like Pampeana INTA was obtained. Later on, in order to improve the frequency of favourable genes and the efficiency of selection, artificial inoculation, together with the introduction of CIP germplasm, was carried out.

The first population introduced from CIP bearing R genes demonstrated the need to work in a background lacking those genes, considering the instability of the resistance shown on many of those clones. On the other hand, several of these clones showed a quite stable performance, indicating some degree of durable resistance. This material has potential for direct use as varieties and as progenitors. Still, there is a need for shortening the growing period and improving the tuber aspect for the local market requirements.

The approach taken with population B, under long days, is showing its advantages: a high level of partial resistance is present, and good tuber aspect and shorter growth cycles are found at increased frequencies. Consideration of genotype \times environment interactions is important if this material is to be used in other regions or programmes: multisite testing will be necessary in order to select the more stable genotypes. Also crossing to *S. tuberosum* clones and cultivars with no R genes is carried on as a way to improve adaptation. Genotype \times environment interactions have proven to be quite important, particularly for the resistance that relies on the existing R genes.

On the diploid side, the Argentine species have shown a high level of partial resistance together with the presence of R genes.

International cooperation to investigate the genotype \times environment interaction for quantitative resistance to late blight

At the initial planning meeting of GILB, the GE interaction was given a high priority as the success of resistance breeding at one location could not be extrapolated to other locations without any further experiments. One previous study by Parker *et al.* (1992) indicated that the variety Alpha, horizontally resistant in Europe and North America, was susceptible to late blight in Toluca, Mexico. In response to the lack of more information on the stability of resistance across environments, CIP and a group of eight collaborators carried out a 3-year GE trial series to study a standard set of varieties at several locations worldwide and with varying pathogenic strains.

The countries and institutions are: Canada (Agriculture Canada), the United States (Cornell and Washington State University), Denmark (LKF), Ecuador (CIP), Argentina (INTA), Scotland (Scottish Crop Research Institute – SCRI), The Netherlands (CPRO), and two sites in France (Institut National de la Recherche Agronomique – INRA). These locations represent nine sites with long-day and one short-day site (CIP, Ecuador).

The data obtained indicate that interaction between quantitatively resistant genotypes and the environment is not significant (Forbes, 1999). Tropically adapted, resistant varieties, such as Cruza-148, also were resistant in the temperate zone, and Torridon, a resistant variety from Scotland, was resistant at CIP–Ecuador. Therefore, although the absolute level of resistance expressed by a variety may depend on the specific local conditions, this variety can be predicted to be relatively more resistant than a susceptible variety regardless of where it is grown.

This first international experiment was performed with unrelated, clonal potato varieties, thus it investigates the interaction of different environmental settings with fixed genotypes. Breeders would, however, like to know the relative contribution to this interaction of resistance alleles that may act in dominant and additive ways. Allelic interactions can be studied ideally in segregating biparental cross progeny, and diploid materials would facilitate the genetic analysis of those alleles. Therefore, a GE experiment using a diploid progeny, denominated PD, from a cross of a horizontally resistant *S. phureja* selection (P) and a susceptible potato dihaploid (D), will be carried out. The PD progeny of 246 individuals will be tested in the field by two institutions in three contrasting environments: CIP (the central Peruvian Andes), BAZ (northeastern Germany) and CIP (Lembang, Indonesia). A genetic map of the PD population is

currently being developed (Ghislain and Trognitz, 1996), and molecular markers of resistance alleles will help to determine relative contributions of alleles to the GE interaction.

Conclusion and Recommendations

The development of durable resistance to late blight in potato has been one of the most challenging tasks in the history of plant breeding. Recurring phases of success through the introduction of resistance from diverse genetic resources and failure due to the pathogen's genetic flexibility to adapt to its hosts have been experienced. International collaboration uniting breeders, pathologists, physiologists and molecular biologists has proved to be crucial for obtaining new insights, as the diversity of plant-pathogen interactions have to be studied in a wide range of agroclimatic settings with their specific *P. infestans* strains.

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25 A Mexican Bean Breeding Programme for Comprehensive Horizontal Resistance to all Locally Important Pests and Diseases

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Introduction

Mexico is one of the centres of origin and domestication of the common bean (*Phaseolus vulgaris*). This country accordingly has a wide genetic variability in beans as well as in bean parasites. Until recently, the local landraces were able to withstand the impact of local pests and diseases. This stable situation changed because of an increase in the areas cultivated by bean coupled with the introduction of intensive cropping systems employing high-yielding pure lines protected either with vertical resistances (i.e. gene-for-gene relationships) or with pesticides (García, 1987b; Pérez *et al.*, 1995). Other possible factors include the global distribution of pathogens, or the appearance of new races (pathotypes) of old pathogens, perhaps due to the unrestricted movement of germplasm within the country and among different countries (Gram, 1960; Thurston, 1984; García, 1987a). The pest and disease populations have now increased to the point where not even the local landraces could be cultivated without crop protection chemicals. As a result of these pest and disease problems, among others, the crop is no longer profitable and it is being abandoned as a commercial crop by farmers in the Mixteca region of Mexico (García, 1987b).

The Mixteca consumers have a strong preference for the local landraces over the considerably cheaper beans now being imported from other countries under the North American Free Trade Agreement (NAFTA).

The challenge was to improve both the resistance and the yield of the local landraces, with a view to offer the Mixteca farmers varieties derived from their own local landraces, but with high enough levels of horizontal resistance to avoid the use of pesticides, and thereby to recover the commercial value of the local landraces. This would

restore the overall stability of bean cultivation, provide the preferred qualities, eliminate the use of pesticides and maintain genetic diversity.

Objective of the Programme

Most plant breeding efforts for resistance to crop parasites have involved single-gene vertical resistance, obtained by gene-transfer breeding techniques (Robinson, 1976). Vertical resistance has two important advantages: it usually provides a complete protection against the parasite in question, and it functions over a wide geographical range. However, it has a number of disadvantages, the most important being its liability to fail on the appearance of a new, matching strain of the parasite (Robinson, 1987).

Horizontal resistance is usually polygenically inherited and its accumulation requires the entirely different breeding technique of recurrent mass selection. Its chief advantage is that it is durable, and it does not fail like vertical resistance. Its main disadvantage is that it is quantitative and it may not always provide a complete protection. Furthermore, the effectiveness of a horizontal resistance, in any one cultivar, is usually limited to a single agroecosystem, because the epidemiological competence of parasites varies greatly from one agroecosystem to another. A cultivar that is in perfect balance within one agroecosystem will then have too much resistance to some parasites, and too little to others, when cultivated in a different agroecosystem (Robinson, 1996). Thus breeding programmes for horizontal resistance must aim for specific adaptation, with selection carried out in the target area.

A comprehensive horizontal resistance bean breeding programme was initiated in 1991 in the Mixteca region in Mexico. The project was conducted by a multidisciplinary team from the Colegio de Postgraduados, Mexico, in cooperation with the University of Guelph, Canada. The objective of the programme was to test the possibility of obtaining both high levels of horizontal resistance to all the locally important bean parasites and the high yields attained by commercial cultivars, while retaining the culinary qualities of the Mixteca landraces

Breeding Strategy

This horizontal resistance bean breeding programme was directed against the two main pathological problems in the region, bean common mosaic virus (BCMV) and bean common blight (*Xanthomonas campestris* pv. *phaseoli*), and the main entomological problem of white fly *Bemisia* sp. and *Trialeurodes* sp., as well as all other parasites that are unavoidably present during the screening process. These less-important parasites included several soil-borne plant pathogens (fungi such as *Pythium* spp., *Rhizoctonia solani*, *Macrophomina phaseolina* and *Fusarium* spp. among others) and several insect pests.

For a successful horizontal resistance breeding programme, it is necessary that the many polygenes responsible for the various quantitative resistances are present in the original parent population, and this necessitates a broad genetic base of the starting material. The breeding programme was initiated with landraces that have a high

inherent variability, making it unnecessary to introduce exotic germplasm. Out of 70 local landraces collected from the highlands of the Mixteca region, seven were chosen as parent populations. These were selected specifically for their susceptibility to a designated pathotype of each of the two main diseases: bacterial blight and BCMV. Since the same designated pathotypes were used in all subsequent screening populations, this ensured that no vertical resistance genes were functioning during the breeding process.

These seven parents were crossed in a half-diallel cross after several (more than three) generations of selfing, and each cycle of recurrent mass selection was subjected to late selection. Late selection is necessary to eliminate any effects of heterosis (hybrid vigour) and to ensure that the effects of any recessive polygenes for horizontal resistance are expressed.

All screening was conducted under field conditions in the Mixteca region, during the normal growing season, and according to the local farming system. Strong selection pressure for resistance was applied by individually inoculating each plant in a population of 6000 plants with bacterial blight and BCMV. The best 1% of plants were kept as parents for the next cycle of recurrent mass selection. The primary screening criterion was yield. This was considered the best proxy for horizontal resistance under the conditions employed (in which every plant had been inoculated with a designated pathotype to ensure that no vertical resistance was functioning). The screening populations were free of all crop protection chemicals. Secondary selection criteria included earliness, growth habit, pod length, and seed size, colour and brightness.

The breeding cycle

The breeding cycle, defined as all the operations that occur between one controlled pollination and the next, included cross-pollination, followed by two or three generations of self-pollination, and family selection in the field. To complete a breeding cycle in the shortest time, the differing climates of various regions within Mexico were exploited. However, screening was conducted only in the area of future cultivation, during the summer, in the Mixteca region. Crossing through hand-pollination was conducted during the winter, at high altitude. This heavy load of very delicate work was done in the greenhouse at the Colegio de Postgraduados by specially trained students. Selfing was conducted in the field, both in the summer at high altitude, and during the winter at low altitude at Veracruz.

Selection pressures

The selection pressures were high in order to maximize the rate of genetic advance. The usual selection coefficient was one plant in 100. Although the selection of parents for the next breeding cycle was done in a single location, the selection of genotypes to be released as new cultivars was based on field evaluations made during 2 years in at least three locations, including the site of future cultivation. Two experiments were established in each location to identify the best genotypes grown with and without artificial fertilizers.

Lines Released and Yields

At the time of writing (June 1999), the programme had produced four new lines, derived from only the third breeding cycle. These are currently in the process of official registration. Out of the 33 parents of the fourth breeding cycle, five new lines were selected as elite lines to develop into new varieties. The 33 parents of the fourth breeding cycle were used in the 1997 crossing process that produced hundreds of new genotypes, out of which the 33 parents of the fifth breeding cycle were selected; out of those, another five elite lines will be selected for official registration. These 33 parents were also used for further crosses in this ongoing programme.

The new lines have been tested under various ecological conditions by farmers in the Mixteca region. This testing had the additional purpose of bulking seed but, in some cases, the production has been so successful that the farmers refused to sell back the seed of some of the lines, which under certain field conditions have yielded as much as 1800 kg ha⁻¹ (the average yield in the region, in a good year is 600 kg ha⁻¹, and in 1998 the local varieties yielded around 200 kg ha⁻¹).

Yields

Table 25.1 shows the gains obtained in the third and fourth breeding cycles in an experiment conducted in the Mixteca region, in which 64 genotypes were included (six original parents, 15 parents of the third and 33 of the fourth breeding cycles, along with some regional and commercial varieties). The experiment was established in 1997 and 1998 under a randomized block design, with three replicates and complete competition among plants. No fertilizers or chemicals for protection were applied.

The accumulation of horizontal resistance

It should be borne in mind that all the screenings were conducted under field conditions and, therefore, under the selection pressure of all locally important parasites. The data discussed below are mainly related to BCMV, although some critical evaluations are described concerning soil-borne diseases. Data concerning bacterial common blight are currently under analysis.

Table 25.1. Yield gains for selection in the third and fourth breeding cycles (Tepexi de Rodriguez, Puebla, 1997).

Parents	Yield (kg ha ⁻¹)	% gain over original parents	% gain of fourth cycle over third cycle
Fourth cycle	650.7	152.9	11.9
Third cycle	581.30	136.6	—
Original parents	425.58	100.0	—

Even though the programme started precisely with seven highly susceptible parents (in order to avoid the possibility of introducing vertical resistance to either of the two diseases targeted), the 1998 results clearly demonstrate the accumulation of resistance in some of the advanced genotypes to both BCMV and soil-borne diseases. Highest yields (significantly different from the rest of genotypes) were obtained by two of the selected parents of the fourth breeding cycle: key numbers 507 and 553, with yields of 865.46 and 854.74 kg ha⁻¹, respectively. Neither genotype showed severe symptoms of BCMV (Fig. 25.1) and only 38% and 50%, respectively, showed mild symptoms (Fig. 25.2).

Lethal diseases, as sometimes BCMV can be for beans, exert very strong selection pressure among plant populations. It has been argued that horizontal resistance against such diseases is of limited value if the crop carries natural genetic flexibility such as the case of allogamous crops like maize. However, this is not a problem for autogamous species, such as common beans.

For this reason, emphasis has been placed on monitoring the incidence of the severe symptoms of BCMV. Nevertheless, even when mild symptoms are considered, it is still possible to observe the accumulation of horizontal resistance against this disease, as shown by the negative correlation between the higher yield of some of the advanced genotypes of this programme and their lower incidence of both types of symptoms (Fig. 25.2).

Since the virus isolate that has been used throughout this programme (the designated pathotype) is capable of producing a continuum of symptoms among the progeny derived from the original parents, from mild, to severe, to the death of plants, it is clear that the most advanced materials of higher yields are showing horizontal resistance when inoculated with the designated pathotype, i.e. produce only mild symptoms (Fig. 25.2).

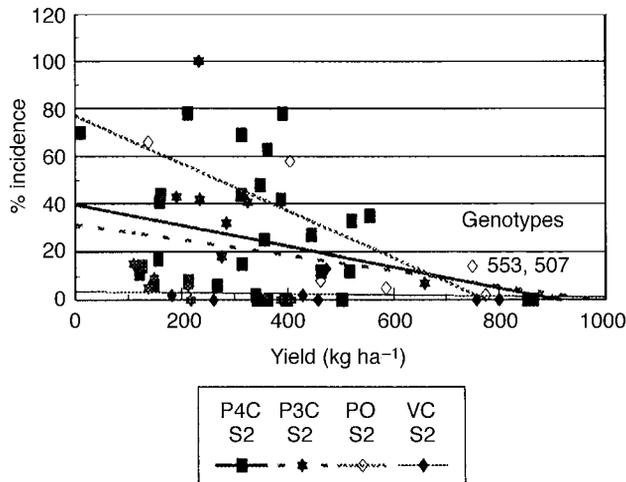


Fig. 25.1. Yield–incidence relationship of severe BCMV symptoms (S2) among the 64 genotypes tested in Tepexi de Rodríguez, Puebla, 1998. Note: % incidence is the proportion of plants affected; each point is the mean of three replicates.

*P4C = fourth breeding cycle progenitors; P3C = third breeding cycle progenitors; PO = original parents; VC = commercial varieties.

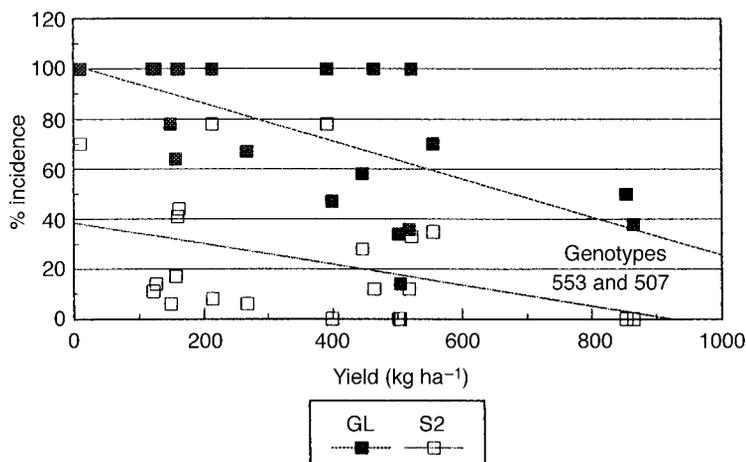


Fig. 25.2. Yield–disease incidence relationship of BCMV, severe symptoms (S2) and severe + mild symptoms (GL) showing the ten best and worst yielding among the included 64 genotypes. Tepexi de Rodríguez, Puebla, 1998.

There is an evident accumulation of horizontal resistance to BCMV when the incidence of both mild and severe symptoms is compared among the original parents and their progeny. The incidence was higher for the original parents than for the parents of the third and fourth breeding cycles. However, the incidence of both symptoms was even lower for those of commercial and regional varieties (Fig. 25.3), but neither group showed the highest yields and some varieties of these groups showed susceptibility to other diseases and pest problems, especially soil-borne diseases that render them

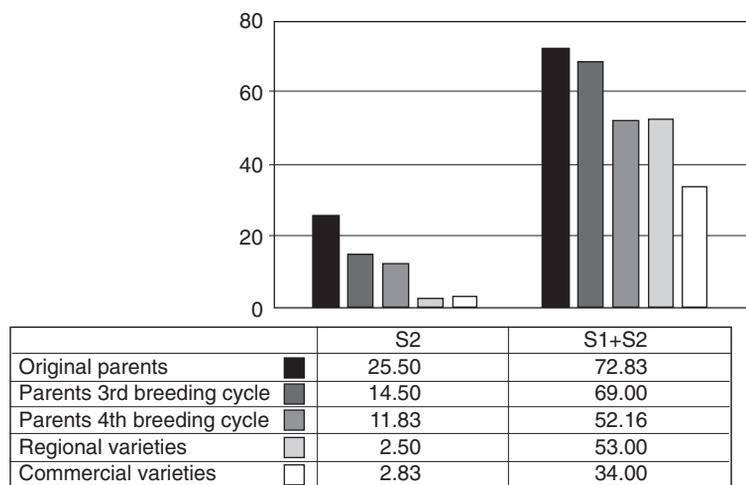


Fig. 25.3. Average percentage incidence of severe symptoms (S2) and mild + severe (S1+S2) symptoms of the six best genotypes among the advanced ones (those of higher yields) and the six and four commercial and regional varieties, respectively.

highly vulnerable in the Mixteca region. In fact, neither of these varieties would have been suitable as original parents in this programme because of the possibility of introducing monogenes of resistance as no information was available regarding their reaction to the inoculation of the pathotypes (BCMV and common blight bacterium). Additionally, the commercial varieties are not accepted by the Mixteca farmers.

One of the clearest improvements observed recently is the accumulation of resistance to soil-borne diseases. In field experiments conducted in 1997, it was easy to identify the plots of some of the commercial varieties because they were destroyed by these kinds of diseases, whereas the most advanced materials of the horizontal resistance breeding programme appeared perfectly healthy. In 1998 field experiments, significantly higher plant survival was observed for the six best-yielding lines of the parents of the fourth breeding cycle, followed by the parents of the third breeding cycle (Fig. 25.4). Although these diseases were not originally included as targets for the project, they have been present throughout the breeding process, acting as selective pressure on the genetic variation of the bean populations used in this programme.

Farmer participation

Many farmers expressed interest in cooperating with the programme, particularly as they are allowed to keep any lines they please. This widespread farmer participation ensures the adoption of the lines best suited to their needs. Because of the relative simplicity and low cost of the breeding process for quantitative resistance compared with that for single-gene, vertical resistance, this method offers new potential for strengthening farmer participation in plant breeding. In the future, the farmers, organized in breeding clubs (Robinson, 1996), could conduct their own breeding programmes, with

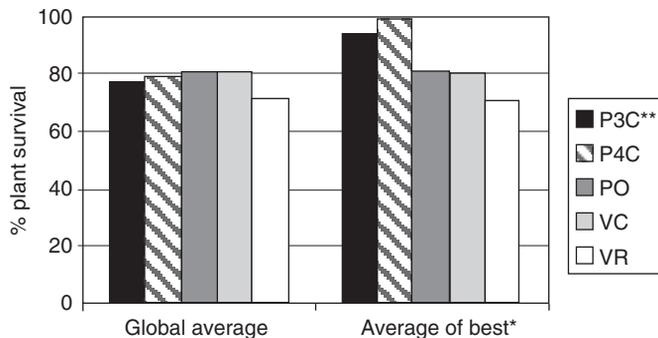


Fig. 25.4. Percentage of plant survival, after the initial attack of soil-borne diseases, showing the levels of resistance for both the total of genotypes per group and the six best-yielding lines, in the Tepexi de Rodríguez, 64 genotypes experiment, summer 1998.

*Global average represents the average percentage of germination of all genotypes belonging to each group, whereas average of best is the average based on the six highest-yielding genotypes of each group. **P4C = fourth breeding cycle progenitors; P3C = third breeding cycle progenitors; PO = original parents; VC = commercial varieties; VR = regional varieties.

assistance from scientists limited to making crosses and the early stages of selection. The total breeding activity could thus be greatly increased.

Unlike breeding for qualitative (single-gene) resistance, breeding for quantitative resistance is a continuous process, with each breeding cycle providing new and better cultivars (Robinson, 1996). The later stages of horizontal resistance breeding in the hands of farmers themselves could produce new high-yielding, high-quality lines capable of withstanding all the locally important parasites. Advanced lines should be tested by a large number farmers under diverse agroecological conditions in the variable, mountainous topography of the Mixteca.

Conclusions

It must be emphasized that this is an interim report on a programme that is far from complete. Nevertheless, the genetic advances obtained in only a few breeding cycles (averaging 18% per cycle in the first three cycles) are greater than anticipated. They more than justify the testing of this method in other crops and in other areas. The results obtained so far provide evidence of the accumulation of horizontal resistance. They suggest that it is feasible to obtain high-yielding, high-quality cultivars that have sufficient durable resistance to all locally important parasites to eliminate the need for crop protection chemicals. This programme demonstrates that breeding for horizontal resistance is quite simple, and could be undertaken by farmers and amateur breeders with only a minimum of assistance from scientists.

Acknowledgement

For the development of our programme we have had the generous support of IDRC of Canada.

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26 The Impact of Decentralized and Participatory Plant Breeding on the Genetic Base of Crops

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Introduction

The use of decentralized methods in crop improvement impacts on the genetic base of crops as deployed in farmers' fields, particularly when participatory methods are employed. Participatory plant breeding (PPB) is increasingly being used in both inbred and open-pollinated crop species (see Sperling *et al.*, Chapter 27, this volume). Two methods, participatory varietal selection (PVS) and participatory plant breeding (PPB), were defined and compared for their impact on varietal biodiversity in farmers' fields by Witcombe *et al.* (1996). The effects of PVS were considered unpredictable as it could result in either an increase or a reduction in varietal diversity at a local level. The outcome depends on the original level of crop diversity and the genetic diversity among the introduced varieties that farmers adopt. The manner of replacement of the existing cultivars – either partial or complete – is also important. In contrast, PPB methods were considered to have a generally favourable impact on varietal biodiversity and could be considered a dynamic form of *in situ* genetic conservation. PPB enhances the effects of traditional farmers' practices, that maintain variability within and between landraces, by improving the efficiency of selection and by increasing the variability on which this selection acts (Witcombe *et al.*, 1996).

Does PPB, when considered either on a local level or on the wider national or international level, tend to narrow or broaden the genetic base of crops? To answer this question, farmer participation has to be considered in relation to decentralization, and distinctions made between the effects of different types of participation, consultative or collaborative, defined by Biggs (1989). This is considered by using examples from rice, wheat and maize, the most widely grown cereals in the developing world.

Decentralization Versus Participation

Decentralization in plant breeding is scale sensitive. It can be from an international to a national level, from a national to a regional level, or from a regional level to ever smaller and ever more precisely defined target zones. The most complete decentralization is when farmers participate in the breeding process in their own fields (Ceccarelli *et al.*, 1994). Hence participation and decentralization are overlapping concepts and the methodological difficulties determining their relative importance are considerable or insurmountable (Witcombe, 1996). Most comparisons were considered too difficult to make because decentralization is nearly always confounded with increased farmer participation. Inevitably, in any decentralized breeding programme, the smaller the target area the more likely it is that the farmers' role in the breeding process will increase, even if that role is only consultative. Hence, although this chapter is largely concerned with the effects of farmer-participatory approaches to plant breeding on base-broadening, most of the conclusions also apply to decentralized breeding.

Using Wide Adaptation in Centralized Plant Breeding

Plant breeding can exploit wide adaptation by selecting varieties that yield well over large geographical areas such as the six mega-environments defined by the International Maize and Wheat Improvement Centre (CIMMYT) for spring wheat (Rajaram *et al.*, 1995). Mega-environments are broad (frequently discontinuous transcontinental) areas, characterized by similar biotic and abiotic stresses, cropping system requirements and consumer preferences. Although the spring wheat breeding programme is mainly conducted in only two research stations in Mexico, varieties bred by the programme are tested in multinational, multilocational trials in the mega-environments. Targeting the mega-environments in this way provides a degree of decentralization whilst having wide adaptation as a major breeding objective. A similar approach is followed by other Consultative Group on International Agricultural Research (CGIAR) centres – such as the International Rice Research Institute (IRRI), which adopts an ecoregional approach where regions are targeted within the main rice ecosystems (Fischer, 1996). For example, there are nurseries targeted at seven irrigated, three rainfed, one deepwater and two upland ecosystems (Chaudhary and Ahn, 1996). This approach of addressing broadly defined environments has been successful and has led to the large-scale adoption of widely adapted varieties in agroecological regions (e.g. Smale *et al.*, 1996; Witcombe, 1999).

Such centralized systems do not have to lead to a narrowing of the genetic base because a genetically diverse set of germplasm, ideally derived from a diverse set of parents and crosses, can be distributed for international testing. However, as the same genotypes are distributed to many countries, and it is common to distribute near-inbred lines, several national programmes may select and release the same one. Moreover, in most developing countries there are very strong filters that prevent much of this varietal diversity from reaching farmers – a centralized system of national multilocational trials and commonly a policy of recommending only a few of the very best performing entries in these trials for official release in the country (Witcombe *et al.*, 1998). As a consequence, there has been a reduction in the varietal diversity deployed

in farmers' fields (at least when weighted by the proportions each variety occupies). For example, rice varieties IR8, IR36 and IR64 occupied, or still occupy, large areas in several geographically distant countries over long periods of time. A few varieties of wheat, such as Sonalika, also dominate over large areas for long periods in countries such as India (Smale *et al.*, 1996).

One way of overcoming this widespread adoption of a few varieties is to decentralize breeding programmes to a more local level. Decentralized programmes will each produce their own, distinct germplasm and farmers should preferentially adopt the varieties bred for their target area. Such preferential adoption should be the common case since decentralized programmes are building on locally adapted germplasm, selecting in the target environment, and taking local farmers' preferences into account.

Decentralization by International Breeding Programmes

Decentralization by refining target areas

International Agricultural Research Centres (IARCs) distribute standard sets of genotypes to many national breeding programmes. These are called international nurseries or trials. For example, the International Spring Yield Wheat Nursery (ISWYN) of CIMMYT is distributed internationally and evaluated by many national research programmes.

DeLacey *et al.* (1996) carried out a pattern analysis of the geographic locations in the ISWYN using the multilocational yield data of the entries in the nursery. A lack of genetic variation towards a stress, e.g. for drought or heat tolerance, among the varieties would mean that the pattern analysis would not be able to discriminate between regions that vary for this stress. However, there was sufficient genetic diversity in the trials for the pattern analysis, carried out on data on varietal phenotypes across locations, to reveal sub-groups of locations within the mega-environments. If all of these sub-environments are targeted with germplasm specifically chosen for them, then such decentralization can lead to improved base-broadening.

Decentralization by targeting national programmes

The barley breeding programme at the International Center for Agricultural Research in Dry Areas (ICARDA) targets individual countries in North Africa by making a different set of crosses for each target country. Since there tends to be a clear geographical distribution of variation within germplasm, the crosses for each target country involve landraces originating from it (Ceccarelli *et al.*, 1994; Chapter 6, this volume). Hence, ICARDA's barley breeding programme is an example of a centrally coordinated programme where the decentralization strategy results in a deliberate maintenance of genetic diversity between the individual programmes. The extent of base-broadening of the crop in farmers' fields between countries will depend on the extent of the differences among the germplasm targeted at the individual national programmes, and on what varieties from the programme's germplasm are adopted by farmers.

Decentralization by shifting responsibilities

When IARCs supply international nurseries or international trials, national programme breeders can depend on them as sources of new varietal variation for promotion to national-programme, multilocational trials. This sometimes has the unintended, but unfortunate, effect of de-emphasizing in national programmes the role of crossing and selection among segregating generations. Resources are limited in many national programmes and basing a breeding programme on finished, or nearly finished, varieties is cheap and has many successful precedents. Traxler and Pingali (1999) have analysed releases by national programmes in wheat and rice according to whether they are the result of crosses made by the national agricultural research system (NARS), or direct introductions from IRRI for rice or CIMMYT for wheat. In rice, the proportion of direct introductions from IRRI has fallen to only 9%. However, in wheat, introductions account for the majority of releases, and this proportion is increasing over time and now exceeds 50%. The reasons for this large difference have yet to be fully investigated, although Traxler and Pingali (1999) offer some explanations such as the greater importance of rice to many national programmes, and the greater diversity of rice ecosystems as compared with wheat.

A desirable shift towards decentralization would be for IARCs to reduce the emphasis on international nurseries and trials and increase support to targeted crossing programmes in which national programme breeders are actively involved. Unfortunately, such a shift increases the demands upon national programmes at a time when many of them are reported by the International Service for National Agricultural Research (ISNAR) to be facing a real decline in resources. However, this change could be facilitated by the adoption of more participatory approaches, which rely less on expensive experimental infrastructure and increase the effectiveness of delivery. IARCs could supply germplasm from crosses targeted at agroecological regions within national programmes in which the minimum of selection has been made – for example, advanced generations produced by single seed descent that, it is suggested below, are ideal for incorporation into PPB programmes. Depending on resources, such activities could replace, or be in addition to, some of the more traditional approaches.

Participatory Approaches to Decentralization by National Breeding Programmes

Decentralization – a case study for maize in Gujarat

In India, breeding programmes are decentralized to the state level, and often agroecological zones are targeted within the state. Lessons on base-broadening can be learnt from a case study of maize breeding in the state of Gujarat, India (J.R. Witcombe, A. Joshi and S.N. Goyal, in preparation). The breeding programme was already decentralized to the state level and to the rainfed agroecological zone. Greater farmer involvement was introduced using consultative methods to identify target traits, such as the need for very short duration, white-endosperm varieties that grow well under low

fertility and rainfed conditions. Collaborative breeding was used in some of the later generations, after random mating was completed, in which mass selection was carried out by farmers. However, since this was done on researcher's land, and not on farmers' fields, the usual benefits of collaborative plant breeding – increasing diversity on participating farmers' fields – were not apparent.

A maize composite was created by crossing both white- and yellow-endosperm maize varieties. Only one of the parents was a local variety; all others were introduced into the area either from breeding programmes in distant states but also from those located within Gujarat and from bordering Madhya Pradesh. All of these varieties had been tested in PVS programmes in Gujarat, so it was known that all of them had at least some attributes that farmers liked and some adaptation to local conditions.

Several varieties, both white and yellow grained, have been produced from this composite. One of them, GDRM 187, has a yield advantage over the local varieties of more than 20%, is considerably earlier to mature, and has superior grain quality. Farmers greatly prefer it over the several cultivars they are currently growing, and it is likely to become the predominant variety in the area. Hence, although there is possibly a huge broadening of the genetic base, because of the diverse ancestry of GDRM 187, compared with the local varieties described by Joshi and Witcombe (1996, 1998), its widespread adoption may well lead to a loss of genetic diversity in farmers' fields. This loss of diversity needs to be defined since there are many types of diversity in agricultural systems (reviewed in Witcombe, 1999). In this case, the reduction will occur in the weighted diversity that takes into account both the genetic diversity between varieties grown by farmers, and the area that each cultivar occupies (Souza *et al.*, 1994). This possible decline in weighted diversity is also a function of the existence of a range of diverse landraces in the target area. If GDRM 187 replaced a single, narrowly based variety, then its impact would be entirely beneficial for the breadth of the genetic base of the crop in the field. Moreover, the genetic base available to breeders and farmers in the state has increased.

Although there were very important collaborative elements, the breeding of GDRM 187 is probably best described as consultative PPB. From a national viewpoint, consultative participation may promote diversity when used to identify parents and target traits in decentralized breeding programmes. It is less likely that individual breeding programmes will depend on the same germplasm: by consulting farmers on their needs for new varieties locally adapted germplasm will often be used in crosses, and the choices of exotic germplasm will also differ according to local needs. Locally adapted germplasm will also usually be locally distributed, although an exception, the rice variety Kalinga III, is discussed below.

Decentralization of plant breeding with collaborative participatory research

Decentralization that employs collaborative techniques is one of the most certain ways to have beneficial effects upon the genetic base because in the process of collaboration farmers grow a diverse range of novel germplasm on their fields. These benefits will tend to be greater in the areas where the PPB programme is being conducted (Witcombe *et al.*, 1996). Only a part of this diversity – the most successful of the farmers' selections – will diffuse from the participating farmers, resulting in geographic

patterns of diffusion from these foci as found by Huke and James (1969) and Witcombe *et al.* (1999).

The extent to which diversity will increase is dependent on the participatory breeding method employed and whether the crop is an inbreeder or outbreeder. In outbreeding crops, such as maize, it is unlikely in a collaborative participatory programme that many composites can be made or selected by farmers in their fields. Indeed, it is probable, given the more limited resources of decentralized programmes, that most will only work on one or two composites at any one time. If collaborative methods prove possible – and they are more difficult in outbreeders because effective progress from selection without undesirable inbreeding depression requires both a minimum population size and genetic isolation from other populations – then base-broadening in the field is possible. A composite can carry a large reservoir of variability, particularly if selection is minimized during the initial random mating generations. It can be given to farmers in a range of specific target environments (both physical and socioeconomic) and selection for local adaptation and local needs of farmers will create and maintain diversity between populations. However, it is difficult to generalize – the ways in which different farmers select and maintain seed will be important in determining eventual changes in varietal diversity (e.g. Louette *et al.*, 1997; see also Berthaud *et al.*, Chapter 4, this volume).

In inbreeding crops – such as rice, wheat and barley – PPB is not constrained by isolation distances and population sizes. Many methods are possible, depending on how early farmers are given seed in the procedure of generation advance after hybridization. Sthapit *et al.* (1996) gave F_5 pedigree bulks (i.e. bulks derived from individual F_2 plants) of rice to farmers located in two high-altitude villages in Nepal. They reported an increase in varietal biodiversity in these villages as several bulks were accepted by farmers. However, in subsequent studies (Joshi *et al.*, unpublished) it was found that only one or two of the F_5 pedigree bulks had persisted, so although there were long-term increases in local varietal biodiversity (new varieties were often additions to farmer varietal portfolios rather than replacements) some of the increases were temporary.

Other methods can be used that should be much more effective in increasing biodiversity than providing farmers with a small number of pedigree bulks. For example, farmers can be given bulk seed that produces highly heterogeneous populations of nearly homozygous plants. These bulks are produced by single seed descent, or variations of this method, that are designed to minimize the effects of selection during the selfing generations in order to maximize between-plant variability in the advanced generations. Since the individual plants in the bulk on a farmer's field are approaching homozygosity the plants will tend to 'breed true', i.e. their offspring will tend to resemble them. This should be more effective than giving farmers earlier generation bulks that are more heterozygous and which require a greater understanding of the difference in the mode of inheritance of traits for selection to be effective. For example, plants selected in early generations for recessively inherited traits will 'breed true'. However, for traits that are dominantly inherited both homozygous and heterozygous plants will be selected and the latter will produce segregants in the subsequent generations. (In brief, the more advanced the selfing generation the higher is the expected between-plant heritability, assuming equivalent environmental variation, and hence the higher the rate of genetic advance from selection.)

Such methods are being used in rice by M. Subedi and K.D. Joshi of LI-BIRD (Local Initiatives for Biodiversity Research and Development), a Nepalese non-governmental organization (NGO), in collaboration with CAZS. They are employing equal seed descent (ESD), that advances the progeny of a cross to homozygosity whilst reducing the effects of selection, and also what can be termed as modified bulk population (MBP) breeding. In this latter technique, a segregating population from a single cross is divided into sub-populations on the basis of highly heritable traits. The cross in this PPB programme is Kalinga III \times IR64, and at least two traits have been used to form the sub-populations: plant height (the cross is between a tall and dwarf variety) and maturity (Kalinga III is much earlier to mature than IR64). In both ESD and MBP breeding, sufficient seed can be produced to distribute it to many farmers for selection in their own fields. Hence, the entire selection process can be replicated across many farmers and environments, a procedure that is impossible to do cost-effectively in a non-collaborative decentralized breeding programme. Assuming there are desirable variants in the bulk, selection within it by several, or many, farmers who grow the bulk in their own fields is the method that is most likely to produce a large, long-term increase in the biodiversity deployed in the field. From the performance of the bulks so far, it is expected that many different lines will be selected and retained by farmers.

The above examples are only some of the many possibilities because participatory breeding programmes need to be adapted to local circumstances. For example, when farmers are reluctant to select from within populations, as is the case in barley in the Middle East and North Africa, then selection between populations of crosses can have greater emphasis (S. Ceccarelli, personal communication). Hence, farmers select from many crosses each of which has been made between parents that do not differ in qualitative traits of importance to them: e.g. in barley the parents would have a common husk colour, and both would either have either two-rowed or six-rowed spikes. Another example is the case of longer-duration varieties of any crop where only one generation a year can be grown. Where doubled haploid techniques are available, their use is advantageous for PPB. Homozygous lines – the doubled haploids – can be produced much more rapidly than by conventional means and farmers can be given homozygous products that breed true.

The size of the target areas of such a programme has important implications for base-broadening. The cross Kalinga III \times IR64 is wide enough to produce segregants that are suitable for both rainfed and upland conditions, and for a range of altitudes in Nepal from 300 to 1300 m. The same cross is also being used by Birsa Agricultural University and a bilateral development project, the Eastern Indian Rainfed Farming Project, in collaboration with CAZS. This very broad target environment is made possible by the adaptation of the parents. Kalinga III has wide adaptation to rainfed environments (it performs well in eastern and western India and Nepal over a range of latitudes) and IR64 has wide adaptation to high potential systems. If this single cross produces varieties that succeed across such a wide range of target areas, then this would lead to a narrowing of the genetic base of rice across the target area. However, estimating varietal biodiversity by considering only the ancestry of these successful varieties may be misleading. Although the coefficient of parentage between any pair of inbred lines derived from the cross will be 0.5, in reality the genetic dissimilarity between lines for two contrasting environments, e.g. upland and irrigated conditions, is expected to

be higher. Divergent selection for adaptation to these two contrasting environments will result in the fixation of different alleles at loci determining adaptation. Moreover, if the recommended method of choosing parents in PPB is followed – using a locally adopted parent – then the Kalinga III \times IR64 cross targets only a small area in Nepal where Kalinga III has been adopted for specialized niches in the February-sown (*Chaité*) rice crop in Nepal. In the PPB programme in Nepal, crosses have also been made to the most important *Chaité* rice, CH45, and the most important main-season rice, Masuli.

Only a few examples of many PPB breeding programmes in rice are described above. The amount of diversity generated by decentralized breeding programmes will depend on the extent of decentralization, i.e. the number of programmes, and on the genetic diversity among the parental germplasm used by those decentralized programmes. However, PPB programmes are still too new and insufficiently widespread for any conclusions to be made on the pattern of varietal diversity that is likely to emerge from them.

Second Cycle Products

It is simple to select the initial parents for targeted crosses in a first cycle of PPB. The best and most obvious strategy appears to be to cross the most adapted, widespread local variety with a few exotic, high-yielding parents from a centralized breeding programme that are carefully selected for having complementary traits (Witcombe *et al.*, 1996). The need for exotic, high-yielding cultivars emphasizes how PPB and centralized breeding complement each other and how there is a continuing need for both of them. PPB can be regarded as adaptive breeding (adapting germplasm for specific target environments), whereas centralized breeding is more strategic (generating novel widely adapted germplasm).

Once farmers accept varieties produced from the first cycle crosses, the most obvious crosses in the second cycle of PPB will be between the best varieties produced in the first cycle of PPB and the latest farmer-adopted releases, i.e. the most elite material from centralized breeding. From a viewpoint of maintaining genetic diversity, attention needs to be paid to minimizing the relatedness of parents from the centralized breeding programme that are used in the first and second cycles. Nevertheless, since the use in the initial crosses of the first-cycle locally adapted parent will also appear in the pedigrees of varieties produced in the second cycle, this will inevitably result in a degree of genetic relatedness between them.

Similar, but less compelling, arguments could be found for a reduction in varietal diversity with conventional breeding. Very popular, widely adapted varieties will tend to be used often as parents and occur in the ancestry of many varieties. However, because local adaptation is not a major criterion for parental selection in centralized breeding programmes, and because many crosses tend to be made in such programmes, new varieties can be genetically distant from the varieties that they replace. For example, HD2329 was the most widely grown wheat cultivar in the Indian Punjab from 1987 to 1996 and, in the space of 3 years, 1997 to 1999, was largely replaced by PBW343 to which it is effectively unrelated (Joginder Singh, Punjab Agricultural University, personal communication).

PPB and Centralized Breeding are Complementary Strategies

Centralized breeding and decentralized participatory breeding can support each other because they utilize different types and ranges of germplasm as parents. Parental choice in centralized breeding can be limited by the need to target mega-environments or entire agroecological zones. Hence, many local landraces would be expected to contribute little or nothing to wide adaptation, but would be ideal parents for the target micro-environments of a PPB programme. Often these will be socioeconomic niches, such as the preference by some farmers, whose livelihoods are more dependent on livestock, for higher straw yields and straw quality rather than simply higher grain yield. On the other hand, in no decentralized PPB programme can anything but a tiny fraction of the available genetic resources be screened, and decentralized programmes cannot enter into strategic breeding that broadens the genetic base by using wide crosses between cultivated and wild species. Such wide crosses have been extremely important in broadening the genetic base of rice and wheat, and much of this work has taken place in centralized breeding programmes in IARCs. Recent examples include the use at the West Africa Rice Development Association (WARDA) of *Oryza glaberrima* in the improvement of *Oryza sativa* (Jones *et al.*, 1997); the introduction of chromosome segments of distantly related species of rice into cultivated rice (Brar and Khush, 1997); and the use at CIMMYT of synthetic hexaploids in wheat breeding derived from crosses between tetraploids and a diploid ancestral species (e.g. Villareal *et al.*, 1996). These wide crosses introduce into the cultivated species novel resistances, in most cases against pathogens, and often the crosses increase the genetic yield potential of the cultivated species.

Partnerships between centralized breeding and participatory plant breeding are needed. However, institutional issues determine how these two approaches can be integrated. For example, in WARDA, progeny from the tissue-culture-facilitated interspecific cross have been entered into participatory trials (WARDA, 1999). Here both the strategic (base-broadening) breeding and participatory varietal selection that broadens the deployed genetic base in farmers' fields are carried out by the same institution. In other cases, the partnership is simply by utilization of germplasm, e.g. where an NGO or national programme uses CGIAR-bred material in crosses to locally adapted and locally distributed germplasm. In the long term, partnerships between centralized breeding and collaborative, participatory breeding can produce the best germplasm and the broadest genetic base in farmers' fields.

Conclusions

Participatory plant breeding (PPB) is increasingly being used in both inbred and open-pollinated crop species. By definition, PPB has significant farmer participation but it also involves decentralization of the breeding process from research station to farmers' fields. From the viewpoint of broadening the genetic base of crops, both decentralization and participation are important. Decentralization, irrespective of the degree of farmer participation, can provide greater diversity than a centralized system. Participation by farmers, particularly when it is collaborative, can result in much greater diversity in the fields of collaborating farmers, and provide a broader range of promising genotypes.

A common strategy in PPB will be to cross locally adapted landraces with genetically unrelated high-yielding varieties from centralized breeding. In subsequent cycles of plant breeding, because locally adapted material will tend to be used as one of the parents, there is an increasing likelihood of genetic relatedness between the products of different cycles.

Decentralization will allow genetic diversity between programmes if they depend on different parental germplasm. However, some varieties, even those for marginal environments, can be widely adapted, and several decentralized breeding programmes could all choose the same widely adapted parent, for in each area in which it is cultivated it will have local adaptation.

Only centralized breeding programmes can undertake strategic research that is designed deliberately to broaden the overall genetic base of crops by, for example, screening perhaps thousands of lines from *ex situ* germplasm collections or by using tissue-culture-facilitated wide crossing. Hence, centralized programmes are involved in strategic research while PPB programmes are at the adaptive end of the research spectrum. Since these strategies will tend to complement each other, neither approach should be adopted exclusively.

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27 **Base-broadening for Client-oriented Impact: Insights Drawn from Participatory Plant Breeding Field Experience**

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Introduction

Broadening of basic germplasm pools can only achieve its goal of promoting agricultural stability if the products are actually sown and resown by farmers on a significant scale. To achieve this end, varieties developed from based-broadened pools need to meet certain criteria: (i) they have to be adapted to farmers' local growing conditions; (ii) they must meet farmers' preferences¹; and (iii) they have to remain accessible to farmers on a sustained basis, that is, in both the short and longer term. In practice, 30–50 years of fundamental base-broadening research will have little value if the resulting primary products remain solely in researcher-controlled fields, laboratories and genebanks. To anticipate some of the more downstream challenges implied by upstream base-broadening work, research and development (R&D) strategies need now to be tested and targeted for widening the base of germplasm use at the 'bottom', among end-users in rural communities. Strategies need to be contrasted and compared to ensure that diverse germplasm pools can provide varieties that are locally adapted, farmer acceptable and farmer accessible.

Current breeding pools offer greater variability than actually reaches the end-user. Further, out of hundreds of varieties in any single national agricultural research system

(NARS), farmers typically receive a handful to be tested each season. For instance, in Rwanda, the initial experimental set of about 250 cultivars narrows down to three to five entries in on-farm trials (Sperling *et al.*, 1993); in Syria (S. Grando, personal communication), a pool of 200 is narrowed down to three or four; and in India (pearl millet), 30–80 entries may enter preliminary yield trials, with one or two reaching farmers only after official release (E. Weltzien, personal communication). The current narrow provision of materials to farmers offers fertile opportunity for testing the principles of ‘local-level base-broadening’ – in anticipation that even wider pools may be available in a ‘base-broadened future’.

This chapter first briefly describes an emerging novel field, participatory plant breeding (PPB), which has among its central aims broadening the diversity of germplasm available to and used by farmers. In practice, upstream base-broadening efforts will have to be linked integrally to ‘compatible’ or ‘like-minded’ downstream R&D field programmes – if diverse and novel products are to be sown in thousands of site-specific contexts. PPB offers one such ‘like-minded’ paradigm, as programmes tend to work very interactively with farming communities and often build in capacity for continued evolution of both genetic materials themselves and farmers’ skills to manage such materials.

Drawing from a large body of actual field experience, this chapter summarizes some of the lessons learned from PPB in terms of meeting the three fundamental principles of adaptability, acceptability and accessibility. While there is accumulating evidence to enhance our ability to meet these three preconditions, and thus to inform the design of base-broadening programmes, critical knowledge gaps remain. As such, each section of this chapter integrates analysis of ‘steps made to date’ with those that ‘still need to be pursued’. Through such reflection, the chapter suggests a practical farmer-level research agenda for enhancing our capacity to widen the base of farmers’ germplasm use.

Overview of Participatory Plant Breeding²

What is PPB?

PPB involves scientists, farmers and others – such as consumers, extensionists, vendors, industry and rural cooperatives – in plant breeding research. It is termed ‘participatory’ because users can have a research role in all major stages of the breeding and selection process. Such ‘users’ become co-researchers as they can help set overall goals, determine specific breeding priorities, make crosses, screen germplasm entries in the pre-adaptive phases of research, take charge of adaptive testing, and lead the subsequent seed multiplication and diffusion process (Sperling and Ashby, 1999). The fundamental rationale for a PPB programme is that joint efforts can deliver more than when each actor works alone.

While some have cogently argued that commercial, private-sector, plant breeding has long been client-driven, or ‘participatory’ under another name, the application of PPB to reach poor client groups, to breed for high-stress, heterogeneous environments and to incorporate diverse traits to meet specific client preferences results in fundamental changes in the way in which plant genetic resources are managed by formal breeding

programmes and farmers. It makes sense, therefore, to analyse PPB as a new approach to germplasm development, especially in the public sector. The Consultative Group on International Agricultural Research (CGIAR) Program on Participatory Research and Gender Analysis for Technology Development and Institutional Innovation (SWP/PRGA) currently has detailed documentation on 65 PPB programmes and projects (Hecht, 1999; McGuire *et al.*, 1999; Weltzien *et al.*, 1999). Most of the cases, whether located in public sector or non-governmental organization (NGO) crop improvement programmes, were begun in the 1990s.

Under the PPB rubric, two broad approaches have been defined: when farmers join in breeding experiments that have been initiated by formal breeding programmes ('formal-led PPB'); and when scientists seek to support farmers' own systems of breeding, varietal selection and seed maintenance ('farmer-led PPB'). Both formal-led and farmer-led work may prove key for enlarging the base of germplasm accessed, modified and evolved through use in farming communities. Table 27.1 indicates the range of crops on which PPB programmes have been initiated, as well as proposals received by the SWP/PRGA. Given its relatively short history, the range of crops is impressive – although few can be considered 'minor'.

Table 27.1. Crop foci of PPB programmes to date.

Crop	Formal-led	Farmer-led	PRGA small grant submissions
Barley	*	*	*
Bean	*	*	*
Black gram	*		
Cassava	*		
Chickpea	*		
<i>Chaite</i> rice	*		
Cotton	*		
Cowpea	*		*
Lentil	*	*	*
Maize	*		*
Pearl millet	*		*
Potato	*	*	*
Rice	*	*	*
Sorghum	*		
Sunflower	*		
Trees	*	*	
Wheat	*		
Peas		*	*
Sweet potatoes		*	
Faba bean			*
Native potatoes			*
Durum wheat			*
Yam			*
Crotalaria			*

What are the goals of PPB?

PPB programmes can have a diversity of overarching goals. The most common goal has been to contribute to increased production in farmers' fields and increased farmer incomes through the development and enhanced adoption of suitable, usually improved varieties. These are the basic goals of any formal-led breeding programme, and participatory approaches are often experimented with to achieve these goals more effectively and more efficiently. In this context, PPB programmes sometimes seek to refine their knowledge of farmers' needs or preferences or re-orient general breeding directions, such as the type of germplasm used, the priority traits sought, and the management of both on-station and on-farm trials.

Enhancement of crop diversity on-farm is another broad goal towards which some PPB programmes strive. Participatory breeding programmes having this goal tend to work more often with the farmers' own germplasm or a combination of local and exotic materials. Many also involve farmers in the screening of a wide range of varieties in the pre-adaptive stages of research, either in on-station trials or in community plots. In several cases, PPB programmes have also released populations or have purposely promoted breeding strategies that result in heterogeneous materials. Chapter 26, this volume, by Witcombe discusses this subject further.

Another important goal of PPB programmes is to provide benefits for specific types of users (e.g. the rural poor, women, farmers with marginal soils) or to address deliberately the needs of a broader range of users. Such a goal necessitates an extensive diagnosis among well-defined types of potential user and stakeholder groups.

While addressing issues related to improved adoption of breeding products and/or enhancement of crop diversity, PPB programmes often find themselves confronted with the need to address modifications in policy, whether these be seed regulations or variety release criteria and procedures. Most modifications are sought to accommodate expansion and institutionalization of approaches that better serve farmers' aims. These may include modifications in the scale of testing and the scale of desired variety adaptation, the kind of data required for release, and the number of varieties released at any one time (see Louwaars, Chapter 5, this volume).

Finally, some programmes specifically work towards enhancing the farmers' own breeding process, i.e. providing technical knowledge and insights so that farmers themselves are more successful in their own selection and seed production efforts. This skill-building goal is often addressed together with a more general effort towards strengthening the capacities of farming communities to demand and derive benefits from the formal research institutions.

Overviews of PPB programmes show that, to date, primary goals set largely parallel those of classic breeding research: to increase production or increase the value of products through enhanced quality traits. However, an impressive 20% of PPB projects also have as an explicit goal varietal diversity enhancement in farmers' fields (McGuire *et al.*, 1999; Weltzien *et al.*, 1999). The strengths, shortcomings and overriding challenges of PPB programmes very directly herald those which might be expected to enrol in more general local-level base-broadening initiatives. Developing strategies for rendering adapted, appreciated and accessible materials to farming communities lies at the heart of both PPB and base-broadening work.

What are the environments in which PPB unfolds?

Based on an inventory of about 65 formal-led and farmer-led PPB cases, maps are being devised to indicate the range of environments in which PPB unfolds. One parameter of the conceptual map describes the type of agroecological context. This has been constructed on a scale for environments from high stress to low stress based on actual vs. expected yields coupled with an index for incidence of crop failure. Agroecological environments potentially range from those that are primarily subsistence-oriented and highly unstable, to systems in which crop production is predictable, highly controlled, and often shaped by significant input use.

The second parameter suggests the broad economic environment of PPB, that is the degree of 'homogeneous demand versus heterogeneous demand' for varieties. Mapping was based on a scale of 1 to 10 according to the leniency/narrowness of varietal characteristics demanded by end-users and the similarity/discordance between varieties' use for home consumption and for sale. Contexts at the higher end (for example, 8 or 9) tend to correspond to a high degree of homogeneity in product and often favour a narrow range of grain, taste and cooking types. Such a strong degree of uniformity is often associated with contexts where farmers are producing for highly specialized markets.

Many plant breeders consider PPB as most appropriate for environments that are high-stress ('marginal') and where agriculture is low-input (i.e. where 'adaptability' is the key issue). Certainly, conventional breeding has been less effective in such difficult environments and in reaching farmers with few resources; so the rationale for testing 'participatory approaches', which are often site-specific, is a solid one. Analysis of actual PPB cases, however, shows a more complex picture. Not all PPB is concentrated in high-stress environments with low-input agriculture. An unexpectedly large number of PPB programmes are being initiated in the intermediate areas where agroclimatic stress is less severe (Fig. 27.1). On the whole, these are cases where quality concerns, i.e. meeting exigent end-user preferences, is defined as the paramount challenge: acceptability is key. Figure 27.1 also shows that a significant amount of PPB work is now occurring in low-stress areas (Green Revolution-type zones) where homogeneous end-user preferences are well defined in the market (for example, the Nepalese Terai: J. Witcombe, personal communication). Two reasons explain most of the cases in these areas. First, some of these PPB programmes aim to expand intracrop varietal diversity in what have become relatively uniform farming areas. Secondly, some programmes are run by NGOs or organized farmer groups with the primary goal of helping communities gain greater control over their breeding process or seed supply (McGuire *et al.*, 1999, Salazar, Chapter 7, this volume). In these sites, the operative driving PPB principles are of increasing 'control' and 'accessibility' over germplasm and germplasm processes.

While the three prerequisites of PPB are integral to each programme, this broad look at the environments of PPB suggests that the weight of each may vary by site. In the harshest zones, adaptability is the prime criterion to be met – that is, getting something that grows. In the mid-potential zones, identifying adapted germplasm is often of equal challenge to finding something that addresses producer and consumer needs (i.e. is acceptable). In the higher potential areas, acceptability holds some weight, but control over breeding and diverse breeding materials (i.e. accessibility) may lay at the base of many PPB programmes.

	Unfavourable	Favourable		
Market integration	Commercial	<p>CORPOICA/CIAT Colombia</p> <p>IRRI/India Partners</p>	<p>CIAT/CIAL/Colombia (beans) PROINPA/Bolivia EAP-Zamorano/Honduras</p> <p>Sokoine/CRSP Tanzania</p> <p>Ethiopia/Awassa</p> <p>Tanzania NARS/CIAT</p>	<p>SE Brazil/EPAGRI USA/popcorn</p> <p><i>CONSERVE/ Philippines</i></p> <p>CAZS/NARC-Nepal PNAP/CIP/Rwanda <i>USDA</i></p> <p><i>Guanxi</i></p>
	Market integration	<p>IRRI India partners EMPMF NE Brazil</p> <p>KRIBHCO/ODA India</p>	<p>PNL/CIAT Zaire</p> <p><i>BBA/India</i></p> <p><i>UPWARD/Philippines</i></p> <p><i>SAVE/Sierra Leone</i></p>	<p>ICRAF/Burundi (trees)</p>
	Subsistence	<p>NARC/DFID Nepal <i>REST/Ethiopia</i> ICARDA/Syria CIMMYT Mexico Sure/ICRISAT India</p> <p><i>Guanxi</i> Narendra Dev/India IER/KIT Mali ICRISAT/Namibia</p>	<p>ISAR/CIAT/COOIBU Rwanda</p>	

Fig. 27.1. Environmental contexts of PPB programmes.

Germplasm Adaptability at the Local Level: Lessons from PPB Field Experience

It is now widely accepted that to identify adapted varieties in the majority of the world's farming communities, much of the selection has to be done, on-site, under comparable agroecological and farmer management conditions. For example, Ceccarelli (1994) highlights the importance of genotype \times environment crossover between farms and experiment stations, advocating testing under more typical conditions to develop varieties that perform best locally with stable yield over time (Ceccarelli *et al.*, 1991). This is a basis for early decentralization and selection under low-input conditions in the barley programme at the International Center for Agricultural Research in Dry Areas (ICARDA) (Ceccarelli *et al.*, Chapter 6, this volume). In the overview paper

on formal-led PPB (Weltzein *et al.*, 1999), many researchers cited high-stress, 'marginal conditions' (including low or erratic rainfall, unpredictable highland climates or low input due to remoteness) as a reason for employing participatory approaches in their programmes. After 15 years of breeding work with little farmer adoption, cassava breeders in a region of Colombia with poor soils and 800–1000 mm rain used PPB to quickly release three farmer-tested varieties. While some varieties identified through highly decentralized testing meet adaptation needs only in specific niches (see Sthapit *et al.*, 1996), others prove to be surprisingly widely adapted (Witcombe *et al.*, 1999). Obviously much depends on how representative the selection is and the heterogeneity of user preferences in surrounding zones. While, in principle, the need for site-specific screening is widely accepted, guidelines for the 'degree of decentralization' necessary (Witcombe, 1996) still have to be elaborated.

Those who use PPB specifically to enhance varietal diversity on-farm (both phenotypic and genetic diversity) face two sets of major challenges to putting into operation decentralization on a broad scale. These challenges will lie similarly at the core of most local-level base-broadening programmes.

Technical approaches to decentralization

The first set of challenges centres on general technical approaches to enhancing varietal diversity at the community level. Theoretically, diversity can be broadened through several strategies:

1. Many fixed lines can be proffered for screening in community-based plots. Farmers can then individually select lines which they project will perform well on their own farms and carry on all further home-based testing. This approach worked quite well in Rwanda, where 21 new bean phenotypes were adopted among three communities in a 3-year period (Sperling *et al.*, 1993).
2. Segregating materials or 'scientifically enhanced populations' can be made available to farming communities who themselves then guide the subsequent adaptation and selection. Berg (1996) describes the theory of this process, drawing from the famous experiment with composite cross populations of barley at the University of California at Berkeley (Allard, 1988, 1992; Soliman and Allard, 1991; see also Ibrahim and Barrett, Chapter 15, this volume). There, populations were exposed to natural selection over many generations and eventually showed good disease resistance and yield stability – although not high yield potential *per se*. In practice, excellent results were achieved in Nepal in identifying adapted and farmer-accepted chill-tolerant rice varieties through the placing of segregating (F_3 to F_4) materials on-farm. This work was heavily shaped by both researcher and farmer input (Sthapit *et al.*, 1996). In another case, in the Philippines, breeders gave F_3 to F_4 rice materials to farmers, with subsequent selection left entirely to communities to F_7/F_8 . The advantages of such a schema is that it is easy to run and can be encouraged at many locations (Witcombe, 1996).
3. A third strategy might focus on upgrading local material itself (in terms of various traits) through recombinations/introgression. This is commonly employed across classic breeding programmes – but is a lengthy and costly process.
4. A focus of 'diversity enhancement' might also be on skill-building itself, rather than

on supplying germplasm. An experimental programme run by Zamarano and Cornell University for farmers from Honduras, Nicaragua and El Salvador considerably honed participants' ability to select and manage maize seed (Gomez, 1995; Gomez and Smith, 1996).

The point is that there are many different strategies that should be tested at the local level for working with farmers and giving them the means to choose among materials or develop and modify varietal materials themselves. The effectiveness of different strategies will probably vary according to such variables as farmer breeding/selecting skills (often related to the degree of previous exposure to diverse materials), the narrowness/laxity of the market environment, and the agroecological 'flexibility' (i.e. there may be few options in the harshest locales). Programmes need to be set up to compare and contrast different approaches simultaneously – and at a scale that allows lessons to be learned. Ultimately, we need sharpened insights into which base-broadening approaches are best for which ecological and socioeconomic environments.

Organizational issues in decentralization

The second challenge revolves around organizational aspects of the base-broadening enterprise. To date, there has been very little work exploring the organizational options for decentralization across many sites (namely the work of the local committees for agricultural research (CIALs) in Central and Latin America, Ashby *et al.*, 1999). This gap is glaring as it is generally believed that client-oriented programmes have to be decentralized to have local-level impact – simply because farmers have differing needs specific to their own agronomic and socioeconomic situations.

Effective decentralization of varietal testing is a task beyond the resources of most public-sector research services: in practice, most NARS' budgets are declining. Might NGOs possibly have an edge in decentralizing efforts – in just one or two communities? And what are the prospects for NGO scaling up? Might the farmer field school (FFS) model be a useful one to link with participatory and decentralized programmes? (The emphasis on skill-building in the FFS approach might be particularly relevant for these innovative breeding efforts.) Would organized groups of farmers have the comparative advantage in leading local testing – and for scaling up? Unless local-level programmes' efforts can enlarge their scale, they remain but interesting, perhaps productive, single-site experiments.

To date, within the field of PPB, there are relatively few cases where the process has been scaled up through the creation of multiple decentralized programmes: that is, where the process of PPB work actually takes place at different sites independently. The CIALs described above are one exception: as of 1999, about 250 CIALs, farmer research committees, in several countries have engaged in independent variety testing on a range of crops (A. Braun, personal communication). Another example of this is PPB work with cassava in Colombia developed around farmer cooperatives dedicated to drying cassava chips: in its 10 years, many cooperatives have been involved and in 1999 alone, the programme (assisted by the Corporación Colombiana de Investigación Agropecuaria (CORPOICA) and the CIAT) is working with 13 different communities (C. Iglesias, personal communication). PPB work in Rwanda also expressly experi-

mented with different 'organizational options' for decentralization, comparing the strengths and weaknesses of collaborating with the formal extension service, women's cooperatives and self-organized farmer research groups (Sperling and Scheidegger, 1997). Evaluation or assessment of organizational options is one of the large and almost total gaps in current PPB work. The choice of collaborators largely determines how much the process can be scaled up and the technical divisions of labour, i.e. devolving responsibility and deciding who does what. The choice of collaborators (and the scale on which one works) also directly influences the cost of the PPB work, both overall, and the cost and benefits for each partner.

It is important to emphasize that almost all scaling-up work in PPB has been done in programmes working with stabilized materials. When one considers generation of genetic variability and selection in segregating populations, there are few examples of farmer participation and all are with very small numbers of farmers (just one to ten). Whether scaling up of farmer participation in these activities is necessary depends on the extent to which they can be centralized while still effectively addressing varietal needs over a broad area (Weltzien *et al.*, 1999; see also Ceccarelli *et al.*, Chapter 6, this volume).

To anticipate base-broadening work, there is a fundamental need to identify decentralization options. Chapter 13, this volume, by Goldringer *et al.* illustrates the potential role of high schools and agricultural colleges in decentralizing formal base-broadening programmes. Most likely, if they are to be cost-effective, they will have to be farmer-initiated and managed. However, this has to be examined systematically. Which organizational forms can handle which type of technical, decentralized experiments? What are the costs and for whom? What are the short-term and longer-term effects on farmer-held diversity?

Germplasm Acceptability at the Local Level: Lessons from PPB Fieldwork

It is easier said than done to identify appreciated varieties. Simply said: adaptation, which is often mistakenly equated with yield, is *not* an adequate predictor of adoption. An increasing number of studies show that traits other than yield strongly affect farmers' cultivar choice (e.g. Haugerud and Collinson, 1990; Nazarea-Sandoval, 1995).

Varietal traits farmers deem important

A great deal of qualitative evaluation has been generated within the course of PPB evaluations. In an overview paper synthesizing some of the critical social issues and analyses associated with PPB work, 54 criteria were highlighted as being routinely cited by farmers in their construction of ideotypes (Hecht, 2001). Table 27.2 outlines the elements mentioned by farmers across crop types, with the broad categories synthesized as 'environmental', 'agronomic' and 'cultural' trait groups. In her thought-provoking social analysis, Hecht comments that slightly fewer than half of these 54

Table 27.2. Farmer selection criteria.

Environmental criteria	Agronomic criteria	Culture, production and use	Ancillary features
Tolerant of soil limitations (fertility; variable water conditions; textural variability)	General (intercropping ability; shade; tolerance; flowering characteristics; dormancy features)	Labour demand (germination characteristics; planting ease; cultivation; weeding; harvesting)	Quality and palatability of leaves for humans
Tolerant of climatic factors (heat; cold; wind; rainfall variability)	Yield (earliness of production; plant form)	Processing (ease of (dehulling; pounding; peeling; milling; humidification; breakage characteristics)	Quality and palatability of leaves for animals
Biotic pressures (insect pests; animal pests; human predators; weed; competition; weed suppression)	Tuber distribution	Culinary (taste; texture; aroma; quality of broths	Calibre of stover fodder
Disease tolerance	Flexibility in planting and harvest	ritual uses; nutritional factors; quality in fermented products)	Ratooning ability
	Crop morphology (size of tuber, grain or cob (bigger is not always better); shape of plant; tillering habits; colour)	Storage	Craft uses of fibres
		Exchange utility	Mulch materials
		Commercial utility	Staking materials
			Construction materials

Source: Hecht, 2000. PRGA Programme.

traits are related to post-harvest, labour, ancillary, culinary or storage features – that is, the ‘cultural’ dimensions of crops. This suggests that farmers, especially women farmers, value these characters a great deal, since these are often highly gender-specific tasks (such as processing). These latter characteristics have rarely been taken into account in the usual pathways of technology development.

Salient among the various farmer criteria cited within PPB evaluations were the following:

1. Cultivar performance in intercropped systems.
2. The importance of ancillary products as food for both humans and animals.
3. Earliness of production.
4. Labour demand characteristics.
5. Post-harvest processing concerns.
6. Culinary dimensions.

While, yield analysis remains the measure of choice for many agronomists for assessing whether the variety is doing well (with some moving toward the measure of yield stability), the data from the participatory evaluation trials suggest other factors pertaining to household needs (i.e. early yield, ancillaries) labour and cultural demands are probably equally important as agronomic criteria.

Diagnostic methods to determine farmer needs

Accurate diagnosis of what users want and need can be effected through a range of techniques. These can include: farmer screening of diverse germplasm nurseries (Ipinge *et al.*, 1996); detailed analyses of ‘weaknesses’ and ‘strengths’ in the materials farmers are already sowing (Weltzien *et al.*, 1996); and exploratory trials using local and exotic material, which explicitly expose farmers to a wide range of traits and/or ranges within traits (ICARDA, 1994). These methods are in addition to the more common formal and informal surveys, focus group sessions or community meeting assessments. The choice of which method to use seems to depend more on the scale of investigation, money and time resources available, and training of the researchers involved – than on the actual results or degree of detail achievable through any one technique. Despite the importance of accurate diagnoses in guiding the development of a lengthy breeding programme, there have been few critical analyses comparing and contrasting the techniques available (Weltzien *et al.*, 1996). One deliberate focus of a PPB programme currently funded by the UK’s Department for International Development in five sites in eastern Africa and Latin America centres on comparing the results of different diagnostic strategies – within the same communities. It aims to evaluate the type of information received (e.g. specificity on varietal traits and trade-off assessments, insights into different user preferences) with the time, skill and scale on which the techniques can be used (L. Sperling, personal communication). One concern is that most diagnostic techniques can only be conducted on a very local level – with larger-scale diagnostic skills (such as conjoint analysis) demanding highly specialized training. This is a methodological area in which much fundamental work remains to be done – to sharpen both PPB and future base-broadening work.

Differentiating among farmers

Good diagnosis of farmers' preferred varietal traits (ranges of criteria/trade-offs) logically needs to be coupled with sufficient means for distinguishing among farmers: it does matter 'who wants what' – if a programme has aims relating to targeting specific groups of potential users. In differentiating between farmers, the current vogue often dictates a focus on gender differences (women may have different preferences to men) or wealth differences (the poor having divergent needs/wants from the rich).

Field evidence from PPB programmes shows that gender can be an important factor in determining differential preferences, but not always. In Mali, maize evaluations showed men putting production and early maturity as the main criteria, with women focusing on organoleptic and processing aspects (DeFoer *et al.*, 1997). Rice work in West Africa had a similar gendered division, with WARDA (West Africa Rice Development Associations) scientists reporting that men focused on yield and yield-related traits such as plant vigour, while women concentrated on quality attributes, such as bold grains (Lilja and Dalton, 1998). However, in many cases, gender-differentiated evaluations do not yield clear-cut preferences.

Field evidence also shows that wealth can be a key distinguishing factor. The review of formal-led PPB programmes showed a number of trends among the financially disadvantaged. Poor farmers often cited earliness as an important factor in shortening the hungry season and in maximizing production on their small landholdings. Poorer farmers also had important criteria related to multiple crop uses (such as cassava in Colombia, pearl millet in Rajasthan (India) and cowpea in Cameroon), as people relied on non-food parts for animal feed, or seasonal excess processed for the market (cassava flour/Colombia). Where farmers rely on selling some of their products for scarce household cash income, quality criteria proved to be determined more by market demands than by grower preferences. With potatoes in Peru and cowpeas in Cameroon, farmers grow modern varieties as cash crops, and benefit by earning as much as double for products with preferred size, colour or shape (Weltzien Smith, 1999).

However, farmers do divide themselves into groups (or construct images of self-identity) beyond gender and wealth. For example, caste, ethnicity or age may be important in any given region. The methodological concern centres on 'how can we find out which populations differences or "user" differences are really key in shaping preferences?'. That is, farmers may differ by age, wealth, religion and politics but not all of these variables are equally important in determining, say, lentil variety preferences. There is a compelling need to develop and refine diagnostic techniques that can be used at different stages of the breeding process (for example, shaping initial priorities and, at the other end, evaluating finishing lines), which can be used at various geographic scales, and which ensure that different user groups are given a voice.

Germplasm Accessibility at the Local Level: Lessons from PPB Fieldwork

PPB work suggests that the earlier farmers are involved in developing germplasm, the higher the likelihood that the resulting varieties and seed will have to be moved outside of formal channels. This proves to be true for several reasons – and especially if the

work is truly participatory: (i) a large range of varieties may be identified for different kinds of users; (ii) the site-specificity of varieties may discourage formal-sector multipliers from devoting their efforts; (iii) the intravarietal heterogeneity might prohibit formal multiplication; and, if farmer–researcher collaboration is taken seriously and ethically; (iv) undefined or shared property rights would deter more routine multiplication.

Seed system issues

Participatory plant breeding programmes often have to go hand-in-hand with recommendations to develop, or build on, local, more decentralized seed systems, which can provide location-specific varieties that farmers themselves effectively multiply and distribute. For instance, prior to the civil strife in the early 1990s, both Rwanda and Burundi, Ministries of Agriculture and Rural Development proposed plans for decentralizing seed services – partly to accommodate more decentralized breeding (L. Sperling, personal communication). PPB programmes are also increasingly incorporating integrated and innovative seed production components to deliver rapidly the positive impacts that PPB can achieve. Good examples of this type of integration come from the PPB and seed work with cassava in Colombia and with potato in Bolivia, Peru and Ecuador through a set of collaborations between the national seed projects and the International Potato Centre (CIP) (Iglesias *et al.*, n.d.; Thiele, 1999).

Overall, relatively little of the current PPB work ties site-specific breeding with seed multiplication work. Either it is assumed that products will go to formal channels (which has happened only in a single case each in India and Nepal) or it is assumed that local seed systems can handle PPB products well, that ‘varieties diffuse by themselves’.

Formal systems have some obvious constraints. In addition to the four points listed above, formal systems generally deal with a relatively narrow range of crops – and reach out to a relatively narrow range of users. Global estimates show farmers accessing about 80–90% of their seed directly on-farm or through local channels (Cromwell, 1997). For non-hybrids, the figure has sometimes been cited as less than 2% of all seed used by small farmers coming from the formal system (CIAT, 1982).

Proponents of local systems sometimes point to the effectiveness of local-level exchange mechanisms and assert that ‘varieties move themselves’. However, the authors know of few studies that actually assess the efficiency of local systems: how fast they move varieties, if they are equitable, if they can handle many new entries, and if they have wide geographic spread. Rather, one detailed case shows local systems to be: (i) variable in efficiency according to agroecological, socioeconomic environment, and degree of varietal appreciation; (ii) of restricted access – unless varieties are diffused in local markets; and (iii) susceptible to frequent loss of specific varieties – especially if genetic materials are in the early stages of diffusion (Sperling and Loevinsohn, 1993). Local seed systems fulfil a range of functions. They provide information about seed sources, seed availability, and new types of seeds and varieties. They govern the actual flow of seed and affect farmers’ seed security and use of external sources of seed. In many regions with marginal conditions for crop production, regions with a very high seasonal or ecosystem diversity, and for relatively minor crops, local seed systems are the only system that provides seed to farmers, especially to poor farmers.

Each seed system (formal, farmer or something in between) has different strengths and weaknesses, and a base-broadening programme should actively understand the opportunities and limitations in each, rather than just slide into one strategy or another. Choice of seed system should be guided by such questions as:

- What number of varieties will be diffused?
- On what scale is diffusion desired and to which target groups?
- Are the property rights associated with each seed system acceptable to partners?
- Is the final material homogeneous or heterogeneous?

In sum, to accommodate both the products of PPB and other types of base-broadening work, there is a clear need to diagnose/test the ability of local systems, or new intermediaries (e.g. cooperatives), to handle multiple new infusions of material – and to distribute such material widely and equitably. This issue is particularly pressing for the cross-pollinated materials.

Property rights

Joint collaboration should mean joint benefit sharing. At this point, there are no ready-made arrangements or ‘best practices’ that one can suggest to guide the diffusion of materials emerging from farmer–researcher collaborations. Neither the farmers’ rights debates nor the formal breeder-rights discussions fully match the bill.

The SWP/PRGA has recently started work to address property-rights issues within the participatory plant breeding arena. The process is unfolding briefly as follows. Eight to ten typical PPB collaborative type cases have been identified. For each case, analysis is taking place in three realms: (i) existing legal frameworks that might constrain or stimulate the PPB relationship; (ii) associated ethical concerns; and (iii) ‘best practice’ actions emerging from widespread public debate with practitioners.

At the moment, most of the PPB programmes have simply skirted the property-rights issues with two very different strategies: materials jointly developed by formal breeders and farming communities have been fed into the formal variety release and seed multiplication system (not recognizing farmers’ input at all), or the PPB-developed materials have been ‘released’ or ‘let go’ into farming communities – with no official launch of any kind. This has had a positive impact among farmers mostly with self-pollinated crops, where seed increase and quality issues are relatively easy for farmers to manage at their own acceptable levels.

Conclusions and Discussion

The term base-broadening most often conjures up images of longer-term commitments to basic evolutions of genepools. This chapter suggests that the success of base-broadening will be highly contingent on whether farmers’ specific needs for adapted, acceptable and accessible germplasm are met. PPB programmes can provide an array of community-based (and tested) approaches for increasing the adaptation, acceptability/attractiveness and accessibility of base-broadened germplasm.

The research agenda for successful base-broadening needs to be considerably

expanded to include such issues as identification of rigorous user diagnostic methods, effective decentralization options (technical and organizational), and creation/support of farmer-responsive seed channels. Intellectual property-rights issues will also require serious attention and consideration as they could pose significant obstacles to use of base-broadened pools and use of PPB products in general.

In several cases, for many crops, current breeding pools are already wide enough to start testing varied strategies for widening the base of farmers' germplasm use. However, it is not clear that they have been focused strongly enough on adaptation and acceptability/attractiveness for the non-commercial farming sector. Exploratory PPB programmes may be critical for moving base-broadened materials out to thousands of communities. However, they may be equally essential for feeding back critical end-user-oriented information to enhance the likely relevance of upstream base-broadening decisions – for rural populations.

Notes

¹We use the terms 'preferences' and 'farmer-acceptance' in a dynamic sense. Obviously concerns of colour, taste and cooking time would be encompassed in these notions. Equally, however, preferences imply a sense of 'attractiveness'. To be used by farmers, base-broadened pools have to offer advantages not currently available to farmers: novel traits or trait combinations, or better levels of existing traits.

²This section draws from Weltzien *et al.*, 1999, and Sperling and Ashby, 1999.

³As one reviewer noted, one might expect that in isolated, economically marginal areas, accessibility would also be an issue – albeit in a different sense – since formal seed supply systems are rarely operating effectively in such areas.

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Final Statement by Participants in the Rome Workshop on Broadening the Genetic Base of Crops, September 1997

It is widely accepted that future sustainable increases in crop productivity will require, amongst other things, an increased use of plant genetic resources, through plant breeding. Yet, despite the great amount of diversity assembled in collections, and available *in situ* in the world at large, lack of diversity/variation within the particular pools of genetic resources available to breeders and to farmers can often limit progress. For some crops, this can result in yield plateaus, inability to overcome biotic and abiotic constraints, or even crop failure. Historical factors such as domestication and crop movements have meant that, at global and local levels, only a fraction of the potential genepool for some crops has been tapped for agricultural production. For many specific agroenvironments there is an extremely limited pool of adapted germplasm available to farmers and breeders, by comparison with what could be made available to them.

There is a need for the increased use of exotic or unadapted plant genetic resources, and this should be based on a clear strategy that is well founded on ecological principles. But a major problem hindering the utilization of plant genetic resources is that of getting genetic diversity into a form that can be more easily used by breeders and farmers. In fact, much of the germplasm available in the primary, secondary and tertiary genepools of crops is not in a form which is of immediate and direct utility.

Much pre-breeding – or genetic enhancement – work is concerned with the introgression of particular genes or gene complexes conferring identified agronomic characteristics into existing elite germplasm. While useful in achieving particular goals for crop improvement, such approaches have little impact on the overall flow of genetic material into the cultivated genepool of the crop in question. There is a need for well-coordinated programmes on a large scale to broaden the genetic base of identified important crops. This would involve the development of several locally adapted pools of genetic resources, from diverse and previously unadapted material. In a sense, such programmes might re-trace crop domestication or evolution. One approach is to establish composite plant populations by crossing a number of genetically different accessions with a view to maximizing the genetic diversity, and then allowing such populations to progressively adapt to local conditions in a range of different locations,

for each of which a need for novel germplasm or new variability is identified. Some scientists have called this 'evolutionary breeding', where natural selection does much of the early-stage work. While the techniques required are cheap and technically rather easy, long-term programmes – of the order of a decade (though this depends on the crop concerned) – are required to generate tangible results, in the form of material which is readily usable in breeding programmes. This approach is fundamentally different from the introgression of selected characteristics from diverse gene pools into existing usable populations, and is complementary to it.

Crops vary, both by species and by region of cultivation, in the amount of diversity present in the material currently available to breeders and farmers, and hence in the contribution that such base-broadening work could make. Priority crops would have to be identified on the basis of assessments of needs at the global, regional, national and local levels, of the extent of genetic diversity potentially available, and on feasibility. It may be useful to develop sets of indicators and criteria to facilitate assessment of which crops, environments or end-users might benefit from genetic base-broadening. Initially the work should focus on key crop and production situations where diversity is available for selection appears in some way to be an important limiting factor in crop improvement.

The adapted pools of crop genetic resources, developed through base-broadening programmes, can feed into formal plant breeding systems, and into informal crop improvement systems of farmers. For some crops and regions, plant breeders in the formal sector have already found the material developed from long-term composite crosses useful. The products of such base-broadening schemes have allowed them to introduce into their breeding programmes substantial new diversity which is already adapted to particular production environments. Such populations have proved to be useful sources of new adapted combinations of useful characters such as disease resistance, phenological adaptation and stress tolerance.

There is a complementary need to broaden the genetic base of crop production at the farmer's field level. Increased access by farmers to diverse genetic resources, within and between species, would allow increased productivity and resilience of farming systems. Appropriately designed base-broadening strategies could provide adapted material for use in developing cultivars for use by farmers, including poor farmers in difficult environments, and potentially they may also make a valuable contribution to direct farmer-based crop-improvement efforts. Additionally, there is much scope for improving the availability to farmers of potentially useful germplasm that is already available in genebanks and formal plant breeding programmes. Decentralized approaches to plant breeding and varietal selection are particularly important in marginal production areas where there are likely to be benefits from direct selection in the target environment. In turn, decentralized selection efforts through farmer-breeder cooperation may allow the development and rational deployment of a range of varieties specifically adapted to local ecologies. Work of this type could build upon the experience of some 50 existing cases of participatory plant breeding, involving national agricultural research systems (NARS), non-governmental organizations (NGOs), farmers' organizations and the international agricultural research system, and upon the methods and experience in farmer research and education pioneered through the Farmer Field Schools and similar decentralized research approaches (e.g. the local committees for agricultural research (CIALs) in Latin America). In turn this will require institutional support and capacity building at the national and community levels.

Already the world's governments have recognized the need for large-scale broadening of the genetic base of some important crops, both in the FAO Global Plan of Action and through the Convention on Biological Diversity's decision on agricultural biological diversity. They have also recognized, however, that this is a classic 'public good' problem where individual incentives to individual nations, breeders, companies and farming communities to enhance and adapt germplasm for strategic long-term needs are insufficient to mobilize action. Thus long-term cooperative approaches among different countries and institutions are needed in this area, most likely led by the public sector. Indeed, for many staple crops of poor people where there is little financial incentive for the private sector, the public sector has a clear responsibility. Such activities must be founded on scientific, ecological principles, and be developed with the full and meaningful involvement of actors at all levels: local communities, national programmes and institutions, and international organizations. The facilitation and coordination of such long-term cooperative programmes is an area where the Food and Agriculture Organization (FAO), the International Plant Genetic Resources Institute (IPGRI) and the other centres of the Consultative Group on International Agricultural Research (CGIAR) have an important role, indeed a responsibility, to play.

Specific recommendations

FAO should launch a 'Base-broadening Initiative' in close collaboration with IPGRI, other CGIAR centres, the NARS, existing crops networks and other relevant institutions, in order to:

1. Facilitate the establishment of international networks of partners (institutions, individuals) to promote base-broadening projects/programmes, on a crop-by-crop basis (making use of existing crop network structures where possible).
2. Carry out reviews of the state of diversity within the cultivated gene pools of crops of importance to global and national food security, and develop indicators and criteria to identify crops in possible need of genetic base-broadening both globally and nationally.
3. Facilitate, for identified crops, the development of long-term projects and programmes on genetic base-broadening through multipartner approaches.
4. Promote, in collaboration with educational institutions, training in approaches to base-broadening and population genetics, especially for developing-country scientists and students.
5. Recognize, strengthen and build upon on-going management of genetic resources by communities, and take steps to increase the diversity of genetic material available to farmers and rural communities (for example, by promoting stronger linkages between formal plant genetic resource conservation institutions, genetic enhancement and plant breeding programmes with farmers, and exploring the potential, as appropriate, of existing mechanisms such as the Farmer Field Schools developed through the FAO IPM programmes).
6. Promote awareness on the need for and modalities of genetic base-broadening, at policy and technical levels, through appropriate meetings, publications and the Internet.

High priority should be given to these areas by FAO, and the international agricultural research system. They should form a central part of the programme of work of FAO's

Division on Plant Production and Protection. Also, support for these activities should be developed within the joint FAO/IPGRI programme to facilitate implementation of the Global Plan of Action, and in collaborative efforts to implement the CBD's decision on agricultural biological diversity. FAO should actively seek the necessary financial resources for such work, including from extra budgetary sources.

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