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Primary productivity of natural grass ecosystems of the tropics: A reappraisal

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Abstract

Studies of net primary production in four contrasting tropical grasslands show that when full account is taken of losses of plant organs above- and below-ground these ecosystems are far more productive than earlier suggested. Previous values have mainly been provided by the International Biological Programme (IBP), where estimates of production were based on a change in vegetation mass alone and would not necessarily have taken full account of organ losses and turnover. Calculation at three of our sites based on established methodology using changes in plant mass alone (*i.e.* that used by the International Biological Programme, IBP) proved to be serious underestimates of when account was taken of losses simultaneously with measurement of change in plant mass. Accounting for the turnover of material at these three sites resulted in productivities up to five times higher than were obtained using the standard IBP procedure. An emergent C_4 grass stand at a fourth site in the Amazon achieved a productivity which approached the maximum recorded for agricultural crops. In this case, productivity values, when organ losses were taken into account, only slightly exceeded that obtained with IBP methods. The findings reported here have wider implications, in prediction of global carbon cycling, remote sensing of plant productivity and impact assessment of conversion to arable cropping systems.

Introduction

The needs of many of the developing countries of the world to increase food production both for home consumption and for export cash crops are, to varying extents and in the short term prospect, satisfied by destruction of natural ecosystems and replacement by agroecosystems. Although destruction of rainforest for agricultural expansion is well known, other communities of the tropics are also being lost. Indeed the areas with the most pressing needs for increasing arable food production are not the tropical rainforest zones, but the semi-arid tropics where grasslands form the natural vegetation. Tropical grasslands, excluding wetlands, occupy 15 million square kilometres and, in terms of both land area and biomass, are second only to tropical forests in importance (Lieth, 1978). In addition, periodically inundated grasslands, a form of wetland ecosystem, occupy 0.7–1.0 million square kilometres in South America alone, of which one-third is in the Amazon basin (W. J. Junk, pers. comm.).

Cursory examination of productivity figures for arable and natural grassland systems of the tropics might suggest that conversion of land to arable would greatly increase total dry-matter productivity (Buringh, 1980; Lieth, 1978). Knowledge of

these natural ecosystems is based mainly on the International Biological Programme (IBP) studies. As we outline below, the methodology used in these studies may have lead to a serious and variable underestimation of production and turnover of plant biomass in these communities.

A comment, on previous productivity studies

Net primary production (P_n) is the total photosynthetic gain, less respiratory losses, of plant matter by vegetation occupying a unit area of ground (Cooper, 1975; Coupland, 1979; Jordan, 1981; Lieth, 1978; Linhurst and Reimold, 1978; Milner and Hughes, 1968; Roberts *et al.*, 1985). Over any one period, this must equal the change in plant mass (ΔW) plus any losses through death (L), both above- and below-ground (Roberts *et al.*, 1985):

$$P_n = \Delta W + L \qquad (1)$$

Essentially, P_n is the measure of the amount of plant matter available to consumer organisms.

Previously, Bourliére and Hadley (1970) reported net above ground production for 22 tropical grasslands. Their values were based on peak standing dry matter alone, whilst below-ground production was not considered. The most extensive data on the productivity of tropical grasslands is provided by the IBP studies, reviewed by Singh and Joshi (1979). They considered 21 studies (8 published) of net primary production in tropical grasslands of India and Africa. The few estimates of below ground net primary production (BP_n) provided by these studies were obtained by 'trough-peak analysis' of the changes in underground biomass with time (Singh and Joshi, 1979). Essentially, this is a method proposed by Milner and Hughes (1968) for the IBP, and will be referred to as the 'IBP standard method'. In this method, when biomass (W) per unit area was found to increase between harvest intervals, BP_n over the interval was considered to equal the increase, but where W decreases or remains unchanged over an interval between harvests, BP_n is assumed to be 0. The annual BP_n is then obtained by summing the estimates for each harvest interval, *i.e.* the positive increments are summed. For this method to yield a value equal to the actual production, formation of new plant material and death must be separated in time – any overlap of the two processes will lead to underestimation of BP_n. Above-ground net primary production (AP_n) of these tropical grasslands was estimated mainly by 'trough-peak analysis' of live and standing dead material (Singh and Joshi, 1979). This is an elaboration of the 'IBP standard method', where AP_n is determined via a decision matrix (Singh *et al.*, 1975). Positive increments in biomass are summed, as in the 'IBP standard method', but where positive increments in the amount of standing dead coincide with positive increments in biomass, these are also added to the total. This procedure would correct for amounts of material lost through death during periods of biomass increase, if no decomposition occurs – however, since this is unlikely the method will again lead to underestimation. Three assumptions which could seriously influence the estimate of production therefore underlie the procedures used in the IBP studies of tropical grasslands:

1) That during any interval between harvests death of material does not occur if production is occurring and vice versa, i.e. *formation of new organs or parts of organs must not overlap with loss through death of organs or parts of organs.* In mixed grasslands this assumption will fail to take account of the different cycles of growth and death in different species, thus a species which is most productive at the time when total biomass is declining would be ignored. Even in monotypic stands this is obviously a gross over-simplification, since sequential senescence of leaves and tillering patterns mean that old leaves and stems will be dying as new ones form.

2) That P_n cannot be negative, either above- or below-ground, since only positive increments are considered. Since these grasslands are dominated by perennials with underground or surface storage organs significant transfers of assimilate between above- and below-ground components will be expected. For example, as dry or cold seasons approach translocation of matter from the shoots to below-ground storage organs can occur. During this period the above-ground biomass will decline and the below-ground biomass rise. The computational procedures used in the IBP studies would give a positive BP_n and zero AP_n, and therefore a

positive total P_n, even though in reality no new material is formed, but existing material reallocated.

3) That all increases in biomass represent P_n. Variability in biomass over the study sites will mean that the average biomass recorded on different dates may vary simply because of random fluctuations in the samples obtained. An apparent positive increment in biomass between two dates could result simply by random chance and although over the year these random fluctuations may be self-cancelling, selection of only positive increments in calculating P_n, will mean that the greater the variability between the samples the greater the overestimation of production (Singh, *et al*, 1984). Singh *et al.* (1975) in their analyses of the US-IBP grassland productivity studies suggest that this error may be compensated for by only including positive increments where the biomass on one sampling date is significantly greater ($p < 0.1$) than on the previous sampling date. However, this will mean that small, but real increases in biomass may go undetected. In a relatively uniform natural coastal grassland, Hussey and Long (1982) found that harvests of 40 quadrats, of the optimum sampling size, placed by a randomised design were necessary to provide a mean estimate of biomass with a standard error within 10% of the mean. Thus, even at this level of sampling a 25% increase in biomass between two dates would not be statistically significant. In the IBP tropical grassland studies sample numbers were considerably lower, *e.g.* 10 quadrats per harvest (Singh and Yadava, 1974).

Assumption 1 would therefore lead to underestimation of P_n, assumption 2 to overestimation and assumption 3 without statistical restraints would also lead to overestimation, but with statistical restraints could lead to substantial underestimation. However, despite these theoretical objections Singh and Joshi (1975) in an analysis of some 30 methods of computing P_n as applied to the data gathered for U.S. grasslands in the IBP studies, concluded that the 'trough-peak' analyses used in calculating P_n in the tropical grassland studies, and many other IBP grassland sites, were among the best procedures. Determination of actual net primary production would require correction of change in biomass for losses due to death, as defined in Equation 1. Losses (L) may be measured by correcting the change in dead vegetation mass between sampling intervals by the amount lost due to decomposition measured by use of litter bags or labelling of dead material (Roberts *et al.*, 1985) or by direct observation of organ death (Jackson *et al.*, 1986). Methods based on simultaneous measurement of ΔW and L of Eqn. 1 make none of the assumptions made in the IBP standard method and other 'trough-peak' analyses. No such method was included in the comparisons made by Singh *et al.* (1975) who only considered methods in which it was assumed that production could be estimated from changes in vegetation mass alone. Methods were evaluated on their ability to discriminate between different grasslands and although 'trough-peak' analysis methods were favoured, it was noted that all methods were closely correlated and that a constant correction factor could be used to relate different methods. For example, multiplication of P_n estimated from the peak biomass method by 1.41 would give P_n as measured by the 'IBP standard method'. Linthurst and Reimold (1978) compared P_n estimated for three U.S. coastal grasslands obtained from peak biomass, as used by Bourliére and Hadley (1971), and from the 'peak-trough analysis', as used by Singh and Joshi (1975), with a method in which P_n was calculated from change in biomass corrected for simultaneous losses through death. Two important conclusions can be reached from this work. 1) That P_n estimated by both use of peak biomass and 'trough-peak' analysis seriously underestimated P_n, by 50%–85% and by 10%–70%, respectively. 2) That the degree of underestimation varied markedly with location and with species composition and that there was no constant conversion factor. This conclusion is in sharp contrast to that of Singh *et al.* (1975), but unsurprising in view of the fact that the errors accruing from the three assumptions underlying the IBP methods will vary independently. Similar conclusions may be drawn from other comparisons of methods made in temperate grasslands (Hofstra and Bradbury, 1976; Long and Mason, 1983). These findings bring the IBP estimates of primary production in tropical grasslands into question, not only may these be serious underestimates, but they may even fail to rank grasslands correctly in terms of their actual productivity. Although the potential

errors in the methods used in most of the IBP studies of grassland P_n were well recognised (Cooper, 1975; Coupland, 1979) the degree of underestimation was not quantified; this would require application of the IBP standard methods and methods correcting for losses on the same vegetation. Overestimation of P_n further affects understanding of ecosystem functioning in tropical grasslands, since the estimates of P_n provided the basis for the extrapolation to rates of vegetation death and decomposition in the IBP syntheses of tropical grasslands (Singh *et al.*, 1979).

This study determines productivity using methods which allow correction for simultaneous losses of biomass through death, both above- and below-ground (Roberts *et al*, 1985) in four tropical grasslands and provides a basis for examining the extent to which previous methodology may have underestimated production.

Study sites

Details of the four study sites are summarised in Table 1.

Site 1: Kenya .

This site was typical dry savannah grassland within the Nairobi National Park. Rainfall is bimodal with the major rains falling in May and a secondary peak of rainfall in October. Growing seasons are normally May–August and October–December. However, in 1984 (immediately preceeding this study) the May rains failed. The site was protected by an exclosure, but would normally be lightly grazed by wildebeest and other game animals. Similar land in Kenya is currently being ploughed for sorghum, cotton and pineapple production.

Site 2: Thailand

Measurements were made at the Prince of Songkhla University field site at Klong Hoi Khong, about 40 km from Hat Yai. The climate here is wet monsoonal, with maximum rainfall in October–December and a brief dry season in February/

March. The site is a semi-natural humid grassland with occasional stands of dipterocarp trees, typical of grassland found throughout southern Thailand. A grass community is maintained by periodic burning. To avoid complications in determining productivity, the site was protected by a fire-break for the duration of this study. This site is now a relict of the original grassland, the surrounding land having been cleared for production of rice, sorghum and a variety of other arable crops.

Site 3: Mexico

The site was a saline grassland at the Colegio de Postgraduados field site, Montecillos (about 50 km from Mexico City). The climate is dry sub-humid, with maximum rainfall in July/August and a dry season from December to February. The study area contained an almost pure stand of a halophytic grass. The grass community is maintained by burning, every 2–3 years.

Site 4: Brazil

The study site was a stand of emergent macrophyte vegetation on the island of Marchantaria, about 40 km from Manaus. This has a tropical rainforest climate, uniformly warm, with heavy rainfall except during a short drier season from August to September. Seasonality of vegetation growth is determined predominantly by the river level rather than by climate, the growing season coinciding with the period of inundation. Many of these sites are now burnt in the dry season and planted to arable crops which can be harvested before the sites are flooded during the next wet season.

Methods

Sites 1, 2 and 3

To determine P_n, following the definition of Equation 1, changes in biomass were measured at monthly intervals. Dry weight of both live and dead vegetation present at each site was determined monthly by clipping to ground level, sets of 20

Table 1. Site descriptions

Terrestrial grasslands	1. Montecillos Chapingo Mexico	2. National Park Nairobi Kenya	3. Klong Hoi Kong Hatya Thailand	4. Marchantaria Manaus Brazil
Location	19°28′N 98 55′W	1°0.5′S 36 49′E	6°0′N 100 56′E	03°20′S 60°00′W
Elevation (m)	2220	1500	100	20
Precipitation (mm yr^{-1})	700	950	2100	3130
Average monthly temperatures (°C):				
Minimum	12 (January)	12 (July)	27 (December)	26 (February)
Maximum	19 (May)	19 (Feb.)	29 (June)	28 (August)
Solar radiation (MJ m^{-2} yr^{-1})	6810	6500	5970	6410
Soil type	Solonet	Black clay vertisol	Humic gley	Alluvial deposits
Grassland type	Saline	Dry Savanna	Humid 'Savanna'	Emergent macrophyte
Dominant species	*Distichlis spicata* (L.) Greene	*Pennisetum mezianum* Leeke *Themeda triandra* Forsk	*Eulalia trispicata* Henr. *Lophopogon intermedius* A. cam.	*Echinochloa polystachya* Hitche
Common crops on conversion to agricultural use	Pasture	Sorghum Pineapple	Sorghum Rice	Maize

quadrats (0.25 × 1.0 m) located by a randomised block design. Soil cores were removed from the centre of 5–20 of these quadrats, to a depth of 15 cm, and organic material extracted by washing over a sieve of 2 mm mesh. Use of 1 mm and 0.5 mm mesh sizes did not recover significantly greater (t, $p > 0.05$) quantities of live root, but the increased capture of dead matter greatly increased the time required for the sorting of samples. For dead material, ability to pass through a 2 mm mesh sieve was used throughout as the arbitrary division between recognisable dead vegetation and particulate organic matter. Preliminary studies suggested that extraction of soil cores to 15 cm depth was adequate to remove more than 90% of the root system by weight. Above-ground material was sub-sampled to approximately 100 g fresh weight before sorting. Below-ground material was divided into fine roots (ca. < 1 mm dia.) and coarser material. Fine root matter was sub-sampled to 1.0 g and the coarser material sorted entirely.

Live leaves were separated from dead on the basis of tissue necrosis, dead portions being removed from otherwise green leaves. Stems were sorted likewise, taking care to remove dead sheaths from living stems. Roots were divided on a similar basis, using vital staining (tetrazolium salts) where visual discrimination was not otherwise possible.

Tetrazolium staining was cross-checked by microscopic examination of cut root tissues where the results of surface staining were ambiguous. The sorted plant material was then thoroughly washed and dried to constant weight at *ca.* 90°C (Roberts *et al.*, 1985).

Losses of live and dead plant material, L in Eqn. (1), were assumed to be by death and decomposition *in situ*, respectively. Large herbivores were excluded from each site by a fence, where necessary. Thus total loss of material (L) equals the change in dead matter (ΔD) plus the loss due to decomposition (A):

$$L = \Delta D + A \tag{2}$$

The quantity ΔD was estimated every month from the harvested samples. Decomposition losses (A) were determined monthly by litter bags. Decomposition of dead shoot material was measured at the ground surface, whilst for roots and rhizomes the litter bags were inserted 5 cm below the ground, with the soil carefully replaced above the bag to minimise disturbance. A portion of dead material obtained at random from each harvest (approx 2 g) was placed in each of 20 litter bags of 2 mm nylon mesh, 8.0 cm × 6.0 cm, and recovered after one month from the field. Contents were washed over a sieve of 2 mm mesh and dried to constant weight.

Table 2. Quantities of vegetation and rates of its decomposition recorded at monthly intervals

Terrestrial grasslands	Montecillos Chapingo Mexico		National Park Nairobi Kenya		Klong Hoi Kong Hatyai Thailand		Marchantaria Manaus Brazil	
	Shoots	Roots/ rhizomes	Shoots	Roots/ rhizomes	Shoots	Roots/ rhizomes	Shoots	Roots
Biomass ($g\,m^{-2}$)								
Max	430	568	337	195	442	520	6840	460
Mean	279	389	222	109	338	340	4450	218
Min	161	229	32	61	244	205	540	40
Dead vegetation ($g\,m^{-2}$)								
Max	821	896	525	218	1048	188	1140	–
Mean	586	573	352	167	782	109	575	–
Min	273	306	66	128	634	70	40	–
Decomposition rates ($g\,g^{-1}\,mo^{-1}$)								
Max	0.28	0.16	0.18	0.32	0.21	0.46		–
Mean	0.09	0.10	0.12	0.21	0.14	0.27		–
Min	0.01	0.03	0.05	0.08	0.07	0.14		–
Total decomposition ($g\,m^{-2}\,yr^{-1}$)	606	686	454	433	1340	414		–

The loss of material from the bags is a measure of the rate at which a random sample of the dead vegetation at the site at the start of each interval between harvests would decompose over the month. Controls in which the litter bags were filled, taken to the field and then immediately returned and processed showed no significant loss of material.

Relative rates of decomposition were expressed as the proportion of initial dry weight lost within the month. In the context of this study decomposition represents loss of dead material due to leaching, breakdown to small particles ($< 2\,mm$ dia.) and consumption by invertebrates. Total decomposition (A) was estimated as the sum of the monthly products of relative decomposition rate and mean quantity of dead material (Table 2).

Site 4

The cyclical inundation of the study site in Brazil is described by Fig. 3. Due to the large size of the plants (up to 12.0 m long), and since the study area is covered by water except during the three-month low-water season, a different approach to measurement of P_n than that used at the first three sites was necessary.

The vegetation of this site was a monospecific stand of *Echinochloa polystachya.* This species forms unbranched annual stems of up to 60 or more nodes. Monthly harvests consisted of 15 individual plants uprooted for dry weight determination. Harvested material was separated into five categories before drying; live stems, leaves (lamina and sheaths), adventitious roots, dead leaves and dead stems. In addition, a further 20 stems were marked and the monthly increase in length and node number recorded. Uprooted plants and quadrats were chosen at random points along a 100 m transect. Production was then calculated as the product of the number of new nodes and the sum of the mean weights of internodes, leaf lamina and leaf sheaths determined from destructive harvests for that month. Direct estimation of new root production was not possible in plants which grew up through several metres of water. Similarly, estimation of root losses to flowing water would be equally difficult. For this community root production could therefore only be estimated from the sum of the positive increments in root biomass between months. However, since roots constituted only a very small ($< 10\%$) fraction of the plant biomass, we assume that this would not have a large effect on the estimate of total production. Production per plant was then multiplied by the mean number of plants counted in 20 quadrats of 1.0 m square to obtain dry weight per unit area.

Results and discussion

Changes in biomass at the first three sites are illustrated in Fig. 1. At all sites living shoot material could be found in every month of the year. On average 50% of the biomass was constituted by undergro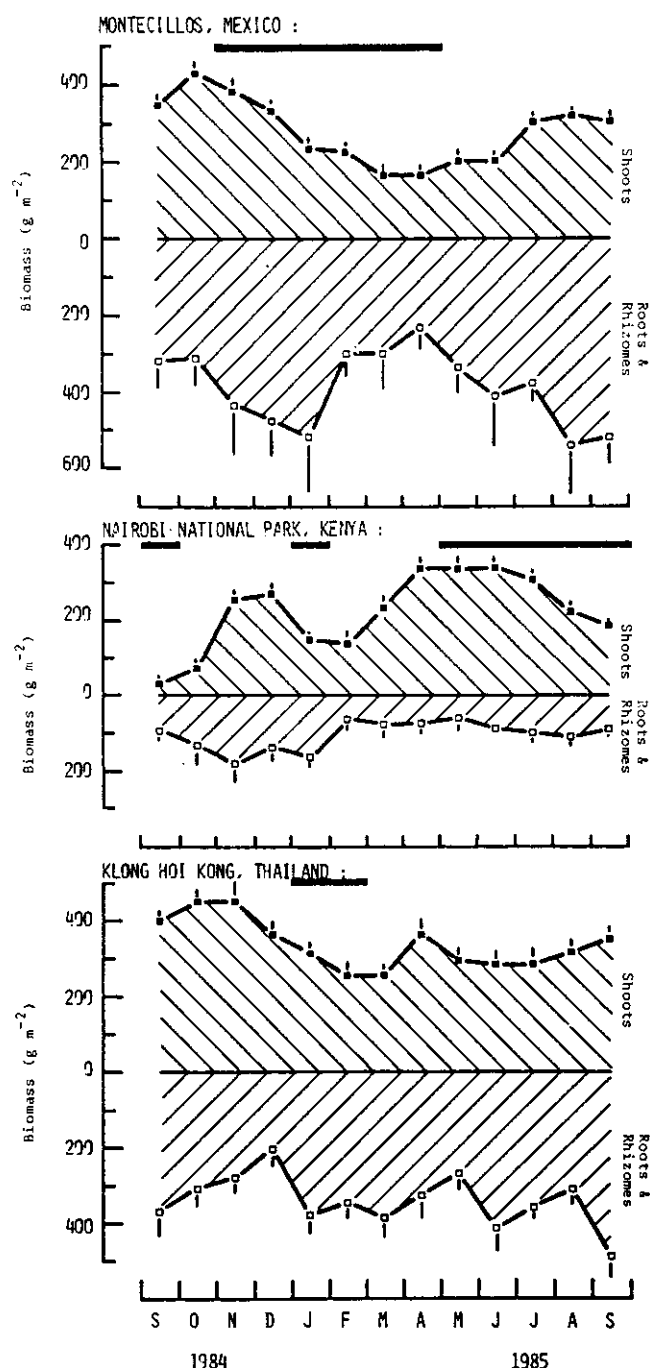und roots and rhizomes. This proportion rose substantially during periods of drought, *e.g.* 70% at Nairobi in September 1984. Amounts of dead material above-ground rose at all three sites over the year, on average by $350 \, g \, m^{-2}$, probably reflecting the exclusion of fire and large grazers from the sites during the year.

At these grassland sites, relative rates of decomposition of dead vegetation varied from 3% to 32% per month, below-ground material decomposing more rapidly than that above-ground (Table 2). The higher rates correlated with periods of high rainfall, the lowest with periods of drought. The total amounts of material decomposed at each site are given in Table 2. Some losses through death were recorded on each interval between harvests at each site emphasising the importance of considering this factor throughout the year. The total amount of material that died during the year (L) was determined (Eqn. 2), and the value substituted into Equation 1, to give the total net primary production (P_n). Figure 2 summarizes the productivities obtained by this procedure. Estimates at all three grassland sites are substantially higher than the P_n of $800 \, g \, m^{-2}$ which has been suggested as an average of annual P_n for tropical grasslands obtained in previous studies (Jordan, 1981; Lieth, 1978). Since both biomass changes and losses through death were measured at regular intervals (Fig. 1), it was possible to use our data to determine the values that would be obtained with 1) the 'standard IBP method' (Milner and Hughes, 1968; Singh *et al.*, 1975) and the peak biomass method (Bourliére and Hadley, 1970) (See Table 3). Both methods underestimate primary production by two- to five-fold in the first three grassland sites. Although substantial changes in amounts of dead vegetation occurred at each site within a year (Table 2) differences between consecutive harvests were not significant (t, $p > 0.1$), and following the recommendations of Singh *et al.*, (1975) should not be included in estimating P_n.

The underestimation of P_n by the IBP standard methods results from failure to include losses through mortality. Our estimate of mortality is heavily dependent on the estimate of decomposition. The mesh size of the litter bags would exclude larger invertebrates, *e.g.* termites, leading to an underestimation of decomposition. Enclosure of material into litter bags will alter the microenvironment for decomposition. Wiegart and
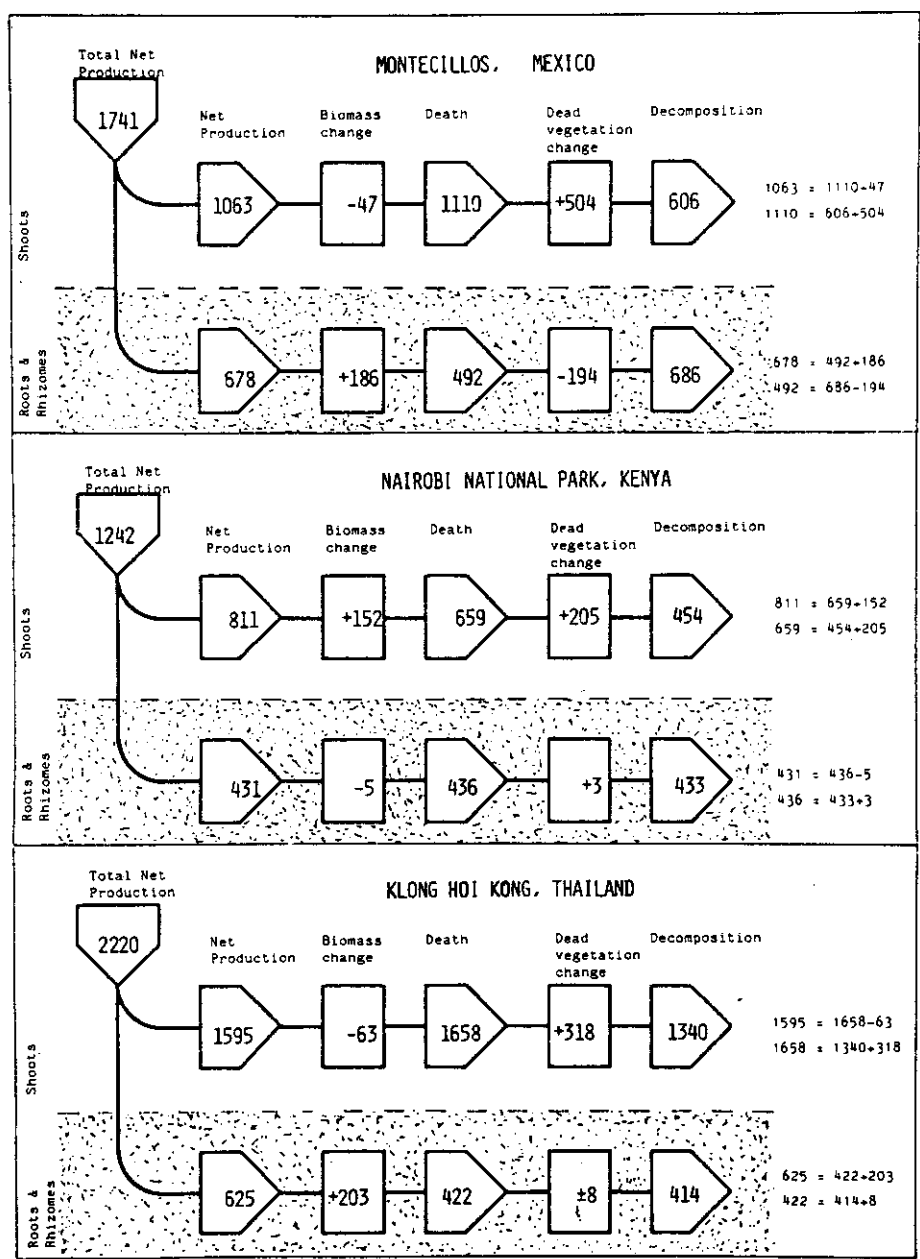

Fig. 1. Changes in shoot and in root and rhizome biomass. *i.e.* living material. Points represent the mean and the vertical bars ± 1 s.e. Horizontal bars indicate periods of low rainfall, *i.e.* months in which precipitation was less than 50 mm.

Fig. 2. Net primary production, its partitioning and fate over the 12 months from September 1984. Fluxes are illustrated by the arrowed boxes and the net changes in conserved quantities by rectangles; units g m^{-2}. From left to right: **Total Net Production**, the sum of above- and below-ground production; **Net Production** (P$_n$), the sum of the change in biomass and the amount of material lost through death; **Biomass Change**, (ΔB) the change in the dry-weight of living material; **Death** (L), the total amount lost through death which equals the sum of the change in dead vegetation and the total amount of dead material decomposed; **Dead Vegetation Change** (ΔD), the change in the dry-weight of dead material; and **Decomposition** (A), the total loss of dead vegetation through decomposition and breakdown. For example, at Montecillos site total net primary production (P$_n$) was 1741 g m^{-2} for the 12 months, this was obtained by summing P$_n$ for shoots (1063 g m^{-2}) and for roots and rhizomes (678 g m^{-2}). Net primary production for shoots was the sum of the changes in shoot biomass over the year (-47 g m^{-2}) and the loss of shoot biomass through dead shoots (504 g m^{-2}), which in turn was the sum of the changes in the weight of dead shoots (504 g m^{-2}) and the amount lost through decomposition (606 g m^{-2}). The same procedure was applied to the below-ground components to obtain the P$_n$ of the roots and rhizomes.

Table 3. Net Primary Production; a comparison of the estimates obtained by taking account of losses through death and below-ground production, with estimates from biomass change alone

Net Primary Production ($g\,m^{-2}\,yr^{-1}$)	Montecillos, Mexico	Nairobi National Park, Kenya	Klong Hoi Kong, Thailand	Marchantaria Manaus Brazil
1) Accounting for mortality (including below-ground organs)	1741	1242	2220	9925
2) Accounting for mortality (above-ground only)	1063 (39%)*	811 (35%)	1595 (28%)	9425 (5%)
3) 'IBP standard method' (including below-ground organs)	740 (56%)	663 (47%)	570 (74%)	8680 (18%)
4) Maximum biomass (above-ground only)	430 (75%)	337 (75%)	442 (80%)	6300 (37%)

*Figures in parenthesis indicate underestimation of productivity as a percentage of net primary production over the 12 months calculated as: 1) the sum of all changes in biomass and losses due to mortality (eqn. 1), for both above- and below-ground); 2) as for 1), but for above-ground vegetation only; 3) the sum of all positive changes in above- and below-ground biomass; and 4) the difference between the peak biomass above-ground during the year.

Evans (1964), in comparing decomposition of dead vegetation in open quadrats and in litter bags, found the latter to under-estimate decomposition losses by about 10%. No account could be taken of the losses of organic matter as root exudates or to mycorrhizal associations, which from the very limited data on this topic may account for as much as 40% of plant productivity (Bowen, 1980). Thus, although our estimates are very much higher than those obtained on the same data by the IBP methods, they are still likely to be conservative relative to the true biological productivity of these plant communities. In considering the first three grassland sites, the 'standard IBP method' would classify Klong Hoi Khong as the least productive and Nairobi National Park as the most productive. When account is taken of losses through death and below-ground production, the ranking is reversed (Table 3). Thus the implicit assumption that the 'IBP' and other harvest methods, even though they underestimate true P_n, would identify the more productive sites must now be questioned.

Changes in biomass at site 4 in Brazil are shown in Fig. 3. Net primary production over one annual cycle is estimated at $9925\,g\,m^{-2}$ (Fig. 4). Root biomass formed a much smaller part of total standing biomass in this ecosystem, at most 8% (Table 2). The plants have an almost continuous supply of water and do not possess below-ground perennating organs, apparently obtaining nutrients via adventitious roots attached to the nodes of the long stems. A low root biomass and productivity would therefore be expected. Root production esti-
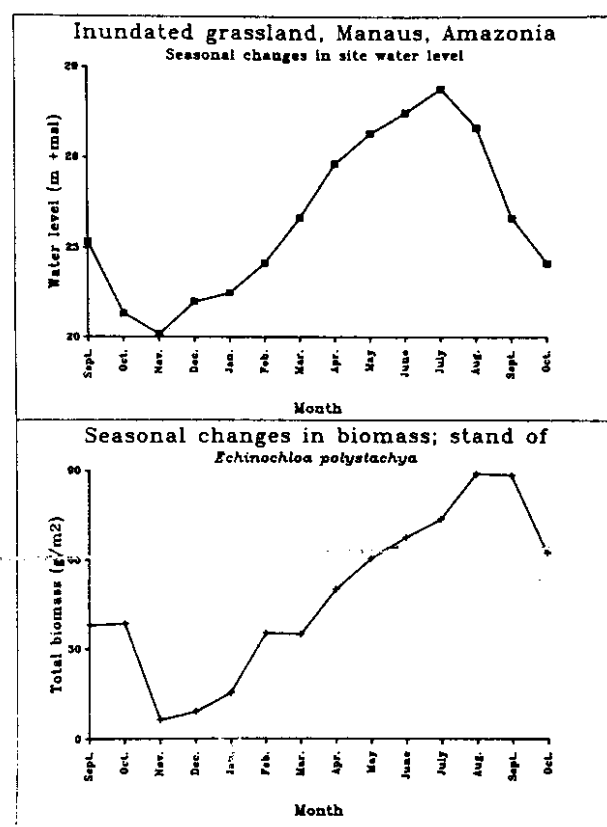

Fig. 3 a. Change in water level at the study site near Manaus, Brazil. The site was at ca. 21 m above mean sea level. b. Change in total dry matter of an *Echinochloa polystachya* stand over the same period in 1985/6.

mated as the positive increments in biomass was $505\,g\,m^{-2}$ (Fig. 4).

Since monthly biomass changes were recorded, it is also possible to estimate production for site 4

Inundated grassland near Manaus, Amazonia
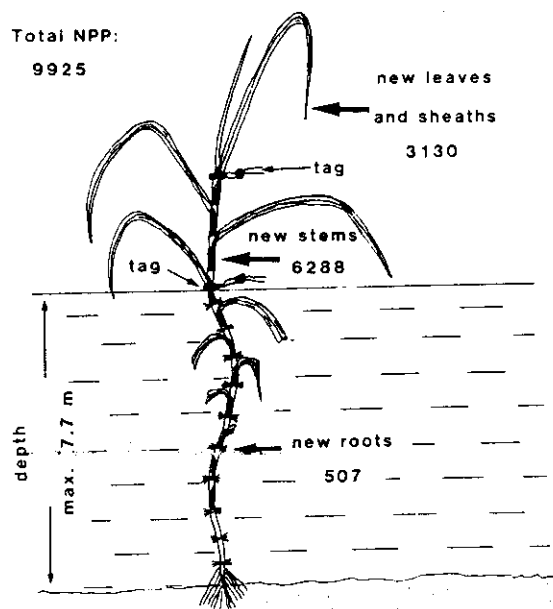(pure stand of Echinochloa polystachya)
Nov./85-Nov./86

Fig. 4. Gains in stem, leaf and root material of an *Echinochloa polystachya* stand determined by monthly growth measurements and demographic data, to determine net primary production (NPP). Figures are dry matter per unit ground area $(g\,m^{-2})$ over the period Nov. 1985–Nov. 1986.

using both the 'IBP standard method' and from peak biomass (Table 3). Both these methods result in slightly lower estimates of productivity than when mortality is taken into account, although the differences are not so marked as for the terrestrial grassland sites. The relationship of P_n estimated by different methods in tropical grasslands is highly variable in contrast to the conclusions of Singh *et al.*, (1975), but in agreement with the variability noted in coastal grasslands by Linthurst and Reimold (1978).

The seasonal growth exhibited by *E. polystachya*, with a large increment in biomass during the year and highly seasonal phenology (a feature more in common with temperate than with tropical grasslands), means that most of the turnover of material recorded here took place towards the end of the growing season. Production of *E. polystachya*, is notable in approaching and exceeding the maximum annual productivity of agricultural crops; for example, $8800\,g\,m^{-2}$ (Beadle *et al*, 1985).

Mean below-ground biomass as a proportion of mean total biomass was 58%, 33%, 50% and 5%, respectively, for the sites in Mexico, Kenya, Thailand and Brazil. The reported values for root biomass are of total dry weight. Although vigorously washed samples could still be contaminated by soil mineral particles leading to overestimation of mass, microscopic examination of samples during sorting did not reveal obvious contamination. Samples from the sites in Thailand and Mexico were combusted in a muffle furnace. The ash contents of these samples were 10%–20%, again suggesting that mineral particle contamination was not leading to serious overestimation. Nevertheless the possibility remains that the values given for root and rhizome masses are overestimated because of some degree of soil particle contamination. However, since we have calculated production and decomposition from changes in mass rather than from maximum amounts, the errors in mass estimates due to soil contamination will be self-cancelling in calculating both decomposition and production (Fig. 1 and Table 2). Below-ground dead matter similarly formed a substantial part of total dead matter at the terrestrial grassland sites (Table 2). Annual below-ground biomass turnovers, estimated as production divided by mean biomass were 1.7, 4.0 and 1.8 for the sites in Mexico, Kenya and Thailand respectively. Annual turnovers of dead matter below-ground measured as decomposition divided by mean dead matter, were 1.2, 2.6 and 3.8, respectively, for Mexico, Kenya and Thailand (Fig. 2). This emphasises the need to consider not only the quantity of below-ground biomass, but also its rate of turnover in any study attempting to determine the productivity of a tropical grassland.

The findings of this study have important implications to ecological understanding of tropical grasslands in three areas: 1) The true input of organic matter to the ecosystem, including that within the soil, will have been undervalued, particularly in the case of the terrestrial grasslands. Thus the potential environmental impact of vegetation removal will not have been fully appreciated in the event of clearance for agricultural use. 2) Assimilation of carbon into plant matter and the input to roots and rhizomes below-ground will have been underestimated. In view of the extent of tropical grasslands, this would have a significant effect on estimates of global carbon cycling and rates of

atmospheric CO_2 rise. Previous studies suggested that productivity of terrestrial grasslands alone in the tropics is $13.5\,Gt\,yr^{-1}$ (Lieth, 1978), about 9% of total terrestrial production. The proportion attributable to grasslands would rise to more than 25% of total terrestrial production if the minimum 3-fold underestimate found here for three grassland sites is generally applicable. If the more modest underestimation of production in other grass ecosystems is also taken into account, the considerable significance of natural grass ecosystems to total terrestrial production becomes apparent. An accurate estimate of productivity of grasses is essential for the establishment of a baseline against which the effects of the global rise of CO_2 levels may be assessed. 3) Recently, techniques for the remote sensing of vegetation biomass have been widely used. Both satellite and aircraft remote sensing give estimates of standing biomass, after calibration of the techniques against 'ground truth' measurements obtained by conventional methods. Productivity is then estimated by, for example, the maximum biomass. However, on the basis of this study such methodology cannot be used alone to provide a reliable estimate of biological production because it ignores death and below-ground production (Table 3) leading to an unpredictable degree of underestimation of actual production. The solution to this problem lies in the development of techniques with adequate ground verification which simultaneously estimate biomass and its death, or which estimate the ability of the vegetation to intercept light for photosynthesis and relate this to biomass production (Tucker *et al.*, 1986; Warrick, 1986).

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References

Beadle C L, Long S P, Imbamba S K, Hall D O and Olembo R J 1985 Photosynthesis in relation to plant production in terrestrial environments. UNEP/Tycooly, Oxford.

Bowen G D 1980 Misconceptions, concepts and approaches in rhizosphere biology. *In* Contemporary Microbial Ecology. Ed. D C Ellwood. pp 283–304. Academic Press, London.

Bourlière F and Hadley M 1970 The ecology of tropical savannas. Ann. Rev. Ecol. Syst. 1, 125–152.

Bradbury I K and Hofstra G 1976 Vegetation death and its importance in primary production measurements. Ecology 57, 209–211.

Buringh P 1980 Limits to the productive capacity of the biosphere. *In* Future Sources of Organic Raw Materials. Eds L E St. Piere and G R Brown. pp 325–383. Pergamon Press, Oxford.

Cooper J P (Ed.) 1975 Photosynthesis and Productivity in Different Environments. IBP Vol. 3. Cambridge University Press, Cambridge.

Coupland R T (Ed.) 1979 Grassland Ecosystems of the World. IBP Vol. 18. Cambridge University Press.

Hussey A and Long S P 1982 Seasonal changes in weight of above- and below-ground vegetation in a salt marsh at Colne Point, Essex. Journal of Ecology 70, 757–771.

Jackon D, Long S P and Mason C F 1986 Net primary production, decomposition and export of *Spartina anglica* on a Suffolk Salt marsh. J. Ecology 74, 647–662.

Jordan C F (Ed.) 1981 Tropical Ecology. Hutchinson Ross, Stroudsberg.

Lieth H F H (Ed.) 1978 Patterns of Primary Productivity in the Biosphere. Hutchinson Ross, Stroudsberg.

Linthurst R and Reimold R J 1978 An evaluation of methods for estimating the net primary production of estuarine angiosperms. J. Appl. Ecol. 15, 919–932.

Long S P and Mason C F 1983 Saltmarsh ecology. Blackie, Glasgow.

Milner C and Hughes R E 1968 Primary Production of Grassland. IBP Handbook 6. Blackwell, Oxford.

Roberts M J, Long S P, Tieszen L L and Beadle C L 1985 Measurement of plant biomass and net primary production. *In* Techniques in Bioproductivity and Photosynthesis, 2nd edition. Eds. J Coombs, D O Hall, S P Long and J M O Scurlock. pp 1–19. Pergamon Press, Oxford.

Singh J S and Joshi M C 1979 Tropical grasslands primary production. *In* Grassland Ecosystems of the World. Ed. R T Coupland. pp 197–218. Cambridge University Press, Cambridge.

Singh J S, Lauenroth W K and Sernhorst R K 1975 Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. Bot. Rev. 41, 181–232.

Singh J S, Singh K P and Yadava P S 1979 Tropical grasslands ecosystems synthesis. *In* Grassland Ecosystems of the World.

Ed. R T Coupland. pp 231–240. Cambridge University Press, Cambridge.

Singh J S and Yadava P S 1974 Seasonal variation in composition, plant biomass and net primary productivity of a tropical grassland at Kurukshetra, India. Ecol. Monogr. 44, 351–376.

Singh J S, Lavenroth W K and Steinhurst R K 1975 Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. Bot. Rev. 41, 181–232.

Singh J S, Lavenroth W K, Hunt H W and Smith D M 1984

Bias and random errors in estimators of net root production: A simulation approach. Ecology 65, 1760–1764.

Tucker C J, Fung I Y, Keeling C D and Gammon R H 1986 Relationship between atmospheric CO_2 variations and a satellite-derived vegetation index. Nature 319, 195–199.

Warrick R A 1986 Photosynthesis seen from above. Nature 319, 181.

Wiegert R G and Evans F C 1964 Primary production and the disappearance of dead vegetation on an oldfield in south eastern Michigan. Ecology 45, 49–62.