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THE ECOLOGY OF A MONTANE GRASSLAND IN SRI LANKA
VII. BIOMASS PRODUCTION

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SUMMARY

(1) Monthly determinations were made of standing crop biomass in two altitudinally, edaphically and floristically different communities in a montane grassland in Sri Lanka, in an attempt to estimate primary productivity, to follow the annual course of dry matter production, and to examine their possible correlations with variations in some of the major environmental factors.

(2) The low productivity of the grassland is attributed chiefly to the low nutrient status of soils, and is contrasted with the productivity of other tropical grasslands.

(3) The community at the higher altitude (900 m), with humus-rich soils, supported a dense turf of *Cymbopogon nardus* and *Themeda tremula*, while that at the lower altitude (560 m), where the quartz-gravel topmost soil dries out rather rapidly, supported a sparse turf of *Cymbopogon nardus* with little *Themeda tremula*; the former was more productive (911.2 g m^{-1} yr^{-1}), and this difference is related to differences in soil moisture regime and species composition.

INTRODUCTION

Estimation of primary productivity is an essential preliminary to the assessment of ecological efficiency of plant communities; it also provides information on their functional characteristics and economic potential. Studies of productivity of montane grasslands of Sri Lanka (patanas) are not only of ecological interest, but also of a agricultural importance; patanas are supposedly of great potential as pastures (Appadurai 1969; Pemadasa 1981). The course of biomass production in pasture species introduced into certain patanas has been documented by, for example, Appadurai & Arsaratnam (1969), Andrew & Jayawardana (1970), Appadurai & Goonawardene (1974), and Sivasupramaniam, Siththamparanathan & Appadurai (1974), but relatively little is known of the productivity of natural patana vegetation.

Note : The first five papers of this series were published in the Journal of Ecology.

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The previous papers of this series (Pemadasa & Amarasinghe 1982; Amarasinghe & Pemadasa 1982) provided evidence of considerable diversity in floristic composition, species-predominance and general physiognomy within the humid-zone dry patana under study, and these are certain to cause distinct variations in productivity. The present experimental investigation was designed to estimate primary productivity of two floristically contrasting communities, to follow the course of changes in standing crop, and also to examine their possible correlations with some of the major environmental variables.

THE SITES

Two communities were selected, one at 900 m altitude and the other at 560 m, which are, for convenience, referred to as the 'upper' and 'lower' site respectively. The upper site supported a dense turf predominantly of **Cymbopogon nardus* and *Themeda tremula*, with *Eulalia trispicata* as the next most frequent species; the three species together contributed as much as 90% of the total cover. The subordinate vegetation was composed of *Cassia kleinii*, *Crassocephalum crepidioides*, *Desmodium heterocarpum*, *D. heterophyllum*, *D. triquetrum*, *Fimbristylis sp.*, *Imperata cylindrica*, *Polygala rosmarinifolia*, *Sacciolepis indica* and *Scleria lithosperma*; woody shrubs *Crotalaria albida* and *Psidium guajava*, and weed species occurred as isolated individuals. The characteristically black topmost soil layer is rich in humus, with relatively little quartz and gravel; rock outcrops are absent. In contrast, the sparse turf at the lower site was dominated by *Cymbopogon nardus*, with *Panicum maximum* as the second most frequent species, their contribution to the total cover being more than 80%. The matrix between the major grasses was composed of *Desmodium heterophyllum*, *Eragrostis* sp., *Fimbristylis* sp., *Hemidesmus indicus*, *Imperata cylindrica*, *Merremia angustifolia* and *Themeda tremula*; woody shrubs *Crotalaria albida*, *Psidium guajava* and *Wikstroemia indica* occurred as isolated individuals. Recent human interference was evident from the occurrence of graminaceous and dicotyledonous weeds, e.g. *Blumea alata*, *Erigeron sumatrensis*, *Hedyotis auricularia*, *Mimosa pudica* and *Pennisetum polystachyon*; in fact, *Pennisetum polystachyon* was the third most frequent species of the community. The soil is heavily eroded and truncated, as evident from the frequent rock outcrops protruding at the surface, with a compact, hardpan-like quartz-gravel topmost layer containing little organic matter. Thus, the two selected sites enable a comparison of productivity in altitudinally, edaphically and floristically contrasting communities in the humid-zone dry patana.

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* Nomenclature follows the provisional check-list of Abeywickrama (1959).

METHODS

Each site was fenced-out, and a 3-m wide strip was cleared right-round to serve as a fire-barrier. The productivity estimation was by the short-term harvest method (Odum 1960). At each site, thirty six 1x1 m plots were arranged in three blocks each of twelve plots. During the first week of each month, the vegetation from three plots was harvested at ground-level, and dry weight of live and dead material of each species was determined separately after oven-drying at 85 ^{0}C for 72 h. At the same time a soil sample was collected from the top 20-cm layer at the centre of each harvested plot; the water content was determined after oven-drying at 85^0 C for 72 h, and expressed as a percentage of the dry weight of soil. The experiments were of randomized-block design with three replicates per harvest, and ran for twelve months (June 1976 - May 1977 at the upper site, and July 1976 - June 1977 at the lower site). Owing to the difficulty of finding reasonably homogeneous and sufficiently large areas, it was not possible to increase the plot-size nor to have more replicates.

Soil, collected from the top 20-cm layer of each site, was also used to estimate Kjeldahl nitrogen, extractable phosphorus, exchangeable potassium, P^H and loss-on-ignition. The techniques employed are described in Pemadasa & Mueller-Dombois (1979).

RESULTS

Environmental data

Some of the environmental data for the experimental period (June 1976 - June 1977) are given in Fig. 1 and Table 1. The mean rainfall and the mean number of sunshine hours were fairly high throughout the year. The monthly rainfall was greater than 100 mm in all months except February. The soil moisture regime was higher during October-November 1976 and May - June 1977 than during the rest of the period. At both sites the same general trend occurred, but the upper site was somewhat more moist than the lower site; this is to be expected because the former is richer in organic matter with lower amounts of quartz and gravel than the latter. The concentrations of total nitrogen, extractable phosphorus and exchangeble potassium were generally low (Table 1). The loss-on-ignition was higher at the upper than at the lower site.

Monthly variations of standing crop

The total standing crop biomass increased progressively during the experimental period, and was appreciably higher at the upper than at the lower site (Fig. 2); there was about a four-fold increase at both sites. At the upper site the amount of live material increased steadily to reach a fairly high value in November 1976, followed by a gradual decline until March 1977 and a progressive rise thereafter. The increment of green matter at the lower site continued until December 1976, remained more or less unchanged during January-February 1977, dropped appreciably in March, and then began to increase rather rapidly; the reduction of living matter in March may be attributed to the low soil moisture regime during the February dry period, which not only hinders growth, but also hastens senescence, while the subsequent renewed growth is a reflection of the advent of the active-growing season synchronized with the increased rainfall (see Fig. 1). At both sites, the amount of dead material was lower than that of live material during the first 5-6 months of the experimental period, but the relationship reversed thereafter (fig. 2), and this was owing largely to death of older tillers of the dominant *Cymbopogon nardus* after flowering and seed production.

As illustrated in Fig. 3, the standing crop of the major species at both sites showed a generally progressive increase during the experimental period; however, there were noteworthy fluctuations of the amount of dry matter of subordinate species, which is a result of inconsistency of their abundance between plots. The sites selected were the most homogeneous available, but even within these there were appreciable variations in the amounts of subordinate species; however, the abundance of major species was reasonably similar in all plots. The inconsistency of occurrence of minor species between plots may not have a significant effect, as their contribution to the total standing crop never exceeded 10%.

Estimation of productivity

If the vegetation is perfectly homogeneous, the productivity can be determined from the difference between the first and the final harvests; but not only do the natural communities contain large numbers of species differing in phenology, but also perfect homogeneity is an exception rather than the rule. It is inevitable, therefore, that there is variation not only between harvests, but also between replicates of the same harvest. In natural communities the time of occurrence of the peak standing-biomass differs between species, and, therefore, the total productivity may exceed the total standing crop at any given time (Odum 1960). The differences between harvests may partly be related to the differential growth of constituent species. Accordingly, the sum total of the differences in standing crop between successive harvests would be a more reasonable estimate of productivity; it also obviates the 'error' due to the carry-over biomass from the previous year. In the present study, the total productivity was calculated as follows:

$$\text{Total productivity} = \sum (H_i - H_j)$$

where H_i and H_j are standing crop biomass values at successive harvests.

The productivity estimates of the upper and lower sites were 911.2 and 679.5 g m $^{-2}$ respectively. Evidently, the upper site is much more productive than the lower site. The standing crop of the upper site was predominantly of *Cymbopogon nardus*, *Eulalia trispicata* and *Themeda tremula*, their percentage contribution being 65.4, 10.1 and

25.4 respectively. In contrast, at the lower site the major constituents were *Cymbopogon nardus*, *Panicum maximum* and *Pennisetum polystachyon*, which respectively contributed 68.6, 13.9 and 7.7% of the total standing crop. There was no significant difference ($P > 0.05$) in the amount of *Cymbopogon nardus* between sites. However, the upper site supported much denser turf of *Themeda tremula* than did the lower site, where this species occurred as isolated tussocks; thus difference in productivity between the two sites is largely a result of differential contribution of *Themeda tremula*, although differences in environmental factors may also have some effect.

DISCUSSION

That the productivity of the humid-zone dry patana is generally low, and differs between communities, is evident from the present data. The annual course of standing crop parallels variations in rainfall and soil moisture regime; with the progress of the south-west monsoonal rains, the biomass production increases until November-December, and then begins to decline during the resting period until the end of dry-spell in February, when the senecsence of older shoots exceeds development of live shoots (Fig. 2).

Estimation of productivity by determining the standing crop at the end of the growing season does not account for losses due to mortality (Kucera, Dahlman & Koelling 1967); the short-term harvest method obviates this limitation (Odum 1960; Hadley & Buccos 1967; McNoughton 1968). In the present study the respiratory losses were not estimated. Moreover, the actual net productivity must be higher than the estimated values, because only the above-ground biomass was harvested; under-ground parts are known to contribute as much as 40% of the total productivity of certain grasslands (Varshney 1972).

The productivity of grassland depends on, for example, the total annual rainfall and its seasonal variations, soil fertility, floristic composition, and grazing pressure (Murphy 1975). Ambasht, Maurya & Singh (1972) estimated a net productivity of 3810 g m^{-1}yr^{-1} in certain Indian grasslands which receive an annual rainfall of over 1000 mm. The values obtained in the present study were much lower (911.2 and 679.5 g m^{-1} yr^{-1} in the upper and lower sites respectively), although the annual precipitation exceeds 2200 mm, and this is a reflection of the low nutrient status of the soil. Nutrient deficiency severely restricts biomass production in grasslands (San Jose & Medina 1976). Our unpublished experimental evidence is that nutrient enrichment can improve the growth of the dominant grasses *Cymbopogon nardus*, *Eulalia trispicata*, *Themeda tremula* and *Pennisetum polystachyon* substantially. Addition of nutrients has also been found to improve biomass production in another type of patana in Sri Lanka (Pemadasa 1981).

The communities examined differ altitudinally, edaphically and floristically. Although both receive the same amount of rain, the upper site is more moist, because of its humus-rich soil, than the lower site, where the quartz-gravel topmost layer dries out rather rapidly; thus, the moisture regime is more favourable in the former than in the latter. Moreover, the turf is more dense in the upper site, where the matrix between *Cymbopogon nardus* is filled with *Themeda tremula*, than in the lower site, where *Themeda tremula* occurs sporadically. Thus, the observed difference in productivity between the two communities is related largely to differences in soil moisture conditions and in floristic composition.

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Table 1. Soil chemistry of the humid-zone dry patana sites (Sri Lanka) used for estimation of biomass production; values are the range of five samples

	Upper site	Lower site
pH	5.2-5.7	5.3-5.6
Loss-on-ignition (%)	12.1-15.3	3.8-6.9
Kjeldahl nitrogen concentration*	81-104	78-98
Extractable phosphorus concentration*	89-115	93-107
Exchangeable potassium concentration*	75-97	84-96

* per unit dry weight of soil ($\mu g\ g^{-1}$).

FIGURE LEGENDS

Fig. 1. Environmental data for the experimental period (July 1976 - July 1977).

(a) mean fortnightly rainfall; (b) mean number of sunshine hours per fortnight. Climatological data are from the Central Agricultural Research Station, Gannoruwa (c.2 Km from the study sites). (c) the monthly course of water content (% by weight) of the top 20-cm soil layer; ■ , upper site; □ , lower site.

Fig. 2. The course of standing crop biomass in the two communities during the twelve-month experimental period. (a) Upper site; (b) lower site. ● , total above ground biomass; Δ , live material; ▲ , dead material. Vertical bars indicate S.E. of harvest means. (c) course of green: dead ratio during the experimental period. ■ , upper site; □ , lower site.

Fig. 3. The course of above-ground biomass production of the major species in the upper and lower sites during the twelve-month experimental period. Vertical bars indicate S.E. of harvest means.

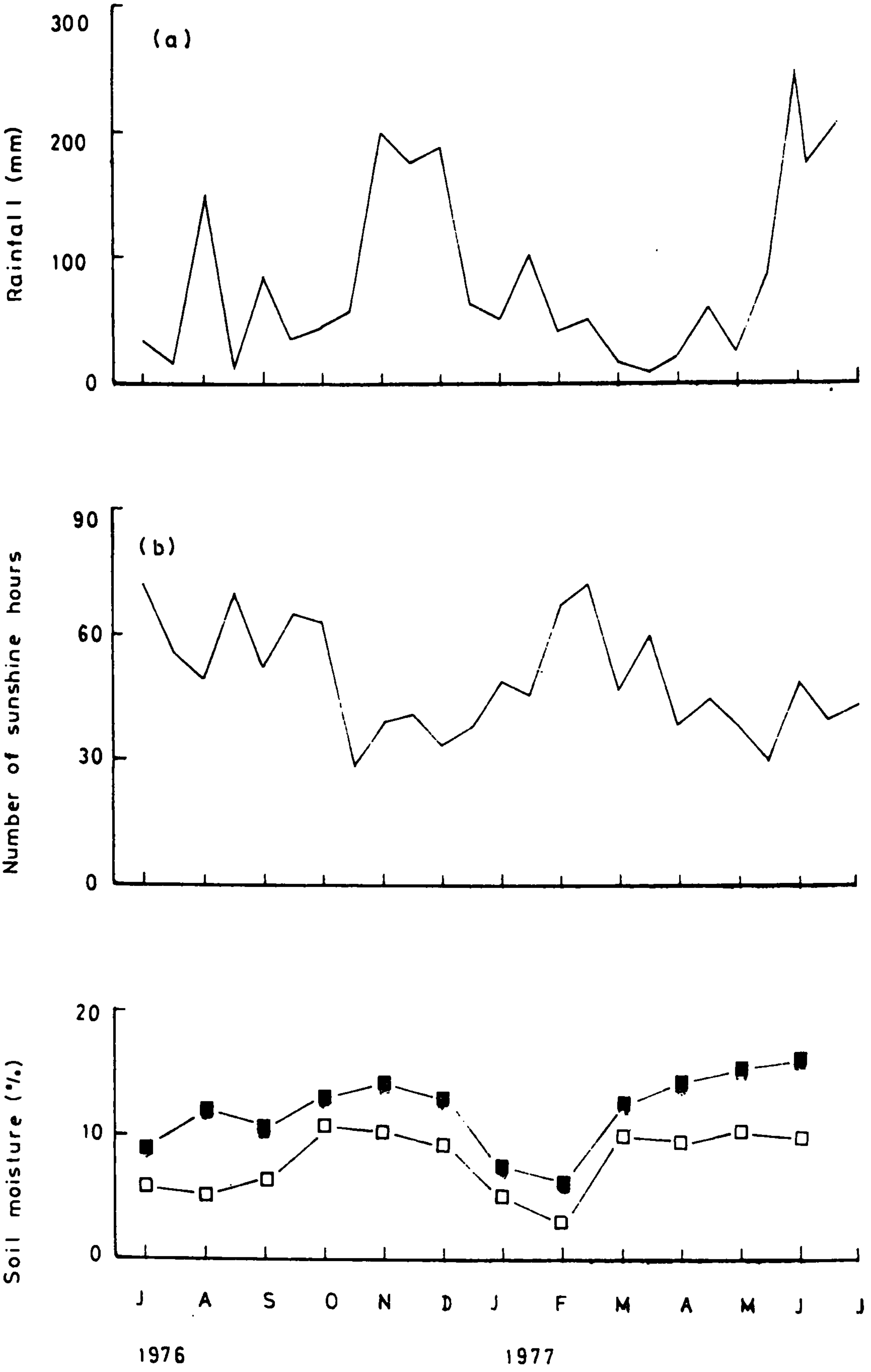
(a)
Rainfall (mm)
300
200
100
0
(b)
Number of sunshine hours
90
60
30
0
Soil moisture (%)
20
10
0
J
A
S
O
N
D
J
F
M
A
M
J
J
1976
1977

Fig. 1

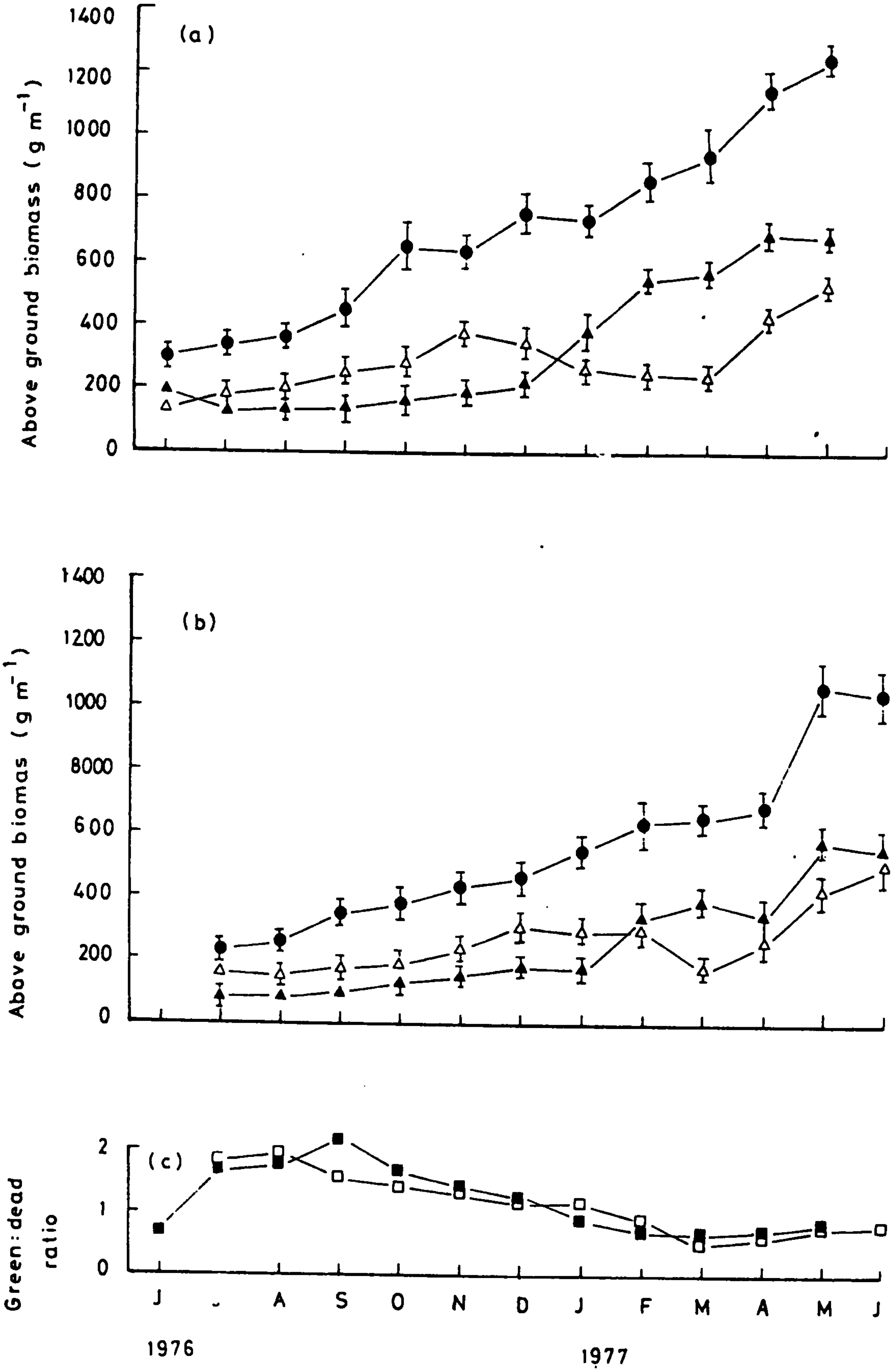
(a)
Above ground biomass (g m^{-1})
1400
1200
1000
800
600
400
200
0
(b)
Above ground biomas (g m^{-1})
1400
1200
1000
8000
600
400
200
0
(c)
Green:dead ratio
2
1
0
J
A
S
O
N
D
J
F
M
A
M
J
1976
1977

Fig. 2

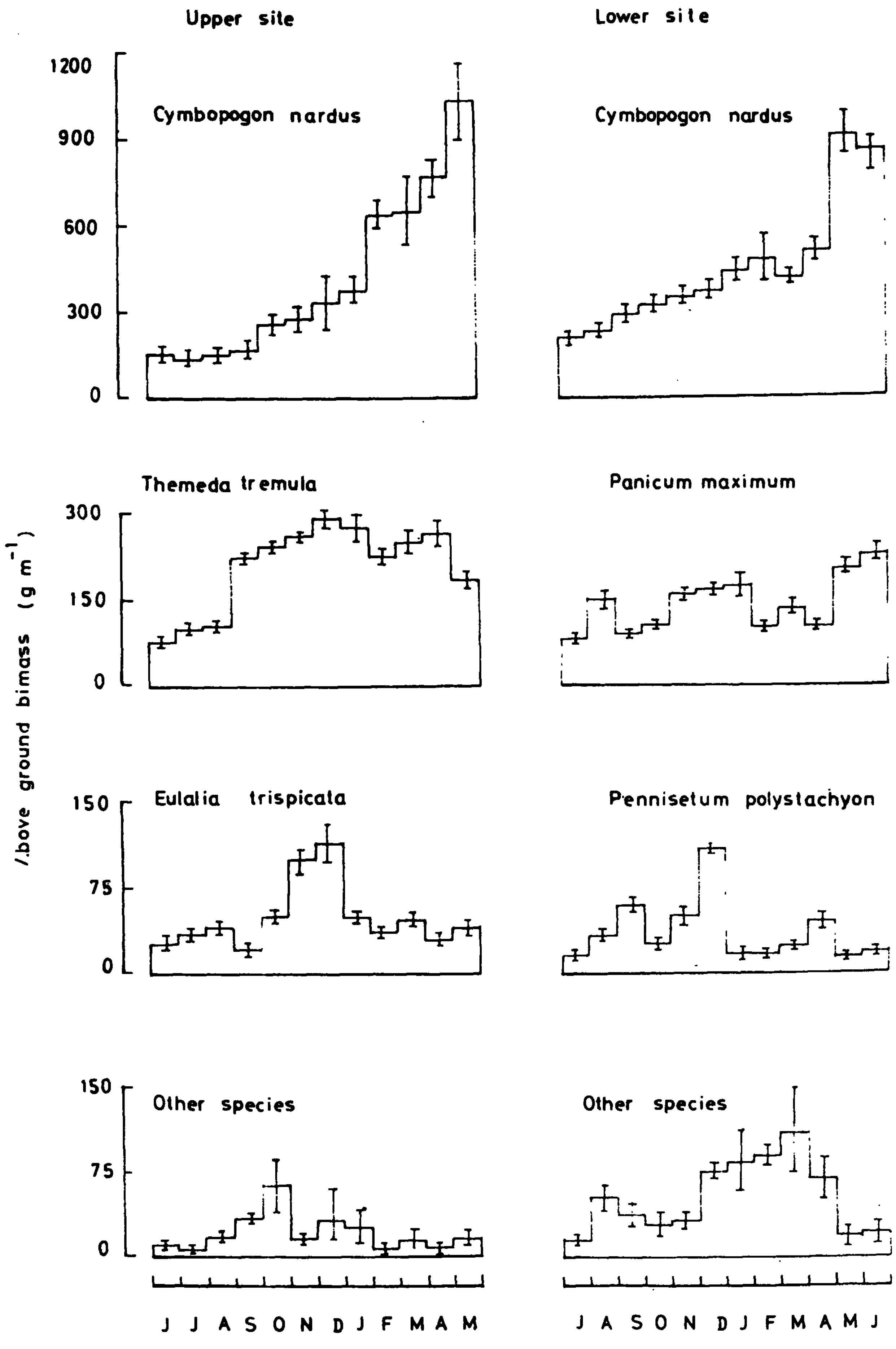
Upper site
Lower site
1200
900
600
300
0
Cymbopogon nardus
Cymbopogon nardus
Themeda tremula
Panicum maximum
300
150
0
/.bove ground bimass (g m^{-1})
150
75
0
Eulalia trispicata
Pennisetum polystachyon
150
75
0
Other species
Other species
J J A S O N D J F M A M
J A S O N D J F M A M J

Fig. 3