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Growth and allocation strategy of some important species of seral grasslands at Cherrapunji in north-eastern India

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Abstract. Growth and allocation patterns of biomass and nutrients of herbaceous species from grasslands at Cherrapunji in north-eastern India were studied under varied nutrient stress situations. Though populations from a nutrient richer soil had better growth rate than those from nutrient poor sites, this difference was not reflected in the tissue concentration of nutrients. Populations in nutrient deficient soils had high allocation to the belowground organs of reproduction than for aboveground parts. Though *Ischaemum* and *Eragrostiella* had generally lower nitrogen uptake efficiencies, their use efficiency was fairly high. Soils that are generally nutrient deficient had more C_4 grass components than the rich soil under *Osbeckia*-type.

Keywords. Growth; resource allocation; nutrient; nutrient uptake efficiency; nutrient use efficiency.

1. Introduction

The grasslands at Cherrapunji, in Meghalaya in north-eastern India, one of the wettest places on Earth, represent various stages of arrested succession of the climax forest (Ram 1986). These are maintained at the grass stage because of climatic stress and is a consequence of clear-cutting the fragile forest ecosystem (Ramakrishnan *et al* 1981). The grasses and forbs of these degraded sites have ecophysiological attributes to survive in infertile soils subjected to frequent disturbance and climatic stress (Ramakrishnan 1985a, b).

Resource allocation strategy, both biomass and nutrients, of the species growing under such stress situations is a reflection of the fitness of the species for survival (Ramakrishnan 1984; Saxena and Ramakrishnan 1984). The present study attempts to look at the ecophysiological attributes of some of the important herbaceous species in grasslands under varied levels of nutrient stress at Cherrapunji.

2. Study area and climate

The study area at Cherrapunji (25°, 15′ N, 91°, 45′ E and 1313 m elevation) located 50 km south of Shillong is one of the wettest places of the world. The climate is monsoonal with an annual average rainfall of 10372 mm (mean for 1973–1983 period) about 96% of which occurs between April–October. The mean monthly

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maximum and minimum temperatures during this period are 24 and 14°C, respectively. November–February are winter months of which February is relatively a dry period. The mean monthly maximum and minimum for the winter period are 17 and 6°C, respectively. The dry summer is just for one transitional month between the winter and the rainy seasons, with mean monthly maximum and minimum temperatures of 20 and 12°C, respectively.

3. Methods

Three grassland types, namely (i) *Osbeckia*–type, which is found in a relatively nutrient rich soil with an average soil profile depth of about 40 cm and which was burnt 6 years prior to the study period, (ii) *Ischaemum*–type, developed on a similar soil type but frequently burnt at 2-year intervals and (iii) *Eragrostiella*–type developed on a nutrient deficient soil at a highly desertified site, were selected.

Arundinella bengalensis, *Carex cruciata* and *Chrysopogon gryllus* are found as part of the *Osbeckia*–type on a nutrient rich soil, as well as on a nutrient poor desertified soil as components of the *Eragostiella*–type. *Ischaemum goeblii* is characteristic of frequently burnt, *Ischaemum*–type. *Eragrostiella leoptera* is found on nutrient poor desertified soils only. These 5 species are subsequently referred by their generic name only. The vegetation analysis of the 3 sites were based on 30 randomly placed quadrats of 1 m^2. Importance value indices (IVI), which is an integrated measure of the relative frequency, relative density and relative dominance (Curtis 1959), was calculated for each species.

Each species was harvested from 3 randomly placed quadrats of 50 × 50 cm at monthly intervals during the growing season. Harvested plants were separated into belowground (roots and rhizomes) and aboveground (stem, leaf and seed) components. Culm was considered as stem. Different components were dried at 80°C for 48 h and weighed. The biomass at sampling time was computed by also considering the number of fallen leaves as suggested by Hickman (1975). Leaf area was measured using a planimeter, and leaf dry weight per unit leaf area was based on 3 replicates, with 50 leaves per replicate. Total leaf area was computed from leaf dry weight per unit leaf area and leaf biomass value. Three growth functions, relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) (Hughes and Freeman 1967; Radford 1967) were calculated as:

$$\mathrm{RGR}=\frac{\ln W_2-\ln W_1}{t_2-t_1},$$

$$\mathrm{NAR}=\frac{(W_2-W_1)(\ln A_2-\ln A_1)}{(A_2-A_1)(t_2-t_1)},$$

$$\mathrm{LAR}=\frac{(A_2-A_1)(\ln W_2-\ln W_1)}{(\ln A_2-\ln A_1)(t_2-t_1)},$$

where W_1 and A_1 are biomass and leaf area at time t_1 and similarly W_2 and A_2, at time t_2.

Plant samples were analysed chemically following standard procedures given by

Allen *et al* (1974). Thus nitrogen was estimated by micro-kjeldahl method, phosphorus by molybdenum blue method and potassium by flame photometry after wet digestion with triple acid. Nutrient uptake efficiency was calculated as mg nutrient absorbed per g root biomass following Blair and Cordero (1978). Nutrient use efficiency was calculated as mg dry matter production per g nutrient absorbed (Brown 1978).

Ten random soil samples collected in July from the 0–10 cm horizon were pooled to give one composite sample for each fallow field. Soil was chemically analysed by standard methods (Jackson 1962; Allen *et al* 1974): organic carbon by Walkley-Black method, total nitrogen by kjeldahl method, nitrate-nitrogen by phenol-di-sulphonic acid method, available phosphorus by molybdenum blue method using Bray and Kurtz's extraction solution, and potassium by flame photometry after extraction in IM ammonium acetate solution at pH 7. All the analyses were replicated 3 times.

4. Results

Under *Osbeckia*–type, the species *A. bengalensis*, *C. cruciata*, *C. gryllus*, *Eulalia quadrinervis*, *Fimbristylis thomsonii* and *Osbeckia capitata* were abundant (table 1). After the burn, some species such as *Gentiana quadrifaria* and *I. goeblii* appeared, others such as *Phyllanthus simplex* increased in number, and yet others such as *Osbeckia crinita* declined. Under *Ischaemum*–type, species such as *A. bengalensis*, *I. goeblii*, *Fimbristylis complanata*, *Gentiana quadrifaria* and *O. capitata* were dominant. These species are also important components under *Eragrostiella* type, along with other species such as *E. leoptera* and *Borreria hispida*.

Table 1. IVI of species of grasslands at Cherrapunji in north-eastern India.

Species	*Osbeckia*–type	*Ischaemum*–type	*Eragrostiella*–type
Perennials			
Arundinella bengalensis (spreng) Druce.	24·6	14·6	12·1
Arundinella nepalensis Trin.	13·4	5·4	—
Carex cruciata Wahenb.	21·3	6·5	4·4
Chrysopogon gryllus (L.) Trin.	24·0	8·2	21·1
Eragrostiella leioptera Stapt, Bor.	—	12·7	40·2
Ischaemum goeblii Hack.	—	52·3	21·9
Osbeckia crinita Benth.	51·5	4·7	23·0
Annuals			
Borreria articularis (L.F) N F William.	—	—	29·5
Dimeria fuscescens Trin.	—	12·1	17·1
Eulalia quadrinervis (Hack) O Ktze.	10·0	—	—
Fimbristylis complanata Link.	—	38·5	26·6
Fimbristylis thomsonii Beeck.	20·1	18·0	2·9
Gentiana quadrifaria Clark non. Bl.	—	24·0	13·2
Osbeckia capitata Benth.	10·2	20·8	18·0
Paspalum arbiculare Forst.	10·5	1·8	10·9
Plectoranthus japonicus Burm (F.) Koidz.	16·3	3·1	—
Pogostemon quricularis (L.) Haosk.	3·1	10·7	2·4
Setaria glauca (L.) P Beauv.	14·0	5·6	—
Others*	80·0	56·9	53·3

*Species with IVI value less than 10.

Nutrient concentration of the soil down the 10 cm soil depth, in July is given in table 2. In general, the soil under *Osbeckia* type was richer in nutrients whereas that under *Eragrostiella* type was poorer. These differences were more pronounced for carbon, total nitrogen and available phosphorus than for NO_3-N and potassium.

All the growth parameters of *Arundinella*, *Carex* and *Chrysopogon* declined sharply ($P < 0.001$) in the nutrient poor soil under *Eragrostiella*-type (table 3). The decline in aboveground/belowground ratio, however, was significant at $P < 0.05$ level only. *Ischaemum* from frequently burnt site had lower value for this ratio and *Eragrostiella* had the least value. However, the values for *Ischaemum* and *Eragrostiella* are comparable to the values for *Arundinella*, *Carex* and *Chrysopogon* from nutrient poor sites.

Relative growth rates and net assimilation rates were generally higher for *Arundinella*, *Carex* and *Chrysopogon* in nutrient rich soil than in nutrient poor soil ($P < 0.001$), with maximum values for *Carex* (table 4). *Eragrostiella* in a desertified site had the least value. Leaf area ratio was very low for *Eragrostiella* followed by *Ischaemum*. The other 3 species in nutrient rich soil had generally higher leaf area ratio ($P < 0.05$) compared to nutrient poor soils, except for *Carex* where the reverse was true.

Concentration of nitrogen in *Arundinella* and *Chrysopogon* was higher in a nutrient poor soil than in a nutrient rich soil, whereas *Carex* showed a reverse trend ($P < 0.05$) (table 5). Inspite of low fertility status of the desertified site, concentration of nutrients in *Eragrostiella* was comparable to some of the species from nutrient

Table 2. Soil analysis (0–10 cm depth) at different sites at Cherrapunji in north-eastern India.

	Vegetation type		
Nutrient	*Osbeckia*	*Ischaemum*	*Eragrostiella*
Organic carbon (%)	2·0 ± 0·01	1·9 ± 0·05	1·4 ± 0·01
Total nitrogen (%)	0·29 ± 0·01	0·21 ± 0·001	0·15 ± 0·01
NO_3-N (mg/100 g)	0·12 ± 0·003	0·12 ± 0·001	0·10 ± 0·004
PO_4-P (mg/100 g)	0·29 ± 0·01	0·10 ± 0·001	0·08 ± 0·003
Potassium (mg/100 g)	0·12 ± 0·01	0·10 ± 0·004	0·10 ± 0·003

Table 3. Growth characteristics (±SE mean) of the different species at Cherrapunji in north-eastern India.

Species	Height (m)	Aboveground biomass (g)	Belowground biomass (g)	Aboveground/ belowground ratio
Arundinella	0·75 ± 0·005	77·96 ± 3·96	82·06 ± 4·17	0·95
	(0·50 ± 0·003)	(27·80 ± 1·18)	(32·71 ± 1·39)	(0·85)
Carex	1·10 ± 0·010	70·78 ± 3·79	67·41 ± 3·61	1·05
	(0·45 ± 0·032)	(14·04 ± 1·20)	(15·60 ± 1·33)	(0·90)
Chrysopogon	0·75 ± 0·061	73·74 ± 3·90	81·93 ± 4·33	0·90
	(0·30 ± 0·021)	(22·64 ± 1·71)	(30·19 ± 2·28)	(0·75)
Ischaemum	0·45 ± 0·035	46·60 ± 2·24	58·25 ± 2·80	0·80
Eragrostiella	0·35 ± 0·002	29·92 ± 1·99	46·03 ± 3·06	0·65

Numbers in parentheses indicate species grown in nutrient poor soil.

Table 4. Mean values (± SE of mean) of growth functions for the different species at Cherrapunji in north-eastern India.

Species	Growth functions Relative growth rate (mg. mg^{-1} day^{-1})	Net assimilation rate (mg (cm^2)$^{-1}$ day^{-1})	Leaf area ratio (cm^2 mg^{-1})
Arundinella	0·0135 ± 0·009	0·123 ± 0·0114	0·117 ± 0·0084
	(0·0095 ± 0·0006)	(0·105 ± 0·0035)	(0·085 ± 0·0054)
Carex	0·0245 ± 0·0017	0·221 ± 0·0151	0·159 ± 0·0114
	(0·0147 ± 0·0011)	(0·135 ± 0·0115)	(0·251 ± 0·0181)
Chrysopogon	0·0106 ± 0·0008	0·121 ± 0·0115	0·082 ± 0·0075
	(0·0026 ± 0·0002)	(0·031 ± 0·0024)	(0·070 ± 0·0062)
Ischaemum	0·0116 ± 0·0012	0·125 ± 0·0101	0·013 ± 0·0011
Eragrostiella	0·0078 ± 0·0061	0·095 ± 0·0071	0·005 ± 0·0003

Numbers in parentheses indicate species grown in nutrient poor soil.

Table 5. Mean tissue concentration of nutrients (± SE mean) during the growth period of different species at Cherrapunji in north-eastern India.

Species	Nutrient concentrations (%) Nitrogen	Phosphorus	Potassium
Arundinella	0·667 ± 0·045	0·098 ± 0·0075	0·733 ± 0·061
	(0·983 ± 0·075)	(0·099 ± 0·0071)	(0·630 ± 0·050)
Carex	0·925 ± 0·065	0·102 ± 0·0091	1·091 ± 0·091
	(0·801 ± 0·071)	(0·135 ± 0·0101)	(1·121 ± 0·101)
Chrysopogon	0·917 ± 0·081	0·168 ± 0·085	0·630 ± 0·051
	(1·283 ± 0·101)	(0·152 ± 0·089)	(0·82 ± 0·071)
Ischaemum	0·85 ± 0·071	0·114 ± 0·0095	0·59 ± 0·041
Eragrostiella	0·667 ± 0·051	0·106 ± 0·0080	0·53 ± 0·041

Numbers in parentheses indicate species grown in nutrient poor soil.

richer soil; the concentration of potassium in *Ischaemum* and *Eragrostiella* was, however, significantly lower than in others ($P > 0{\cdot}05$).

Starting with an initially high belowground biomass, a decline was observed in all the species in July–August, followed by an increase towards the latter part of the growing season (figure 1). Leaf biomass was initially much higher declining during the latter part. In *Arundinella*, *Carex* and *Chrysopogon*, belowground biomass was significantly higher ($P < 0{\cdot}05$) in the nutrient poor soil than in nutrient rich soil, with highest values recorded for *Eragrostiella* and *Ischaemum*. It may be noted that *Eragrostiella* and *Chrysopogon* have no stem component, as the leaves arise directly from the rhizomatous base. Further, seed production in *Chrysopogon*, did not occur in the nutrient poor soil.

Nitrogen allocation to belowground organs of *Arundinella*, *Carex* and *Chrysopogon* was lower ($P < 0{\cdot}01$) in nutrient poor soils than in the richer soils (figure 2). While in *Arundinella* the allocation to the stem was higher in the nutrient poor soil, ($P < 0{\cdot}05$) the reverse was true for *Carex*. Leaf allocation of nitrogen was significantly higher ($P < 0{\cdot}01$) for *Arundinella* and *Carex* but lower for *Chrysopogon* ($P < 0{\cdot}01$), in nutrient poor soils. Belowground allocation of nitrogen was maximum in *Eragrostiella* followed by *Ischaemum*.

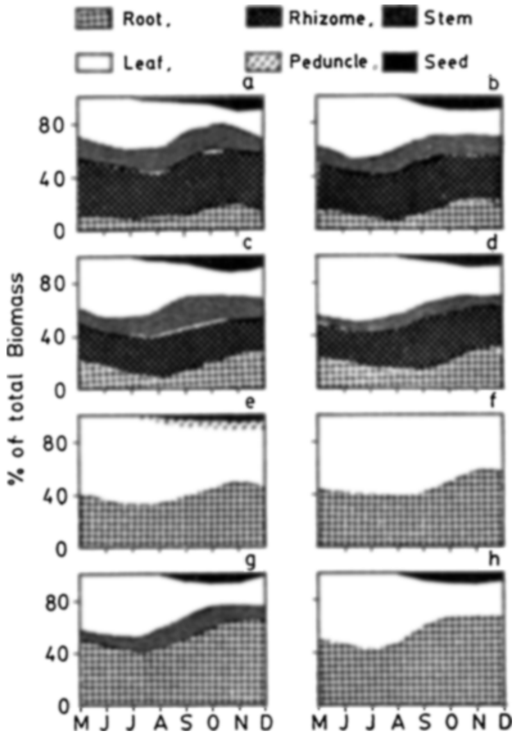

Figure 1. Growth and allocation strategies of *Arundinella* (**a**, **b**), *Carex* (**c**, **d**) and *Chrysopogon* (**e**, **f**) in grasslands at Cherrapunji in north-eastern India, under nutrient rich (**a**, **c**, **e**) and nutrient poor (**b**, **d**, **f**) sites and of *Ischaemum* (**g**) and *Eragrostiella* (**h**).

Allocation of phosphorus to the root component of *Arundinella*, *Carex* and *Chrysopogon* was significantly higher ($P < 0{\cdot}05$) in nutrient poor than in nutrient rich soil (figure 3). Phosphorus allocation to the rhizome, however, was significantly higher on nutrient rich soil only in *Arundinella*. Allocation to the leaf component was significantly higher in nutrient poor soil ($P < 0{\cdot}01$) in *Arundinella* and *Carex* but not very different in *Chrysopogon*. Maximum allocation of phosphorus to the root component was observed in *Ischaemum* and *Eragrostiella*. Allocation to the leaf and the seed components in *Eragrostiella* was higher ($P < 0{\cdot}05$) than in *Ischaemum*.

Allocation of potassium to the belowground parts in *Arundinella* alone was significantly lower ($P < 0{\cdot}05$) in nutrient poor than in richer soil (figure 4). Maximum allocation of potassium to the root component was observed in *Eragrostiella*. Allocation to the leaf component was maximum in *Ischaemum*.

A significantly lower ($P < 0{\cdot}01$) nutrient uptake efficiency in nutrient poor than in richer soils was observed only for nitrogen (table 6), with least values for *Ischaemum*.

A significantly higher ($P < 0{\cdot}05$) nitrogen use efficiency was seen for *Arundinella* and *Chrysopogon* in nutrient rich than in nutrient poor soil (table 7). *Eragrostiella* had maximum values for nitrogen and potassium use efficiency compared to all other species; even phosphorus use efficiency of this species was high. While *Chrysopogon* had a higher phosphorus use efficiency in nutrient poor than in rich soil, the reverse was true for *Carex*. Potassium use efficiency of *Chrysopogon* in nutrient poor soil was lower than in richer soil.

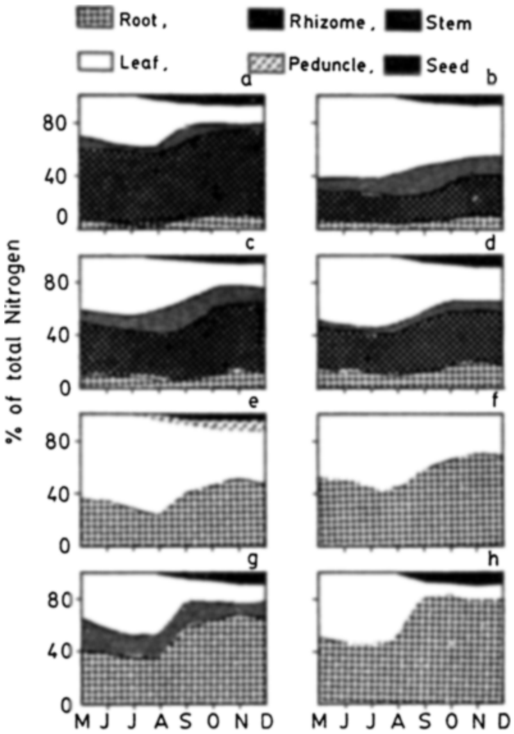

Figure 2. Same as figure 1; allocation of nitrogen.

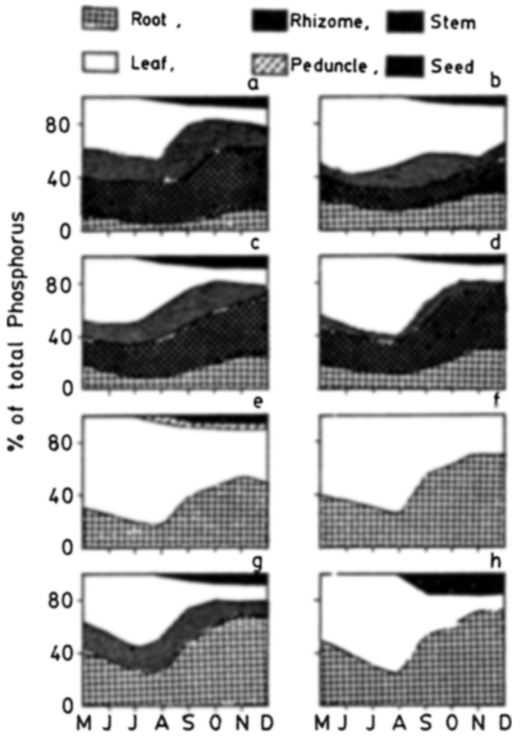

Figure 3. Same as figure 1; allocation of phosphorus.

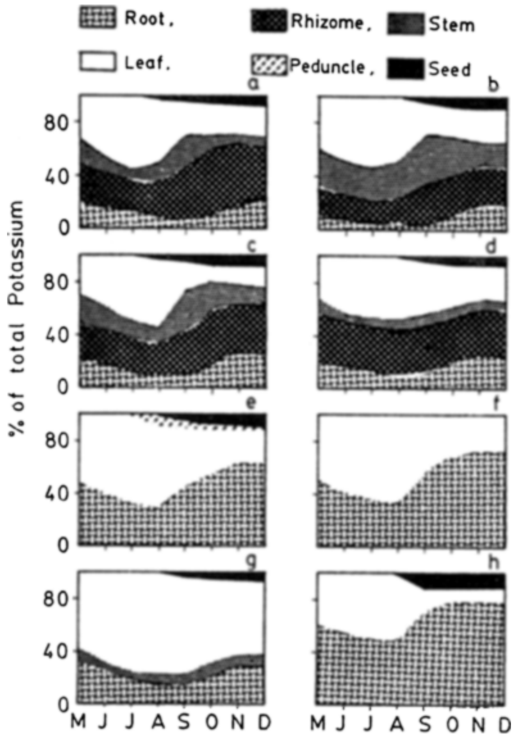

Figure 4. Same as figure 1; allocation of potassium.

Table 6. Nutrient uptake efficiency during annual growth period (mg nutrient absorbed/g root biomass) of different species at Cherrapunji in north-eastern India.

	Nutrient uptake efficiency		
Species	Nitrogen	Phosphorus	Potassium
Arundinella	107·02 ± 8·5	11·7 ± 9·5	53·05 ± 5·1
	(56·05 ± 4·2)	(10·4 ± 8·9)	(58·13 ± 4·9)
Carex	71·50 ± 4·1	13·76 ± 11·5	71·5 ± 4·5
	(61·50 ± 5·0)	(11·39 ± 10·1)	(68·1 ± 4·1)
Chrysopogon	102·10 ± 8·9	12·83 ± 1·9	54·09 ± 5·0
	(88·09 ± 7·5)	(11·51 ± 2·0)	(53·66 ± 5·1)
Ischaemum	45·69 ± 4·3	12·37 ± 0·10	47·05 ± 0·6
Eragrostiella	65·13 ± 6·1	13·40 ± 1·5	60·67 ± 4·10
Least significant difference ($P = 0{\cdot}01$)	6·53	1·62	7·88

Numbers in parentheses indicate species grown in nutrient poor soil.

5. Discussion

The 3 grasslands under consideration here are degraded types with soils that are relatively deficient, compared to the climax forest type of the area (Khiewtam 1986). However, among these 3 grasslands, the soil under *Osbeckia*-type is relatively nutrient rich compared to that under *Eragrostiella*-type, the *Ischaemum*-type falling

Table 7. Nutrient use efficiency (mg dry matter produced/mg nutrient absorbed) of different species at Cherrapunji in north-eastern India.

	Nutrient use efficiency		
Species	Nitrogen	Phosphorus	Potassium
Arundinella	149·9 ± 12·5	1020·4 ± 95·4	136·4 ± 12·5
	(101·7 ± 9·7)	(1010·1 ± 91·7)	(158·7 ± 14·5)
Carex	108·1 ± 9·1	980·4 ± 75·9	91·7 ± 8·5
	(124·8 ± 11·1)	(740·4 ± 61·4)	(89·2 ± 7·1)
Chrysopogon	109·1 ± 9·4	595·2 ± 41·5	158·7 ± 13·7
	(77·94 ± 5·4)	(657·9 ± 51·3)	(122·0 ± 10·5)
Ischaemum	117·6 ± 9·7	877·2 ± 73·4	169·5 ± 14·3
Eragrostiella	150·9 ± 12·7	943·40 ± 81·4	188·7 ± 17·1
Least significant difference ($P = 0{\cdot}01$)	3·99	31·1	4·86

Numbers in parentheses indicate species grown in nutrient poor soil.

in between. It is therefore reasonable to expect larger biomass with a faster growth rate for the species under *Osbeckia*–type than under *Ischaemum* or *Eragrostiella* types. This is reflected not only through differences in the growth rate of species such as *Ischaemum* and *Eragrostiella* under these two grassland situations but also through differential growth rates of the other species on nutrient rich versus poor soils.

A useful strategy for survival of plant species growing in nutrient poor soils is to have greater allocation of biomass to the belowground organs as compared to aboveground parts. This is a mechanism to maximize nutrient intake through a larger root surface (Chapin 1980) rather than through a high nutrient absorption capacity (Nye 1977; Nye and Tinker 1977). This is seen in the present study too with respect to *Chrysopogon*, *Ischaemum* and *Eragrostiella*. *Eragrostiella* growing in a desertified site had maximum root biomass compared to all other species. This is also a mechanism to store organic food and nutrients in the belowground rhizomatous tissue and thus contribute to more efficient vegetative reproduction using the food reserves. Greater allocation of resources to belowground organs is thus an adaptation for survival under stress environment, S-strategy of Grime (1979). With larger allocation of available resources to the belowground organs of regeneration, species such as *Carex* and *Arundinella* have lesser allocation to sexual reproduction (Keeley and Keeley 1977). In fact, for the 3 tussock perennial grasses *Chrysopogon*, *Ischaemum* and *Eragrostiella* of stressed sites, with sprouts appearing from the base, the emphasis on sexual reproduction is minimal; this is unlike ruderal environment where resource availability is unpredictable.

An important characteristic that is of value for survival in a nutrient poor soil is a slow growth rate (Chapin 1980). Thus, species such as *Eragrostiella* had least growth rate compared to other species. Further, species occurring on and off nutrient rich soils such as *Arundinella*, *Carex* and *Chrysopogon* had drastically reduced relative growth rate and net assimilation rate in nutrient poor than richer soils. This helps to have comparable tissue concentrations of nutrients in nutrient poor soils as under nutrient richer soils. Thus, the reduction in nutrient concentration in the species growing under infertile soils is not very different from those growing in more fertile soils; in some cases the concentration is the same or even higher when under nutrient stress.

Species from infertile sites may have generally lower nutrient concentrations than from fertile sites, owing to ready availability and absorption. However, slow growing plant species from infertile sites may respond to nutrient stress by maintaining high tissue nutrient concentration through luxury consumption and or reduced growth rate (Auclair 1977). Contrary to this more rapid growth of a species in fertile sites may have dilution effect on the plant nutrient pool. Consequently, tissue concentrations of wild plants are less sensitive indicators of soil availability (van den Driessche 1974).

It is interesting to note that a C_3 species such as *C. cruciata* showed a higher growth rate compared with some C_4 species. This is perhaps related to a much higher leaf area ratio for this species compared with others. A similar observation was made by Saxena and Ramakrishnan (1984) while comparing C_3/C_4 strategies of early successional herbs after slash and burn agriculture (Saxena and Ramakrishnan 1981, 1983), with a C_3 species such as *Eupatorium odoratum* having a higher growth rate due to higher leaf area ratio. For comparing the productive potentials of C_3 and C_4 plants the importance of the extent of the light interception surface has been emphasized by a number of workers (Bull 1971; Caldwell 1974; Hafstra and Steinstra 1977) rather than the photosynthetic rate per unit leaf area as stressed by others (Black *et al* 1969; Black 1971). Gifford (1974) concluded that the large potential advantage of the C_4 species is progressively attenuated while moving from microscopic to macroscopic parameters and there remains no apparent difference between the two photosynthetic pathways at the level of crop growth rate when each species is grown in its own preferred environment.

The C_4 species, having a generally higher nutrient uptake and use efficiencies compared to C_3 species, are adapted to occupy nutrient deficient soils (Brown 1978; Saxena and Ramakrishnan 1983, 1984). It is therefore reasonable to find that *Ischaemum* and *Eragrostiella* types of grassland on relatively nutrient poorer soils have more C_4 species than the *Osbeckia* type under nutrient richer soils (Ram 1986).

The results, presented here, thus show a close adaptation of species to the environmental conditions in which they occur. Under nutrient stress conditions, as exists in many of these grassland types, the allocation strategy is largely geared to clonal propagation, with greater emphasis on C_4 species that are generally nutrient use efficient.

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