Proc. Indian Acad. Sci. (Plant Sci.), Vol. 99, No. 4, August 1989, pp. 343–351.

Growth strategies of early and late successional shrubs from a sub-tropical moist forest under two light regimes

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MS received 7 January 1988; revised 3 July 1989

Abstract. Two early successional shrubs *Mallotus indica* Muell. and *Clerodendron infortunatum* Gaertn. and two late successional shrubs, *Litsea khasiana* Meissn. and *Combretum flagrocarpum* Herb. were studied under both open and shade environments. The early successional species had greater dry weight allocation to the stem and leaf components and lesser allocation to the root component. Thus the early successional species had an exploitative strategy for effective light capture and utilization of nutrient enriched surface soil after clear-cutting of a forest. On the other hand, the late successional shrubs showed a reverse pattern in allocation. This was related for their survival and to make adequate growth in a competitive environment. These differential strategies of the two categories of shrubs was also reflected in the lower nutrient uptake efficiency and higher use efficiency of the late successional species compared to the early successional ones. Under shade the dry weight production of late successional species was reduced to a less extent than that of early successional species. This would presumably have a competitive advantage for the former category of species.

Keywords. Allocation strategies; succession; tropical forest; light adaptation of shrubs.

1. Introduction

The effect of shading upon the growth and morphogenesis of shade tolerant and intolerant plant species has received much attention (Blackman and Wilson 1951; Bordeau and Laverick 1958; Grime 1966; Loach 1970; Mygren and Kellomaki 1983). These studies suggest that plant species often maximize dry matter production in shade through increase in leaf area and shoot/root ratio. The success of an organism in a particular environment is mainly dependent upon its relative apportionment of biomass for diverse purposes such as growth and reproduction, which is referred to as the allocation strategy of the species (Abrahamson 1979). Allocation of photosynthates to different components of a plant has been associated within the stand light condition (Mousi and Murata 1970; Horn 1971). Biomass allocation strategy for light demanding early versus shade tolerant late successional tree species was examined by Shukla and Ramakrishnan (1984) and was related to the successional environments.

Studies on growth strategies of shrubs have dealt with evergreen versus deciduous habit (Schlesinger and Gill 1980; Gray and Schlesinger 1983). The behaviour of shrubs under sun and shade environments across a successional gradient have not received much attention. With drastic changes in microenvironmental conditions during succession, it is expected that the dry weight allocation strategies of shrubs would vary. The present study, therefore, deals with growth and resource (biomass

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and nutrients) allocation pattern of 4 selected shrub species. Two of these, *Mallotus indica* Muell. and *Clerodendron infortunatum* Gaertn. are light-demanding early successional species and invade abandoned fields during secondary succession after slash and burn agriculture (Singh and Ramakrishnan 1982; Toky and Ramakrishnan 1983) at lower elevations of Meghalaya in north-east India. *Litsaea khasiana* Meissn. is a mid-successional species and grows in the open but has the ability to tolerate shade of a closed canopy. *Combretum flagrocarpum* Herb.* is a late successional shade tolerant species occurring under a close canopy of forest. These two early successional species have continuous growth and are leaf-exchanging types periodic whereas the two late successional species growth evergreen types (Longman and Jenik 1974).

2. Study area

The study area is located at Lailad (26° N and 92° E) at an elevation of 296 m and is about 70 km north of Shillong. Slash and burn agriculture is prevalent agricultural practice of the region. It involves cutting of forest, burning of slash, cultivating a mixture of crops for a year or two and then leaving the land for regeneration till the next clearing. The regeneration phases were dominated by herbaceous vegetation such as *Mikania micrantha*, *Imperata cylindrica*, *Saccharum spontaneum* and *Eupatorium odoratum* up to 5 years. This is followed by a shrubby early successional woody stage consisting of species such as *Mallotus indica*, *Clerodendron infortunatum* and *Lagerstroemia parviflora*. Bamboos such as *Dendrocalamus hamilttonii* the tree species such as *Schima wallichii*, *Macaranga denticulata* and *Dillenia pentagyna* also occure up to 20 years of fallow regrowth (Toky and Ramakrishnan 1983). The late successional stages are dominated by trees such as *Artocarpus chaplasha*, *Castanopsis indica*, *Shorea robusta* and *Mesua ferrea* with a dominant shrub stratum (Singh and Ramakrishnan 1982).

The soil is a sandy loam (0–40 cm) and is of lateritic origin (Oxysol) on metamorphic rock parent material. The pH ranges from 5·8–6·3. Detailed information on soil characteristics of the study site is given elsewhere (Ramakrishnan and Toky 1981). The climate is typically monsoonal with about 80% of the total annual rainfall (2200 mm) occurring during May–September. The rest of the period is relatively dry (435 mm). The monsoon season is followed by a mild winter from mid-November to mid-February. March and early April represent a brief dry summer period (figure 1).

3. Methods

Seeds of *Mallotus*, *Clerodendron*, *Litsaea* and *Combretum* were collected during November 1982 to February 1983. Five hundred earthern pots, 30 cm high and 48 cm diameter filled with garden soil were used to raise seedlings of each shrub species. Five hundred pots each of the two early successional species were placed under full day light (light intensity variation during the year was 6×10^4 to $7{\cdot}1 \times 10^4$ lux).

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*Henceforth referred to by the generic name.

Like wise seedlings of the two late successional species were raised in 500 pots each under a closed canopy of the forest (light intensity variation during the year was $0{\cdot}9 \times 10^4$ to 10×10^4 lux). Fifteen days after germination seedlings were thinned down to one individual per pot. After growth for one month in the two environmental situations, 250 potted seedlings of each species were transferred to the contrasting light environment (i.e. open to closed and vice versa). After one year of sapling establishment, 10 individuals each of the 4 species from both open (sun) and closed (shade) environments were harvested at monthly intervals, during April 1984 to April 1985. The harvested plants were separated into root, stem and leaf, dried at $80° \pm 5°C$ for 48 h and weighed. Leaf area estimation using a planimeter and leaf dry weight per unit area were based on 3 replicates of 50 leaves per replicate.

Growth functions such as relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) were calculated as:

$$\text{RGR (mg mg}^{-1}\,\text{d}^{-1}) = \frac{\ln W_2 - \ln W_1}{t_2 - t_1},$$

$$\text{NAR (mg cm}^{-2}\,\text{d}^{-1}) = \frac{(W_2 - W_1)(\ln A_2 - \ln A_1)}{(A_2 - A_1)(t_2 - t_1)},$$

$$\text{LAR (cm}^2\,\text{mg}^{-1}\,\text{d}^{-1}) = \frac{(A_2 - A_1)(\ln W_2 - \ln W_1)}{(\ln A_2 - \ln A_1)(W_2 - W_1)},$$

where W_1 and A_1 are total dry weight (aboveground + belowground) and leaf areas values respectively, at the sampling time t_1 and W_2 and A_2 at time t_2 (Hughes and Freeman 1967; Radford 1967).

Concentration of nutrients in the different plant components were determined following the standard methods given by Allen *et al* (1974). Thus, nitrogen was analysed by microkjeldahl method, phosphorus by molybdenum blue method and potassium by flame photometry, after dry ashing. Nutrient uptake efficiency was expressed as mg nutrient absorbed per g of root biomass (mean monthly values), following Blair and Cordero (1978). Nutrient use efficiency was calculated as mg dry matter production per mg nutrient absorbed (Brown 1978). Statistical analysis using one way ANOVA was made to detect differences between the two categories.

4. Results

Table 1 shows mean growth measurements on 2-year old individuals growing in sun and shade. The two early successional shrubs grown in the sun had higher values ($P < 0{\cdot}05$) for growth attributes such as height, basal stem diameter (at 10 cm height from ground) and shoot dry weight compared to the late successional shrubs. The root dry weight, however, was not significantly different for both categories of species. Consequently, the shoot/root ratio was lower for late successional species compared to early successional ones. Under shade, there was a decline in all growth attributes studied; this decline was generally more pronounced for the early successional species ($P < 0{\cdot}05$).

The RGR and NAR were generally higher ($P < 0{\cdot}05$) for early successional shrubs under open and shade conditions (table 2). RGR and NAR were less under shade than in the open ($P < 0{\cdot}05$) for all the species. On the other hand, LAR was higher ($P < 0{\cdot}05$) for late successional species than early successional ones. LAR was higher

Table 1. Mean growth measurements (terminal harvest) (±SE) of early and late successional shrubs in open and shade environments.

Species	Treatment	Height (cm)	Stem diameter (cm^2)	Aboveground biomass (g)	Belowground biomass (g)	Shoot/root ratio
Early successional						
Mallotus	Open	79·5 ± 2·1	0·91 ± 0·04	70·5 ± 2·1	12·4 ± 0·2	6·4 ± 0·20
	Shade	31·3 ± 1·3	0·37 ± 0·01	21·5 ± 0·3	5·5 ± 0·3	4·2 ± 0·05
Clerodendron	Open	66·4 ± 1·5	0·70 ± 0·01	73·6 ± 0·9	13·4 ± 0·2	5·5 ± 0·13
	Shade	30·0 ± 0·6	0·31 ± 0·01	25·5 ± 0·4	6·2 ± 0·1	4·1 ± 0·06
Late successional						
Litsaea	Open	42·9 ± 0·8	0·50 ± 0·03	48·4 ± 0·4	11·6 ± 0·1	4·2 ± 0·03
	Shade	22·6 ± 1·1	0·28 ± 0·01	20·2 ± 0·2	7·2 ± 0·1	2·8 ± 0·04
Combretum	Open	54·9 ± 1·7	0·61 ± 0·02	60·1 ± 0·6	14·1 ± 0·2	4·3 ± 0·04
	Shade	21·4 ± 0·6	0·25 ± 0·01	25·6 ± 0·3	8·5 ± 0·1	3·0 ± 0·05

Table 2. Mean values of 12 monthly sampling (±SE) of growth functions of early and late successional shrubs in open and shade environments.

Species	Treatment	Relative growth rate ($mg\ mg^{-1}\ d^{-1}$)	Net assimilation rate ($mg\ (cm^2)^{-1}\ d^{-1}$)	Leaf area ratio ($cm^2\ mg^{-1}$)
Early successional				
Mallotus	Open	0·032 ± 0·0012	0·246 ± 0·0028	0·136 ± 0·0015
	Shade	0·015 ± 0·0003	0·107 ± 0·0041	0·159 ± 0·0008
Clerodendron	Open	0·025 ± 0·0008	0·202 ± 0·0048	0·147 ± 0·0016
	Shade	0·014 ± 0·0004	0·095 ± 0·0017	0·170 ± 0·0019
Late successional				
Litsaea	Open	0·019 ± 0·0004	0·134 ± 0·0023	0·189 ± 0·0014
	Shade	0·011 ± 0·0004	0·053 ± 0·0012	0·239 ± 0·0021
Combretum	Open	0·022 ± 0·0006	0·153 ± 0·0047	0·173 ± 0·0029
	Shade	0·009 ± 0·000	0·048 ± 0·0013	0·222 ± 0·0021

($P < 0·05$) under shade compared to the open and this increase was greater for the late successional species than early successional ones.

The dry matter allocation pattern from first and second year saplings expressed as a percentage of the total is shown in figure 1. Both early and late successional species showed a decline in biomass allocation to the leaf component under shade. The allocation of dry matter to the stem and root components of early successional species was not affected by light availability, whereas the allocation to the root increased under shade for late successional ones.

Nitrogen allocation to the leaf component in both early and late successional species declined under shade whilst that for the root component increased (figure 2). Early successional species generally had a higher allocation of nitrogen to the leaf compared to the late successional species. The patterns for phosphorus and potassium allocations were similar to nitrogen and therefore are not presented here.

The nutrient uptake efficiency was generally higher ($P < 0·01$) for early succes-

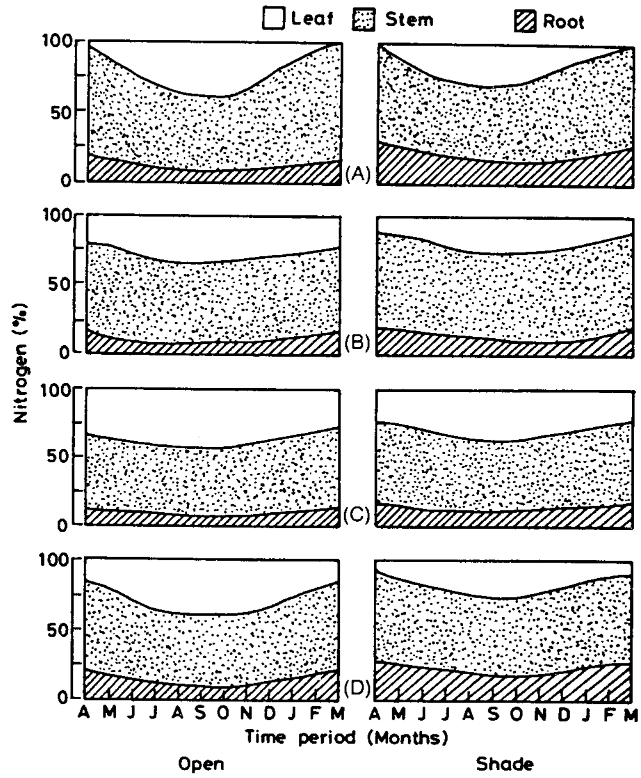

Figure 1. Allocation pattern of biomass to different components (expressed as percentage of the total capital) of early and late successional species in open and shade environments. **(A)**, *Mallotus*; **(B)**, *Clerodendron*; **(C)**, *Litsaea*; **(D)**, *Combretum* (the monthly variation was within 95% confidence limit).

sional shrubs compared to late successional ones (table 3). A decline ($P<0{\cdot}01$) in nutrient uptake efficiency was observed for all the species under shade.

The nutrient use efficiency (table 4) for late successional species was significantly higher ($P<0{\cdot}01$) compared to early successionals. Nutrient use efficiency of all species improved under shade ($P<0{\cdot}01$) compared to those in the open, but this improvement was more pronounced for the late successional species.

5. Discussion

The ability of a forest species to survive and grow beneath a forest canopy is related, among other things, to its shade tolerance. Species differ in their ability to tolerate shade and this is often interpreted in terms of their relative efficiencies in biomass accumulation (Grime 1966; Loach 1970). Early successional shrubs which are light demanders have a high above ground biomass production in an open environment, contributing to quick shoot growth (Boojh and Ramakrishnan 1982; Ramakrishnan and Shukla 1983; Shukla and Ramakrishnan 1986). The proportional allocation of the biomass to the root system of early successional shrubs was less than that of the late successional ones, an observation similar to that on tree

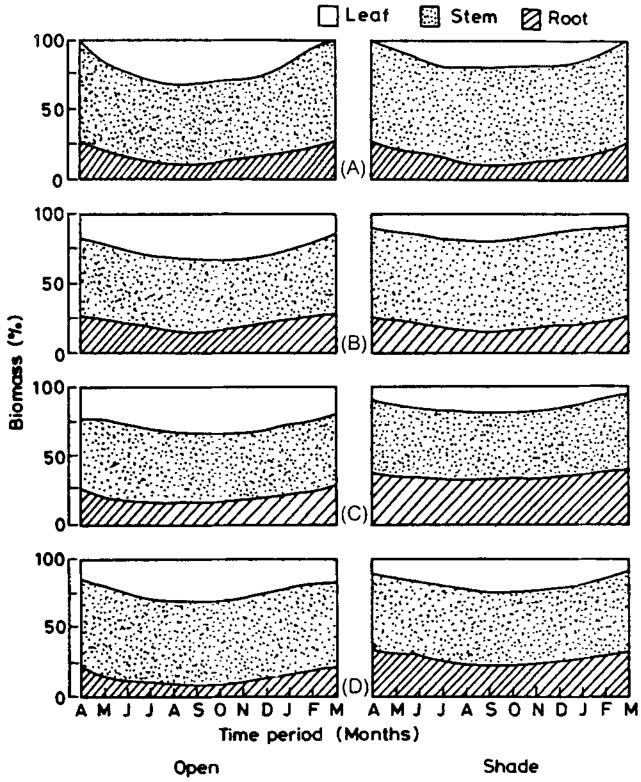

Figure 2. Allocation pattern of nitrogen to various components (expressed as percentage of the total capital) of early and late successional species in open shade environments. (**A**), *Mallotus*; (**B**), *Clerodendron*; (**C**), *Litsaea*; (**D**), *Combretum* (the monthly variation was within 95% confidence limit).

species made by Shukla and Ramakrishnan (1984). Perhaps, the early successional species growing in a nutrient-rich surface soil after clear-cutting of a forest or as a large gap species could possibly do with a reduced shoot/root ratio compared to late successional shrubs which may have to compete with many other species for the limited soil nutrients of a closed forest.

The light-demanding early successional shrubs responded to shading by a greater reduction in biomass (about 3 times) than the late successional shrubs (about two times), also observed by Bordeau and Laverick (1958), Grime (1966, 1977) and Loach (1970), such a differential response with greater tolerance to shade by the late successionals as expressed by biomass production would confer greater competitive ability under a closed forest canopy. However increased biomass production in the open by the shade-tolerant shrubs is perhaps suggestive of their ability to survive under shade rather than to maximize light interception and biomass production.

Nutrient allocation pattern of early and late successional species differed. The former had more allocation of nutrients to the leaf component, than the latter. Leaf being the chief photosynthetic organ, this allocation strategy may be an adaptation for quick growth by early successional species. With a fast turnover of leaves in early successional trees (Boojh and Ramakrishnan 1982; Shukla and Ramakrishnan

Table 3. Mean monthly nutrient uptake efficiency (±SE) (mg nutrient absorbed per g root dry weight) of early and late successional shrubs in open and shade environments.

		Nutrient uptake efficiency		
Species	Treatment	Nitrogen	Phosphorus	Potassium
Early successional				
Mallotus	Open	137·2 ± 1·3	7·1 ± 0·04	122·0 ± 1·0
	Shade	80·9 ± 0·6	4·0 ± 0·02	65·6 ± 1·3
Clerodendron	Open	94·8 ± 1·0	5·0 ± 0·06	91·3 ± 1·4
	Shade	58·5 ± 1·6	3·2 ± 0·01	45·0 ± 1·1
Late successional				
Litsaea	Open	67·3 ± 1·4	4·1 ± 0·02	59·4 ± 0·8
	Shade	39·6 ± 0·3	2·2 ± 0·01	46·6 ± 1·6
Combretum	Open	74·8 ± 1·0	4·6 ± 0·03	66·6 ± 1·6
	Shade	42·6 ± 0·6	2·4 ± 0·01	35·0 ± 0·6

Table 4. Mean nutrient use efficiency (±SE) (mg dry matter) produced per mg nutrient absorbed of early and late successional shrubs in open and shade environments.

		Nutrient use efficiency		
Species	Treatment	Nitrogen	Phosphorus	Potassium
Early successional				
Mallotus	Open	67 ± 1	1062 ± 15	82 ± 1
	Shade	80 ± 1	1268 ± 10	105 ± 1
Clerodendron	Open	82 ± 1	1320 ± 14	97 ± 3
	Shade	99 ± 2	1547 ± 18	131 ± 2
Late successional				
Litsaea	Open	102 ± 2	1464 ± 14	125 ± 3
	Shade	140 ± 2	1909 ± 29	183 ± 3
Combretum	Open	116 ± 2	1657 ± 12	136 ± 3
	Shade	162 ± 3	2273 ± 38	210 ± 2

1984) and shrubs (U Baruah and P S Ramakrishnan, unpublished results) a greater allocation of nutrients to these organs ensure a faster turnover of a larger mass of nutrients through cycling for use by the developing vegetation.

The higher nutrient uptake efficiency and the lower nutrient use efficiency of early successional shrubs, and the reverse of it for late successional shrubs suggest of a close adaptation to the soil environment in which these category of species exist early successional shrubs normally occurring in a temporarily nutrient enriched soil and the late successional shrubs occurring in a nutrient depleted soil. These results also suggest the importance of considering nutrients in allocation strategy studies (Benzing and Davidson 1979; Clark and Burk 1980; Abrahamson and Casewell 1982; Saxena and Ramakrishnan 1984). It may be reasonable to conclude that the early successional shrubs with an exploitative strategy as reflected through this study and through our earlier studies on tree species (Ramakrishnan *et al* 1982) is designed to capitalize upon a temporarily resource (light and nutrients) rich environment, after slash and burn of the forest (Ramakrishnan and Toky 1981). On the other hand, the late successional shrubs have a competitive strategy that has evolved to survive and to make adequate growth in a closed late successional environment, over a period of about 50 years of forest succession.

Acknowledgements

This research was supported by the Department of Science and Technology, New Delhi and the work was done at the Centre for Eco-Development of the North-Eastern Hill University, Shillong. One of the authors (UB) is thankful to the Director, Tocklai Tea Experimental Station, Jorhat for facilitating the work through study leave.

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