New Phytol. (1984) 97, 697–706

LEAF DYNAMICS OF TROPICAL TREES RELATED TO SUCCESSIONAL STATUS

BY R. P. SHUKLA AND P. S. RAMAKRISHNAN*

Department of Botany, School of Life Sciences, North-Eastern Hill University, Shillong 793014, India

(*Accepted 28 March 1984*)

SUMMARY

Leaf dynamics of two early successional and two late successional species of a tropical humid forest at Lailad in north-eastern India were studied. Leaves produced during different months were found to have markedly different longevity, for all the species studied. The early successional species showed higher leaf turnover rates, reduced leaf longevity, more uniform production and fall of leaves under forest-grown conditions than in open-grown conditions (though with some fluctuation during the year) and an evergreen or leaf-exchanging pattern of leafiness. The late successional species had slower leaf turnover rates, longer leaf longevity, a peak of leaf production and a deciduous habit. It is concluded that differences in leaf dynamics of early and late species are related to the successional niches they occupy in the forest community.

Key words: Leaf dynamics, tropical tree growth, succession, strategies.

INTRODUCTION

Leaf area available for photosynthesis plays a crucial role in biomass production: the change in total leaf area being primarily determined by the patterns of production and fall, and the longevity of leaves (Watson, 1956; Newhouse & Madgwick, 1968). Seasonal or other variation in leaf size will also affect the total photosynthetic area (Smith & Nobel, 1977). Several studies on leaf expansion of temperate angiosperm trees (Büsgen & Münch, 1931; Kozlowski & Clausen, 1966) suggest variations based on the type of shoot and the environment to which they are exposed (Kozlowski, 1971).

Much less is known about the leaf dynamics of tropical trees. While temperate angiosperm trees characteristically shed their leaves during autumn, tropical trees show a wide variety of patterns of leaf production, longevity and fall (Holttum, 1940; Alvim, 1964; Longman & Jenik, 1974). Because of the implication of light in leaf dynamics (Addicott & Lyon, 1973), strategies found in trees over a successional gradient might be expected to vary. Such a relationship between leaf dynamics and changing light conditions in the community has been shown by Boojh & Ramakrishnan (1982) for temperate elements of high altitude trees of north-east India. However, little is known on these aspects for tropical trees; this has stimulated the present study on leaf dynamics of two early successional (ES) tropical tree species (*Duabanga sonneratioides* Ham. and *Anthocephalus cadamba* Miq.) and two of a late successional (LS) stage (*Dillenia petagyna* Rox. and *Artocarpus chaplasha* Roxb.). The successional status of these trees was determined on the basis of our earlier studies (Singh & Ramakrishnan, 1982; Toky & Ramakrishnan, 1983; Ramakrishnan & Shukla, 1983).

---

* Author to whom all correspondence should be addressed.

0028-646X/84/080697+10 $03.00/0

MATERIALS AND METHODS

The work was performed at Lailad, about 70 km north of Shillong, Meghalaya in north-eastern India (25° 45′ latitude, 91° 45′ longitude) at an elevation of 300 m. The climate (Fig. 1) is monsoonic with about 84% of the total annual rainfall (2200 mm) during May to September. The winter (November to mid-February) is mild. The warm dry summer extends from mid-February to mid-April.

Five-year-old open-grown trees of all the four species were identified, on the basis of growth morphology considering extension growth markings on the leader axis and the number of yearly suits of first-order branches developed on them (Shukla, 1981), in a 10-year-old naturally regenerated secondary forest, (Ramakrishnan *et al*, 1981) along the periphery of a 50-year-old reserve forest at Lailad (Singh & Ramakrishnan, 1982). Forest-grown trees of *Anthocephalus* and *Artocarpus* of the same age were also identified in the 50-year-old reserve forest at Lailad (Singh & Ramakrishnan, 1982). Identified trees were protected from herbivores by fencing and spraying with insecticides as required during the study period. All observations are based on five replicate trees. The average dimensions of the sample trees are given in Table 1.

All the existing and the newly forming leaves on each tree were tagged with small and lightweight colour-coded aluminium tags. Detailed observations at weekly intervals on emergence, fall and area were obtained for individual leaves, on the main axis, and all first- and second-order branches on the tree, starting from January 1979 to December 1979.

Apparent plastochron (in days) was derived on the basis of the total number of leaves produced per month, considering only the main axis of the tree (Gill & Tomlinson, 1971). Because the rate of leaf production was slow in forest-grown individuals of *Anthocephalus* and *Artocarpus*, the average plastochron was obtained by dividing the total growth period for all the axes by the total number of leaves produced by them.

Leaf area was calculated on the basis of 50 leaves harvested from another 5-year-old tree and using regression equations developed relating blade length × breadth and leaf area for each species (Shukla & Ramakrishnan, 1981).

Ten 1-year-old first-order branches from the upper half of the canopy of 5-year-old open-grown trees of each species were harvested at the peak of the growing season in November 1979. The total leaf area on each branch was computed. Dry weights of each branch and the leaves on them were obtained separately after oven-drying at 80 ± 2 °C for 25 h.

RESULTS AND DISCUSSION

In earlier studies on the leaf dynamics of temperate trees of high elevations in north-east India, differences were observed in the seasonal behaviour of trees related to their successional status (Boojh & Ramakrishnan, 1982). The results discussed here on leaf dynamics extend our earlier work, showing that differences in leaf production, fall and longevity of ES vs LS trees result in faster turnover rates for the former compared to the latter category.

Leaf production

Under open conditions, the ES species had higher leaf area than the LS species; *Duabanga* had the highest (Fig. 2). Forest-grown trees had a smaller leaf

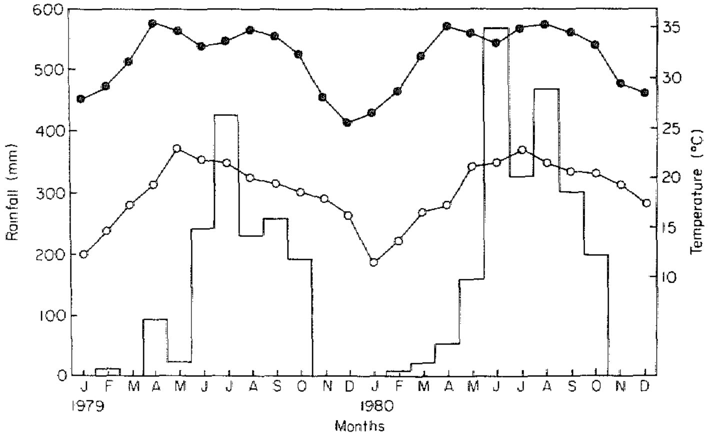

Fig. 1 Rainfall and temperature at the study site. Histogram, rainfall; closed circle, mean monthly maximum temperature; open circle, mean monthly minimum temperature.

Table 1. *Dimensions of four species of trees used in the study*

Species	Light conditions	Height (m)	Diameter at breast height (cm)
Duabanga sonneratioides	Open	5·8±0·2	7·2±0·2
Anthocephalus cadamba	Open	7·4±0·4	8·8±0·4
	Forest	3·7±0·1	3·0±0·1
Dillenia pentagyna	Open	4·3±0·1	4·9±0·1
Artocarpus chaplasha	Open	6·1±0·004	8·0±0·4
	Forest	4·8±0·3	4·5±0·3

Values are the means for five replicates ±standard error.

area than open-grown ones. The reduction in leaf area of the forest-grown individuals compared to open-grown ones of *Anthocephalus* was more than that for *Artocarpus* suggesting better shade tolerance by the latter species (Boojh & Ramakrishnan, 1982). The ES species are never completely leafless during the year even during the period of peak leaf fall in February to April. On the other hand, the LS species became totally leafless in March (*Dillenia*) or April (*Artocarpus*), although, forest-grown *Artocarpus* retained a few old leaves even during April.

The monthly leaf production, as a percentage of the total number of leaves produced in a year, (shown here for open-grown trees only) was markedly different on different axes (Fig. 3). Though all the four open-grown species showed fluctuations in leaf production in different months, the ES species showed less monthly variation while the LS ones had a major peak during April and June in the case of the main axis and the first-order branches. Such a continuous and steady production of new leaves in ES species may be significant in maximizing photosynthesis under the high irradiances of the ES environment and thus lead to faster growth rate (Boojh & Ramakrishnan, 1982; Ramakrishnan, Shukla & Boojh, 1982). Rapid growth of some of ES tropical trees has been related more

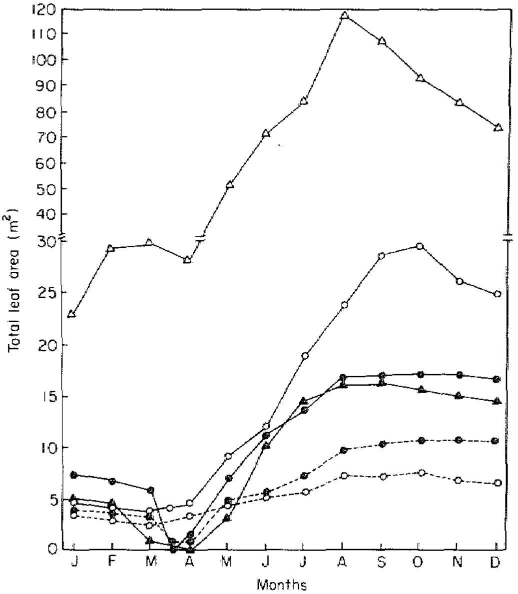

Fig. 2. The monthly pattern of change in total leaf area on early successional (open symbols) and late successional (closed symbols) species. Open triangles, *Duabanga*; open circle, *Anthocephalus*; closed triangles, *Dillenia*; closed circle, *Artocarpus*. Continuous line, open-grown individuals; and broken line, forest-grown individuals.

to their ability for unrestricted leaf production than to efficient energy conversion per unit leaf area (Coombe & Hadfield, 1962). For the second-order branches, the ES species showed a major peak in leaf production during April to May (*Duabanga*) and July to August (*Anthocephalus*). Leaf production on the second-order branches of *Anthocephalus* started a month later than on the first-order branches, perhaps as a response to shading. The pattern of leaf production on the second-order branches of LS species was not greatly different to that observed on the first-order branches for the same species. Leaf production stopped during the dry period of November to March except in *Duabanga* where it continued throughout the season, although at a low rate during winter months.

The frequency of leaf emergence on the main axis at different times is shown in Table 2 for all the open-grown species. The pattern for the upper and lower canopy position branches was similar and is not presented. The apparent plastochron for the ES species was least during July and August, but leaf production occurred throughout the year. The shorter apparent plastochron in the early phase of the shorter growth period of LS species results in a larger leaf population on the tree, and may be significant for optimizing photosynthesis in the low right regimes within the forest.

A comparison of the mean apparent plastochron for *Anthocephalus* and *Artocarpus* showed that the forest-grown trees of both species had a longer apparent plastochron than open-grown trees at all canopy positions (Table 3). This is related to reduced growth under the low light regime in the forest. However, no clear-cut differences could be found between the two species.

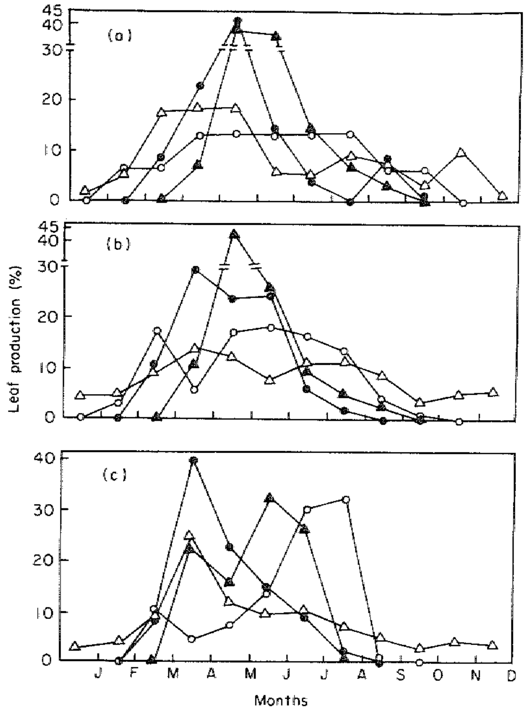

Fig. 3. The pattern of leaf production in early successional (open symbols) and late successional (closed symbols) species over the growth period, expressed as percentages of total number of leaves produced in a year on (a) main axis, (b) first-order and (c) second-order branches of open-grown individuals. Open triangles, *Duabanga*; open circles *Anthocephalus*; closed triangles, *Dillenia*; closed circles, *Artocarpus*.

Table 2. *Apparent plastochron (in days) for the main axis leaves of open-grown trees*

Month											
J	F	M	A	M	J	J	A	S	O	N	D
				Duabanga sonneratioides							
6·2 ±1·2	3·5 ±0·4	2·8 ±0·2	3·3 ±0·4	2·3 ±0·4	1·9 ±0·2	2·8 ±0·3	2·2 ±0·2	3·3 ±0·3	3·4 ±0·4	6·0 ±0·4	7·8 ±0·6
				Anthocephalus cadamba							
—	—	23·0 ±0·8	16·0 ±0·5	17·0 ±0·6	19·0 ±0·8	11·0 ±0·8	13·0 ±0·5	20·0 ±0·9	24·0 ±0·8	28·0 ±1·2	—
				Dillenia pentagyna							
—	—	—	—	4·4 ±0·2	6·0 ±0·4	5·2 ±0·5	4·4 ±0·3	15·0 ±0·4	31·0 ±	—	—
				Artocarpus chaplasha							
—	—	—	3·8 ±0·4	3·9 ±0·4	5·0 ±0·4	6·2 ±0·9	15·5 ±0·7	15·0 ±1·1	15·5 ±1·6	—	—

Dash denotes a month without leaf production. Values are the mean ± standard error of five replicates

Table 3. *Average apparent plastochron (in days) over the whole growth period for leaves on branches of two species growing in open and forest conditions*

Species	Light condition	Main axis	Upper branches	Lower branches
Anthocephalus cadama	Open	19·00	19·44±0·58	18·20±1·40
	Forest	30·86	34·06±1·79	45·50±2·06
Artocarpus chaplasha	Open	9·26	13·41±1·48	9·39±0·85
	Forest	13·07	19·78±2·13	27·96±1·40

Values are the mean±standard deviation of five replicates.

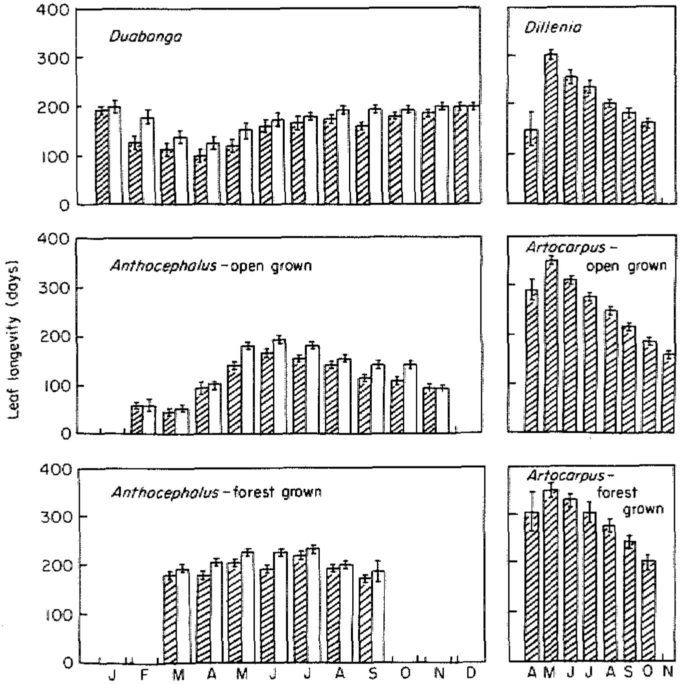

Fig. 4. Changes in longevity of leaves according to the month of emergence on main axis (hatched bars) and first-order branches (open bars). Vertical lines in the bars indicate standard error values.

Leaf longevity

The longevity of the leaves of ES species was shorter than that for the LS ones (Fig. 4). The longevity of the main axis leaves of ES species was often significantly shorter ($P < 0.05$) than that of those on the first-order branches; this was not true for LS species. The leaves of *Duabanga* produced during March to April survived for a shorter period than those produced in other months. The forest-grown *Anthocephalus* showed smaller fluctuations in life-span of leaves produced during March to September. The open-grown trees of this species showed greater fluctuation over the whole year. Thus the life-span of the leaves produced during May to July was more than three times that of those produced during February and March and about two times that of those produced during October. Leaf longevity for LS species was the longest for those emerging in May with a gradual decline through subsequent months. The leaves emerging in April also had a shorter life-span.

The significance of these findings is not clear. Apparently leaf longevity is not related solely to climate as different species show different patterns. The shorter life-span of the leaves of the ES species and the consequent rapid turnover may be associated with the tendency of these species to achieve fast growth by always placing most of the leaves in a favourable light environment as suggested earlier (Boojh & Ramakrishnan, 1982). The presence of a larger population of younger leaves in ES species may help in maximizing photosynthesis since photosynthetic efficiency of a leaf tends to decrease with age (Mooney, 1972; Johnson & Tieszen, 1976).

Leaf fall

The pattern of leaf fall in open- and forest-grown trees and in different branch orders did not differ and only the leaf fall from open-grown trees is shown in Figure 5. Leaf fall peaked during the dry period of March and early April and was followed by a marked decline in leaf shedding in subsequent months in the LS species. In ES species, this pattern of peaking and decline in subsequent months was less pronounced. Such a leaf fall pattern in tropical trees may be related to the dryness of the season (Longman & Jenik, 1974).

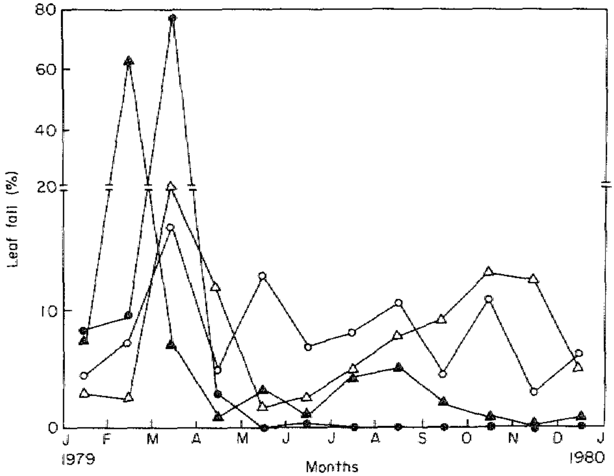

Fig. 5. The pattern of leaf-fall over the year expressed as the percentage of total leaves fallen in a year from the individuals of early successional (open symbols) and late successional (closed symbols) species growing in the open. Open triangles, *Duabanga*; open circles, *Anthocephalus*; closed triangles, *Dillenia*; closed circles, *Artocarpus*.

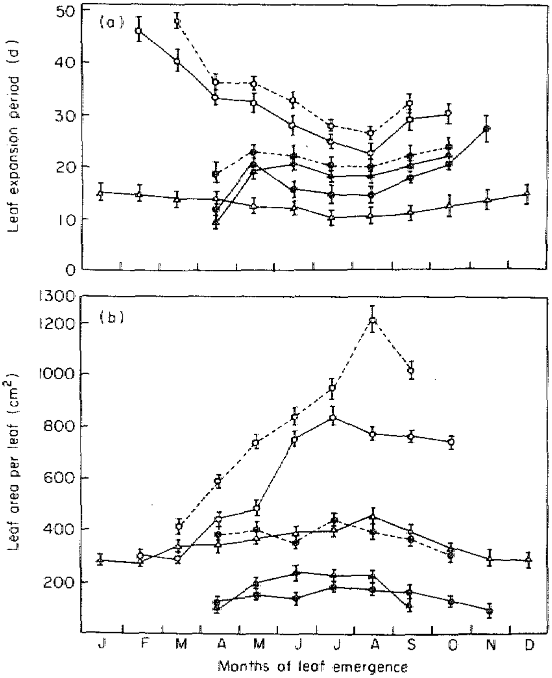

Fig. 6. Seasonal changes in (a) leaf expansion period (days) and (b) final area (cm^2) of leaves emerging in different months. Continuous line, for first-order branches of open-grown individuals; broken line, forest-grown individuals of early successional (open symbols) and late successional (closed symbols) species. Open triangles, *Duabanga*; open circles *Anthocephalus*; closed triangles, *Dillenia*; closed circles *Artocarpus*. Vertical lines indicate ± standard error.

Changes in overall leafiness

Seasonal patterns in the length of the leaf expansion period and in the final individual leaf area achieved did not differ for the different orders of branches, and only that for the first-order branches is presented (Fig. 6). The expansion period was the shortest for leaves produced during July and August in the case of the ES species and during April for the LS ones. The trends in expansion agree broadly with those for the apparent plastochron (cf. Table 1), the LS species tending to show more active leaf production during the early part of the growing season. The expansion period, in general, was greatest for *Anthocephalus* and least for *Duabanga*, the latter also had the least monthly variation. The forest-grown trees of *Anthocephalus* and *Artocarpus* showed slower leaf expansion than open-grown ones. The largest individual leaf area was attained by the ES species in July and August though the expansion period during these 2 months was shortest; LS species also showed larger leaf area of individual leaves during July and August, a period when moisture and temperature conditions are optimum for growth. As expected, forest-grown trees of *Anthocephalus* and *Artocarpus* had larger individual leaf area than open-grown trees of the same species.

Table 4 shows leaf area and leaf dry weight in relation to the weight of the

Table 4. *The ratio of leaf area or leaf weight per unit branch weight*

Species	Leaf area/ branch weight	Leaf weight/ branch weight
Duabanga sonneratioides	272·08 ± 36·20	2·71 ± 0·38
Anthocephalus cadamba	242·93 ± 36·00	2·30 ± 0·31
Dillenia pentagyna	152·30 ± 23·40	1·30 ± 0·19
Artocarpus chaplasha	118·60 ± 21·60	1·22 ± 0·08

The values are the mean ± standard error of 10 replicates.

branches bearing these leaves for open-grown trees only. This ratio was markedly higher for the ES species than for the LS ones which allocated less biomass to the leaves than to the branches on which they were borne. These results are in agreement with the studies of Montenegro *et al.* (1979) on the growth strategies of some shrubs, considering the leaf as a source and the branch as the immediate sink and the allocation strategies of a number of tropical trees (Ramakrishnan & Shukla, 1983; Shukla & Ramakrishnan, 1984).

Considering leafiness on the basis of leaf production and leaf fall, the two ES species studied here belong to 'continuous growth–evergreen type' (*Dubanga*) or 'periodic growth–leaf exchanging type' (*Anthocephalus*) while both the LS species strictly follow the pattern of 'periodic growth–deciduous type' (Longman & Jenik, 1974). Our studies on general phenology of a sub-tropical forest in this region (Shukla & Ramakrishnan, 1982) suggest that a large number of LS trees are deciduous compared to the ES trees which are evergreen.

The overall leafiness of the ES trees can be seen as an exploitive strategy (Bormann & Likens, 1979) linked to the plants ability to utilize the enriched resources in the soil after clear-cutting, and to take advantage of gap environments and make quick growth under the high light regime. The LS trees, on the other hand, show a conservative strategy, attuned to the more competitive environment of a closed forest.

ACKNOWLEDGEMENTS

We are grateful to J. B. Fisher, Fairchild Tropical Garden, Miami, Florida and to P. L. Marks, Cornell University, Ithaca of USA for their helpful comments on the original draft of this manuscript.

REFERENCES

Addicot, F. T. & Lyon, J. L. (1973). Physiological ecology of abscission. In: *Shedding of Plant Parts* (Ed. by T. T. Kozlowski), pp. 85–124. Academic Press, New York.

Alvim P. de T. (1964). Tree growth periodicity in tropical climate. In: *The Formation of Wood in Forest Trees* (Ed. by M. H. Zimmermann), pp. 479–496, Academic Press, New York.

Boojh, R. & Ramakrishnan, P. S. (1982). Growth strategy of trees related to successional status. II. Leaf dynamics. *Forest Ecology and Management*, **4**, 375–386.

Bormann, F. H. & Likens, G. E. (1979) *Patterns and Process in a Forested Ecosystem*. Springer-Verlag, New York.

Büsgen, M. & Münch, E. (1931) *The Structure and Life of Forest Trees* (Translated by T. Thomson), 3rd Edn. John Wiley, New York.

Coombe, D. E. & Hadfield, W. (1962). An analysis of the growth of *Musanga cecropoides*. *Journal of Ecology*, **50**, 221–234.

GILL, A. M. & TOMLINSON, P. B. (1971). Studies on the growth of red mangrove (*Rhizophora mangle* L.) 3. Phenology of the shoot, *Biotropica*, **3**, 109–124.

HOLTTUM, R. E. (1940). On periodic leaf-change and flowering of trees at Singapore. *Garden Bulletin, Singapore*, **11**, 119–175.

JOHNSON, D. A. & TIESZEN, L. L. (1976). Above ground biomass allocation leaf growth and photosynthesis patterns in tundra plant forms in Arctic Alaska. *Oecologia*, **24**, 159–173.

KOZLOWSKI, T. T. (1971). *Growth and Development of Trees*, vol. I. Academic Press, New York.

KOZLOWSKI, T. T. & CLAUSEN, J. J. (1966). Shoot growth characteristics of heterophyllous woody plants. *Canadian Journal of Botany*, **44**, 827–843.

LONGMAN, K. A. & JENIK, J. (1974). *Tropical Forest and its Environment*. Longman, London.

MONTENEGRO, G., ALJARO, M. E. & KUMMEROW, J. (1979). Growth dynamics of Chilean matorral shrubs. *Botanical Gazette*, **140**, 114–119.

MOONEY, H. A. (1972). The carbon balance of plants. *Annual Review of Ecology and Systematics*, **3**, 315–346.

NEWHOUSE, M. E. & H. A. I. MADGWICK (1968). Comparative seedling growth of four hardwood species. *Forest Science*, **14**, 27–30.

RAMAKRISHNAN, P. S. & SHUKLA, R. P. (1983). On the relation among growth stategies, allocation pattern, productivity and successional status of trees of a sub-tropical forest community. In: *Improvement of Forest Biomass* (Ed. by P. K. Khosla), pp. 403–412. Solan, India.

RAMAKRISHNAN, P.S., SHUKLA, R. P. & BOOJH, R. (1982). Growth strategies of trees and their application to forest management. *Current Science*, **51**, 448–455.

RAMAKRISHNAN, P. S., TOKY, O. P., MISHRA, B. K. & SAXENA, K. G. (1981). Slash and burn agriculture in north-eastern India. In: *Fire Regimes and Ecosystem Properties* (Ed. by H. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan & W. A. Reiners), pp. 570–586. USDA *Forest Series General Technical Report*, WO 26, Hawaii.

SHUKLA, R. P. (1981). *Studies on the Adaptive Strategy of a Few Selected Tree Species in North-Eastern India*. Ph.D. Thesis, North-Eastern Hill Univ., Shillong, India.

SHUKLA, R. P. & RAMAKRISHNAN, P. S. (1981). The nature and ecological significance of heterophylly in *Artocarpus chaplasha* Roxb. *Proceedings Indian National Science Academy*, **B47**, 551–556.

SHUKLA, R. P. & RAMAKRISHNAN, P. S. (1982). Phenology of trees in a sub-tropical humid forest in north-eastern India. *Vegetatio*, **49**, 103–109.

SHUKLA, R. P. & RAMAKRISHNAN, P. S. (1984). Biomass allocation strategies and productivity of tropical trees related to successional status. *Forest Ecology and Management*. (In press.).

SINGH, J. & RAMAKRISHNAN, P. S. (1982). Structure and function of a sub-tropical humid forest of Meghalaya. I. Vegetation, biomass and its nutrients. *Proceedings Indian Academy of Sciences* (Plant Science), **91**, 241–253.

SMITH, W. K. & P. S. NOBEL (1977). Influence of seasonal changes in leaf morphology on water use efficiency for three desert broad leaf shrubs. *Ecology*, **58**, 1033–1043.

TOKY, O. P. & RAMAKRISHNAN, P. S. (1983). Secondary succession following slash and burn agriculture in north-eastern India. I. Biomass, litterfall and productivity, *Journal of Ecology*, **71**, 735–745.

WATSON, D. J. (1956). Leaf growth in relation to crop yields. In: *The Growth of Leaves* (Ed. by F. L. Milthorpe), pp. 178–191. Butterworths, London.