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Leaf dynamics of early versus late successional shrubs of sub-tropical moist forests of north-eastern India

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Abstract. The two early successional shrubs (*Melastoma malabathricum* L. and *Mussenda frondosa* L.) are periodic growth leaf-exchanging-types (leaf fall is associated with bud break; leaf span of leaves being approximately 12 months), whereas the two late successional ones (*Litsaea khasiana* Meissn and *Oxyspora vagans* Wall.) are periodic growth evergreen types (leaf fall is completed well after bud break; life span of leaves being a little over one year). Early successional shrubs have larger leaf production and faster turn-over rates, unlike late successional shrubs with production confined during the early part of the growing season (April–May) is geared to expose larger area over a longer time period, for survival under shade. The early successional shrubs have an exploitative strategy whereas the late successionals are conservative in nature for survival under shade.

Keywords. Leaf dynamics; succession; tropical shrubs; strategies.

1. Introduction

The leaf along with its auxillary bud is the basic construction unit in higher plants (Harper and White 1974; Harper and Bell 1977). The leaf being the chief photosynthetic organ in woody species, productivity is primarily determined by the patterns of production, fall and longevity of the leaves (Newhouse and Madgwick 1968). There are many studies on temperate tree species with respect to leafing patterns (Kozlowski and Clausen 1966; Newhouse and Madgwick 1968), but relatively fewer studies exist on tropical trees (Boojh and Ramakrishnan 1982b; Shukla and Ramakrishnan 1984). The leaf dynamics of the shrub stratum in a forest has received little attention. Because of the implication of light in leaf dynamics (Addicott and Lyon 1973), strategies over a successional gradient might be expected to vary (Ramakrishnan *et al* 1982). The present study is a comparative evaluation of the leaf dynamics of early versus late successional shrubs in the secondary successional tropical forests developed after slash and burn agriculture in north-east India (Ramakrishnan *et al* 1981).

2. Study area

The study area is located at Lailad (26° N and 92°E) which is about 70 km north of Shillong, north-east India, at an elevation of about 300 m. The climate is typically monsoonic with about 80% of the total annual rainfall occurring during May–September. The rest of the period is relatively dry. The mild winter extends from mid-November to mid-February. March and early April represent a brief dry

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summer period. The mean monthly maximum and minimum temperature during summer are 37 and 28°C respectively and the corresponding values for whaer are 26 and 11°C respectively.

3. Methods

On the basis of their architectural design, 3 replicates of 4-yr old individuals of two early successional shrubs, namely, *Melastoma malabathricum* L. and *Mussaenda frondosa* L. and two late successional shrubs, namely, *Litsaea khasiana* Muell. and *Oxyspora vagans* Wall. were identified at the study site. The early successional shrubs were selected under open situations, as they do not grow in shade. The two late successional species were found in older forests and are shade tolerants. Since the late successional shrub (*Litsaea*) was found to grow in open conditions also, this species was selected from both environments; *Oxyspora* could be considered under forest-grown conditions only.

The census of leaf numbers was made for each individual at the beginning of the study. Monthly estimates of leaf production, fall and leaf area were made starting from December 1983 to November 1984 by constantly giving fresh tags to newly recruited ones using small and light, colour-coded aluminium tags. Dormancy period is measured as the period between cessation of flushing and fresh bud-break. Apparent plastochrons (in days) were derived on the basis of the total numbers of leaves produced per month on a given branch order. The total leaf area per plant was computed from leaf length into breadth measurements using a correction factor to estimate the leaf area. Statistical analysis using one way ANOVA was made to detect differences between the two categories of species.

4. Results and discussion

The two early successional shrubs are evergreen leaf exchanging types (leaf fall is associated with bud break; life span of leaves being approximately 12 months). However, the two late successional shrubs are typical evergreen types (leaf fall is completed well after bud break; life span of leaves being a little over one year) (Longman and Jenik 1974).

In general, early successional shrubs had early leaf emergence and delayed onset of dormancy compared to late successional shrubs, so that the former had a relatively longer period of leaf production (table 1). The leaf being the chief organ for photosynthesis of woody species, early successional species have a larger leaf population to exploit the early successional environment and to make quick growth. This contrasts markedly with the forest grown late successional species. Further, open grown *Litsaea* had a longer period of leaf production than the forest grown ones, with the consequent larger leaf population for the former category. Though monthly leaf production pattern for individual branch orders were considered seperately, for each species, the patterns were almost similar to that of branch order zero, except peaking was delayed by a month. Therefore percentage monthly production are shown only for zero order branches (figure 1). On the zero order branch, monthly leaf production by early successional species peak in April whereas for late successional species the peak occurred in May. Peaking in monthly leaf production was more pronounced for late successional species compared to early successional ones.

Table 1. General leafing characteristics of early and late successional shrubs species in north-east India.

	Early successionals		Late successionals		
	Melastoma	*Mussaenda*	*Litsaea*		*Oxyspora*
	Open-grown	Open-grown	Open-grown	Forest-grown	Forest-grown
Date of leaf emergence	Mid-Jan.	Early-Feb.	Mid-March	Early-April	Early-April
Onset of dormancy	Late-Oct.	Late-Sept.	Mid-Sept.	Early-Sept.	Early-Sept.
Leaf production period (days) in a year	280	234	195	159	153
Dormancy period (days) in a year	86	132	171	209	215
Total/number of leaves produced per year per shoot	2026	850	545	341	276
Total leaf area ($\times 100\ cm^2$) per year per tree (shoot)	554	342	187	115	48
Leafing behaviour	Leaf exchanging	Leaf exchanging	Evergreen	Evergreen	Evergreen

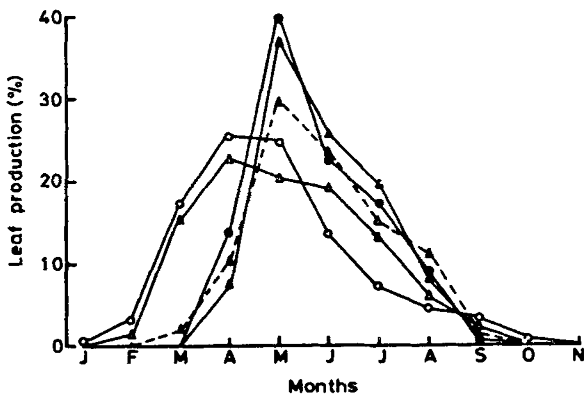

Figure 1. Leaf production pattern (%) on leader axis of early successional (open-symbols) and late successional (closed-symbols) shrubs species. (○), Open-grown *Melastoma*; (△), open-grown *Mussaenda*; (▲), open-grown *Litsaea*; (--▲--), forest-grown *Litsaea*; (●), forest-grown *Oxyspora*.

Leaf fall was maximal in March–April for all the species though this was more pronounced for early successional shrubs (figure 2). Open-grown *Litsaea* had sharper peaking of leaf-fall compared to forest-grown individuals. This would contribute a faster turn-over of leaves in the case of early successional species than the late successional ones. Leaf expansion time of early successional species was maximum in the initial stages of leaf production in February gradually declining up to July, followed by a sharp increase in subsequent months (figure 3). On the other hand, leaf expansion period was less variable for late successional species.

Plastochron length in a given month generally increased for all the species with increase in branch order though the monthly pattern was similar. In figure 4 the values for the zero order alone is given. Plastochron time for the two early successional species declined gradually from February reaching the lowest value in July followed by a sharp increase in subsequent months. On the other hand, for late successional species plastochron time increased gradually during the growing

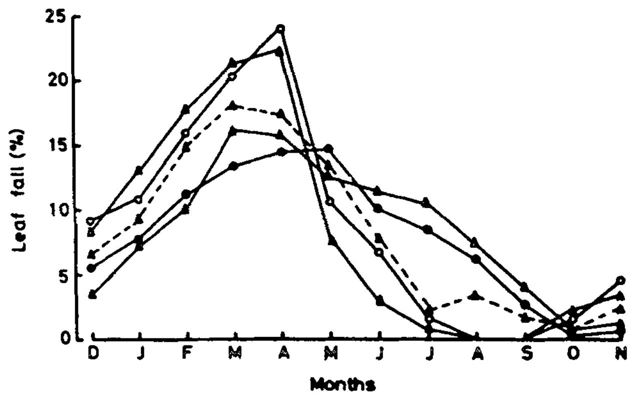

Figure 2. Leaf fall pattern of early successional (open-symbols) and late successional (closed-symbols) shrubs species. (○), Open-grown *Melastoma*; (△), open-grown *Mussaenda*; (▲), open-grown *Litsaea*; (--▲--), forest-grown *Litsaea*; (●), forest-grown *Oxyspora*.

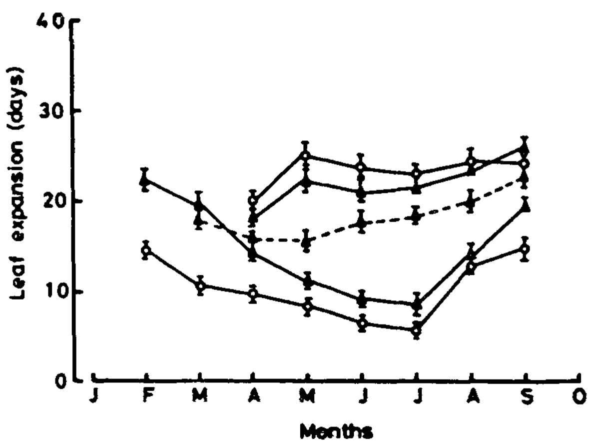

Figure 3. Monthly changes in leaf expansion period (days) of early successional (open-symbols) and late successional (closed-symbols) shrubs species. (○), Open-grown *Melastoma*; (△), open-grown *Mussaenda*; (▲), open-grown *Litsaea*; (--▲--), forest-grown *Litsaea*; (●), forest-grown *Oxyspora*.

season from March–April to September. Plastochron values for early successional species were significantly lower ($P < 0{\cdot}01$) compared to late successional species. Open-grown *Litsaea* had generally lower values than for forest-grown individuals. These results suggest faster leaf production in the case of early successional species. Further, more active leaf production and expansion rate for late successional shrubs in the very early part of the growing season is similar to that of trees (Shukla and Ramakrishnan 1984) and is geared to expose larger leaf area over a longer time period, in a shaded environment.

The life table (table 2) shows generally larger production of leaves for early successional shrubs compared to late successional ones. Some of leaves from the previous year are carried over to the current year in late successional species giving a turn-over time of slightly more than a year, unlike early successional species

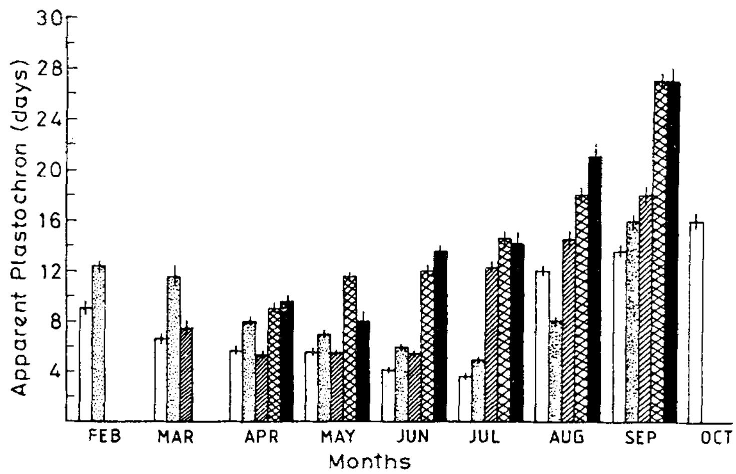

Figure 4. Monthly variation in the apparent platochron (days) of early and late successional shrubs in north-east India. (□), Open-grown *Melastoma*; (▤), open-grown *Mussaenda*; (▨), open-grown *Litsaea*; (▩), forest-grown *Litsaea*; (■), forest-grown *Oxyspora*.

Table 2. Population flux of leaves of early and late successional shrubs in north-east India.

	Early successionals		Late successionals		
	Melastoma	*Mussaenda*	*Litsaea*		*Oxyspora*
	Open-grown	Open-grown	Open-grown	Forest-grown	Open-grown
(a) No. of leaves per plant in December 1982	1744	696	556	355	266
(b) No. of leaves per plant in December 1983	1754	705	591	375	290
(c) Net change (a − b)	+10	+9	+35	+20	+24
(d) Annual rate of increase (b/a)	1·01	1·01	1·06	1·06	1·09
(e) No. of leaves per plant produced between December 1982 and December 1983	2026	850	545	341	276
(f) No. of leaves lost between December 1982 and December 1983	2033	861	510	324	240
(g) No. of leaves present between December 1982 and December 1983	0	0	64	48	53
(h) Percentage survival (g) leaves in (a), (× 100 g/a)	0	0	11·51	13·52	19·92
(i) Expected time for complete turnover (year)	1·0	1·0	1·13	1·16	1·25
(j) Total leaves recorded during study	3770	1545	1101	690	542
(k) Percentage annual mortality of total leaves $\left(\frac{b}{j} \times 100\right)$	53·93	55·73	46·32	46·55	44·28

which had a turn-over time of one year. Mortality in the leaf population was also higher for early successional species compared to late successional ones.

The leafing behaviour of the shrub strata as shown here, and also shown through extensive phenological observations on over 70 shrub species in successional forests of 5–60 years of age (Baruah and Ramakrishnan 1989) suggest that the early successional shrub are predominantly deciduous or leaf-exchanging-types and the late successional shrubs are largely evergreen. This contrasts with early successional trees which are evergreen but with fast leaf turnover rates, mid-successionals that are typically deciduous and the climax species that are evergreen but with slow leaf turnover (Boojh and Ramakrishnan 1982b; Shukla and Ramakrishnan 1986). Such a contrast between trees and shrubs may be related to micro-environmental differences for light at upper and lower canopy positions in the forests. The evergreen versus deciduous habit in species has often been related to a single factor such as soil fertility status (Chapin 1980) and such explanations are perhaps too simplistic. Obviously, more critical studies on tropical forest phenology are needed.

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