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The Growth Pattern of Two Species of *Schima*

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ABSTRACT

The growth patterns of two closely related deciduous tree species, *Schima wallichii* (at 100 m and 1600 m altitude), and *S. khasiana* (at 1900 m) in Meghalaya, north-eastern India, were compared. Both species conform to Rauh's model of architecture. Sylliptic lateral branches formed on *S. khasiana* during periods of vigorous growth of the main shoot. Although stem extension and leaf production were continuous throughout the growing season, they exhibited (endogenous?) periodicity which was most marked in *S. wallichii* at lower altitude. *Schima wallichii* at lower altitude had the fastest turnover of leaves.

THE DYNAMICS OF SHOOT INITIATION AND EXPANSION in tropical trees has been studied qualitatively by Hallé and Martin (1968) for rubber, Borchert (1969) for *Oreopanax*, Gill and Tomlinson (1971) for *Rhizophora*, and Hallé *et al.* (1978), but the morphometric analysis of growth characteristics of tropical trees has received relatively little attention (Fisher 1978, Borchert and Slade 1981).

Many studies (Njoku 1963, Frankie *et al.* 1974) have shown close correlations between the growth of tropical deciduous trees and seasonal climatic changes (*e.g.*, leaf fall/drought relationships). However, correlations between phenological events and environmental change are often difficult to determine in evergreen forests (*e.g.*, Alvim 1964), and the environmental cues may depend upon interaction with internal controls (Borchert 1978).

MATERIALS AND STUDY SITES

The two species of *Schima* Reinw. ex. Blume (Ternstroemiaceae) studied, *S. wallichii* (DC) Korth and *S. khasiana* Dyer, are important timber trees of north-east India. *Schima wallichii* ranges in altitude from 100 to 1600 m, while *S. khasiana* is restricted to 1600 to 1900 m. These secondary successional trees follow slash and burn fallows, coppice well, and are dispersed by light, wind-blown seeds. They mature at an average height of 25 to 30 m and 12 to 20 m at lower and higher elevations, respectively. Whitmore (1975) observed *S. wallichii* colonizing man-made clearings in lowland and lower montane forests of Malaya and considered it a marginal pioneer.

Schima wallichii was studied at Shillong (25°34'N, 91°56'E, alt. 1600 m) and Burnihat (90 km North of Shillong, alt. 100 m). *Schima khasiana* was studied at Upper Shillong (10 km South of Shillong, alt. 1900 m). The study areas have four distinct seasons: a monsoon season of heavy rain during May to September; a transitional period of low rainfall in October and November; a "winter" season during December to February with scattered rainfall; and a dry "summer" during March and

April. Average annual rainfall during the study period was 2350, 1800, and 1550 mm at Upper Shillong, Shillong, and Burnihat, respectively. The average maximum and minimum temperatures for the monsoon and winter seasons, respectively, were 16–22°C and 2–15°C at Upper Shillong (Fig. 1a), 16–24°C and 6–16°C at Shillong, and 24–32°C and 12–24°C at Burnihat.

METHODS

Extension growth of the main leader was measured on five 5-year-old, open-grown, saplings chosen randomly on each study site. Branch development was studied by following the fate of buds on current increments of the main axis and 1-year-old first order branches. In the description of branch ordering, the tree trunk was designated zero, and the branches identified as first, second, and third order in chronological sequence (Hallé *et al.* 1978). Radial growth was measured with a dendrometer. Phenological observations on flushing, flowering, fruiting, seed-dispersal, and growth cessation were made on adult trees marked at the three altitudinal study sites.

A leaf census was taken for each tree at the beginning of the study. Monthly estimates of leaf production and leaf fall were made by tagging all previously opened leaves and giving fresh tags to newly emergent ones. The leaf area was calculated using the formula $A = C \times L \times W$, where A is the area of the leaf, C is a correction factor, L is the length, and W is the width of the leaf. The correction factor C (Dolph 1977) is obtained for each population by dividing the planimeter-measured area of 100 leaves by the product of their lengths and widths. Dry weights of leaves were estimated after oven drying for 24 hours at 85°C, or to constant weight.

RESULTS

EXTENSION GROWTH.—The two species of *Schima* follow the architectural model of Rauh, as defined by Hallé *et al.* (1978). As shown in Table 1, extension growth for

TABLE 1. Phenology of growth and reproduction in *Schima* species. The dates are the average of ten 5-year-old marked trees in 1979.^a

	Start of flushing	Beginning of dormancy ^b	Growing period (days)	Dormant period (days)	Flowering date	Fruiting date	Seed dispersal
<i>Schima wallichii</i>							
Lower altitude	Mar 1	Dec 25	300	65	Apr 1	May 25	Feb 20–Mar 15
Higher altitude	Mar 20	Nov 25	250	115	Apr 25	Jun 1	Mar 1–Apr 15
<i>S. khasiana</i>	Apr 5	Oct 1	180	185	May 15	Jul 25	Jan 20–Feb 15

^a Daily observations were made for major phenological events, otherwise all observations were made weekly.

^b Cessation of extension growth was used as the criterion for dormancy.

S. wallichii at lower altitude started earlier and ended later than at higher altitude, so that the growing period at lower altitude was longer. *Schima khasiana* had the shortest growing period with the onset of dormancy much earlier than for *S. wallichii* at the same altitude. Flowering and fruiting occurred earlier for *S. wallichii* at lower altitude compared with that at higher elevations, and was delayed even more for *S. khasiana*.

The growth in height (Fig. 1b) showed two peaks, one in April–May, and another in July, the latter being lesser than the former. At lower altitude a questionable growth peak occurred in September for *S. wallichii*. In all situations, more than 50 percent of the annual extension growth was completed by May. The growth of the monopodial trunk is periodic, being characterized by the presence of shorter internodes along the axis alternating with longer internodes during the same growing season, a periodicity which was also manifest in changes in leaf area (Fig. 2) and formation of sylleptic lateral branches. The presence of a series of short internodes at the end of the growing season delimits a year's growth and helps in aging the tree. Radial growth (Fig. 1c) was in all cases maximal on a date subsequent to that for maximum extension growth.

The branches are produced sylleptically (Hallé *et al.* 1978) on the leader axis (Fig. 3, left) but with a large number of buds remaining dormant. The periodicity of lateral branch formation is correlated with that of extension growth. At lower altitude *S. wallichii* produced two sets of branches, one in April and the other in July (seven to eight branches per set); while this species at higher elevation, and *S. khasiana*, produced only a single set of four or five branches in May. The periodic pattern of branching was repeated on the laterals. The first order branches of the current year did not produce the second order branches during the same growing season for *S. khasiana*, but they did for *S. wallichii* (with greater numbers at lower than at higher altitude). Since the branching on the laterals is confined chiefly to the lower (abaxial) side, the crown is broadened. If the terminal axis is dam-

aged, the resting axillary buds of older shoots may give rise to proleptic shoots (Fig. 3, right). As the flowers are axillary on the shoots, these have no direct effect on tree geometry.

LEAF DYNAMICS.—Leaves of *S. wallichii* are entire, whereas those of *S. khasiana* are serrate. Leaf blade area was significantly greater (*t*-test, $P = 0.05$) for *S. wallichii* from the lower elevation than from the higher elevation *S. wallichii* and *S. khasiana* (Table 2). The high elevation *S. wallichii* showed significantly greater leaf biomass

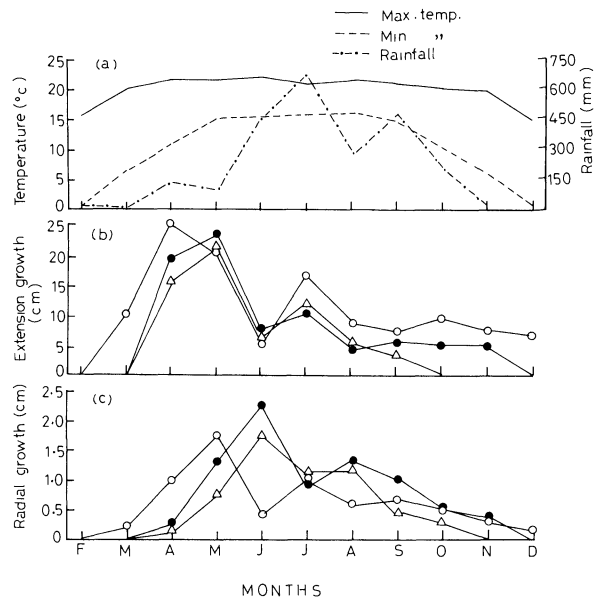


FIGURE 1. Climate and growth data for *Schima* spp. a) Maximum (—) and minimum (---) temperatures, and rainfall (....) totalling 2350 mm at Upper Shillong (1900 m). b) and c) Seasonal extension and radial growth, respectively, for *S. wallichii* at lower altitude (O), higher altitude (●), and *S. khasiana* (Δ).

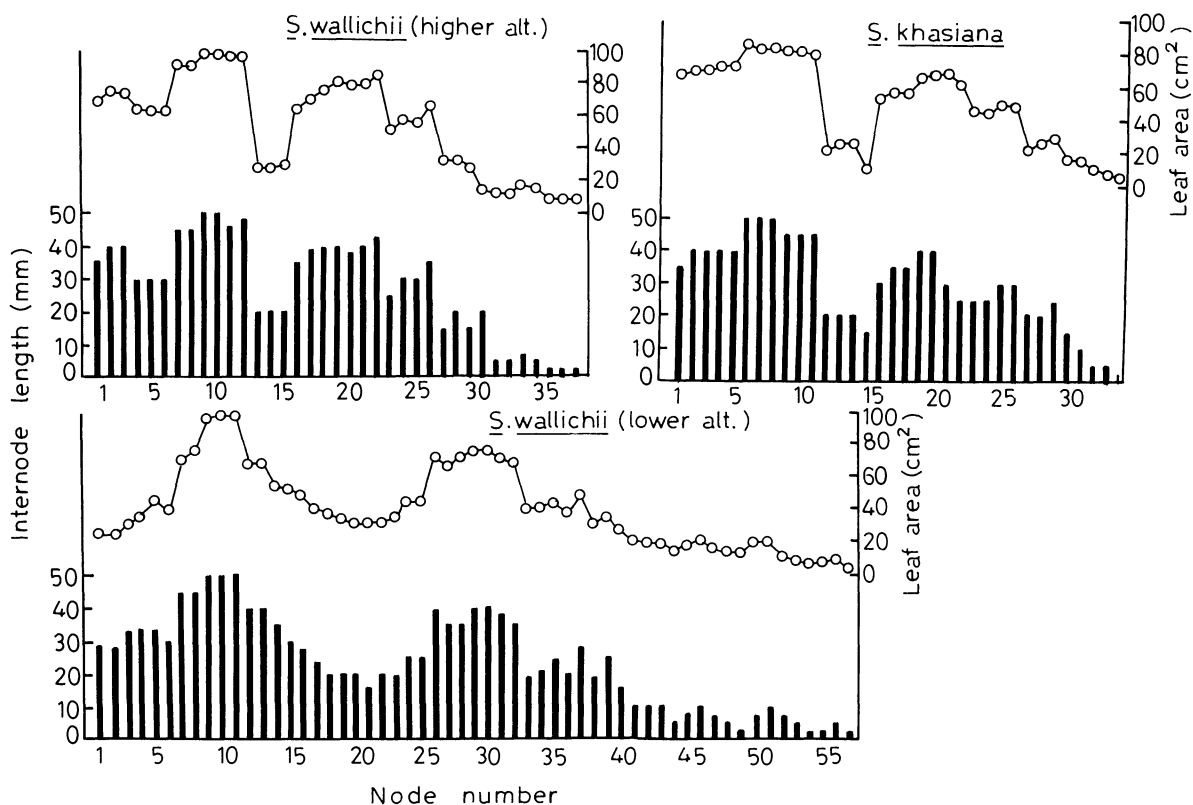


FIGURE 2. The annual growth rhythms in *Schima* species represented by internodal elongation (bars), and corresponding leaf area changes (circles) on the leader axis.

(*t*-test, $P = 0.05$) compared with the conspecific low elevation population; significantly, *S. khasiana* had the lowest leaf biomass (Table 2). However, live leaf thickness was not measured.

Flushing of young, pink leaves occurred during early March for *S. wallichii* at lower altitude, about 20 days later at higher altitude, and another 15 days later in early April for *S. khasiana*. The high altitude populations of

S. wallichii and *S. khasiana* had similar leaf production and fall pattern in all respects, except that high-altitude *S. wallichii* retained about 15 percent of its leaves; low-elevation *S. wallichii* and *S. khasiana* were totally deciduous for about one month at the end of the growing season. Data for *S. khasiana* and low altitude *S. wallichii* are presented in Figure 4.

Leaf production during the growing season showed

TABLE 2. Variations in leaf characteristics (\pm SE) of *S. wallichii* and *S. khasiana*. A sample of 70 leaves was taken on five replicate trees from three (upper, middle and lower) canopy positions for each species population.

Leaf characteristics	<i>S. wallichii</i>		<i>S. khasiana</i>
	Lower altitude	Higher altitude	
Petiole length (cm)	1.11 \pm 0.03	0.93 \pm 0.02	1.09 \pm 0.02
Blade length (cm)	16.02 \pm 0.31	13.85 \pm 0.33	15.92 \pm 0.29
Blade width (cm)	6.48 \pm 0.12	5.69 \pm 0.15	4.45 \pm 0.09
Correction factor	0.67 \pm 0.01	0.67 \pm 0.01	0.65 \pm 0.01
Leaf area (cm²)	71.49 \pm 2.46	54.72 \pm 2.54	46.49 \pm 1.64
Leaf biomass (mg)			
Petiole	16.50 \pm 0.80	18.50 \pm 0.70	11.00 \pm 0.60
Blade	381.80 \pm 16.00	437.70 \pm 22.00	279.10 \pm 9.80



FIGURE 3. Left, sylleptic branching in *Schima wallichii*. The branches have developed as axillary meristems that began proliferation immediately after their formation, and contemporaneously with the terminal bud of the shoot that bears them. Right, development of a proleptic shoot by the activation of a dormant axillary meristem after damage to the main leader.

peaks in April and July for both species (Fig. 4, inset). Low-altitude *S. wallichii* showed a small, questionable peak of production in September. Leaf production declined sharply in subsequent months with complete cessation in late December in the case of the low altitude *S. wallichii*, and early October for *S. khasiana*. Both species produced more than 50 percent of their annual leaf pro-

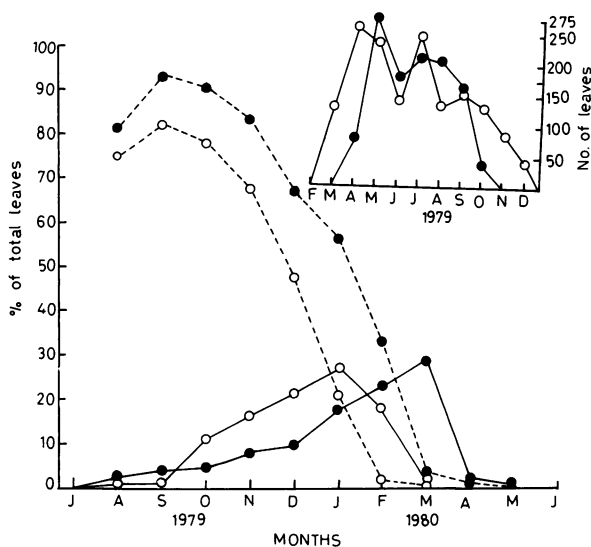


FIGURE 4. The dynamics of production and fall of leaves in lower altitude *S. wallichii* (○) and *S. khasiana* (●). Solid lines represent percentage of leaves fallen in a given month out of the total annual leaf production, and dotted lines represent standing crop of leaves. Inset figure shows the pattern of new leaf production.

duction by June. Annual cumulative leaf area production for the low altitude *S. wallichii* population was 63,000 cm² whereas it was 41,000 cm² for *S. khasiana*. Considering the cohort of leaves produced in 1979, the standing crop of leaves reached its peak in September–October for both species. During subsequent months the standing crop of leaves declined sharply due to leaf fall and all leaves of that cohort were shed by February in the case of low altitude *S. wallichii*, and by March–April for *S. khasiana*. However, leaf fall began as early as August for both *S. wallichii* and *S. khasiana* with a peak in January for the low altitude population of *S. wallichii*, and in March for *S. khasiana*.

Leaves produced early in the season generally had a longer life than those produced later. In general, the leaves of *S. khasiana* and the higher altitude population of *S. wallichii* had a longer life than those of the low-altitude populations of *S. wallichii* (Fig. 5).

DISCUSSION

The branch production through syllepsis for both species occurs during periods of rapid growth, as observed for *Alnus* (Champagnat 1954), for *Avicennia* (Gill 1971), and for *Rhizophora* (Gill and Tomlinson 1971). Thus, the occurrence of two sets of lateral sylleptic branches for *S. wallichii* at lower altitude is another facet of the two peaks of vigorous stem elongation. Such correlations between growth vigor and lateral shoot production have been well documented by Champagnat (1965).

Schima species have periodicity in shoot growth and leaf expansion that apparently is not directly related to climatic fluctuations during the growing season. Even under the most favorable environmental conditions of high

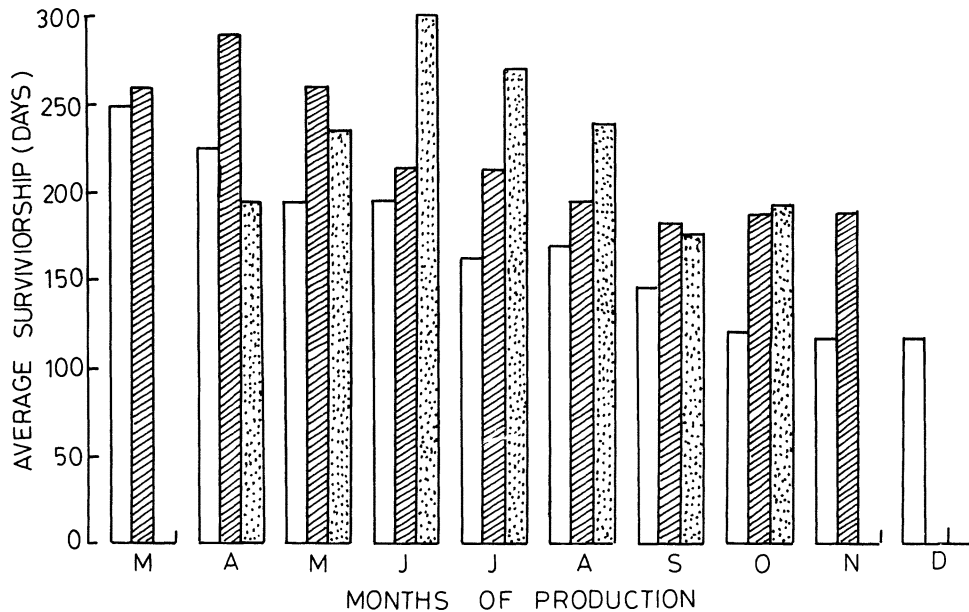


FIGURE 5. Life span of leaves in relation to the month of their emergence for *S. wallichii* (open bars for lower and hatched bars for higher altitude) and *S. khasiana* (stippled bars).

rainfall and temperature, there are periods of slower growth (cf. Figs. 1a, 1b, and 2). While many workers have attributed environmental variables such as wet and dry seasons to periodicity (Alvim 1964, Gaertner 1964), absence of correlations with the environment has prompted others (Koriba 1958; Greathouse *et al.* 1971; Borchert 1978, 1980) to consider this phenomenon endogenous. The presence of rhythms during the same monsoon season in the present case is suggestive of such endogeneity.

In all cases, radial growth started and terminated later than extension growth, as also reported for many temperate (Kozłowski 1971) and some tropical trees (Choudhury 1957). Such a late start and cessation of cambial growth has been explained by the hormone production of the expanding bud being transported basipetally (Wareing 1958, Romberger 1963).

Leaf size was inversely related to altitude, a phenomenon which may be a response to differences in ambient temperature (Longman and Jeník 1974, Milthorpe 1976). Genetic control seems more likely than purely environmental, but this aspect has not been studied.

A variety of patterns of leaf renewal and leaf fall have been described for tropical trees (Holttum 1940, Koriba 1958, Longman and Jeník 1974), with most cases of pre-rain or equinoctial flushing (Alvim 1964, Frankie *et al.* 1974) being related to the expansion of leaves at the time of maximum solar insolation and to other favorable growth conditions (Longman and Jeník 1974). Borchert (1980) has suggested that the timing of flushing depends

primarily upon the timing of leaf fall, which in turn is a function of leaf age, leaf structure, water relations, and other factors. He has proposed that in tropical trees the timing of bud break will result from the interaction between the endogenous shoot-growth periodicity and variations in the water status of the environment.

The pattern of leaf flushing reported here also suggests that the flushing is a result of drought-induced shedding of old leaves. Tree water stress enhances leaf senescence and hence leaf shedding. The longer life span of leaves at higher altitudes and the evergreen nature of the species in Indonesia (Hallé, pers. comm.) may be attributed to site-dependent stress conditions. As the duration of growth cycles depends on the life span of the leaves, the differences in longevity of leaves probably accounts for the differences in timing of leaf fall and pattern of leafiness observed.

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