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The Nature and Ecological Significance of Heterophylly in *Artocarpus chaplasha* Roxb.

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The qualitative and quantitative changes in leaf shape from seedling to emergent tree stage in *Artocarpus chaplasha* Roxb. were studied. The number of lobe and deepness of lobing in leaves were found to be closely related with light intensity, branch order, branch length and tree age. The plasticity in leaf shape characteristics and the ability of the species to grow under open as well as under different degrees of shade, suggest its success as a mid-successional species.

Key Words: Heterophylly, Lobed and {unlobed leaves, Ecological adaptation, *Artocarpus chaplasha*

Introduction

Broad leaves are found in a number of shapes and the variation in size, shape and structure of leaves with climate and environment has been discussed and reviewed from time to time (Clements 1904, Bailey & Sinnott 1916, Brown 1919, Ryder 1954, Cain et al. 1956, Talbert & Holch 1957, Jackson 1967, Gentry 1969). Leaf shape variation in a single individual may be a direct consequence of morphogenetic effects of light (Heslop-Harrison 1964) and/or of other factors of the physical environment during their ontogeny (Piersall & Hanby 1926, Milthorpe 1959, Milthorpe & Newton 1963, Givnish & Vermeij 1976). However, many plant species may have the intrinsic ability to produce different sizes and shapes of leaves in different micro-environments (Parkhurst & Loucks 1972). *Artocarpus chaplasha* Roxb., a sub-tropical, emergent deciduous tree species, produces leaves of more than one shape and size during its lifetime. This work, undertaken as part of a detailed study on the growth pattern and architecture, deals with the pattern of distribution of different types of leaves and their ecological significance in this species.

Material and Methods

The study was carried out in a sub-tropical humid forest of north-eastern India, at

Lailad (25°45″—26° N lat; 91°45″—92° E long; and 296 m alt.). Saplings of *A. chaplasha* growing in the open (80–90 thousand lux) and under different degrees of shade (800–30,000 lux) in the forest were selected. Saplings of different age groups (1–8 yr) were available in good numbers under varying light conditions. The age of the saplings was determined on the basis of growth pattern analysis of this species. Saplings and branches of old trees (5 replicates), harvested at the end of the growing season in November 1980, were categorized into different branch orders and analysed for their length and number of lobes and/or unlobed leaves on them. After categorizing the leaves into four different classes on the basis of size and shape, the length and maximum breadth of the leaves as well as the number of lobes on them, if any, were noted. The leaf area was measured by planimeter. Leaf measurements are based on 100 observations at different sites. Correlation factors between length × breadth and leaf area were developed for each shape under each light regime and these were used to compute the leaf area of other leaves.

The depth and frequency of lobing of leaves was determined following Horn's (1971) procedure (figure 1A). The area of the large circle drawn, was equal to the area of the leaf while the smaller one was the largest circle that could be inscribed within the boundary of the leaf. Lobing pattern was expressed as a ratio of the diameter of the two circle (large/small). Plant age, branch age, branch order, branch length and light intensity were related to different leaf characteristics.

General characteristics of growth

The architecture in *A. chaplasha* conforms to Rauh's model (Halle et al. 1978). The trunk (main axis) is monopodial i.e. grows by original seedling meristem. After germination in August-September the seedlings produce smaller ovate leaves with dentate margin until growth cessation in November, and lobed leaves with entire margin during the second growing season (March–November) after a period of rest during winter (November–February). The phase change from small unlobed to large lobed leaves (figure 1B) occurred earlier under shade. The production of lobed leaves continues on the main axis until the damage of the original main shoot tip; otherwise the substitution growth by subterminal bud produces one to few unlobed leaves during its initial phase of extension. The trunk remains unbranched (monoaxial) until the 3rd or 4th growing season. Usually, a single tier of branches is produced each year during the most favourable part of the growing season through prolepsis (by the activation of resting buds laid during the last growing season), but occasionally one more tier of branches may be produced during the same growing season through syllepsis (by the extension of lateral buds on the current year's shoot during the extension phase of terminal bud). A single tier may have 3–7 branches depending upon the growth conditions and the age of the tree and could be separated from a tier of the preceding and succeeding year by a gap of 2–11 internodes on the main axis (as was observed among saplings of 3-8 years of age). The branches and leaves are arranged spirally. During proleptic development of a I order branch from an axillary bud, the first few leaves are unlobed and the rest are lobed. One or two of the first produced unlobed leaves may be smaller and ephemeral. The terminal bud which is always protected by a pair of stipules, produces one leaf at a time which, while expanding, discards the outermost pair of the stipules. The proportion of unlobed leaves to the lobed ones increases gradually with age of the tree resulting in the exclusive production of unlobed leaves in old emergent trees.

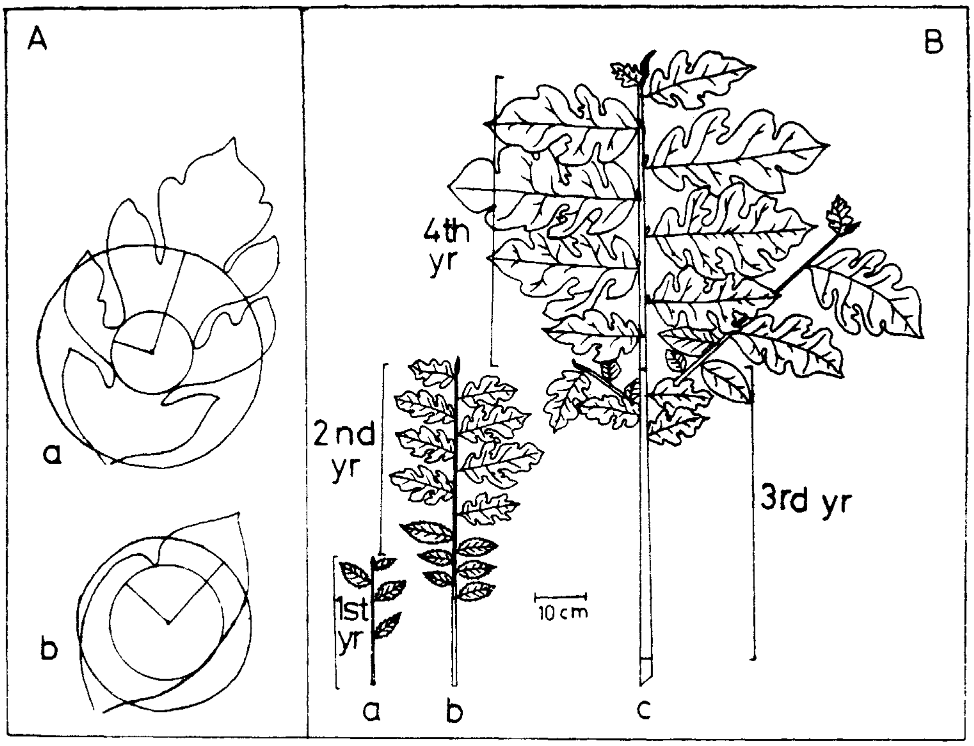

Figure 1A Diagramatic representation of Horn's procedure. The outer circle is equal to the area of the leaf and the inner one is the largest possible circle which could be inscribed within the boundary of the leaf. The relative sizes of two circles in terms of diameter ratio were used as a measure of frequency and deepness of lobing. *a* and *b* show the comparison of two shapes of leaves.

Figure 1B Diagramatic sketch of growth of *A. chaplasha* up to 4 years of age. *a*, production of small dentate leaves during the 1st year of growth after germination; *b*, growth during 2nd year showing phase change and production of lobed leaves; and *c*, growth of main axis and proleptic development of axillary branches during 4th year of growth. These branches produce few unlobed leaves before starting the production of lobed leaves, the first one or two leaves being the smallest. Almost leafless part of the shoot shows the extension growth during third year.

Younger trees may have all the three types of shoots: (i) heterophyllous, bearing both lobed and unlobed leaves, (ii) with only lobed leaves, and (iii) with only unlobed leaves.

Results

Table 1 shows the leaf characteristics of 7 year old trees of *A. chaplasha* growing under two different conditions of light. The main axis did not produce any unlobed leaves under any light condition. However, the length, breadth and area of leaves and the frequency and depth of lobing were higher in shade compared to that in the open. Similar differences were observed for the leaves on the I, II and III order branches. In these branch orders the ratio of the number of lobed to unlobed leaves increased in shade. Both in the open-grown and in shade-grown trees, all these leaf characteristics tended to decline with increase in branching order. Short shoots (<15 cm) of I order branches were mostly confined to the mid-part of the tree canopy and had only unlobed leaves on them but their leaf dimension was greater

Table 1 *Leaf characteristics in 7 years old trees of A. chaplasha growing under two different light intensities (open, 80,000–90,000 lux and shade, 800–2000 lux). Values given in parenthesis are for shade-grown trees and upper values are for open-grown trees (Values = Mean ± St. er.)*

Parameters	Ordinal numbers of shoots bearing leaves				
	0 order (leader)	I order	II order	III order	I order (short shoots)
Ratio of number of lobed to unlobed leaves	all lobed (all lobed)	4.87 (8.90)	1.46 (3.31)	1.40 (2.38)	all unlobed (all unlobed)
Lobing frequency (lobe/leaf)	3.6 ± 0.6 (6.5 ± 0.3)	2.6 ± 0.3 (3.4 ± 0.3)	1.6 ± 0.4 (2.2 ± 0.2)	0.9 ± 0.3 (1.2 ± 0.3)	0 (0)
Leaf length (cm)	35.7 ± 1.9 (47.1 ± 1.7)	22.4 ± 0.7 (31.1 ± 1.1)	10.9 ± 1.1 (15.4 ± 2.2)	8.8 ± 1.2 (14.3 ± 2.1)	13.7 ± 1.0 (20.4 ± 1.5)
Leaf breadth (cm)	24.7 ± 1.5 (41.0 ± 2.4)	14.5 ± 0.6 (20.6 ± 0.6)	6.0 ± 0.6 (10.1 ± 1.3)	5.8 ± 0.9 (7.5 ± 1.2)	8.5 ± 0.4 (14.1 ± 1.7)
Leaf area (cm^2)	491.1 ± 37.9 (705.3 ± 26.1)	218.6 ± 13.0 (464.0 ± 34.1)	52.9 ± 8.7 (145.1 ± 37.4)	37.2 ± 8.8 (92.5 ± 22.4)	88.2 ± 9.4 (253.8 ± 36.4)
Ratio of diameter of large to small circle	1.40 (3.23)	1.34 (1.43)	1.27 (1.39)	1.25 (1.28)	1.22 (1.23)

Table 2 *Correlation coefficients of different parameters of leaf characteristics with different factors affecting leaf shape and size in A. chaplasha*

	Ratio of No. of lobed to unlobed leaves	Lobing frequency (lobe/leaf)	Area/leaf	Ratio of dim. of large to small circle (depth of lobing)	Degree of freedom
Plant age[1]	—0.784**	—0.961*	—0.761**	—0.894*	5
Branch age	—0.758**	—0.766**	—0.792**	—0.901*	5
Branch order	—0.929*	—0.982*	—0.966*	—0.880**	4
Branch length[2]	0.708**	0.898*	0.756**	0.395^{ns}	6
Light intensity	—0.890**	—0·918*	—0.834**	—0.886**	4

[1]After phase change from small dentate to lobed leaves i.e. from second year of growth.
[2]Only monopodial branches were considered.
* = 1% and ** = 5% level of significance and ns = not significant.

than those on the II and III order branches and less than those on the fully developed I order branches.

Table 2 presents the correlation coefficients of various leaf characteristics related to plant age, branch characters and light intensity for trees up to 8 years of age. All the leaf characteristics were negatively correlated with plant age, branch age, branch order or light intensity. However, branch length alone was found to be positively correlated with leaf characteristics. All correlations were significant ($p<0.05$) except that between branch length and depth of lobing.

Discussion

The distribution of entire and non-entire (lobed and unlobed) leaves in relation to climatic factors within an individual is more marked in woody dicotyledons than in herbaceous plants (Bailey & Sinnott 1916). This is attributed to the differences in growth forms of these two categories, as the herbaceous plant, due to its short stature and life-span, is less subjected to changes in prevaling environmental conditions.

Artocarpus chaplasha, which establishes itself making fair growth under a forest canopy, soon overtops the other species and becomes stabilized as an emergent. Thus, during its growth the tree is exposed to diverse light regimes. The prevalence of lobed leaves in the shade and the gradual disappearance of lobing in the open suggests that the shape of leaves, in this species, is more related to light intensity, as was also shown by Horn (1971) in *Betula* and *Quercus* species. The larger number and deeper lobing in shade leaves may help in better distribution of light amongst the leaves placed at different strata of the canopy, increasing the effective leaf area of the plant. Thus the average diameter of the two circles related to leaf area and leaf boundary, discussed earlier, determine the efficiency of vertical distribution of light to leaves as the maximum light under forest canopy comes from the top (Horn 1971). The pattern of variation in leaf shape in this species, therefore, seems to be selected for later stages of succession in the forest, rendering the species capable of growing fairly well under shade as well as in the open. Further, the production of lobed leaves in younger saplings, irrespective of the light regime in which they grow, indicates that this species, in the evolutionary process, was adapted for a late successional status in the forest.

Though light seems to play an important role in controlling the proportion of lobed to unlobed leaves, the interaction of other factors like branch length or vigour, branch age and branch order also affect this proportion, as evident from the correlation coefficients. Thus, the lower order of branches which are more vigorous, have a higher proportion of lobed leaves. On the other hand, short shoots, despite their rank as first order branches, hardly produced any lobed leaf.

The ontogenetic development of leaves in *A. chaplasha*, therefore, seems to be governed by changing light regime and also by branch order, age and vigour which are related to the diversification of nutrient channels. The importance of nutrient pool in determination of lobing was observed in epicormic branches and reiterating units, which produced several lobed leaves before the production of unlobed ones, irrespective of the age of parent tree and prevailing light conditions. It may be concluded here that heterophylly in this species is an adaptive mechanism to ensure its survival and growth under different light regimes.

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