Studies on the Adaptive Strategy of a few Selected Tree Species of the North-Eastern India

ABSTRACT

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The thesis embodies the results on two aspects: (i) the adaptive strategy of a sub-tropical humid forest community including seasonal adaptations, growth and allocation pattern, seed germination and seedling establishment of some important species representing the tree component of the community, and (ii) detailed analysis of pattern and architecture of growth of four important tree species, viz., *Duabanga sonneratioides* Ham., *Anthocephalus cadamba* Miq., *Dillenia pentagyna* Roxb. and *Artocarpus chaplasha* Roxb., the former two being the early successional while the latter two the late successional species.

These species grow during the process of secondary succession after Jhum (shifting agriculture) in north-eastern India. The studies mentioned above were carried out in a sub-tropical humid forest at Lailad (Lat. 25°45" - 26°0" N, long. 91°45" - 92°0" E and alt. 296 m) which is 70 Km north of Shillong. The results of the present study may be useful for the practical forest management in the region.

Section A. COMPARATIVE STUDY ON ADAPTIVE GROWTH STRATEGY OF FOUR EARLY AND LATE SUCCESSIONAL TREE SPECIES.

Chapter I. Pattern of architecture and extension growth:

The study deals with the pattern of architecture, extension growth and branch display of two early successional (*Duabanga sonneratioides* Ham. and *Anthocephalus cadamba* Miq.) and two late successional (*Dillenia pentagyna* Roxb. and *Artocarpus chaplasha* Roxb.) species. While the early successional species showed heterogeneous axes (trunk orthotropic and branches plagiotropic) and conform to Massart's model (*D. sonneratioides*) or Roux's model (*A. cadamba*), the late successional species showed homogeneous axes (all axes orthotropic) and conform to Scarrone's model (*D. pentagyna*) or Rauh's model (*A. chaplasha*) of tree architecture. The extension and radial growth of axes of early successional species were very rapid and more in comparison to those of late successional species. The sparse branch arrangement facilitating leaf exposure to a greater degree and longer growth period of early successional species accounted for the faster growth. On the other hand, late successional species showed shorter growth period and densely packed canopies with mutual shading of leaves which accounts for their slower growth rate. In the early successional species production and contribution of I order branches to the total framework of branch system was much higher than that in late successional species. Plasticity in orientation and overall display of branches in relation to light intensity was noted in these species. The significance of these results are discussed in relation to the niche occupancy of these species.

Chapter II. Leaf dynamics:

Leaf dynamics of two early successional (*D. sonneratioides* and *A. cadamba*) and two late successional (*D. pentagyna* and *A. chaplasha*) species has been studied here. The early successional species showed higher leaf turnover rates, reduced leaf longevity, more uniform production and fall of leaves with some fluctuation during the year and evergreen or leaf-exchanging which had higher allocation to the root compartment. The early successional species with a shallow root system had most of the root biomass within the upper 20 cm of the soil profile while the late successionals with deeper roots had higher proportion of root biomass below the 20 cm depth. Root p production of the early successional species was significantly higher over the late successional species only upto 5 years of age after which the differences were less marked. However, the higher production of the shoot system was consistently maintained by the early successional species.

Section B. ADAPTATION OF TREES IN THE FOREST COMMUNITY

Chapter V. Phenology of trees in the forest community:

Phenological observations on 122 tree species were made. The forest had a higher proportion of evergreen compared to deciduous species. Leaf-fall of most of the tree species coincided with the dry season. Flushing in a majority of the tree species started towards the end of the dry season after different degree and period of leaflessness. Leaf production in the overstorey species extended over a longer time period compared to the understorey species. For most of the species, flowering coincided with leaflessness. Proportionately more number of overstorey species flowered during the dry season and wet season flowering was more for the understorey species. A majority of the species produced fruits during the wet season in which case the fruits were mostly of fleshy types. Fruits produced during the dry season were mostly of dry types. The significance of these results are discussed.

shade, steep slope and deep burial (5 cm) adversely affected the germination percentage of these species. Mid- and late successional species responded little to differences in these conditions. The survivorship of seedlings of early successional species at the end of rainy season was more adversely affected than that of mid- and late successional species. This was related to the generally lighter seeds of early successionals. The higher seedling survival of late successional species in shade than in the open and the reverse behaviour of the early successional species are related to their adaptation to different light regimes in the forest community.

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I certify that the thesis entitled "STUDIES ON THE ADAPTIVE STRATEGY OF A FEW SELECTED TREE SPECIES OF THE NORTH-EASTERN INDIA" submitted by Shri Ravindra Prasad Shukla, M. Sc. for the degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong embodies the record of original investigation carried out by him under my supervision. He has been duly registered and the thesis presented is worthy of being considered for the award of Ph. D. degree. This work has not been submitted for any degree of any other University.

Date: July 31, 1981.
Place: Shillong.

Signature of the
Supervisor

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CONTENTS

SECTION A

COMPARATIVE STUDY ON ADAPTIVE GROWTH STRATEGY OF FOUR EARLY AND LATE SUCCESSIONAL TREE SPECIES.

SECTION B

ADAPTATION OF TREES IN THE FOREST COMMUNITY.

PREFACE

The thesis embodies the results obtained on two aspects: (i) the adaptive strategy of a sub-tropical humid forest community as a whole with chapters dealing with the phenology, seed germination and establishment, general growth pattern and allocation pattern of the major tree components of the community, and (ii) detailed architecture and growth pattern analysis of four important tree species, namely, Duabanga sonneratioides Ham. and Anthocephalus cadamba Miq. which are two early successional species and Dillenia pentagyna Roxb. and Artocarpus chaplasha Roxb. which represent two late successional species. Apart from the fact that informations on tropical trees are meagre in these areas of study, it is hoped that this will be useful from the point of view of practical forest management in the region.

The thesis is divided into chapters, each chapter dealing with one aspect of the study. General Introduction gives a review of literature and places the study in its right perspective. Literature cited in the text is given at the end. As the different chapters are written in the form of papers eventually to be published, some overlapping in writing could not be avoided.

GENERAL INTRODUCTION

About 38 per cent of the continental area of the earth is covered by the forests but India has only about 22 per cent of its land under forest cover. The forest produces meet the basic necessities of human civilization in the form of raw materials for several industries. The woody plants of the tropics which is a vast renewable source of energy, must be given attention in a situation when the world's fossil fuel stock is depleting fast. The present era, could be known as the era of secondary vegetation, as with few exceptions, there is no country on earth which has a substantial land surface cover of primary vegetation (Richards,1963; Gomez-Pompa and Vazquez-Yanes, 1974). These secondary species (species of secondary vegetation) today represent probably the most important biota of the tropical lowland areas because of their abundance and remarkable versatality of their response to disturbances.

Studies with different approaches and interests have been carried out in the tropics mostly at the community level. The reactions and adaptations of the primary producers to varied environmental factors and successional niche can be better understood when we intensify our investigations at lower levels of biological organization. Of the several important aspects dealing with adaptive features of trees, the aspects of architectural pattern and growth coordination of trees form a basis for the differences in photosynthetic or production efficiency of giant terrestrial producers. The studies on their allocation and productivity pattern, their preferences to different environmental set of conditions for germination, establishment and growth and the compatibility of their different phenophases with seasonal climatic changes may prove to be rewarding for the evaluation of species mixtures for better forestry practices and social forestry programmes through a knowledge of their specific requirement and production efficiency in different environments. Such studies may also be helpful in efficient forest management for sustained utilization of these resources (Ramakrishnan, 1978).

The present study is of particular relevance to north-eastern India where the forest resources, particularly timbers have a sizable impact on the economy of this region. The studies on these long neglected aspects may also help in understanding the adaptive growth strategies of tree species of the tropics.

PHENOLOGY

Phenology is generally described as the art of observing the phases of the life cycle or the activities of the organisms as they occur through the year (Lieth, 1970, 1971). Two different approaches in phenological work can be distinguished. In the first, average calender dates are established with specific phenological events. This process is called bench-making and the second indicates the quantitative development of plants and animals throughout the season and is called phenometry. Both approaches have great value in productivity studies. The phenologists select the beginning or the end of phenophases-any distinguishable phase in the life cycle of plants in which changes occur in a short period of time. Some phenologists take the entire community as a unit and describe the seasonal changes as phenophases. The way in which the entire sequence of phenophases occurs around the year is called the phenodymamics and the elaboration of this for all the species in one community entering in a given phenophase is called phenological spectrum (Lieth, 1971).

Beginning with the early elaboration of seedling, flowering and harvesting calenders, phenology evolved and resulted in impressive maps about the geographical patterns (isophenes) of certain phenological events. Quantitative relationships of the time between seeding and harvests of many crops, finally enabled Thornthwaite (1952) to propound his phenological slide rule. This last achievement was possible through detailed growth analysis of certain crops which was called phenometry. There are many aspects of productivity which can be categorized, predicted and evaluated on the basis of phenological attributes.

Phenology of different vegetation types from different climatic zones are available such as for tundra (Sorensen, 1941; Mooney and Billing, 1961), Rocky Mountains (Holway, 1965) and Rock Valley in the northern Mojave Desert (Shreve, 1942;

the 'Caatinga' drop their leaves with the onset of drought and replace them when rains resume (Alvim, 1964). According to Jackson (1978) the most advantageous strategy of leaf replacement in a perennial plant in an aseasonal environment would be retention and photosynthetic use of an old leaf until a new leaf is grown. Drought stress in tropical forests increases gradually through the dry season and drought-adaptive leaf fall is correspondingly more gradual than cold-adaptive leaf fall in temperate forests. In tropical forests the maximal differential between dry season and wet season leaf-fall varies from 2 (Klinge and Rodrigues, 1968; Fittakau and Klinge, 1973) to 10 times (Madge, 1965). The studies of Jackson (1978) divided the adaptive strategies of leaf replacement into 8 types and the leaf-fall replacement pattern of Frankie _et al_ (1974) provides examples of two adaptive strategies, namely, (i) dry season leaf-fall — wet season flushing and (ii) dry season leaf-fall — dry season flushing.

Studies in tropical forests have revealed massive dry season flowering (Duke and Black, 1953; Snow, 1962; Janzen, 1967). Frankie _et al_ (1974) found twice as many seasonally-flowering species in bloom in the dry season as in the wet season. Alternate year or irregular flowering has been demonstrated for certain species in the tropics (Holttum, 1931; Fedorov, 1966; Ashton, 1969; Janzen, 1970). Although moisture-related factors may play the biggest role in controlling flowering in tropical trees, African studies by

Njoku (1958, 1963) and Lawton and Akpan (1968) suggest that a change in photoperiod may be an important stimulus in triggering flowering. Njoku (1958) demonstrated that a difference of 15 minutes in photoperiod at Ibadan is sufficient to initiate the flowering process in many herbs and shrubs and he suggested that these small photoperiodic change may also trigger flowering in trees.

Frankie et al (1974) found that the precipitation pattern is meaningful for fruit development besides several other biotic and abiotic factors which may also be involved. The need for high moisture level for proper development of fleshy fruits was shown by Zahner (1968). Several flowering and fruiting pattern suggest that animal-plant interactions may have a subtle but important influence. Flowering patterns that may be influenced by pollinating animals were found in recent studies like that of Frankie et al (1974), Heinrich and Raven (1972) and Levin and Anderson (1970). Bawa (1974) has found that a high proportion of tree species are incompatible or dioceous. Consequently, since most of these are obliged to cross, and since wind pollination in the tropics is rare (Whitehead, 1969; Baker, 1970), they are dependent upon animals for effective pollen transfer.

TREE ARCHITECTURE

Trees are fascinating organisms if only because they represent the world's oldest and largest living beings (Kozlowski, 1972).

The essential elements of the definition of a tree are crown and trunk or bole. It is interesting to consider different ways in which a plant becomes a tree. The pipe model theory (Shinozaki et al, 1964) maintains the constant proportion in parts like crown, trunk and root, and the developmental basis for the construction method, according to this model, is the ability of the trunk to increase in diameter as it grows in height. This theory is based on the observation that the amount of leaves existing above a certain horizontal level in a plant community is always proportional to the sum of the cross-sectional area of the stems and branches found at that level.

The initiation of a tree starts from seedling stage which is the most critical phase in the life cycle of a plant (Ramakrishnan, 1972; Harper and White, 1974). The consideration of stages or phases is of significance in architectural development in trees because many trees as saplings show many morphological and physiological features which either are lost or change with age. The organisational status of the meristem of the tree may change by its position regardless of its age for which Molisch (1922) coined the term topophysis; the changes in organisational status of meristem with age were termed as cyclophysic. Two types of changes from juvenile to adult tree stage may take place: one is gradual and the other is abrupt termed as homoblastic and heteroblastic respectively (Goebel, 1928-33). The appreciation of phase change is relevant in architectural analysis because it signals the branching pattern, a characteristic of the trees.

The form of woody plants is determined by the differential elongation of buds and branches and the expression of a particular growth habit is commonly associated with the phenomenon of apical dominance. Basically three types of crown forms have been recognised (Brown, 1971): (i) columnar, without branches due to absence of lateral buds, exemplified by some arborescent monocots where the unbranched main axis simply terminate in a tuft of leaves, (ii) excurrent, the main axis outgrows the lateral branches resulting in a conical crown form common for most gymnosperms and a few angiosperms and (iii) deliquescent or decurrent, where the lateral branches grow as fast or faster than the main axis causing virtual loss of identity of the main axis in the crown (Kramer and Kozlowski, 1960). Although the basic patterns of tree form are genetically controlled, since the trees are exposed continuously to varying environmental conditions during their active growth phase from germination to maturity, the phenotypic changes in crown form in response to these changes are obvious. Crown form adapted to a particular situation was termed as ideotype (Brunig, 1970, 1976).

Architecture is a dynamic concept and should not be confused with shape or physiognomy which is a static concept. Size of the plant is not considered in architecture and small herbs and giant forest trees may precisely have the same architecture. Richter (1970) mentioned the statement of Leonardo da Vinci about the proportional relations between axes, 'all the branches of trees at every stage of their height, united together, are equal to the thickness of their trunk below them'. This is of course, the basis of the pipe model theory of trees developed by Shinozaki et al (1964). Corner gave two principles which maintain the regularity in construction of higher plants (i) axial conformity and (ii) diminuition or ramification (cf. Halle et al, 1978).

The shapes and crown forms are more variable in the tropics than in temperate regions. A comprehensive account of architectural models was given by Halle and Oldeman (1970). According to Halle et al (1978) the architecture of a plant is 'the visible morphological expression of its genetic blue print at any one time'. To get the complete spectrum of architectural phases, the tree must be of seed origin and it must flower and seed. Based on different morphological characteristics of plant growth, Halle et al (1978) distinguished over 23 architectural models. These characters are in pairs: monoaxial (unbranched) or polyaxial (branched), branches orthotropic (erect) or plagiotropic (horizontal), axes homogeneous or heterogeneous (orthotropic and/or plagiotropic), construction modular (all axes morphologically equivalent) or non-modular (distinct branch and trunk), branches at the base (basitony) or from the upper part (acrotony) of the trunk, branches axillary or dichotomous, branches short-lived or long-lived, growth monopodial (by original terminal bud) or sympodial (by substituted bud) and inflorescence hapaxanthic (terminal) or pleonanthic (lateral). The other important features influencing tree architecture are primary and secondary orientation of leaves and shoots, the behaviour of lateral buds producing the branches either in continuation of growth since inception (sylleptic) or after a rest period (proleptic) and branch polymorphism in the form of long and short shoots. Short shoots are identified to grow less than 2 cm per year and bear no lateral branch (Wilson, 1966). The trees rarely conform completely to their architectural model even under optimal conditions for tree functioning. The process of architectural adjustment by which the damaged tree accomodates itself to its environment is called reiteration (Oldeman,1974). Architecturally, the most significant morphological feature of the tree is the lowest major branch and as the branches are progressively shed, so the crown is gradually displaced vertically. It is convenient to refer to this level characterized by the first living branch or reiterated trunk as the morphological inversion point (Oldeman, 1974). The usefulness of morphological inversion point is that it provides an easily measurable value for the ratio between crown depth and total height and so of the bioenergetic status of a tree.

The recognition of buds as a unit in modular construction of plants is traditional (recently reviewed by White, 1979). According to Harper (1980), such modules should be considered as a basis of demographic treatment of growth as the heirarchy of branch orders and the form of architecture is ultimately determined by the distribution of births and deaths in a population of buds. Such a treatment of growth has started receiving attention only in recent years (Hunt, 1978; Hunt and Bazzaz, 1980). The study on tree architecture as a whole is still a neglected field. Further, no work in this area has been done on Indian forest tree species. Since the architecture of the crown form has major effect on forest production and yield (Nelson et al, 1981), architectural analysis of tree species in relation to their adaptation to a given ecological niche would be rewarding both from an academic as well as applied view point.

EXTENSION AND RADIAL GROWTH OF TREES

"Growth of a tree is a complex phenomenon compounded of responses of its primary apical meristems and secondary cambial meristems to both intrinsic and extrinsic forces which are not uniform either in time or space". This brief definition was given by Forward and Nolan (1961) after extensive studies on tree growth.The first comprehensive account on shoot growth of temperate trees was the publication of a classical book by Busgen and Munch (1931) dealing largely with temperate species. Kozlowski (1964) reviewed the current state of understandings on shoot growth particularly of north-temperate trees.

Two widely different patterns of shoot growth occur in temperate trees. In one group of species the shoots are fully preformed in the winter bud and the extension growth is limited to the expansion of the predetermined components of the bud in summer. Only one type of leaves occur e.g. Pinus, Acer, Fagus (Kozlowski, 1958, 1963). In a second type shoots are not fully preformed in the winter bud and both early and late leaves are produced (Critchfield, 1960; Kozlowski and Clausen, 1966). Kozlowski (1972) subsequently recognized three different patterns of shoot growth in trees: predetermined, heterophyllous and recurrent flushing type. Of these the last type of growth is represented by sub-tropical and tropical trees involving the recurrent formation and expansion of a series of bud at the tip of the same elongating shoot. Gill (1971) studied the composition and expansion of bud of Fraxinus americana and called the predetermined shoot as determinate and all other extension type as indeterminate. The tendency to distinguish second flushes in north-temperate trees as 'lamma's shoots' is due to the fact that it is regarded to be normal for these trees to exhibit only one flush of growth per growing season.

There is little understanding of the growth of tropical trees as compared to the information available on temperate tree species. In older literature, the studies specific to tropical trees growth, largely refer to comprehensive investigations of phenology (Busgen and

Munch, 1931). Some factual basis for our understanding of growth expression in tropical trees comes from a study of method of extension growth on woody plants mostly derived from the examination of shoot morphology (Tomlinson and Gill, 1973). For instance, Koriba (1958) collected a lot of valuable information about over 500 species in Singapore but as the observations are largely based on qualitative morphological examination, they may not be meaningful in some cases where the growth type exhibit no morphological change in shoot.

However, two main patterns of extension growth in tropical trees was distinguished by earlier workers:
(i) Rythmic, where shoots have marked endogenous peridicity of extension (Halle and Martin, 1968). This term is synonymous with episodic (Romberger, 1963); intermittent (Koriba, 1958); or articulate (Tomlinson and Gill, 1973).
(ii) Continuous, where shoots have no marked endogenous periodicity of extension. This is synonymous with evergrowing (Koriba, 1958) and non-articulate (Tomlinson and Gill, 1973).

The historical phase of generalized observation is now passing over to one of detailed analysis of individual species over longer periods of time. Some of the studies with this approach include the work of Bond (1942, 1945), Holdsworth (1963), Halle (1966), Halle and Martin (1968), Purohit and Nanda (1968), Borchert (1969), Greathouse and Laetsch (1969), Taylor (1970), Gill and Tomlinson (1971) and Greathouse *et al*

(1971). Of these, Halle and Martin's work on rubber is a model type because it is a union of anatomy, morphology and physiology. Shoot growth of tropical woody plants is very diverse and the classification of growth patterns of many species is difficult because they vary widely in different regions. For example, species of *Thespasia* and *Duabanga* are considered evergrowing in Singapore but deciduous in India (Koriba, 1958). Similarly our studies show that *Duabanga sonneratioides* exhibits no conspicuous feature of rythmic growth and grow continuously throughout the year but the observations of Halle in Malaysia show that the growth units in these species is marked by some scale leaves between any two tiers of branches (Halle *et al*, 1978).

One of the most important environmental factors influencing the rate of stem extension is light intensity because of its controlling effect on the rate of photosynthesis which in turn influences the other metabolic processes involved in growth. In addition, there is the problem of distinguishing between direct effects of light on photosynthesis and indirect effects such as higher leaf temperature, increased water loss, etc. (Kozlowski and Keller, 1966; Hughes, 1966). Grime and Jeffrey (1965) noted an inverse correlation between growth rate and survival of tree seedlings at low light intensities and suggest that slow growth rate may play a role in adaptation to shade. The growth of woody plants in relation to water has also been very widely studied (Kramer and Kozlowski, 1960; Rutter and Whitehead, 1963; Zahner, 1968).

Evidence accumulating suggests that growth rate may be very sensitive to temperature change also. A number of species also grow faster in longer than in shorter day length (Longman, 1972).

Internode elongation of many tropical trees can be very rapid. Examples of rapid height growth were given by Longman and Jenik (1974): *Terminalia superba*, 2.8 m/yr; *Musanga cecropiodes*, 3.8 m/yr; *Ochroma lagopus*, 5.5 m/yr. Such higher growth rate is often determined for open-grown trees or at the forest border. Within the forest community the rates tend to be much slower and often decline with increasing age of the tree (Kramer and Kozlowski, 1979). The higher growth rate of these open-growing trees may be attributed to higher photosynthetic rate of these species which can be easily acclimated to a high light environment as evidenced by the performance of gap phase species like *Acer rubrum*, *Cornus florida* and *Liriodendron tulipifera* (Wallace and Dunn, 1980).

The duration of growth per year is variable among different species and individuals of the same species of different age group. In Nigeria, older trees of *Bombax buonopozense*, for example, were dormant for 9-10 months or more whereas 3-year old seedling stopped their growth only for 3-4 months (Njoku, 1963, 1964). Controlled environmental studies have shown that shoot extension growth can be halted in a number of tropical trees by reducing the day length

(Njoku, 1964; Longman, 1966, 1969). In temperate zone, height growth often begins before the threat of frost is over and is completed during a short part of frost-free season (Kienholz, 1941; Kramer, 1943; Kozlowski, 1962). Kramer (1943) found the date of growth cessation more variable than that of growth initiation. In tropics, the wet and dry season often control the periodicity of growth (Gaertner, 1964). However, the evidence accumulating suggests that there are several species which may show continuous growth throughout the year as in _Rhizophora mangle_ L. (Gill and Tomlinson, 1971).

The phenomenon of shoot tip abortion which induce sympodial growth is common in many woody plants (Romberger, 1963; Kozlowski, 1964; Zimmermann and Brown, 1971). The timing of shoot tip abortion varies with age, vigour and environment. In many genera such as _Ulmus_, _Fagus_, _Tilia_, _Syringa_ and _Vaccinum_, shoot tip aborts with decline in growth as the shoot and its leaves complete expansion in the spring (Millington, 1963). Accelerated abortion in short days and delay in long days has been well documented in _Ulmus americana_ (Millington, 1963).

Cambial growth of tropical trees is very diverse. In many species xylem increment may continue to be during most or all the year. Growth rings may or may not be correlated with periods of shoot growth (Kramer and Kozlowski, 1979). For example, in rubber tree saplings, shoot growth occurred in flushes at 42 days intervals, each flush being associated with an increment of xylem leading to distinct growth rings. By comparison some tropical pines produce as many as five shoot growth flushes in a year but form only one ring (Tomlinson and Gill, 1973). Daubenmire (1949) found cambial growth related to length of the day rather to air or soil temperature. This was further supported by Fraser's findings (1952) on both the growth initiation and growth cessation. The same external and internal factors which control the bud break and leaf fall also control the timing of the period of cambial activity (Longman and Jenik, 1974). But Hummel (1946) showed that in the leafless _Khaya grandifolia_ also cambium did not become fully dormant. Continuous cambial growth in most evergreen tropical trees was observed by Alvim (1964).

TREE BRANCHING PATTERN AND ORIENTATION

A tree is a photosynthetic device consisting of assimilating units (leaves) arranged on one or more woody self supporting axes (Tomlinson, 1978). The woody framework of branches presents leaves, the photosynthetic surface, to sunlight in a manner that is primarily related to photosynthetic efficiency of the leaf and the distribution of light in the environment of the tree.

In most of the trees, the number of leaf-bearing units (shoots) increases by the proliferation of original seed-borne or plumular shoot meristem. This increase is determined by the genetic make-up according to a precise pattern. In trees two types of branch production can be distinguished: (i) Prolepsis produces a branch axis (proleptic shoot) that has basal bud scales (reduced prophylls or persistent scars), initially congested nodes (no hypopodium) and a gradual transition in leaf morphology and size at the first few nodes, usually from bud scales to foliage leaves; (ii) Syllepsis produces a branch axis (sylleptic shoot) that lacks basal bud scales, has a long basal internode (hypopodium) and has little or no transition in leaf morphology and size at the first few nodes. These terms were given by Spath (1912) but defined precisely by Tomlinson and Gill (1973). Syllepsis is a predominantly tropical phenomenon. Examples like coffee are interesting in which a sylleptic and proleptic shoot may originate successively from the same node.

The branching pattern is established only after an initial period of seedling development in which the axis is unbranched. The subsequent development of lateral meristem whether by syllepsis or prolepsis, bears a relation to the periodicity of growth activity of the parent terminal meristem. Where growth of the terminal meristem is continuous, branching itself may be either continuous or diffuse (intermittent). Intermittent branching involves the production of one or more tiers of branches at irregular intervals as the development of lateral meristems into branches (usually by syllepsis) seems correlated with the vigour of the terminal meristem. Where growth of a shoot is rhythmic (with regular alternation of growth and rest) branching is also rythmic and is clearly correlated with the activity of the terminal meristem (Tomlinson, 1978). The recognition of distinct branch tiers or branch complexes leads to a discussion of the essential differences that exist between trunk and branch axes. The elaborate organisation of the tree largely depends on this differentiation.

Many trees show a clear differentiation between orthotropic and plagiotropic shoots, which may be distinguished by a combination of morphogenetic features and physiologic responses (tropisms). An orthotropic shoot has an erect orientation (negatively geotropic), radial symmetry and phyllotaxis most commonly deccussate or spiral. A plagiotropic shoot has a hrozontal or oblique orientation (more or less diageotropic) and dorsiventral symmetry either by virtue of distichous phyllotaxis or, if spiral or deccussate by secondary orientation. In many trees orthotropic shoots correspond to trunk axes and plagiotropic shoots to branch axes. In Terminalia-branching each sympodial unit is initially plagiotropic and finally orthotropic (Fisher, 1978). This demonstrates that the degree of differentiation of a meristem may be changed either by external influences or by modification of internal conditions (Tomlinson, 1978). Of special interest are those woody plants in which there is an inherent change of expression within a single meristem producing axes of architectural significance. Such axes are described by Halle and Oldeman (1970) as 'mixed'. Secondary changes in axis orientation may have important consequences mostly mediated via the influence of reaction wood (Zimmermann and Brown,1971).

Branching pattern governs the features of adaptive significance like effective leaf display and minimization of non-photosynthetic tissue (Horn, 1971; Whitney, 1976; Honda and Fisher, 1978), and structural strength (McMohan and Kronhauer, 1976). Strahler (1957) developed a method for analysing branching pattern in trees on the basis of geomorphologist's law of stream number. The method for calculating bifurcation ratio (Rb) involves ordering of branch segments; the ultimate branch as I order and in that series the trunk as the highest order. The method serves as an index of the degree of branching. More recently, this was used to characterize branch system in many plants (Holland, 1969; Leopold, 1971; Oohata and Sidei, 1971; McMohan and Kronauer, 1976; Whitney, 1976; Thornley, 1977; Niklas, 1978). Oohata and Shidei (1971) subjected seedlings of *Quercus phyllyraeoides* to different planting densities and found that bifurcation ratio was insensitive to changes in light environment. Whitney (1976) compared bifurcation ratio of open and shade grown *Fraxinus americana* and similarly concluded that bifurcation ratio value is a species-specific constant. Steingraeber et al (1979) found significantly different Rb values in the open and forest grown saplings of sugar maple (*Acer saccharum* Marsh.), and attributed this to the phenotypic plasticity of branching which is an adaptive strategy for survival of this species under varied light conditions. Little is understood about the contribution of different order of branches in total make-up of tree frame-work in different ecological situations. Steingraeber et al (1979) found significant differences between open grown and forest grown sugar maple seedlings with respect to the proportional aid of different order of branches in the form of total number and total length.

The orientation or display angle of branches results in maximum effective leaf surface possible for a branch system (Honda and Fisher, 1978; Fisher, 1979). Markedly variable response to open vs. closed habitat in the branch display angle was observed by Pickett and Kempf(1980) and Kempf and Pickett (1981) in a few early successional shrub species.

LEAF DISPLAY

The leaf orientation affects significantly the canopy structure. De wit (1965) divided plant canopies into several types, based on the distribution of leaf angles within them. The two extreme forms are the planophile canopy in which horizontal leaves are more frequent and the erectophile canopy in which vertical leaves predominate. Simulations based on light interception theory (Monsi et al, 1973) have shown that canopy productivity is higher in erectophile canopies than in planophile ones when foliage is dense. The results of Turitzin and Drake (1981) support the hypothesis that the normal seasonal decline in photosynthesis is due at least in part, to the shift in canopy structure. Fine scale features of leaf display have been found to differ in model and real plants (Fisher, 1979). Efficaceous leaf display in response to open vs. shade conditions was shown by Honda and Fisher (1978), Pickett and Kempf (1980) and Kempf and Pickett (1981) in a few early successional shrubs and understorey tree species.

LEAF DYNAMICS OF TREES

The flushing or bud burst in tropical and temperate trees mostly demonstrate rythmic growth but in the tropics continuous production and growth of leaves throughout the year is also not uncommon (Tomlinson and Gill, 1973; Ashton and Brunig, 1975). Increased number of flushing at certain times and less at other times have been shown by different workers (Taylor, 1960; Njoku, 1963; Hopkins, 1970). Some trees are reported to flush regularly in a uniform climate (Holttum, 1940). In evergreen seasonal forests, flushing frequently occurs in the dry season before the start of the rains (Longman and Jenik, 1974). Rainfall, therefore, cannot be assumed as a triggering agent for flushing (Njoku, 1964). Temperature is in many ways the most likely environmental factor to control bud-break. Thus cocoa buds may tend to flush when maximum temperature exceeds about 20^{o}C (Hardy, 1958, 1964; Alvim, 1967). Experiments in growth rooms have shown that bud-break in some tropical trees is closely influenced by day length (Longman, 1969).

In the tropics, the deciduous habit cannot be sharply demarcated from the evergreen (Holttum, 1940; Koriba, 1958). Therefore, on the basis of relative timing of bud-break and leaf abscission Longman and Jenik (1974) recognised four patterns of leafiness: (i) periodic growth - deciduous type, in which leaf fall occurs well before bud break with longer period of nakedness, (ii) periodic growth - leaf exchanging type, in which naked period is very short and new leaves come just after leaf fall, (iii) periodic growth - evergreen type, in which leaf fall occurs throughout the year but at slower rate and the trees never appear naked, and (iv) continuous growth - evergreen type, in which continuous production and fall of leaves occurs throughout the year with little change in the appearance of the tree. The number of flushes varies widely in different tree species which do not show continuous growth. Chowdhury (1964) described the flushing pattern of Indian trees and found a maximum of four flushes per year. Purohit and Nanda (1968) also reported four flushes of growth per year in *Callistemon viminalis* with no correlation between alternate period of rest and extension and the seasonal climatic change.

Growth rate of leaves is normally closely linked with shoot elongation and is often quite rapid during the middle part of the growing season (Longman and Jenik, 1974). In tea plant it has been noted that a single deciduous bud scale amongst expanding foliage leaves has a corresponding short internode beneath it (Bond, 1942). The high vigour in the middle part of the growing season may also shorten the plastochron interval (Gill and Tomlinson, 1971).

The variation in leaf size and shape in relation to macro- and micro-climatic conditions is much discussed (Bailey and Sinnott, 1916; Piersall and Hanby, 1926; Ashby, 1948; Richards, 1952; Ryder, 1954). Warmer period of growing season also favour the expansion rate and final size of the leaves (Rboerts, 1920; Kozlowski and Clausen, 1966). The final leaf size and the seasonal duration of leaf expansion varies greatly among species, type of shoot and the environment (Kozlowski, 1971). Smaller leaves are produced just before the onset of dormancy or after the bud burst (Halle and Martin, 1968). Shading often influences the growth of leaves of cocoa and coffee (Murray and Nicholas, 1966). Temperature is also known to play an important role in determining final leaf size (Milthorpe, 1959, 1963). Parkhurst and Loucks (1972) developed a model of leaf size on the basis of its water use efficiency in different environment. Baker (1950) divided tree species into 3 shade tolerance classes on the basis of leaf characteristics: tolerant, intermediate and intolerant. Fedorov (1966) regarded the variation in leaf size of little adaptive significance though Heslop-Harrison (1964) supposed this feature within the same genotype as of some adaptive value. Smith and Nobel (1977) used a more empirical approach to determine the adaptive significance of seasonal variation in leaf size in a few desert shrubs.

Aging in common deciduous tree leaves is known to be rapid (Kozlowski, 1971). Length of life of leaves is important and retention of a large leaf surface is likely to increase dry matter production (Zavitowski et al, 1974). Bentley (1979) studied the leaf longevity in many understorey species of tropical forests. He found that longevity of leaves was correlated with light intensity and discussed the longer retention of leaves unfavourable for production due to increasing epiphylls. Further, the photosynthetic efficiency of a leaf decreases with age after full expansion (Mooney, 1972; Johnson and Tieszen, 1976). The turnover rate of the leaves of shade intolerant species was shown to decrease under shade (Newhouse and Madgwick, 1968). Further, the turnover rate of leaves of shade tolerant species is generally low with longer retention of leaves (Bentley,1979).

Therefore, an understanding of the strategy of different tree species as far as this feature is concerned, would be significant.

ECOLOGICAL STRATEGIES OF TREES IN SUCCESSIONAL ENVIRONMENT

'Strategies in an economic sense is the reciprocal sets of action and reactions between two conflicting groups directed to the attainment of their ends by each group' (cf. Halle _et al_, 1978). For the plants the ends sought is to preserve their genotype and occupy as large a part of the available biotope as is necessary.

The idea of two main trends in selection of specific strategies comes from the work of animal biologists (**MacArthur** and Wilson, 1967). The notion of r, the intrinsic rate of population increase and K, the equilibrium size is essential for the comparison of two main strategies in a given environment. Grime (1974, 1977) considered stress tolerance as a distinct strategy evolved under intrinsically unproductive environments or under extreme resource depleted condition, imposed by the vegetation itself. In this three-strategy model (C-, S-, R-) ruderal and stress tolerant strategies correspond to the extremes of r and K selection respectively while the highly competitive species occupy a position in between the two (Grime, 1979). Halle _et al_ (1978) used the notion of ecotype, the combination of niche and habitat favoured by ecologists (Whittaker _et al_, 1973;

Oldeman, 1974).

Seed production, germination and establishment:

The strategy of seed production and seed longevity is much different in early successional species from that of late successional species. The former produce very small seeds which have been found in the soils of primary forest in several areas of the tropics (**Richards**, 1952; Keay, 1960; Ashton and Brunig, 1975). Among early successional species there are differences in germination with respect to various kinds of successional environments (Bazzaz and Pickett, 1980). For example, bare soil is initially invaded by Trema guineense but Musanga cecropioides becomes established after a vegetative cover has been formed (Ross, 1954). In Thailand, Macranga denticulata, Aralia armata and Polygonum chinense germinate in the forest at some distance from a clearing but Trema orientalis and Melastoma malabarica seeds germinate in the high light of the clearing (Cheke et al, 1979). On the other hand, late successional species (shade-tolerant) can invade the environments with different degree of light intensity and generally they germinate more successfully under the shade of the forest canopy (Richards, 1952).

Seed germination of early successional species with smaller seeds is epigeal (Richards, 1952; Budowski, 1965; Ng, 1974; Gomez-Pompa and Vazaquez-Yanes, 1974). The frequency of epigeal germination declines with seed size in late successional species (Ng, 1974). This type of germination is advantageous as the cotyledons become photosynthetic soon after. Sheldon (1974) found that the deep seated seeds of species producing small and light seeds may fail to germinate because of the low potential of seedling due to meagre seed reserve to penetrate through soil profile. Seed burial is favoured for large seeds and Shaw (1968) found 50% more germination from the buried acorns of *Quercus petraea* than from surface lying seeds. This is mainly due to heavy predation of large seeds of species like *Astrocaryum mexicanum* (Sarukhan, 1978). Tropical forest seeds and seedling predation may be very heavy (Burgress, 1972; Janzen, 1974; Ng, 1974; Whitmore, 1975). The duration of suitable conditions and the seed's response to these are major factors which control the germination and establishment (Harper *et al*, 1961).

The seed germination of most of the species remain unaffected by light intensity (Sarvas, 1950; Black and Wareing, 1954; Grime and Jarvis, 1976). However, there are several pioneer species which require light for germination. This is consistent with the ecology of pioneer species suggesting a mechanism whereby the seeds of these species might be prevented from germination below a closed canopy (Grime and Jarvis, 1976). Initial survivorship of seedlings of late successional species has been reported to be more in the shade (Kinnaird, 1974). Most of the early successional species cannot withstand shade. Moreover, the shade-intolerant species are reported to be more susceptible to fungal attack under the shade than the shade-tolerant species (Vaartaja, 1962; Grime and Jeffrey, 1965).

Gaps created in the forests through death or fall of mature phase trees, are important for the seedling dynamics of different species at different successional status (Bazzaz and Pickett, 1980). These gaps are not so frequent and may occur in some tropical forests at an average of 100 years (Hortshorn, 1978). A gap is a heterogeneous environment with an increase in light, soil and air temperature, rainfall input and nutrient availability but a decrease in relative humidity (Schulz, 1960, Longman and Jenik, 1974). Whitmore (1975) has constructed the most comprehensive classification of tree species relative to gaps but he recognises that each species is unique in its strategy (Whitmore, 1978). The creation and filling of different sizes of gaps may be responsible for much of the organisation of forest communities and for much of the differentiation and coexistence of plants (Bazzaz and Pickett, 1980).

Growth, production and allocation pattern:

Growth of early successional trees in the tropics is extremely fast. Reports of annual height growth of upto 5 m yr^{-1} are common with fast diameter growth (Leburn and

Gilbert, 1954; Lamb, 1968; Ewel, 1971; Jordan, 1971; Longman and Jenik, 1974; Ashton and Brunig, 1975). Diameter growth of 2-3 cm yr^{-1} are common in pioneers. In contrast later successional trees grow more slowly (Richards, 1952). There is a continuum of growth rates from early successional to late successional species of mature phase (Schulz, 1960). This differences in the amount of growth is attributed to the differences in leaf display, photosynthetic rates, LAI and allocation pattern in early and late successional species.

Lugo (1970) compared photosynthetic and respiration rate of two early successional (Cecropia peltata and Anthocephalus cadamba) and two late successional (Sloanea berteriana and Dacryodes excelsa) species. The early successional species reach light compensation points at 150 - 400 fc and saturate at 2500 fc (Odum et al, 1970). Cecropia photosynthesizes at the rate of 11.1 mg CO_2 dm^{-2} hr^{-1} and Anthocephalus has a value of 10.7. In many trees of secondary forests, the shoot growth is continuous while the late successional species usually show intermittent growth (Ashton and Brunig, 1975). Large leaves supported by sparse branch framework may be a major mechanism for reducing structural cost in pioneers and the fast turnover rate of leaves in early successional species may account for the faster growth of these (Coombe and Hadfield, 1962). The pioneers also have comparatively soft wood of low density. The priority here is given not to the durability but to the quick use of available resources and effective competition with neighbours (Bazzaz, 1979). Marks (1975) found that maximum LAI is attained between 4 to 6 years of age in pin cherry (*Prunus pensylvanica* L.), an early successional tree species, and biomass accumulation was also most rapid during this period. The LAI of early successional species are generally lesser than that of late successional species which determine the greater area of exposed leaf surface accounting for high photosynthetic rates, growth and production (Bunting, 1976). The studies on productivity through succession are rare but the available data show that there is a rapid production during the early stages of succession (during 5 to 10 years) and then a stabilization through time as the forest matures (Jordan, 1971; Farnworth and Golley, 1974).

The strategy of allocation pattern of available resources for various life activities is the result of various ecological and evolutionary factors which favour natural selection (Cody, 1966). The success of an organism depends on its relative apportionment of biomass (MacArthur and Wilson, 1967). Much of the work in the case of plants pertains to herbaceous and shrub species (Harper and Ogden, 1970; Jaksic and Montenegro, 1974; Abrahamson, 1975; Ramakrishnan and Kanta, 1976; Bell *et al*, 1979; Williams and Bell, 1981). Considerable attention has been given to the root-shoot balance of temperate tree species (Drew and Ledig, 1979; Farmer, 1980; Grier *et al*, 1981).

Study of partitioning of dry matter or biomass among various parts of plants is more difficult in trees than in herbaceous plants because their large size restricts sampling (Kramer and Kozlowski, 1979). The production of dry matter in leaves, branches, bole and roots must be measured on trees of uniform size or age because the proportion of total biomass in the various compartments vary with tree age and size (Switzer _et al_, 1968). The shoot:root ratio is often considered to be stable for a species under any given set of environmental conditions (Wareing, 1970). On this basis, Thornley (1972) developed a model to account for the partitioning of assimilates between leaf, stem and root. Marks (1975) found that the early successional species possess superficial roots just sufficient to anchor the tree poorly but increasing the absorptive surface for quick exploitation of short term increase in nutrient availability and water in disturbed land (Marks and Bormann, 1972). The higher shoot:root ratio in early successional species and proportionately much higher allocation to the bole and leaves here is implicated as an adaptive strategy which favour the high production rate through fast vertical move of the canopy in high light environment (Marks, 1975). On the other hand, late successional species shows greater allocation to the root for sustained but long term utilization of the resources and grow slow because of their lower resource demand (Grime, 1979; Bazzaz, 1979).

Tree architecture:

The morphological-developmental models of tree architecture (Halle *et al*, 1978) may be related to a r-K continuum In general light demanding early successional species which colonize gaps maintain their model construction throughout the life and may reiterate poorly while the more tolerant species can reiterate successfully (Bazzaz and Pickett, 1980). As long as a tree conforms to its initial model, where vegetative growth and sexual reproduction are integrated in a standard pattern, its place along K to r line is fixed. Quantitative data are required to place the architectural models precisely on this line. It may be suggested that the orthotropic branches have different energy requirement from plagiotropic branches. The former maximize volume production for support and conduction, while the latter place emphasis on surface production. The plagiotropic axes are more commonly met in early successional species than in late successional ones.

Two theoretical strategies of leaf distribution was given by Horn (1971): a monolayer with leaves densely packed in a single layer and a multilayer with leaves loosely scattered among many layers. The multilayer can expose much more leaf area and no leaf completely eclipse the other. This strategy is generally represented by early successional species. A monolayer can expose no more than one unit of self-sustaining leaf area for each unit of the ground area and is mostly represented by late successional species. Horn also derived that the multilayer can grow faster than monolayer only when exposed to between about 54% and 100% of full sunlight. Under conditions much shadier than 54% of full sunlight, monolayer can grow faster than multilayer. This is consistent with the strategy of early successional species which exploit and compete for the high light environment. Thus architectural analysis is a necessary preliminary for the study of bioenergetic status of the tree. In addition to the branching pattern and leaf display parameters like overall shape, reproductive periodicity, seed crop size and ability to reiterate are required for the detailed architectural analysis. This type of approach may lead to an understanding of the ecological strategies of the architectural models (Halle _et al_, 1978).

THE PRESENT STUDY

The present investigations deal with the adaptive growth strategies of some early and late successional tree species coming during secondary succession after Jhum (shifting cultivation). An attempt has been made to compare the growth strategies, production and allocation pattern of these two group of species. Apart from this detailed study on a few early and late successional species, over 20 important tree species of a sub-tropical humid forest community has been studied for their general growth characteristics, production and allocation pattern relating these characteristics to successional status of the species concerned. The germination and establishment strategy of a number of tree species of this community was also studied. The phenological behaviour of the community as a whole was correlated with seasonal changes in climate. The tree species studied here form a part of a sub-tropical humid forest at Lailad (25°45" - 26°N lat; 91°45" - 92° long.) at an elevation of 296 m in the Khasi Hills of Meghalaya.

STUDY AREA AND CLIMATE

The study area (Fig. 1) is located at Lailad which is about 70 Km towards the northern side of Shillong city, the capital of Meghalaya in the north-eastern region of India. It lies between $25^{o}45''$ - $26^{o}0''$ N latitude and $91^{o}45''$ - $92^{o}0''$ E longitude at an elevation of about 296 m. The pre-cambrian rocks are represented by gneiss, schists and granites. The soil is red, sandy loam and is of laterite origin. The pH ranges from 5.8 to 6.3. Angles of the slopes generally range from 20^{o} to 60^{o}. The climate is typically monsoonic with about 84% of the total annual rainfall occurring during May to September. April and October are also quite wet. The rest of the period is practically dry. The monsoon season is followed by a mild winter during mid-November to mid-February. March and early April represent a brief dry summer period (Fig. 2).

The study site is a part of a reserve forest known as Nongkhyllem reserve which is under Meghalaya Forest Department since 1910. The peripheral zone of this forest is disturbed and developing forest communities at different stages of succession may be found. The forest is bounded on the north and northwest by Kamrup district and on the north-west by Nowgong district of Assam. The southern side of the forest is covered by Shillong sub-division. The age of the reserve forest is approximately estimated to be 50 years.

Fig. 1 Location of study area.

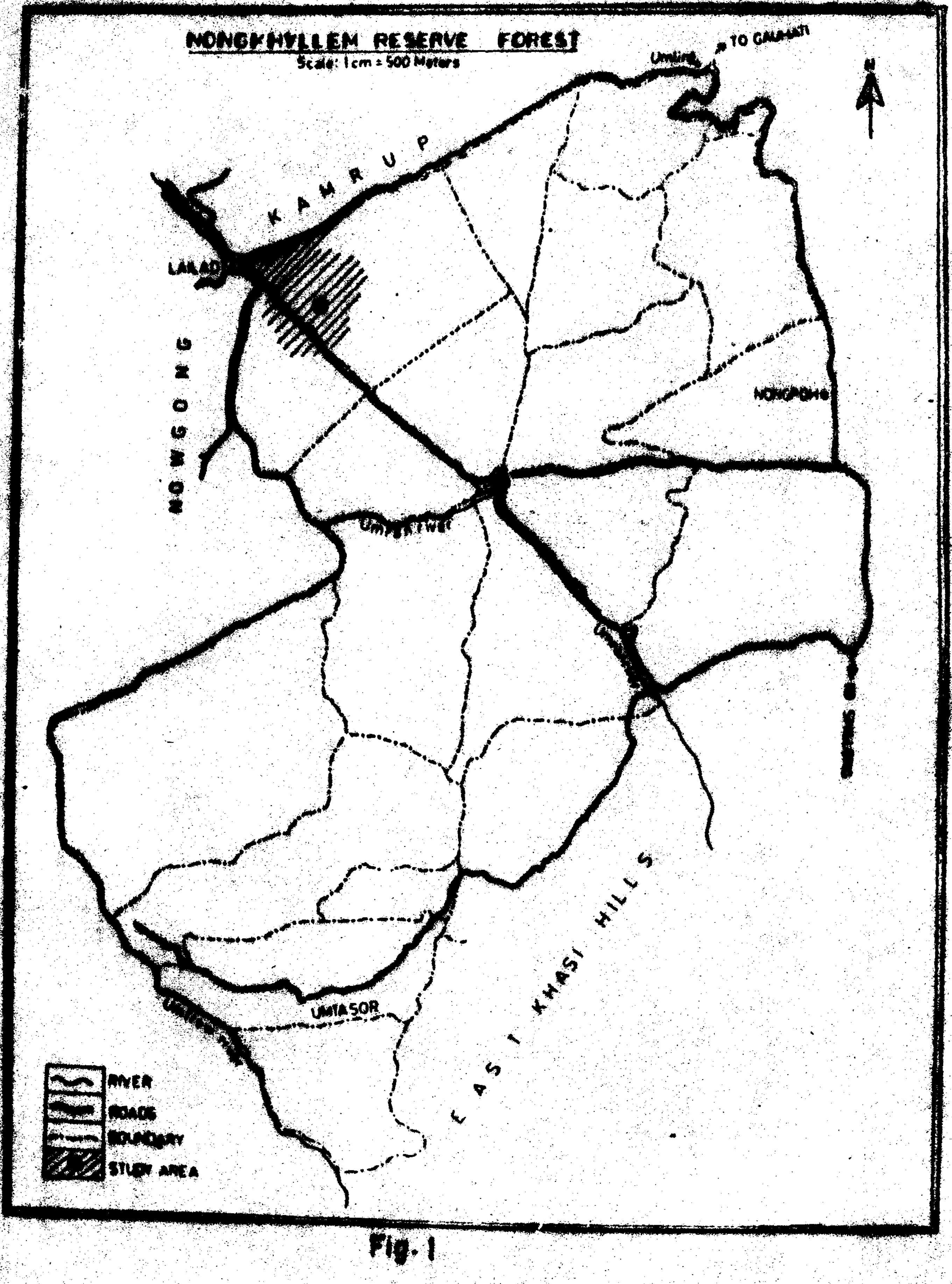
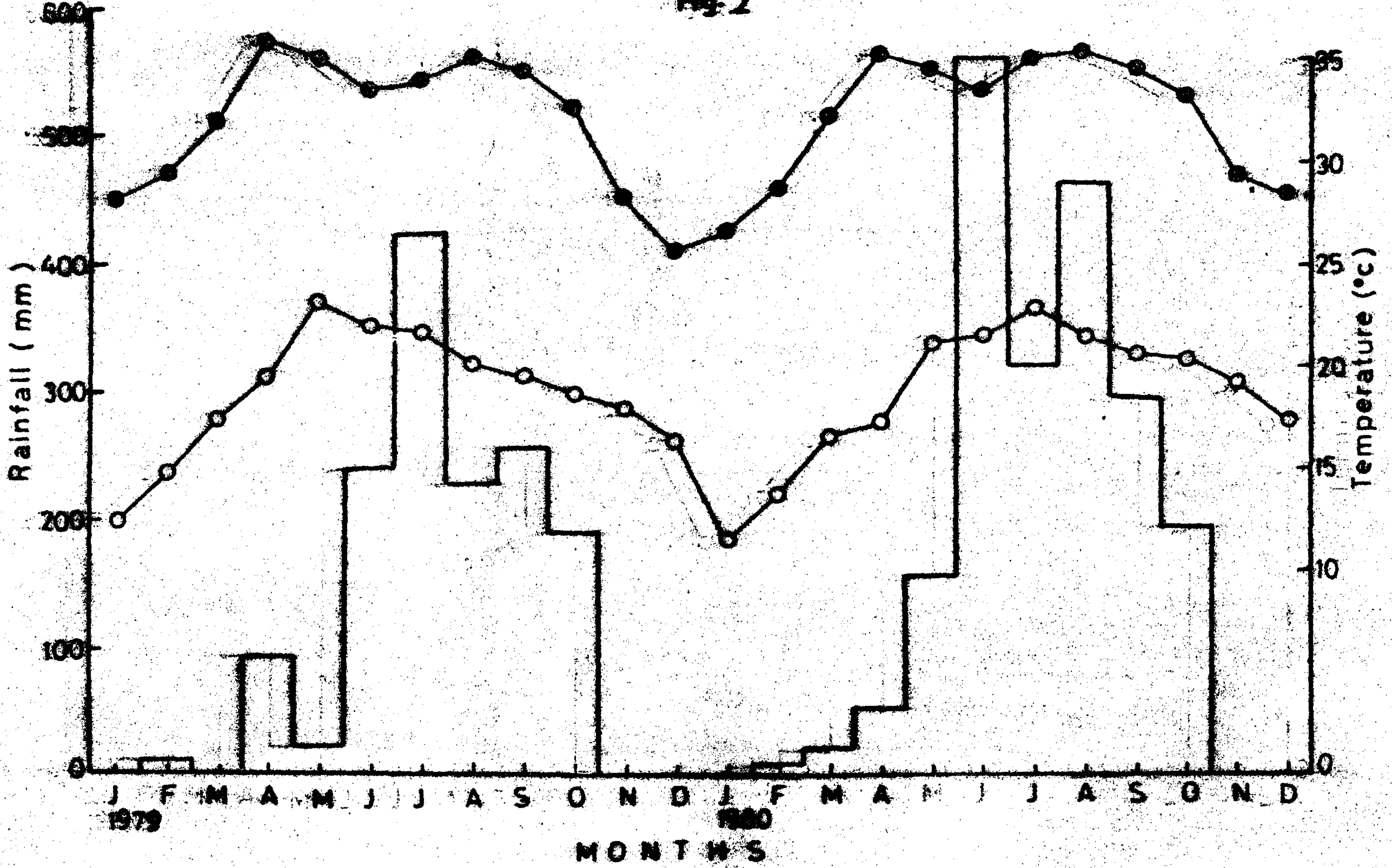

NONGKHYLLEM RESERVE FOREST
Scale: 1cm = 500 Meters
Umling
TO GAUHATI
N
KAMRUP
LAILAD
NOWGONG
NONGPOH
UMTASOR
EAST KHASI HILLS
RIVER
ROADS
BOUNDARY
STUDY AREA

Fig. 1

It represents the oldest fallow of the Jhum practised at lower elevations of the Khasi Hills of Meghalaya by the local tribal population, namely the Khasis and Garos (Ramakrishnan and Toky, 1978).

Fig. 2 Ombro-thermic diagram for the study area, open bar, rainfall; closed circle, mean maximum temperature; open circle, mean minimum temperature.

Fig. 2


Rainfall (mm)
0
100
200
300
400
500
600
Temperature (°c)
0
10
15
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SECTION-A

COMPARATIVE STUDY ON ADAPTIVE GROWTH STRATEGY OF FOUR EARLY AND LATE SUCCESSIONAL TREE SPECIES

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CHAPTER - I

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PATTERN OF ARCHITECTURE AND EXTENSION GROWTH

INTRODUCTION

Growth of tree is a complex phenomenon which is governed in time and space by several intrinsic and extrinsic factors (Forward and Nolan, 1961). Most of our knowledge on tree growth has been based upon the studies of their temperate representatives (Cook, 1941; Kozlowski and Ward, 1957, 1961; Kozlowski, 1964, 1972). Temperate trees offer very limited diversity of pattern of architecture and growth. Though some intensive studies on growth pattern of tropical trees are available (Holdsworth, 1963; Halle and Martin, 1968; Borchert, 1969; Halle, 1971; Gill and Tomlinson, 1971), the need of deeper understanding of tree growth pattern in tropical forests was emphasized by Tomlinson and Gill (1973). Recently, the canopy form in relation to prevailing environmental condition has got much attention (Bruing, 1976; Nelson et al, 1981) and several quantitative studies on branching pattern has been made (Whitney, 1976; Fisher, 1978, 1979; Steingraeber et al, 1979; Pickett and Kempf, 1980). The pattern of growth in relation to the successional status of tree species (Marks, 1975) suggests distinct strategies for early and late successional species (Ramakrishnan et al, unpublished). Halle and Oldeman (1970) and Halle et al (1978) discussed the architectural pattern of tropical trees giving more than 23 architectural models.

The present study on shade-intolerant (*Anthocephalus cadamba* Miq. and *Duabanga sonneratioides* Ham.) and shade-tolerant (Dillenia pentagyna Roxb. and Artocarpus chaplasha Roxb.) tree species is a comparative analysis of the strategy of architectural development, amount and pattern of extension and radial growth, dynamics and distribution of branches and characteristics of internodal length in relation to rythmicity of growth.

METHODS OF STUDY

The forest community at Lailad is a 50 year old humid sub-tropical semi-evergreen forest, developed after slash and burn agriculture. All the four species, A. cadamba, D.sonneratioides, D. pentagyna and A. chaplasha were found growing in the open and the last two species were also occurring under different degrees of shade in the forest. A. cadamba and D.sonneratioides were abundant along the disturbed periphery of the forest as well as in other younger forest communities. Young trees of all the species were identified under open situations. A single tree of A. cadamba was found to grow in partial shade and this was also considered for study. Trees of A. chaplasha were identified in shaded sites whereas D. pentagyna, though found to grow in shade, could not be considered as most of them were found to be of sprout origin. The initial age, height (ht) and diameter at breast height (dbh) of the trees of all the four species studied, were as follows:

Species	Light condition	Initial age (yr)	ht(m)	dbh(cm)
A. cadamba	open	4	7.43	8.76
" "	shade	4	3.68	3.02
D. sonneratioides	open	4	4.78	6.15
A. chaplasha	open	6	6.12	8.63
" "	shade	6	4.77	4.53
D. pentagyna	open	6	4.26	4.94

Observations on growth characteristics was initially started in January 1979 on the main axis (trunk) and actively growing branches of all the trees. The tops of the trees were approached through a wooden platform. Fortnightly observations were made on girth increment of the main axes at breast height (1.3 m) and extension growth of the main axes and individual branches. Branch orientation was measured by noting the angles of their attachment. Ordinal numbers were used to denote branch orders for referring all growth characteristics except bifurcation ratio (Rb). Trunk or main axis was designated as 0, primary branches originating from main axis as I order and secondaries originating from primaries (I order) as II order branches and so on. However, for calculating bifurcation ratio, Strahler's method (1957) was followed — the ultimate branch was designated as first order, where two first order branches come together, the resulting proximal segment was designated second order. Where two branches of unequal orders met, the resulting branch maintained the higher order. Bifurcation ratio (Rb) of branching system of the trees was derived on the basis of Motomura's (1947) formula modified by Steingraeber <u>et al</u> (1979):

$$Rb = N. - N\,max/N. - N_1$$

Where N. is the total number of branches of all orders, N max is the number of branches of the highest order and N_1 is the number of branches of first order.

The degree of branch formation on the main axis and I order branches were calculated as percentages of total lateral buds forming branches in current or subsequent growing season. The monthly pattern of production of I and II order branches were calculated as percentages of total branches produced on respective branch order in a year. Branch angles were measured by protractor.

Three open-grown trees of each species (age 5-6 Yr) were harvested at the end of the growing season in November 1980 and the branches were segregated into different orders. The length of each branch was measured to the nearest centimeter. The branches were categorized into different branch length classes and were analysed with respect to I and II order branches respectively.

The total content of the apical bud was determined by dissection under the binocular microscope. Examination of buds was made several times during the year (February, May, August, November). Some general growth observations like growth initiation and cessation, shoot tip abortion, self-pruning and reiteration were made on the basis of 3-5 replicates of different age groups of trees (1-8 years) of a given species.

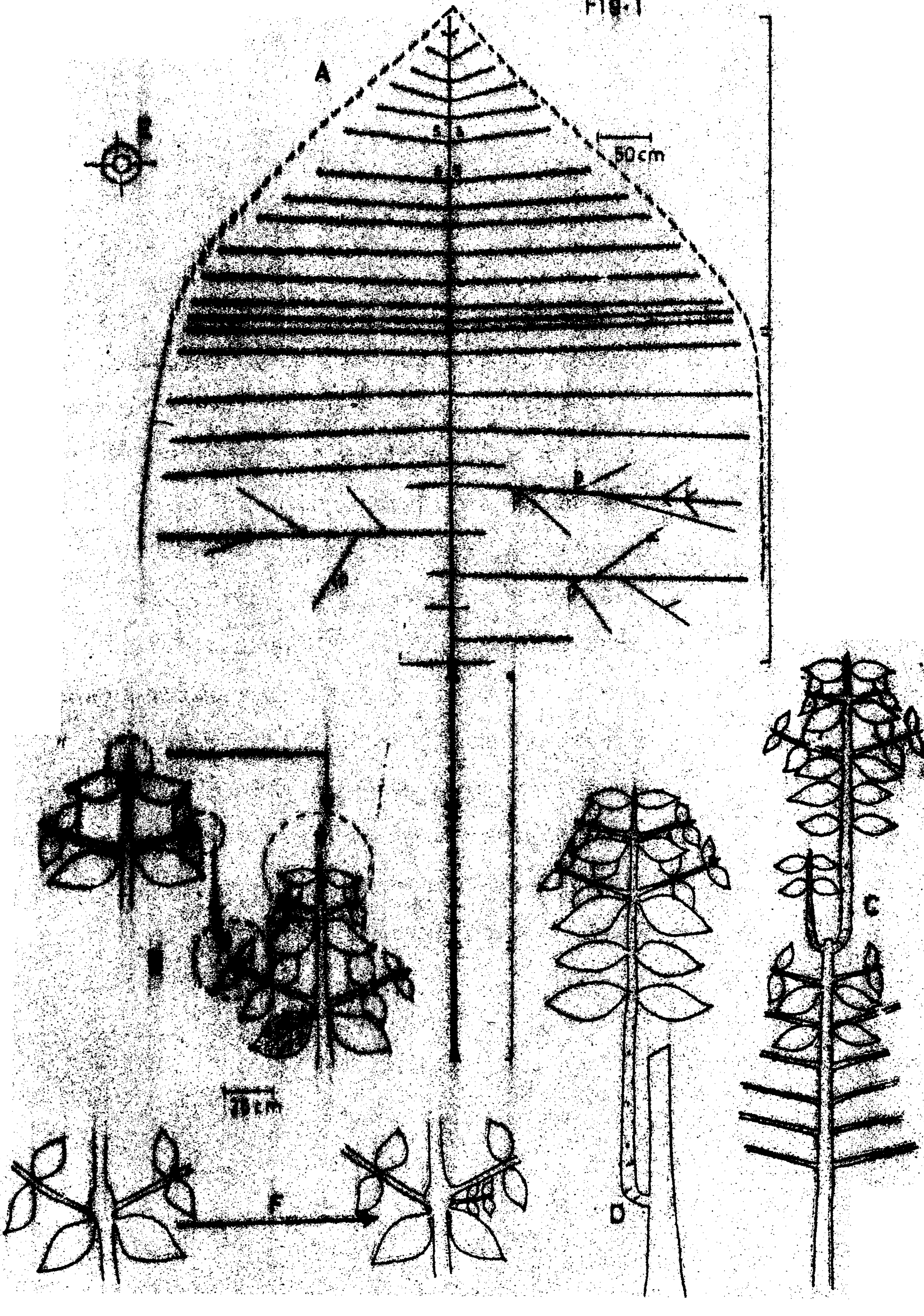
Architecture and General Growth Characteristics

Anthocephalus cadamba Miq.

The architecture (used in the sense of Halle and Oldeman, 1970) built in *A. cadamba*, is the result of continuous growth of a monopodial trunk (Fig.1A). The leader (main axis) produces deccussately arranged leaf pairs with interpeticlar stipules and branches (Fig. 1 B,E). Branch dimorphism is evident because while the trunk is an orthotropic monopodium, the precocious I order branches which arise sylleptically (by the continued growth of lateral buds laid during the current year's growth), are all plagiotropic (tend to be horizontal) monopodia. These branches have long first internode (hypopodium) before bearing leaves. Branches other than the I order are produced proleptically (by the activation and growth of lateral buds laid during the last year's growth). The leaf arrangement on plagiotropic units shows dorsiventrality by secondary orientation of blades in a single horizontal plane, exhibiting apparent discordancy with that of the trunk where the deccussately arranged leaves may be oriented in several planes.

Fig. 1 Architectural pattern of *A. cadamba*: A, architectural skeleton (demarcation on main axis represents the shortest internode and termination of annual growth; S, sylleptic and P, proleptic origin of branches); B, terminal bud growth (a, growth of main axis bud, producing pair of leaf and sylleptic branch, b, growth of terminal bud of branches producing leaf pair only); C, substitution growth after tip damage; D, reiteration of the model; E, branch arrangement; F, development of supernumerary branch.

Fig. 1



During the dormant phase in winter, the terminal vegetative buds are protected by a gummy substance. The trees start their growth in February- March and enter the dormant phase in November. During growth initiation, the terminal bud of the leader axis is the first to burst open into a pair of opposite leaves with a pair of sylleptic branches somewhat extra-axillary to the last leaf pair of the previous year (Fig. 1 Ba). The growth continues and this pattern of bud growth, production of pairs of leaves and corresponding branches is checked only in November at the onset of bud dormancy. A 4 or 5 year old tree may produce 10 pairs of I order branches in a year. The shortest internode of the year on main axis and branches indicates the termination of annual growth. This short internode (articulation) is helpful in determining the age of the tree. Bud-burst on the main axis is followed within a week by the same on the I order branches but without the production of any sylleptic branch (Fig. 1Bb).

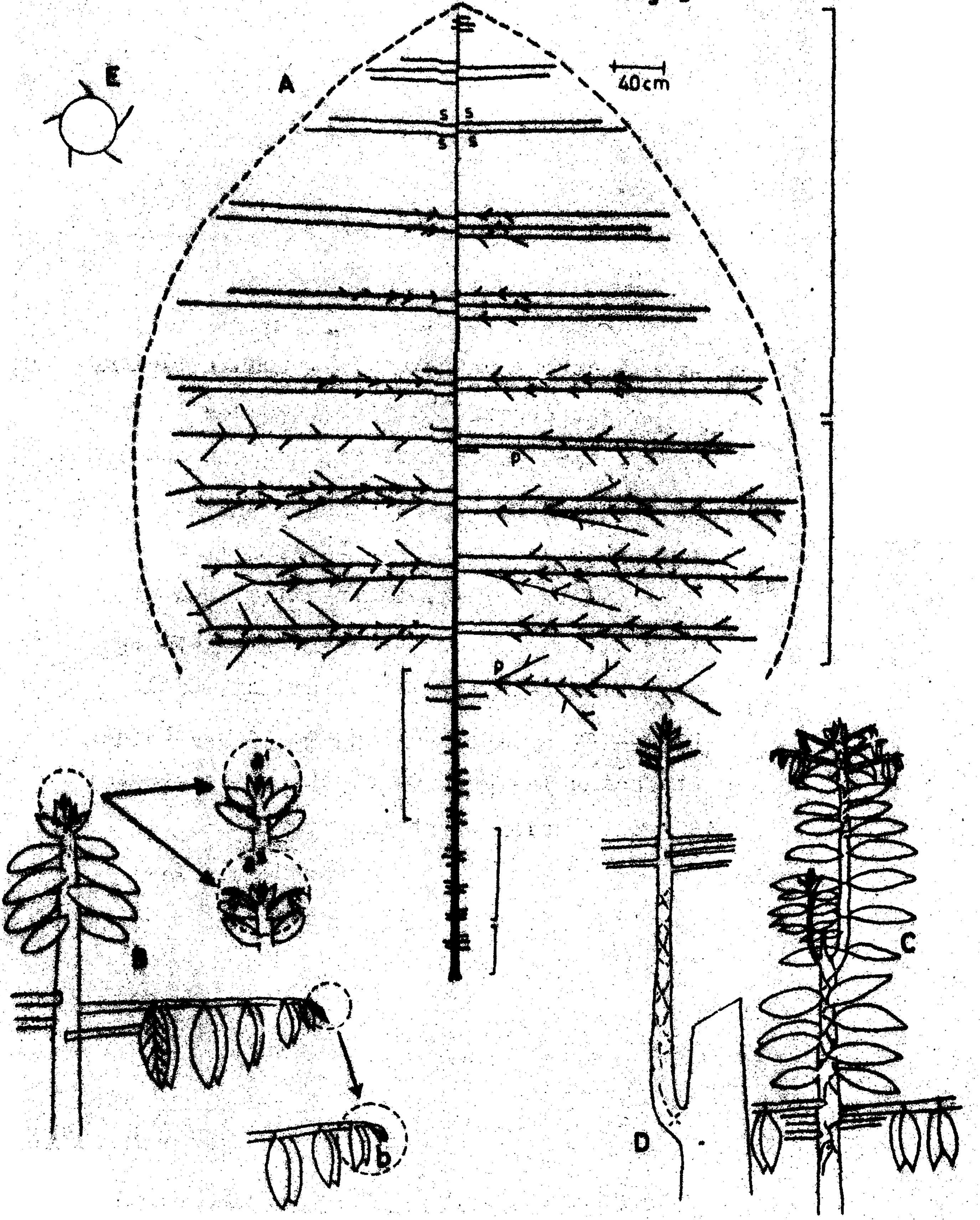
The architectural development in _A_. _cadamba_ is affected by shoot tip abortion in lower branches. They die and decay resulting in self-pruning. If the main axis growth is disturbed or checked by the destruction of terminal bud, substitution growth takes place. Initially, the top pair of the branches assumes leadership and become orthotropic but later on one is suppressed by the other. In this process leaf orientation is changed as on the main axis. (Fig. 1 C). Bayonet-joints become ill-defined in this species.Reiteration of architectural model takes place when the whole canopy or major aerial part is destroyed or broken (Fig. 1 D). The development of a few supernumerary branches (branch arising between a leaf and corresponding sylleptic, I order branch on main axis). As a consequence of any disturbances in general growth pattern was also observed in this species (Fig. 1F). The vegetative juvenility period was found to be about 5 years and the trees bore inflorescence on the III order branches only.

Duabanga sonneratioides Ham.

The architecture (Fig. 2 A) is determined by an orthotropic monopodial trunk which produces tiers of sylleptic (I order) branches with hypopodium seperated by a gap of 20-80 cm. A 4-5 year old tree may produce about 5 tiers of branches in a year. The leaves are arranged spirally at short intervals on main axis but are opposite on branches with longer internodes (Fig. 2 B). Branch dimorphism is very clear as all other branch complexes except main axis, are plagiotropic. Similar to *A. cadamba* branches other than the I order, are produced proleptically. The plagiotropic branches become pendulous with age. The growth units (tiers of branches) were neither demarcated by scale leaves nor had a period of rest unlike that reported by Halle *et al* (1978). Growth in this species was continuous with fluctuation in growth rate during the year.

Fig. 2 Architectural pattern of *D. sonneratioides*: A, architectural skeleton (branch tiers and canopy form, main axis without demarcation of annual growth, S & P representing sylleptic and proleptic branches); B, terminal bud growth (a_1,terminal bud of main axis simply producing leaves and a_2, producing both the leaves and sylleptic branches; b, terminal bud of branch always producing leaves); C, substitution growth; D, reiteration; E, branch arrangement.

Fig. 2



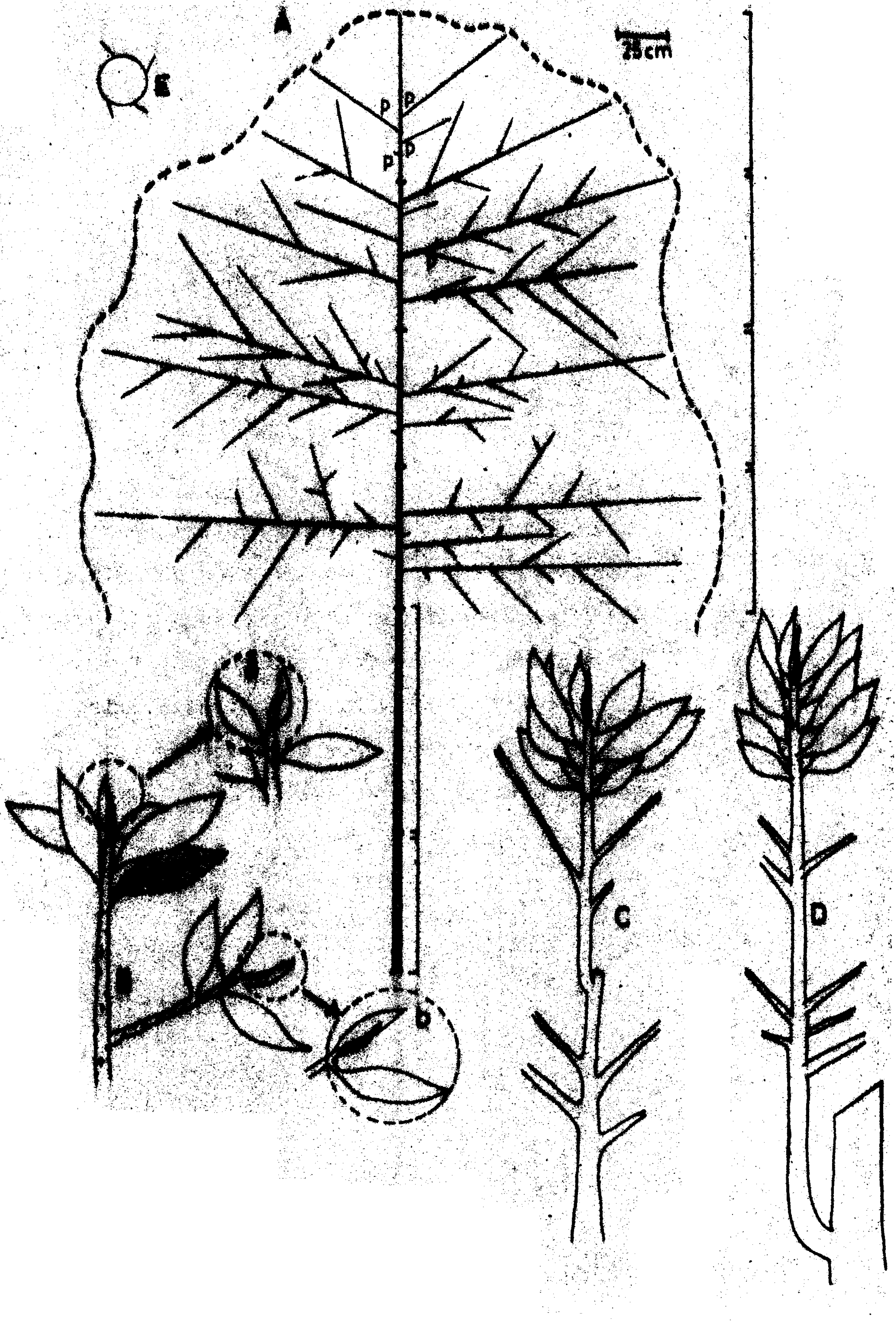
The architectural model in this species is usually disturbed by termites and ants due to which substitution growth occurs when the branches of top tier assume leadership (Fig. 2 C). They grow vertically but only one of them takes over suppressing the others, where the leaf arrangement becomes spiral as on the main axis. As in A. cadamba bayonet-joint in this species is not well pronounced. If the top of main axis is severely damaged at an early stage of growth, all the five branches of top tier may assume leadership simultaneously. Reiteration process is very efficient in this species and after destruction of major aerial part of the old trees, it regenerates by repeating its architectural model (Fig. 2 D). The inflorescence is terminal but does not affect the model. The vegetative juvenility period is about 6 years.

Dillenia pentagyna Roxb.

The architecture (Fig. 3 A) is governed by an orthotropic monopodial trunk. All the branches are equivalent and orthotropic, produced proleptically only after the fall of axillant leaves. The arrangement of leaves and branches is spiral (Fig. 3 B,E). A 6 year old tree may produce 3-5 I order branches in a year, the branches being loosely arranged in tiers. The branch growth is monopodial during the period of vegetative juvenility but become sympodial after the onset of the terminal inflorescence. The lower branches of the canopy show 'plagiotropoid phenomena'

Fig. 3 Architectural pattern of D. pentagyna. A, architectural skeleton (all branches of proleptic origin, demarcation on main axis denotes the annual extension growth); B, terminal bud growth (production of single leaf by terminal bud of main axis, a; and of branches, b); C, substitution growth with bayonet-joints; D, reiteration; and E, branch arrangement.

Fig. 3



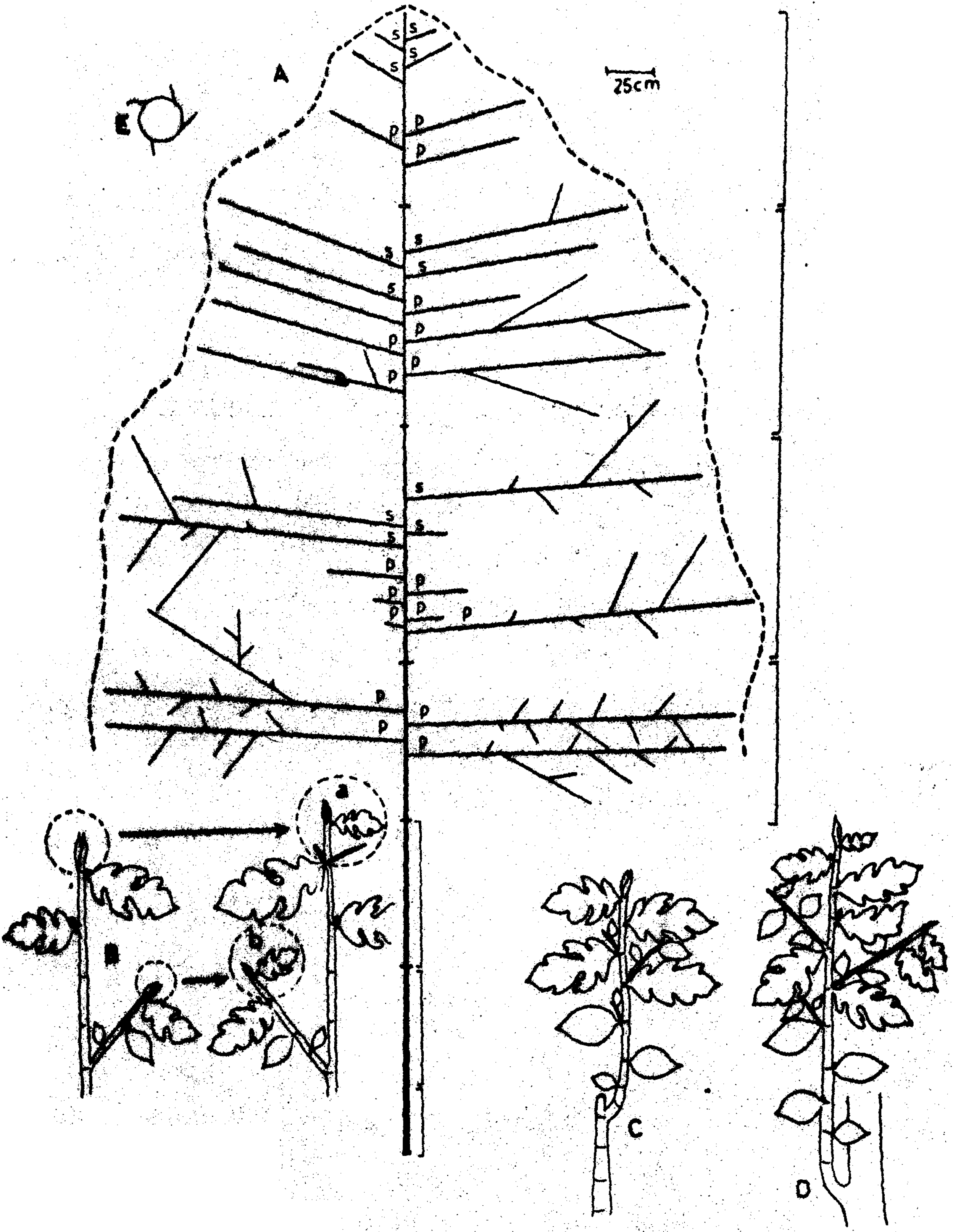
(Halle *et al*, 1978) and may become pendulous with age. The spread of branches is very assymetrical as compared to *A. cadamba* and *D. sonneratioides*. Growth starts in April to second week of May and growth cessation occurs during September-October with winter dormancy from October to April. The termination of annual extension growth could be marked by aggregation of leaf scars on the main axis and branches. During the winter, the terminal bud is protected by scale leaves but during the growth period, it is naked. The architectural model in this species is rarely damaged by pests but the predominance of branch growth always render the trunk short. Bayonet-joint, developed rarely after substitution growth (Fig. 3 C), is very prominent. Reiteration of the model, after major damage in aerial part of the tree, is very successful in this species and the trees of sprout origin are hard to identify from that of seed origin (Fig. 3 D).

Artocarpus chaplasha Roxb.

An orthotropic monopodial trunk determines the architecture in this species. All the branch complexes are orthotropic and equivalent to the trunk and are loose in tiers. The arrangement of branches and leaves is spiral (Fig. 4 B,E). The growth starts in April and is checked in October-November due to the onset of winter dormancy. The trunk remains unbranched (monoaxial), until the 3rd or 4th

Fig. 4 Architectural pattern of *A. chaplasha*: A, architectural skeleton (demarcation on main axis represents annual extension growth; S, sylleptic branch; P, proleptic branch). B, terminal bud growth (a, of main axis and b, of branch producing leaf and axillary bud); C, substitution growth with prominent bayonet-joint; D, reiteration; E, branch arrangement.

Fig. 4



growing season. Usually only a single tier of branches is produced each year during the most favourable part of the growing season through prolepsis but occassionally under more favourable conditions, one more tier of branches may be produced during the same growing season through syllepsis (Fig. 4 A). A single tier may have 3-7 branches depending upon the growth conditions and the age of the tree and could be separated from the preceding or succeeding tier by a gap of 2-11 internodes on the main axis. 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 stipules (Fig. 4 B). The trees rarely grow true to the model due to damage by pests and animal herbivores. The latter include deers who eat the shoot apices of this species at younger ages. As a consequence of damage of terminal bud, substitution growth occurs which may be well marked in this species by conspicuous bayonet-joints (Fig. 4 C). Trunkated tree repeats its original model by reiteration (Fig. 4 D).

RESULTS

Growth period

D. sonneratioides exhibited continuous growth throughout the year except for a slower rate during November-December. Other species had winter dormancy and the growth period decreased with increase in the age of the tree resulting in a corresponding increase of dormant period. A 4 year old open-grown tree of A. cadamba had longer growth period compared to the forest-grown tree of the same age. In the latter, dormancy sets in almost a month ahead of the open-grown individuals. The date of bud burst in all the species was more variable than the date of onset of dormancy in relation to age and this was more pronounced in A. cadamba. D. pentagyna and A. chaplasha had shorter growing period compared to the other two species (Table 1).

Bud content

Fig. 5 shows the schematic representation of the terminal bud contents (Fig. 5a) for different species. The analysis revealed that the number of embryonic leaves with their associated stipules, if any, were constant throughout the year for a particular species. The buds of D.sonneratioides were naked and actively growing throughout the year; the bud of the main axis had three differentiated leaves (spirally arranged) and that of branches had 3 pairs of leaves (opposite). Others were in primordial form. A. cadamba had two pairs of leaves in the bud with protective stipules while D. pentagyna had four leaves but not protected by any stipule. The outer most leaf was thicker and coloured in the dormant bud of latter species as a protective cover. During the active phase, the bud was covered over by the winged leaf base of the last expanded leaf. A. chaplasha had three leaves with a pair of

Table 1. Variation in time of growth initiation and cessation and in growth period of three tree species in relation to tree age (only open-grown trees were considered).

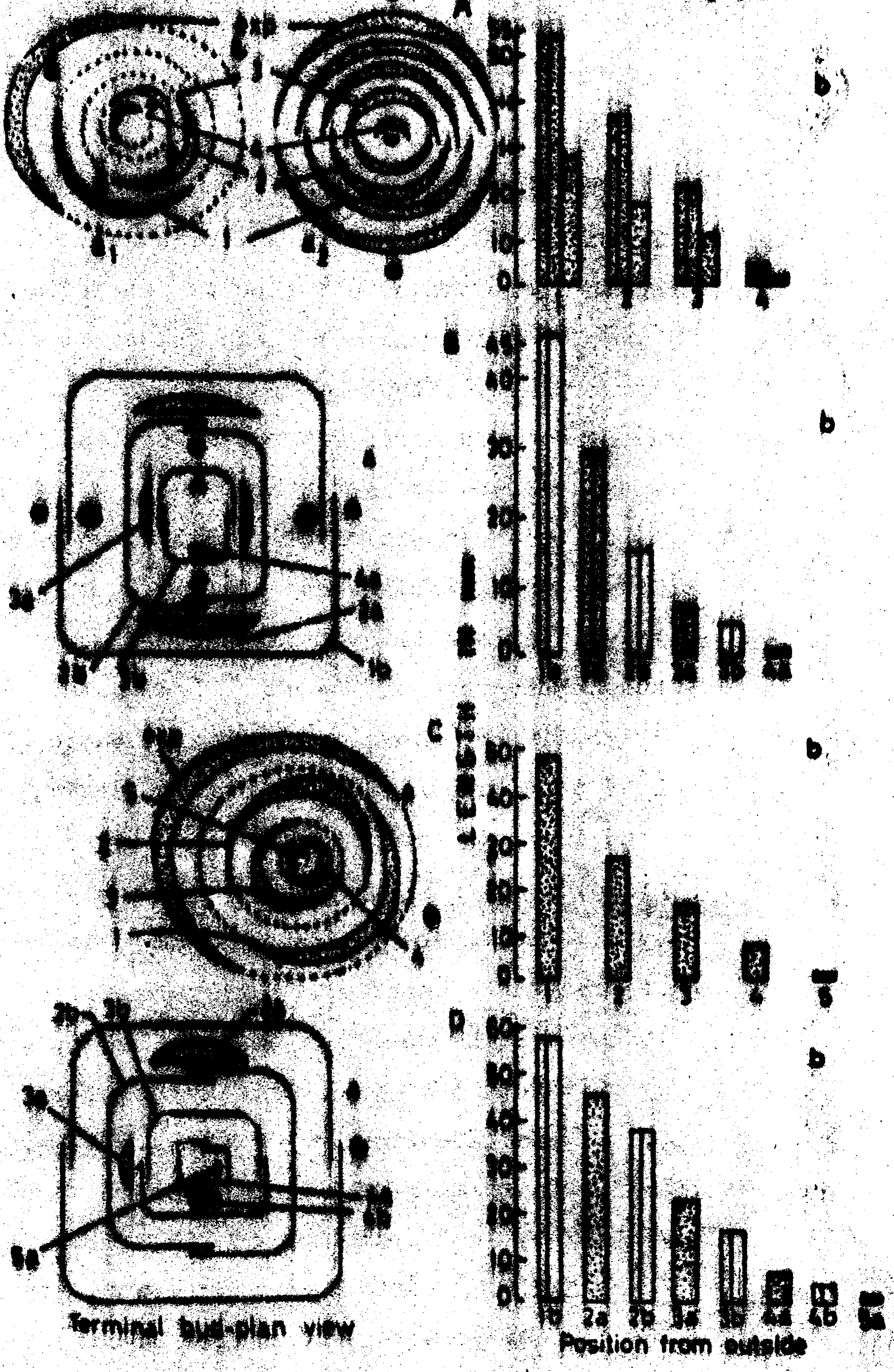
Tree age (yr)	Anthocephalus cadamba			Dillenia pentagyna			Artocarpus chaplasha		
	Initiation	Cessation	Growth period (weeks)	Initiation	Cessation	Growth period (weeks)	Initiation	Cessation	Growth period (weeks)
1	Jan. IV	Nov.IV	44	Apr. II	Oct. IV	32	Mar. I	Nov.III	38
2	Feb. I	Nov.IV	43	Apr.III	Oct. IV	31	Mar. II	Nov.III	37
3	Feb. II	Nov.III	41	Apr.III	Oct.III	30	Mar.III	Nov. II	35
4	Feb.III	Nov.III	40	Apr. IV	Oct.III	29	Mar. IV	Nov. II	34
5	Mar. II	Nov. II	36	Apr. IV	Oct. II	28	Apr. I	Nov. II	33
6	Mar.III	Nov. I	34	May. I	Oct. II	27	Apr. II	Nov. I	31
7	Mar. IV	Nov. I	33	May. II	Oct. I	25	Apr.III	Nov. I	30
8	-	-	-	May. II	Oct. I	25	Apr.III	Oct. IV	29

Note — (i) I, II, III and IV represent the 4 different weeks of a month.
(ii) Duabanga sonneratioides had continuous growth throughout the year.

Fig. 5 Terminal bud structure. The plan view (a) on the left shows the stipular primordia by solid lines and embryonic leaves or leaf primordia by stippled arcs and those of axillary structure by hatched circles. The small crossed circles outside the bud indicate the position of youngest expanded leaves. On the right (b) the length of the leaves and stipules are shown for mature buds about to open. Lengths of stipular primordia are shown as open bars, those of leaf primordia as stippled bars. Vertical line indicates paired embryonic leaves or primordia. A

A, D. sonneratioides;(a_1, of main axis and a_2, of branch; b, lengths of leaf primordia; longer bar, primordia of branch leaves; shorter bar, primordia of main axis leaves, 1-4); B, A. cadamba,(stipular primordia, 1b-3b, and leaf primordia 2a-4a; all in pair);C, D. pentagyna, leaf primordia in single 1-5; D, A. chaplasha,(stipular primordia in pair 1b-4b; leaf primordia in single 2a-5a.

Fig. 5


A
B
C
D
a
b
b
b
b
LENGTH
0
10
20
30
40
50
1a
2a
2b
3a
3b
4a
4b
5a
Terminal bud-plan view
Position from outside

stipules in between. The fourth leaf was in primordial stage. The size characteristics of the bud contents are presented in Fig. 5b in the form of histograms.

Growth rythm

Gradual increase and decrease in internodal length and area of corresponding leaves along the main axis was found in all the species. This intrinsic rythm was more conspicuous in *D. sonneratioides* and *A. cadamba* than in *D. pentagyna* and *A. chaplasha*. The number of peaks in rythm as well as the number of internodes produced in a year were fewer in the forest-grown trees of *A. cadamba* and *A. chaplasha* than in open-grown trees of these species (Fig. 6 A,B,C,D).

The total internodes produced in a year are presented for *A. cadamba*, *D. pentagyna* and *A. chaplasha* whereas only one tier of branches along with the gap represented by a number of internodes alone are presented for *D. sonneratioides*. It may be noted that 4-5 such tiers of branches along with gaps are produced in a year; *D. sonneratioides* produced a large number (70-100) of short internodes whereas *A. cadamba* produced fewer but longer internodes during the year. *D. pentagyna* and *A. chaplasha*, however, produced fewer and shorter internodes in a year.

Pattern of extension and radial growth of main axis

The duration of extension growth in the case of

Fig. 6 Rythmical changes in internodal length (open bars) and corresponding leaf area (undulating line with open circle amidst the bars) on main axis of *D.sonneratioides* (A), *A. cadamba* (Bo, open-grown and Bf, forest-grown trees), *D. pentagyna* (C), and *A. chaplasha* (Do, open-grown and Df, forest-grown trees).

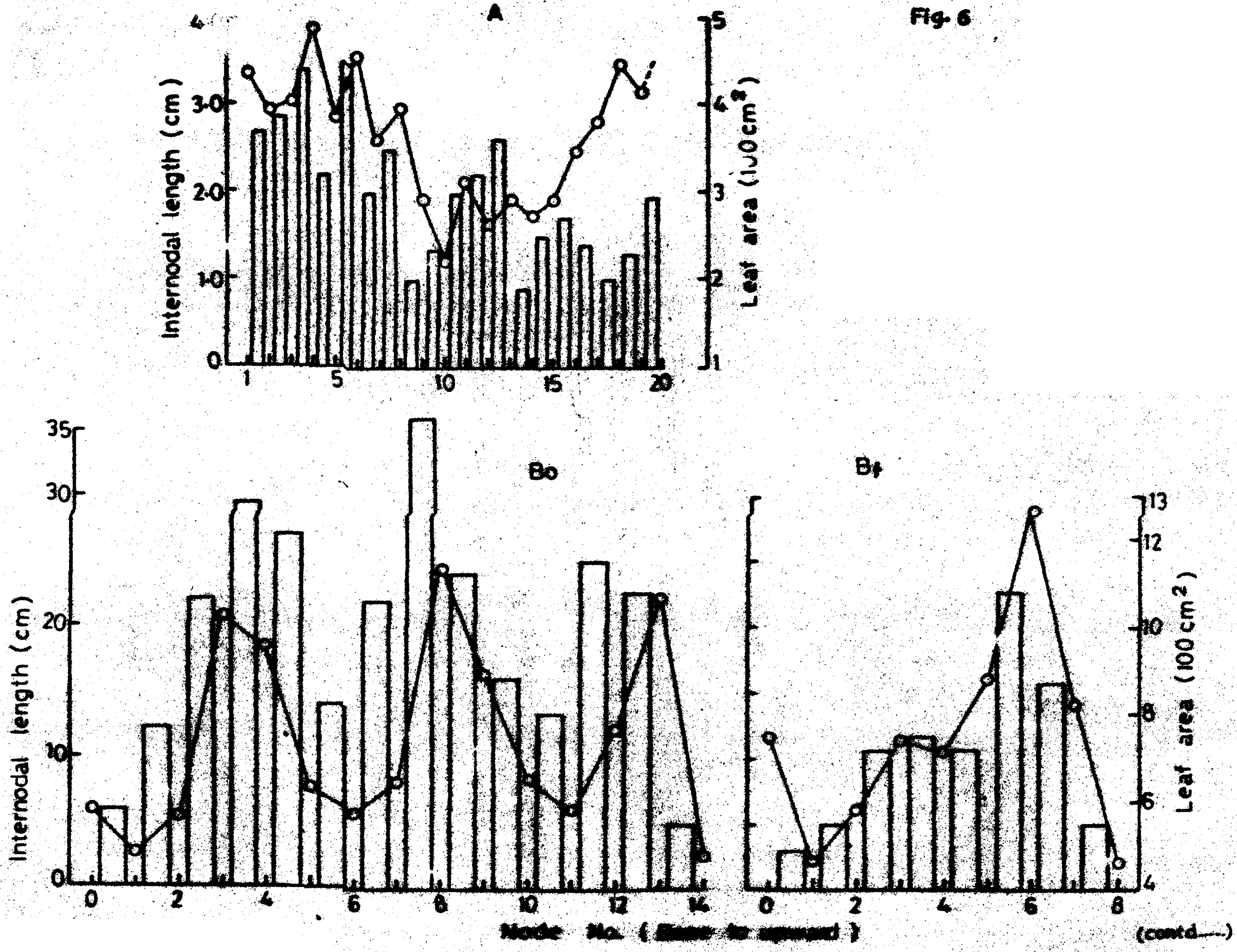
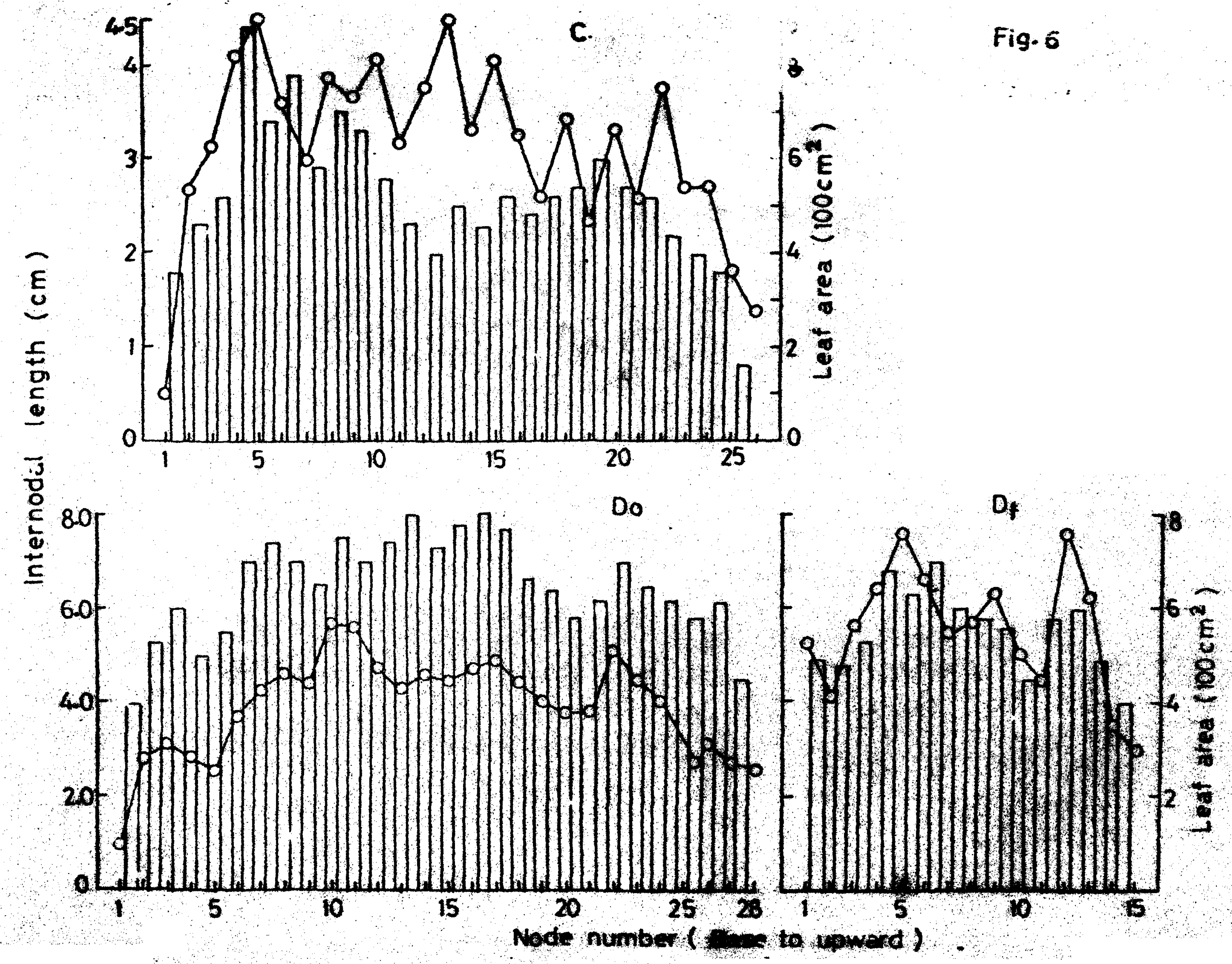

A
Internodal length (cm)
0
1·0
2·0
3·0
4
Leaf area (100 cm²)
1
2
3
4
5
1
5
10
15
20
Bo
Internodal length (cm)
0
10
20
30
35
0
2
4
6
8
10
12
14
B₁
Leaf area (100 cm²)
4
6
8
10
12
13
0
2
4
6
8
Node No. (Base to upward)

Fig. 6

(contd.....)

Fig. 6


C.
Do
Df
Internodal length (cm)
Leaf area (100cm²)
Leaf area (100cm²)
Node number ([illegible] to upward)
0
1
2
3
4
4.5
0
2.0
4.0
6.0
8.0
0
2
4
6
8
1
5
10
15
20
25
28

D. sonneratioides and *A. cadamba* was longer than that for *D. pentagyna* and *A. chaplasha*. The former two showed a number of peaks in growth compared to the other two where only one peak was observed. The forest-grown tree of *A. cadamba* showed decrease in duration of growth period with less conspicuous rythm compared to open-grown trees whereas this decrease in duration of growth in forest-grown *A. chaplasha* was less marked but with two distinct peaks of growth. This was more pronounced in the open-grown trees of *A. cadamba* and *A. chaplasha* than in the forest-grown trees. Further, the decline in cumulative growth in the forest-grown *A. cadamba* was significantly higher than that in *A. chaplasha* so that the cumulative extension growth of these two species were not different in shade (Fig. 7 A,B). *D. sonneratioides* and *A. cadamba* showed more uniform growth during the growth period as compared to the other two species in which the major part of the annual extension growth was completed within few months.

In *D. sonneratioides* and *A. cadamba* radial growth occurred throughout the year but it was slower during winter months. The other two species showed no radial increment during December to March (Fig. 8 A). The peak in radial increment was during August-September for *D. sonneratioides*, July-August for *A. cadamba* and *D. pentagyna* and June-July for *A. chaplasha*. This peak for forest-grown *A. cadamba* and *A. chaplasha* was similar to that in open-grown trees.

Fig. 7 Extension growth of main axis. A, cumulative and B, percentage extension growth; A_1 B_1, open-grown trees and A_2 B_2, forest-grown trees. Open triangle, D. sonneratioides; Open circle, *A.cadamba*; closed triangle, *D. pentagyna*; and closed circle, *A. chaplasha*.

Fig. 7

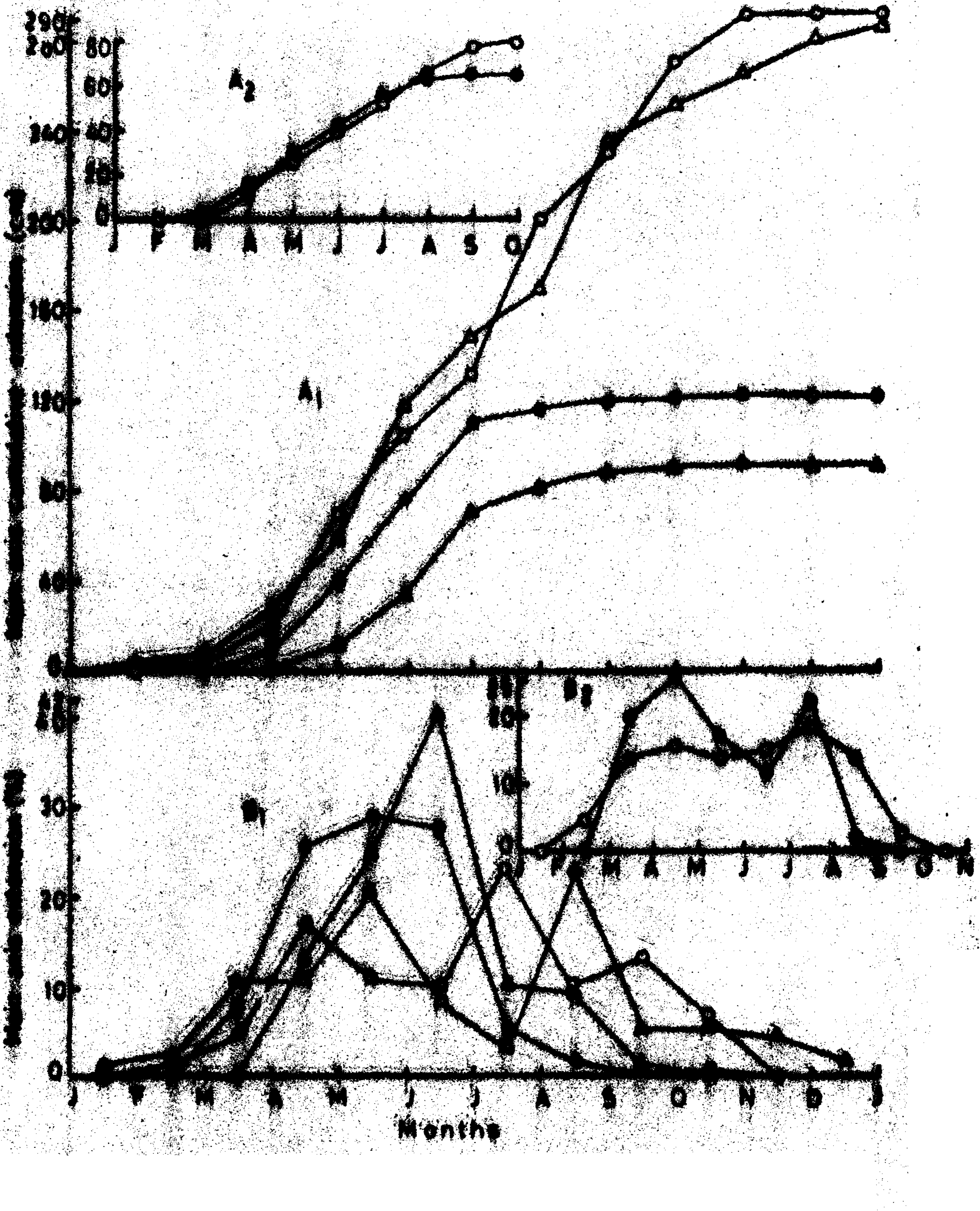
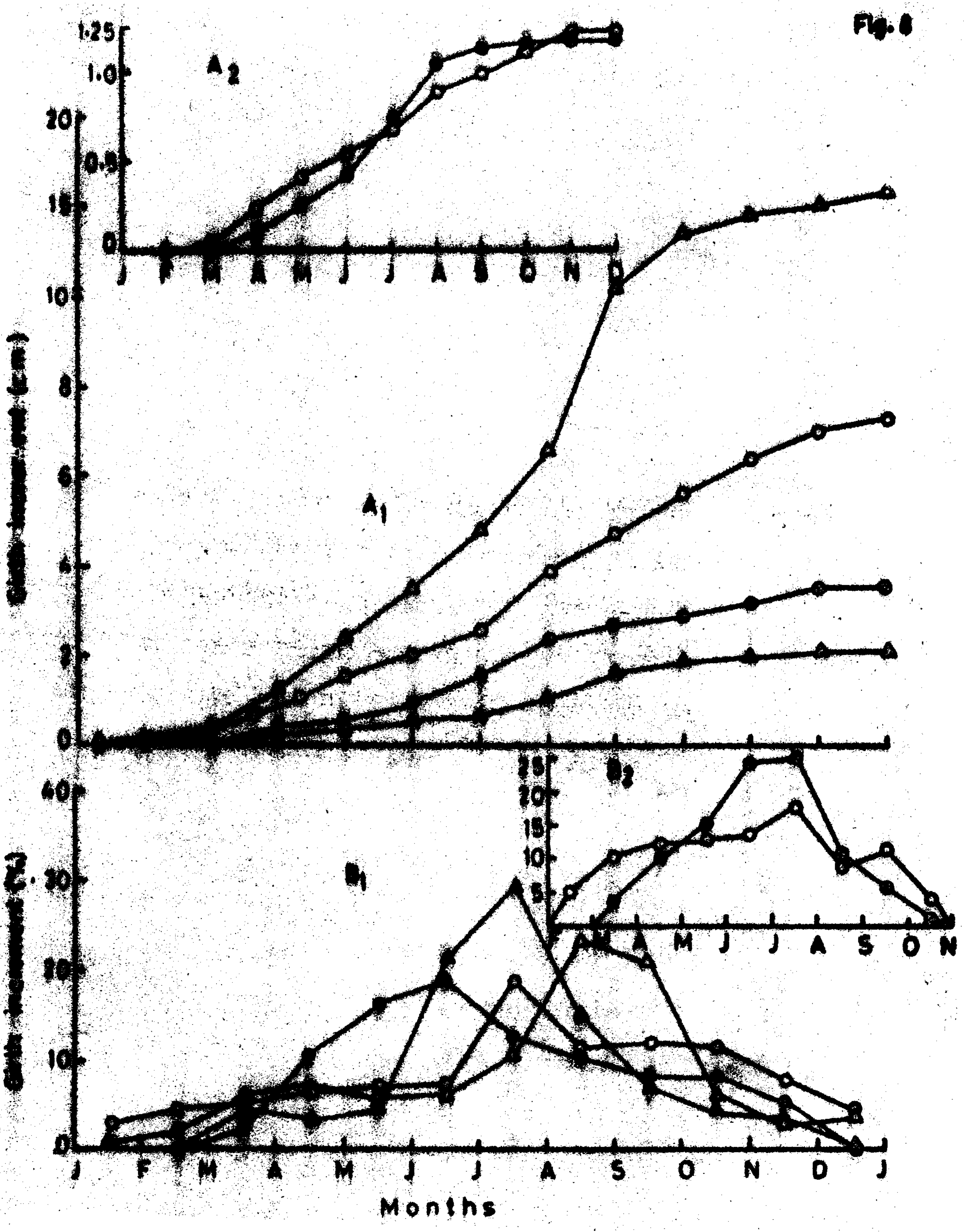

A2
A1
B1
B2
290
200
80
60
40
20
0
240
200
160
120
80
40
0
40
30
20
10
0
30
20
10
0
J F M A M J J A S O
J F M A M J J A S O N D J
J F M A M J J A S O N
Months

Fig. 8 Radial growth of main axis. A, cumulative and B, percentage radial growth. A_1 B_1, open-grown trees, A_2 B_2, forest-grown trees. Open triangle, *D. sonneratioides*; open circle, *A. cadamba*; closed triangle, *D. pentagyna*; and closed circle, *A. chaplasha*.

Fig. 8


A2
1.25
1.0
0.5
0
J F M A M J J A S O N D
A1
0
2
4
6
8
10
15
20
B2
5
10
15
20
25
M A M J J A S O N
B1
0
10
20
30
40
J F M A M J J A S O N D J
Months

However, the forest-grown A. cadamba did not show any radial increment during winter months. The period of radial growth was lesser in forest-grown A. chaplasha in comparison to open-grown one. (Fig. 8 A,B).

Annual extension growth of axis and branches

Table 2 shows the total annual extension growth of the main axis and the I and II order branches of different species. The extension of the main axis was more for D. sonneratioides followed by A. cadamba, A. chaplasha and D. pentagyna in that order. The forest-grown A. cadamba and A. chaplasha both showed lesser extension growth compared to the open-grown ones except for the fact that this difference was less marked for A. chaplasha. The annual extension growth of I order branches was lower than that of the main axis for all the species. The annual extension growth of I order branches of D. sonneratioides and A. cadamba declined sharply from top to bottom of the canopy and this was less pronounced in the other two; The forest-grown trees of A. cadamba and A. chaplasha showed a similar pattern as the open-grown ones except for the lesser extension growth made under the former condition. The II order branches were not present in the top part of the canopy of A. cadamba and D. sonneratioides but those in the middle and bottom part of the canopy made very little growth. The II order branches of D. pentagyna and A. chaplasha also made lesser growth than I order branches.

Table 2. Annual extension growth (cm) of main axis and I and II order branches placed at three different positions of the canopy of four tree species. Values in parenthesis are for forest-grown trees

Order of shoot	D.sonneratioides	A.cadamba	D. pentagyna	A.chaplasha
0 order (Main axis)	298.2±32.24 (-)	286±36.42 (79.5)	102.2±13.68 (-)	123±28.05 (66.5±8.64)
I order				
top canopy	259.4±32.78 (-)	262±24.63 (122±16.04)	35.7±14.01 (-)	104.2±32.60 (74.0±17.82)
middle canopy	174.1±34.26 (-)	208.6±28.36 (86.0±9.43)	31.72±11.53 (-)	86.0±29.64 (48.4±16.42)
bottom canopy	44.4±16.50 (-)	127.4±28.84 (42.4±8.62)	22.2±12.92 (-)	54.62±18.6 (29.0±17.2)
II order				
top canopy	(- (-)	- (-)	6.36±7.02 (-)	43.20±20.24 (27.5±5.89)
middle canopy	53.8±21.64 (-)	34.6±13.24 (-)	6.93±3.34 (-)	65.24±20.80 (47.5±13.13)
bottom canopy	23.0±9.65 (-)	45.2±14.50 (-)	2.3±1.40 (-)	23.7±16.24 (12.8±8.48)

± standard deviation

While in the case of D. pentagyna both middle and top canopy II order branches made more growth than bottom branches, in case of A. chaplasha it was maximum for the middle canopy II order branches only, followed by top and bottom branches.

Branch production and shoot tip abortion

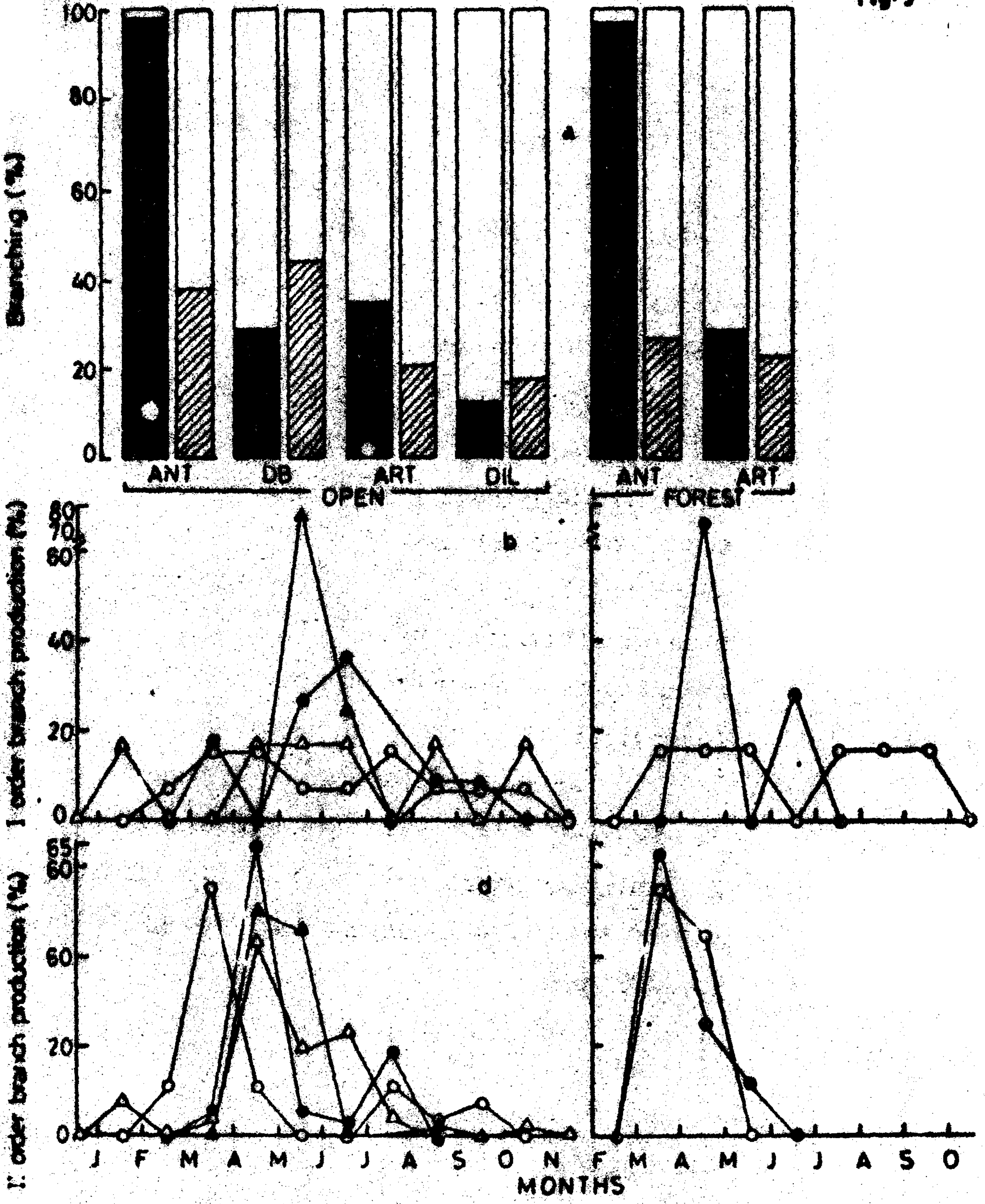
Fig. 9a shows the axillary branch production as a percentage of total axillary buds on the main axis and I order branches of all the 4 species. A. cadamba had maximum number of branch production on the main axis followed by A. chaplasha and D. sonneratioides whereas D. pentagyna had the least number. Branch production on I order branches showed decreasing trend from D. sonneratioides, A. cadamba, A. chaplasha to D. pentagyna. Branch production for forest-grown A. cadamba alone showed difference from the open-grown tree with respect to that on the I order branches.

Fig. 9b, c show the monthly production (% of production out of the total for the year) of I order branches and Fig. 5d, e are for II order branches. The I order branch production in D. sonneratioides and A. cadamba was more or less uniformly distributed throughout the growth period except for rythmicity. The production of I order branches was chiefly restricted to a few months (May-July) in the case of D. pentagyna and A. chaplasha. The forest-grown A. cadamba behaved similarly to its open counterpart but A. chaplasha produced most of its I order branches during

Fig. 9 Branch production. 9a, % of axillary buds producing branches. Closed bar, on main axis; hatched bar, on I order branches. ANT - *A. cadamba*; DB - *D. sonneratioides*; ART - *A. chaplasha*; DIL - *D. pentagyna*; OPEN - open-grown trees; FOREST - forest-grown trees.

9b,c, monthly production (%) of I order branches in open-grown (b) and forest-grown (c) trees. 9d,e, monthly production (%) of II order branches in open-grown (d) and forest-grown (e) trees. Open triangle, *D. sonneratioides*; open circle, *A. cadamba*; closed triangle, *D. pentagyna*; closed circle, *A. chaplasha*.

Fig. 9



100
80
60
40
20
0
Branching (%)
a
ANT
DB
ART
DIL
ANT
ART
OPEN
FOREST
80
70
60
40
20
0
b
I order branch production (%)
65
60
40
20
0
d
II order branch production (%)
J
F
M
A
M
J
J
A
S
O
N
F
M
A
M
J
J
A
S
O
MONTHS

April-May and very few in June-July. The peak for II order branch production was during March-April for A. cadamba and April-May for D. sonneratioides, D. pentagyna and A.chaplasha. However, the forest-grown A. cadamba and A. chaplasha produced most of their II order branches during March-April. While these two species showed only one peak in forest-grown situation, two peaks were observed in open-grown conditions.

The gradual yellowing and blackening of shoot tip of lower I and II order branches of A. cadamba started in July and continued upto September-October. The frequency of shoot tip abortion varied with age (Table 3). It was markedly higher in II order branches than in I order ones with the result that the III order branches were fewer in number. This phenomenon was more severe in shade than in the open.

Branch orientation

The branch angle increased from the top to the base of the canopy in all the species studied and this was more marked for forest-grown trees. In general, D. sonneratioides and A. cadamba had branches with wider angles than D.pentagyna and A. chaplasha. The branches of forest-grown tree of A. cadamba were more obtuse than that of the open-grown ones and this was not evident for D. pentagyna and A. chaplasha. However, the top part of the canopy of a forest-grown tree of these two species showed slightly acute branch angles compared to the open-grown trees of the same two species (Table 4).

Table 3. Shoot tip abortion in A. cadamba (Values = Mean ± Standard deviation)

Age (yr)	I order		II order		III order	
	Total	aborted	total	aborted	total	aborted
1	-	-	-	-	-	-
2	9.5±1.0	0.8±0.74	-	-	-	-
3	17.8±1.70	2.0±0.81	-	-	-	-
4	28.5±1.29	2.3±0.95	25.5±4.40	5.8±1.71	-	-
5	37.0±2.16	3.5±1.30	98.3±11.78	23.5±9.15	1.3±0.63	0.3±0.43
6	38.8±0.96	4.5±1.30	98.0±9.09	30.3±7.14	2.5±1.30	1.0±0.56
7	42.5±3.41	2.8±0.96	97.3±6.90	25.5±8.23	3.3±0.95	1.3±0.63

Note— A 5 year old forest-grown tree showed shoot tip abortion in 7 out of 16 branches.

Table 4. Branch angles (°) of I order branches at three different canopy positions of four tree species growing in the open and under the forest canopy (except for *D. sonneratioides*)

Species	open-grown trees			forest-grown trees		
	top	middle	bottom	top	middle	bottom
D.sonneratioides	72.2±1.45	81.0±1.86	88.6±2.36	-	-	-
A.cadamba	68.2±2.42	81.7±2.2	86,2±1.84	72.4±3.42	86.0±2.34	89.5±1.42
D.pentagyna*	51.0±1.75	53.0±2.14	63.8±3.14	50.6±1.67	52.6±2.31	62.2±3.51
A.chaplasha	55.0±2.65	57.2±2.32	60.4±2.58	54.2±2.04	58.5±3.12	64.6±2.72

*, trees of the sprout-origin were also considered.
± standard deviation.

Branch distribution and bifurcation ratio (Rb)

The values showed in Fig. 10 are the percentage of total number (10a) and total length (10b) of all I order branches falling under different classes of branch length. Most of the I order branches on D. sonneratioides and A. cadamba belonged to higher length classes ranging from 300-400 cm. On the other hand, D. pentagyna and A. chaplasha had most of the branches in length class of 30-150 cm. Thus, the contribution of length to total framework of I order branch system of D. sonneratioides and A. cadamba was exclusively supported by longer branches (20-80 cm)contributed considerably to the total number and total length of the I order branch system.

The pattern for II order branch distribution (Fig. 11a,b) was somewhat similar to that of the I order branch system except that the difference noted above are not so pronounced. More II order branches of higher length classes were present in species like A. chaplasha. The total length of I order branches produced by 5 year old trees of A. cadamba and D. sonneratioides was 3-4 times more than that by D. pentagyna and A. chaplasha of the same age. The relative total length of II order branch produced by D. pentagyna and A. chaplasha in relation to I order branches was more than that by A. cadamba and D. sonneratioides (Table 5).

The bifurcation ratio (Rb) of D. sonneratioides and A. cadamba was significantly higher than that of other two

Fig.10 Distribution of I order branches under different length classes (class 1, 0-10 cm; 2, 10.1-20 cm; 3, 20.1-30 cm and so on). a, % of total number and b, % of total length of branches. Open triangle, *D. sonneratioides*; open circle, *A.cadamba*; closed triangle, *D. pentagyna*; closed circle, *A. chaplasha*.

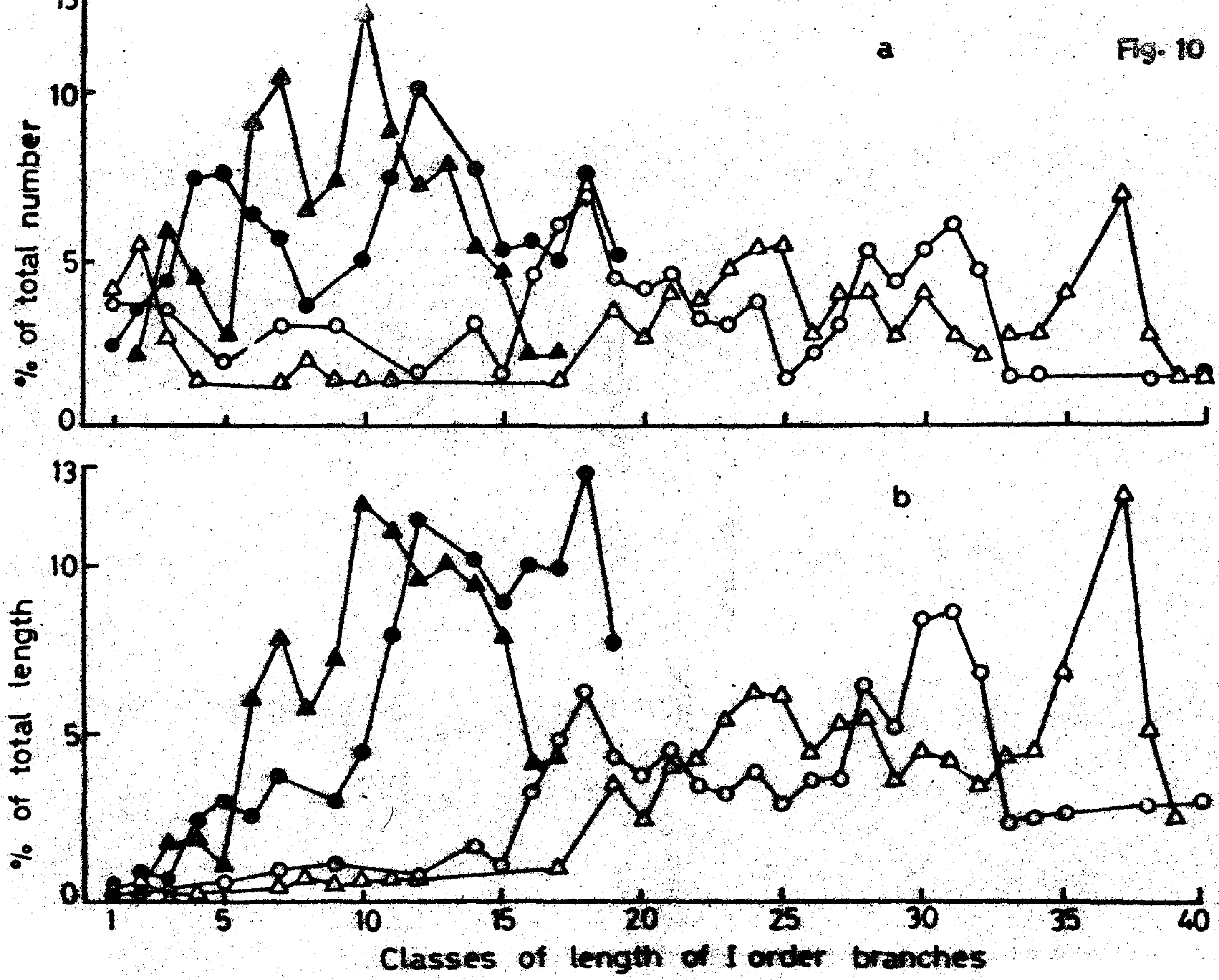

a
b
% of total number
% of total length
0
5
10
13
1
5
10
15
20
25
30
35
40
Classes of length of I order branches

Fig. 10

Fig.11 Distribution of II order branches under different length classes (class 1, 0-10 cm; 2, 10.1-20 cm; 3, 20.1-30 cm and so on). a, % of total number and b, % of total length of branches. Open triangle, *D. sonneratioides*; open circle, *A. cadamba*; closed triangle, *D. pentagyna*; closed circle, *A. chaplasha*.

Fig. 11

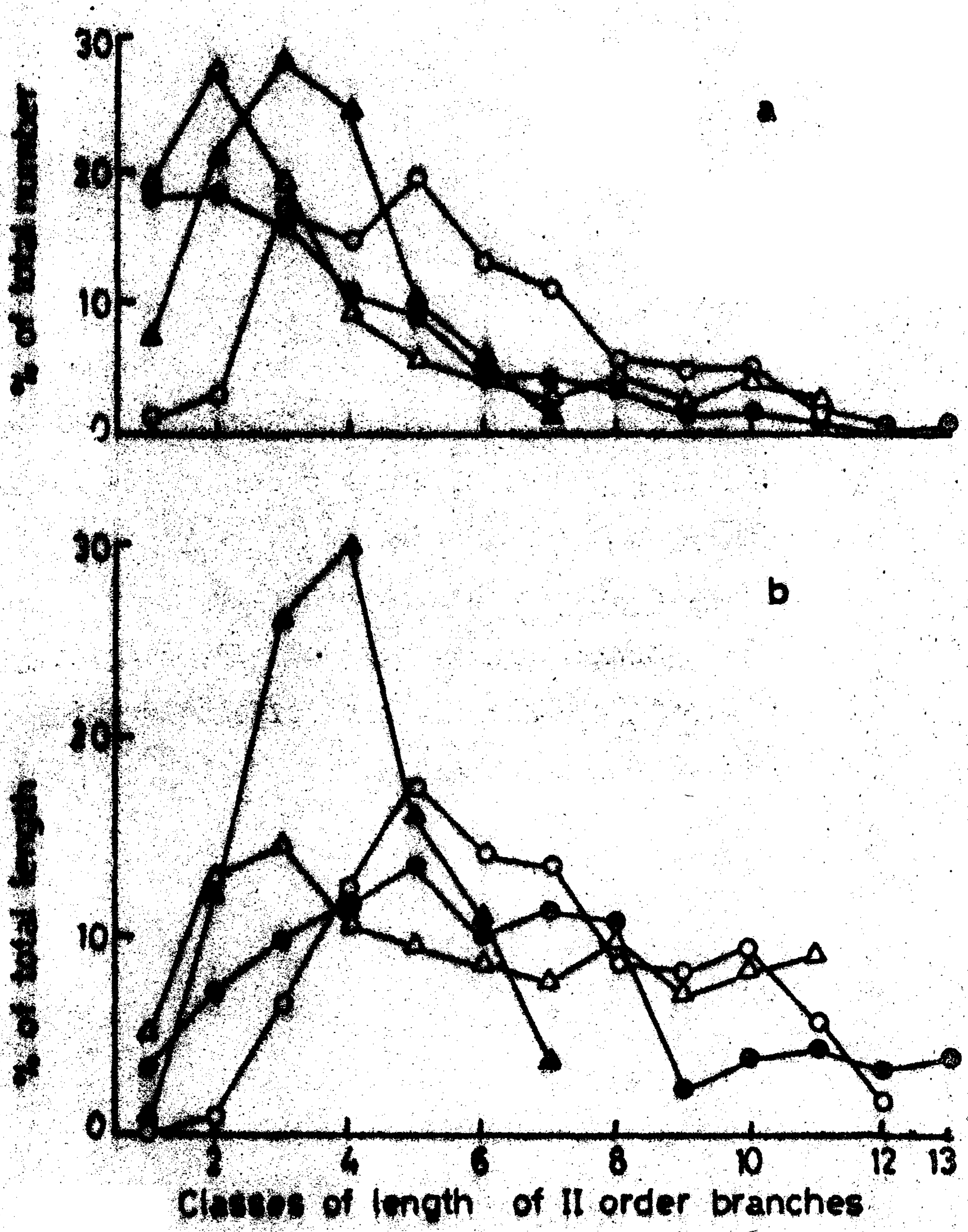

a
b
30
20
10
0
% of total number
% of total length
2
4
6
8
10
12
13
Classes of length of II order branches

Table 5. Contribution of I and II order branches to the total length of branch system of the trees. Values are shown in absolute form as well as in the form of the percentage of the total length of all branch system (The absolute values are the sums of three 5-yr old open-grown tree in each case).

Species	I order		II order		III order		Total length of all branch system (cm)
	Length (cm)	%	length (cm)	%	length (cm)	%	
D.sonneratioides	15017	80.56	3624	19.44	-	-	18641
A. cadamba	13856	69.34	6127.5	30.66	-	-	19983.5
D. pentagyna	3806	52.47	3447	47.53	-	-	7253
A. chaplasha	4324	57.44	3046	38.67	306	9.30	7876

species under open conditions. The forest-grown tree of *A. cadamba* exhibited a very low bifurcation ratio in comparison to its open counterpart. The Rb values for forest-grown *D. pentagyna* and *A. chaplasha* was markedly **lower** than that for the open-grown ones (Table 6).

DISCUSSION

Architecture

The four species viz. *D. sonneratioides*, *A. cadamba*, *D. pentagyna* and *A. chaplasha* studied here, occupy distinct successional niches in the sub-tropical humid forest community in north-eastern India. *D. sonneratioides* and *A. cadamba* are early successional shade-intolerant species also occurring as a gap species in older forests. *D. pentagyna* regenerates chiefly in the open but can tolerate shade after seedling establishment placing itself in the category of a mid-successional species while *A. chaplasha* has the ability to regenerate well in shade and can make adequate growth under the shade cast by a closed canopy placing itself in the category of a typical shade-tolerant late successional species.

The pattern of growth in these four species is in marked contrast to that of temperate woody plants where in both the determinately and indeterminately growing broad-leaved species, the growth is characterised, at least initially, by a determinate flush of leaf production (Kozlowski, 1972).

Table 6. Bifurcation ratio (Rb) for different species growing in the open as well as under the forest canopy (Values = ± Standard deviation).

Species	open-grown trees			t-value	forest-grown trees		
	Rb	range	sample size		Rb	range	sample size
D.sonneratioides	9.27±2.01	6.2-12.02	10	-	-	-	-
A.cadamba	8.71±2.08	5.85-11.4	10	-	3.3	-	1
D.pentagyna*	6.30±0.57	5.05-7.85	10	3.7	5.53±0.78	4.02-6.80	10
A.chaplasha	5.84±0.85	4.20-6.86	10	3.1	4.82±0.62	3.14-5.32	10

*, trees of the sprout-origin were also considered.

Here we find that after bud burst only one leaf/leaf pair is produced at a time in a continuous manner throughout the growth period as also reported in *Rhizophora mangle* (Gill and Tomlinson, 1971), with a constant and low number of embryonic leaves in the bud (Gill, 1971).

The architectural models of trees are mainly based on morphological expression of growth though there are numerous ways in which growth may be expressed in tropical trees (Tomlinson and Gill, 1971). *D. sonneratioides*, though with continuous growth throughout the year, had a morphological rythm in growth pattern with diffuse branching in well separated tiers placing this species in the Massart's model of tree architecture (Halle *et al*, 1978). The general feature of growth of *A. cadamba* is also continuous (except for a rest period during winter dormancy with slight articulation) without any organisation of branches in tiers corresponding to Roux's model. *D. pentagyna* and *A. chaplasha* have all axes orthotropic and equivalent with the same topophysic status (in contrast to the other two species in which the topophysic status for branch and main axis is different). Both these species produce diffused branches in loose tiers and are similar in most of the vegetative growth characteristics. However, the position of flowering ultimately determines the model conformation in these two species. Thus *D. pentagyna* have terminal flowering and conforms to Scarrone's model while A. chaplasha have lateral flowering and conforms to Rauh's model of tree architecture (cf. Halle et al, 1978).

The Roux's and Massart's models which are characterised by plagiotropic branches, provide the individual of D. sonneratioides and A. cadamba a fast growth which is made possible by maximum light interception by leaves, little obscured by one another. While these architectures are well suited for rapid vegetative growth (K-strategy) the small and numerous disseminules in these two species, at the same time ensure their higher reproductive efficiency. D. pentagyna (Scarrone's model) though basically produce orthotropic branches but the lower branches of older trees show plagiotropoid phenomena (cf. Halle et al, 1978). In the case of A. chaplasha, however, orghotropy with repetitive monopodial growth produces the Rauh's model without any plagiotropoid phenomena. Thus the Scarrone's model is more primitive than Rauh's model. The sequence of evolution of architectural model among these species seems to be as Roux's (A. cadamba), Massart's (D. sonneratioides), Scarrone's (D. pentagyna) and Rauh's (A. chaplasha) which fairly conforms to the sequence of successional niches the four species occupy in the forest community.

Growth characteristics

The bud burst in temperate tree species is relatively constant whereas the date of growth cessation is more variable (Kramer, 1943) and this is in contrast to the present situation where the time of bud burst was found to show more variation. Bud-burst in A. cadamba occurring anywhere between late January (winter) to late March (a warmer period) suggests that temperature has lesser controlling influence and that endogenous factors related to age is important. D. sonneratioides having continuous growth throughout the year, all the other three species initiated growth during drier period of January-May and this is in agreement with the earlier observations on most of the tropical tree species (Longman and Jenik, 1974). The rythmicity in growth observed in all the four species seems to be intrinsic as it occurs throughout the year irrespective of climatic changes.

The early successional tree species had extension growth over a longer period compared to late successional species. This could be related to the requirement of early successional species for fast vertical move of the canopy to avoid shading. On the other hand, both the early successional species showed continuous radial growth throughout the year whereas late successional species had cessation in cambial activity for about two months during the winter. Besides, such a cessation of cambial activity was also observed in forest-grown A. cadamba. These observations suggest that extension and radial growth need not always be related to one another (Hummel, 1946) and that this may be a specific character also related to the external environmental influences.

The early successional species, with their synchronous sylleptic I order branch production, seems to achieve quick growth and rapid extension of plagiotropic branches ensuring least overlapping of the leaves, so that they are able to capitalize upon the resources before light becomes limiting factor. Further, the hypopodium of sylleptic branches helps extending the branch to avoid the shade offered by leaves of the parent shoot (White, 1979). The tip damage or heavy shoot tip abortion in the II order branches checking their further growth in the case of early successional species, also seems to be intended to avoid shading of the leaves placed in the interior of the canopy. Further, greater shoot tip abortion of the lower I order branches due to their competitive disadvantage (Kramer, 1958) under low light intensities and their self-pruning helps in moving the canopy of the early successionals to greater heights. This is further supported by the greater emphasis placed by the early successional species on I order branch extension over the II order system, so that an excurrent crown form is attained. On the other hand, the production of proleptic I and II order branches, in late successional species, over a brief period of time with greater emphasis being placed on production and extension of II order branches, helps in developing broader tree crown where the leaves are placed more peripherally so that they are able to maximize photosynthesis under the shade of forest canopy.

The early successional species exhibited longer and comparatively less forked axes leading to the more open canopies (Multilayer; Horn, 1971) whereas late successional species produced more frequent and forked stem leading to a denser peripheral arrangement of leaves (Monolayer; Horn,1971). Whitney (1976) observed the same thing and according to him the leaf arrangement and branching pattern are specific for a tree species. However, the lower bifurcation ratio of forest-grown individuals in comparison to that of open-grown ones, is consistent with the contention of Steingraeber et al (1979) that trees may show plastic response in forking of branches under different light conditions to arrange their leaves for maximum light interception.

Besides other characteristics, the overall geometry of a living tree is a manifestation of its adaptive strategy and depends upon branch orientation. The angles and orientation of branches result in maximum effective leaf surface possible for a branch system (Honda and Fisher, 1978; Fisher, 1979). The fast increase in I order branch angle down the tree in early successional species results in greater increase in gap between two successive plagiotropic I order branch complexes from their base to the tip. In late successional species also there is an increase in I order branch angle from top to the base of the canopy but the orthotropic nature of the trees does not affect the gap size and the leaves are pushed to the periphery of the crown due to exclusively developed II order branch system.

In conclusion it may be pointed out that early successional species like *D. sonneratioides* and *A. cadamba* show exploitive strategy where the aim is to maximize vertical growth over a short period of time when light is not a limiting factor whereas late successional species like *D. pentagyna* and *A. chaplasha* have conservative strategy where the aim is to make growth, though slowly, even under shaded situations in a late successional community and survive till such a time they are able to make more rapid growth either through gap formation or after gradual emergence over the general canopy of the forest.

SUMMARY

The study deals with the pattern of architecture, extension growth and branch display of two early successional (*Duabanga sonneratioides* Ham. and *Anthocephalus cadamba* Miq.) and two late successional (*Dillenia pentagyna* Roxb. and *Artocarpus chaplasha* Roxb.) species. While the early successional species showed heterogeneous axes (trunk orthotropic and branches plagiotropic) and conform to Massarts's model (*D. sonneratioides*) or Roux's model (*A. cadamba*), the late

successional species showed homogeneous axes (all axes orthotropic) and conform to Scarrone's model (*D. pentagyna*) or Rauh's model (*A. chaplasha*) of tree architecture. The extension and radial growth of axes of early successional species were very rapid and more in comparison to those of late successional species. The sparse branch arrangement facilitating leaf exposure to a greater degree and longer growth period of early successional species accounted for the faster growth. On the other hand, late successional species showed shorter growth period and densely packed canopies with mutual shading of leaves which accounts for their slower growth rate. In the early successional species production and contribution of I order branches to the total framework of branch system was much higher than that in late successional species. Plasticity in orientation and overall display of branches in relation to light intensity was noted in these species. The significance of these results are discussed in relation to the niche occupancy of these species.

Plate 1

Plate 2

A

B

Plate 3

SHOOT TIP ABORTION IN PROXIMAL
SEC. & TERT. BRANCHES OF *A. cadamba*

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CHAPTER - II

****

LEAF DYNAMICS

INTRODUCTION

Growth, expressed as dry matter accumulation, depends on the size of total leaf area on the plant (Watson, 1956; Matthews, 1963; Newhouse and Madgwick, 1968) which is determined mainly by the pattern of production, fall and longevity of leaves. Seasonal variation in leaf size may also affect the total photosynthetic area (Smith and Nobel, 1977). Several studies on leaf expansion of temperate angiosperm trees are available (Busgen and Munch, 1931; Mounts, 1932; Kozlowski and Clausen, 1966) and they suggest variations based on the type of shoot and the environment to which they are exposed (Kozlowski, 1971).

Very little is known on the leaf dynamics of tropical tree species. While temperate angiosperm trees shed their leaves characteristically during autumn (Kramer and Kozlowski, 1960), tropical trees may differ widely in this regard showing a variety of pattern for production, longevity and fall (Holttum, 1940; Beard, 1946; Alvim, 1964; Longman and Jenik, 1974). Apart from this, leaf dynamics of trees over a successional gradient may also vary, as temperature and light regimes have been implicated for differences in the pattern (Roberts, 1920; Addicott and Lyon, 1973), though little has been done to examine this aspect of problem.

The present study is, therefore, intended to analyse quantitatively the leaf dynamics in four tree species occupying different successional status in a sub-tropical humid forest. Of these, *Duabanga sonneratioides* Ham. and *Anthocephalus cadamba* Miq. are two light demanding early successional species while *Dillenia pentagyna* Roxb. and *Artocarpus chaplasha* Roxb. are two shade-tolerant late successional species at lower elevations of Meghalaya in north-eastern India.

METHODS OF STUDY

Individuals of *D. sonneratioides*, *A. cadamba*, *D. pentagyna* and *A. chaplasha*, considered for studies on the architecture and extension growth (Chapter I) were used for present study also. The already present and the new leaves coming up on open-grown individuals of all the four species and the forest-grown individuals of *A. cadamba* and *A. chaplasha* were tagged by metallic labels. Detailed observations on emergence, fall and leaf area were maintained for individual leaves. Leaf area was calculated on the basis of correlation factor developed between blade length x breadth and leaf area. In the case of *D. sonneratioides*, *A. cadamba* and *D. pentagyna* the leaf area calculations were done on the basis of one correlation factor developed for each species separately, considering 50 mature leaves of different sizes. In the case of *A. chaplasha*, since the tree had leaves of different shapes (Chapter III), four different correlation factors had to be developed on the basis of 50 leaves in each case in order to account for these differences.

Plastochron lengths (days) were derived on the basis of total number of leaves produced per month (Gill and Tomlinson, 1971). It represented the time interval between the emergence of two successive leaves emerging in different months of the growth period. The higher the leaf number per month, the lower was the plastochron length and vice versa. Only the main axis and I order branches (current year's and last year's) were considered for this study. Since the rate of leaf production was very slow in forest-grown trees of *A. cadamba* and *A. chaplasha*, the average plastochron length for these individuals and their open counterparts (for comparison) was derived by dividing the total growth period of axis by the total number of leaves produced on that axis.

Ten one-year old top I order branches of each species growing in the open were harvested in November. The total leaf area of leaves on the branches were computed on the basis of correlation factors. Dry weight of leaves and branches were obtained after drying them at 80±2°C to constant weight. These data were used to calculate the pattern of resource use between leaves and their supporting branches in different species.

RESULTS

The pattern of variation in total leaf area during the year, given in Fig. 1, shows that the early successional species differ from the late successional ones. The open-grown early successional species, in general, had higher leaf area than open-grown late successional species with D. sonneratioides having maximum leaf area. The early successional species never became naked during the year and bore some leaves even during the peak leaf fall period of February-April. The late successional species were deciduous becoming totally naked in March (D. pentagyna) or April (A. chaplasha). However, the forest-grown A. chaplasha retained a few old leaves during April also. In general, forest-grown trees had lesser leaf area compared to open-grown ones. The leaf area of A.cadamba was more adversely affected under forest conditions than that of A. chaplasha.

The monthly leaf production, as a percentage of total numer of leaves produced in a year, is shown in Fig. 2. The open-grown trees differed markedly in leaf production on the different axes, viz., main axis, I order and II order branches. Though all the four (open-grown) species showed fluctuations in leaf production in different months, the early successional species showed lesser monthly variations while the late successionals showed a major peaking during April-June in the case of main axis and I order branches.

Fig. 1 The monthly pattern of change in total leaf area on early successional (open symbols) and late successional (closed symbols) species. Open triangle, *D. sonneratioides*; open circle, *A. cadamba*; closed triangle, *D. pentagyna*; and closed circle, *A. chaplasha*. Continuous line, open-grown individuals; and broken line, forest-grown individuals.

Fig. 1

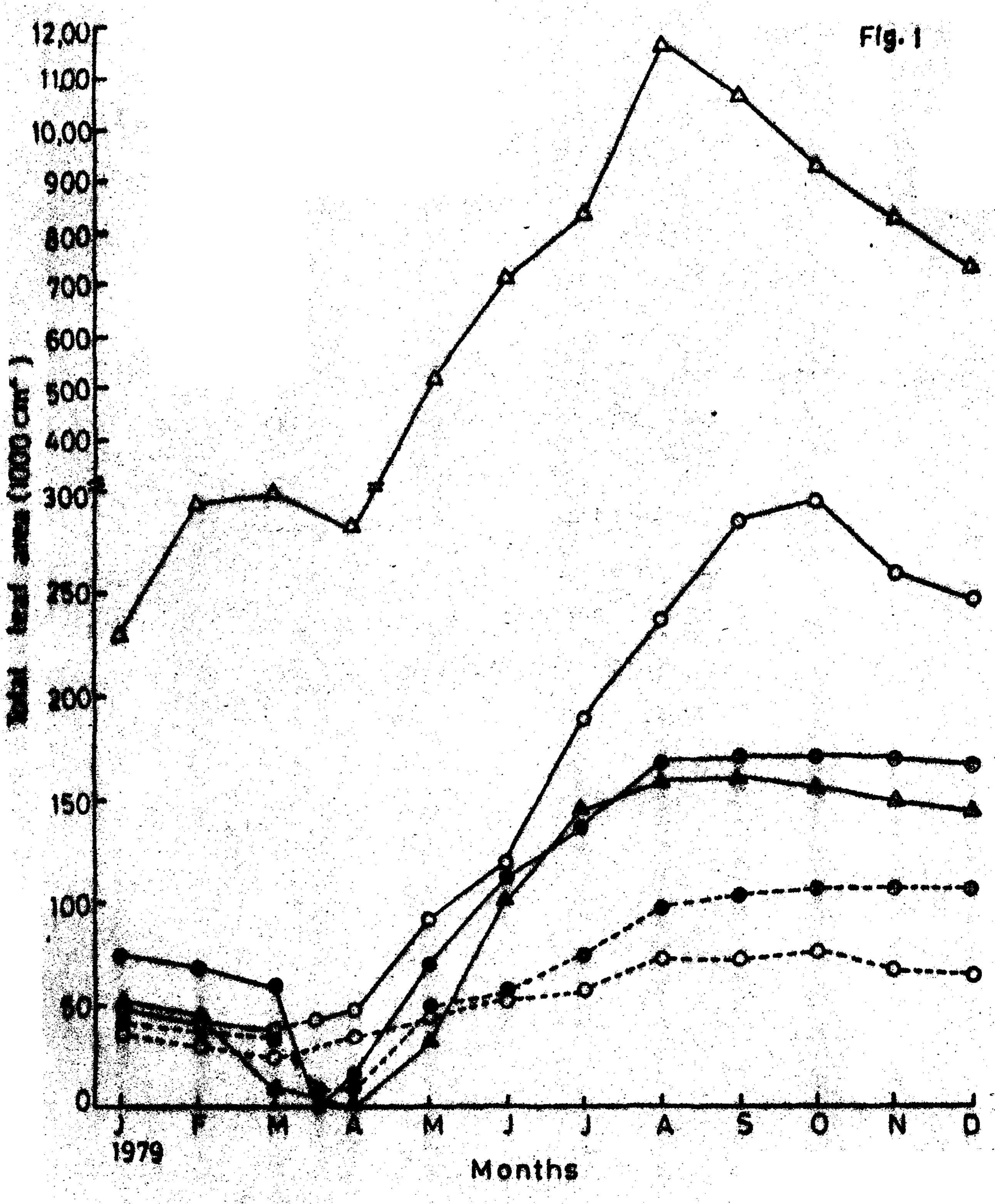
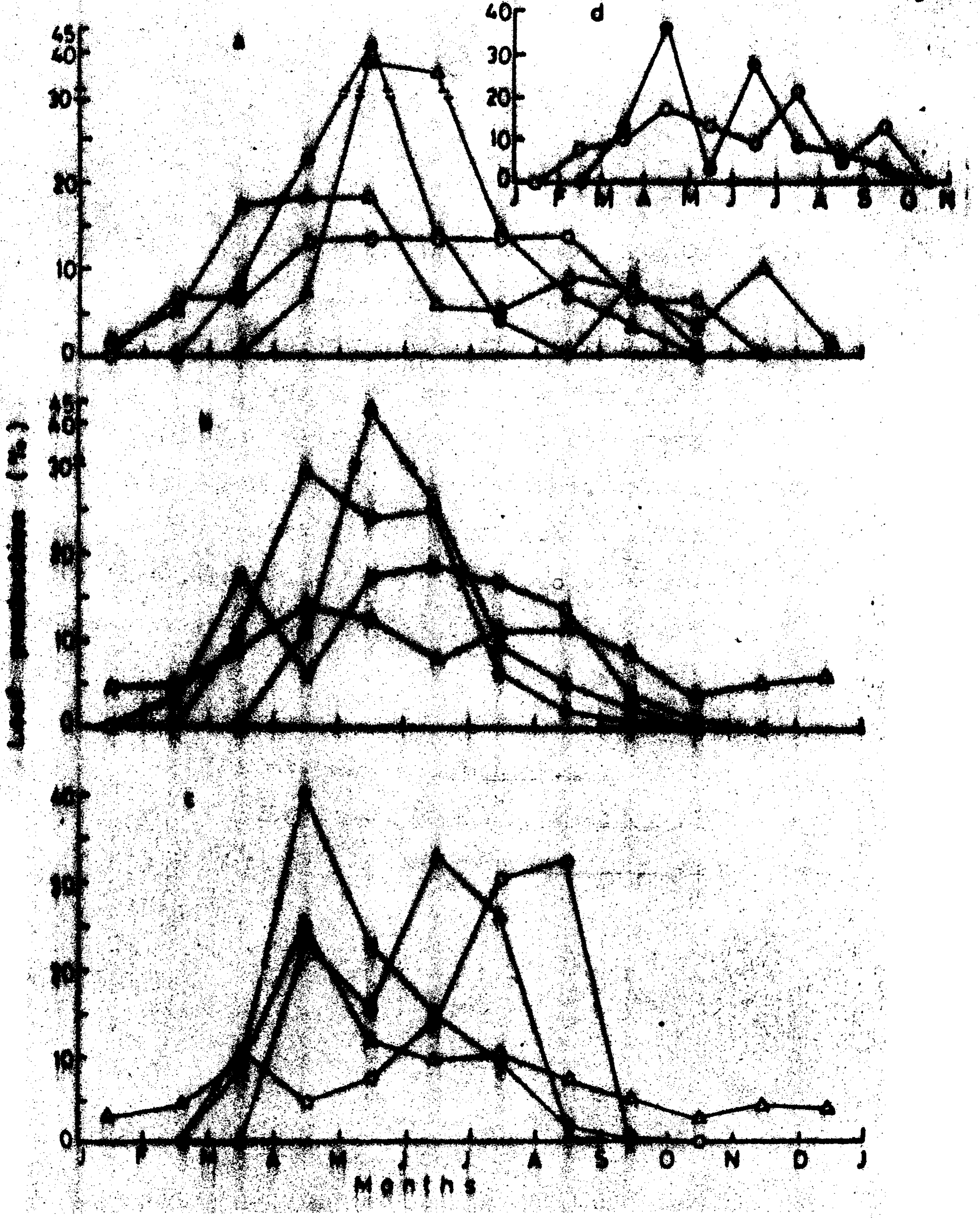

Total leaf area (1000 cm²)
12,00
11,00
10,00
900
800
700
600
500
400
300
250
200
150
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D
1979
Months

Fig. 2 The pattern of leaf production in early successional (open symbols) and late successional (closed symbols) species in different months of the growth period, expressed as the percentages of total leaves produced in a year on main axis (2a), I order (2b) and II order (2c) branches of open-grown individuals. The inset figure (2d) is for the forest-grown individuals.

Open triangle, *D. sonneratioides*; open circle, *A. cadamba*; closed triangle, *D. pentagyna*; and closed circle, *A. chaplasha*.

Fig. 2



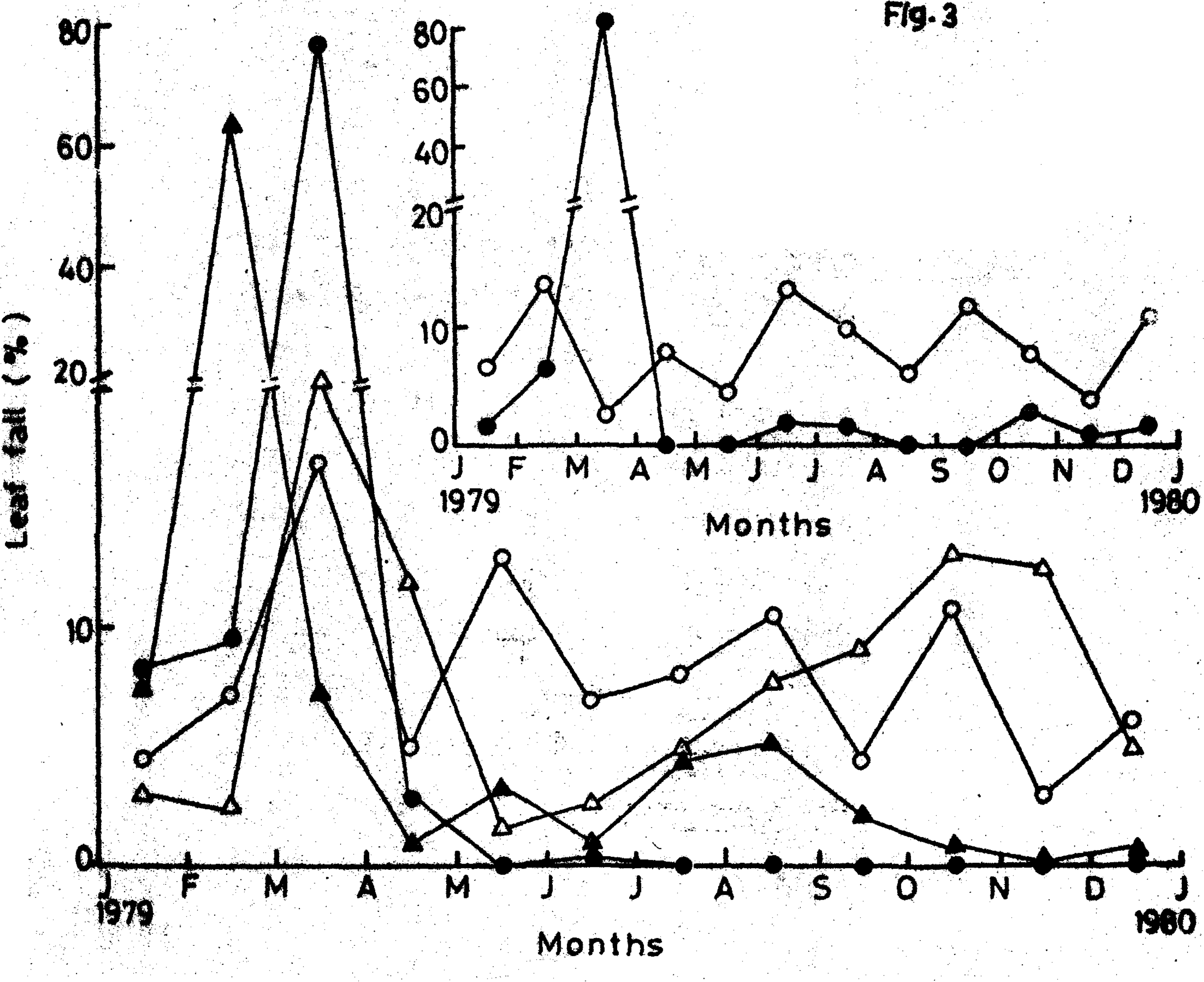
In the case of II order branches, the early successional species showed a major peaking in April-May for D. sonneratioides and in July-August for A. cadamba. The pattern of leaf production for the II order branches of late successional species was not very different from that observed on the I order branches of the same. Further, on the II order branches of A. cadamba leaf production started a month later than that on the I order branches. In all the species leaf production stopped during the dry months of November-March except in the case of D. sonneratioides where leaf production continued throughout, though with low percentage during the winter months. The inset figure shows the leaf production pattern in the forest-grown A. cadamba and A. chaplasha. The rate of production was slower under forest conditions with a number of small peaks during the growth period.

The leaf fall pattern in the different branch orders was not different from each other. Leaf fall in all the open-grown individuals was maximum during March-April followed by a sharp decline in subsequent months. However, this pattern was more pronounced in the late successional species while in the early successional ones, the leaf fall was more uniformly distributed throughout the year (Fig. 3). The leaf fall pattern in the forest-grown trees of A. cadamba and A. chaplasha also showed that this peaking pattern was obvious only in the latter species.

Fig. 3 The pattern of leaf fall in different months of the year expressed as the percentages 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 and under forest (inset figure) conditions.

Open triangle, *D. sonneratioides*; open circle, *A. cadamba*; closed triangle, *D. pentagyna*; and closed circle, *A. chaplasha*.

Fig. 3



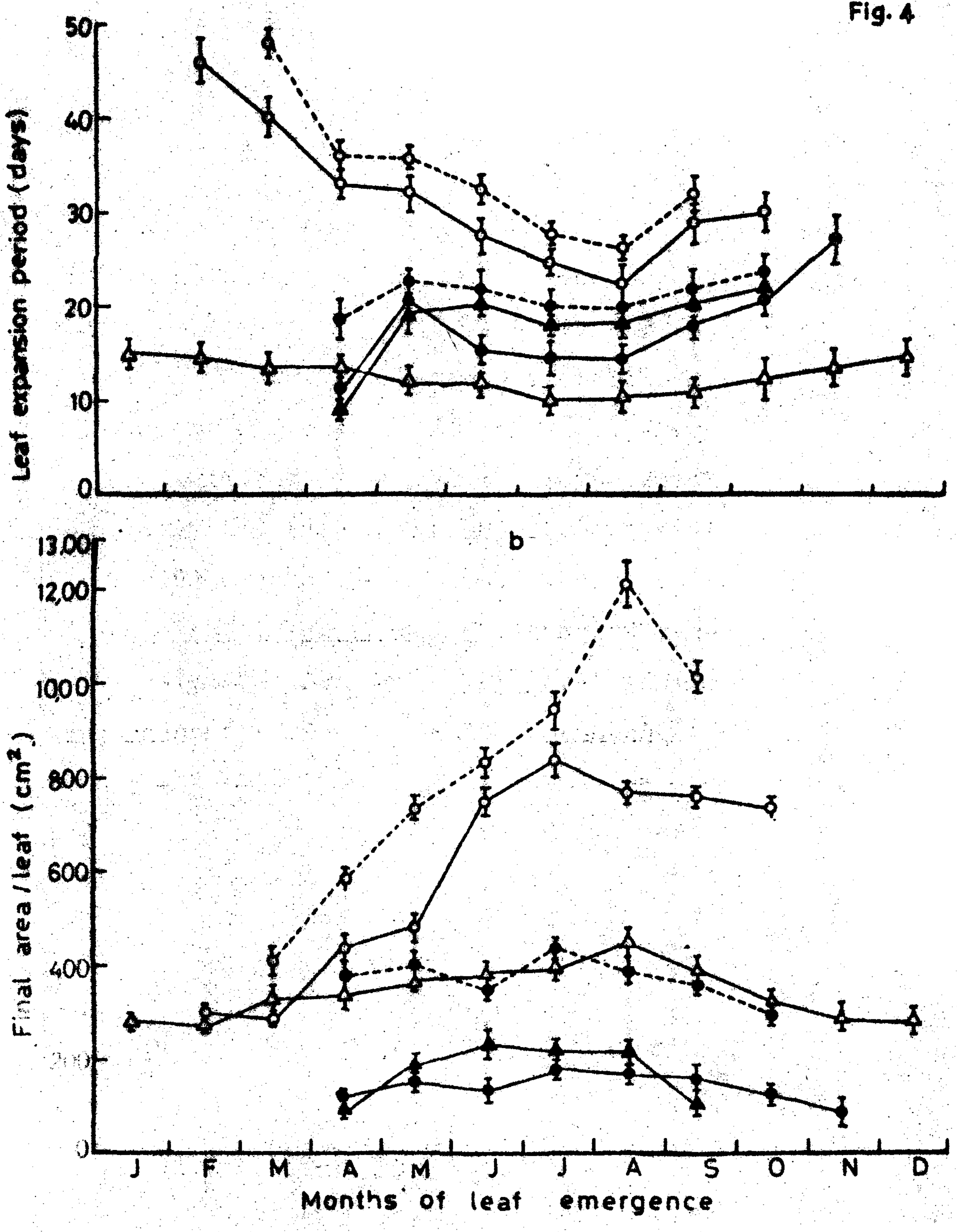
Since the pattern of change in leaf expansion period and final leaf area for the leaves emerging in different months of the growth period, was not very different for the different orders of branches, that for the I order branches alone is presented here. Leaf expansion period was the briefest for the leaves produced during July-August in case of all the species, irrespective of light conditions. On either side, the time taken tended to increase gradually. Expansion period, in general, was maximum for *A. cadamba* where again forest-grown tree took more time than open-grown ones. The open-grown and forest-grown trees of *A. chaplasha* followed a similar pattern as that of *A. cadamba*. Expansion period was minimum for the leaves of *D. sonneratioides* which also showed lesser monthly variations (Fig. 4a).

The final leaf area attained by the leaves produced in different months showed a pattern different from that of expansion period mentioned above. Maximum area was attained by the leaves produced in July-August with decline on either side. Forest-grown trees of *A. cadamba* and *A. chaplasha* had larger leaf size compared to open-grown trees of the same species (Fig. 4b).

The longevity of the leaves produced during different months of the year on the early successional species was generally shorter than those produced on the late successional ones. The leaves produced on the main

Fig. 4 The pattern of change in expansion period (a) and final area (b) of leaves emerging in different months. Continuous lines, open-grown individuals and broken lines, forest-grown individuals of early successional (open symbols) and late successional (closed cymbols) species. Open triangle, D. *sonneratioides*; open circle, A. *cadamba*; closed triangle, D. *pentagyna*; closed circle, A. *chaplasha*.

Fig. 4


Leaf expansion period (days)
50
40
30
20
10
0
b
13,00
12,00
10,00
800
600
400
200
0
Final area / leaf (cm²)
J
F
M
A
M
J
J
A
S
O
N
D
Months of leaf emergence

axis showed significantly shorter longevity than those produced on the I order branches of early successional species in both the light conditions. In the case of D. sonneratioides, the longevity was more or less the same throughout the year except for the leaves produced in March-April where it was shorter. In A. cadamba, the maximum longevity was observed for the leaves produced in May-July with decline on either side. The longevity of leaves of the forest-grown A. cadamba was more and was not significantly different in different months. Starting from May, the late successional species showed decline in longevity of leaves produced in different months with minimum for leaves of October-November. The April-born leaves of these species had shorter life-spans (Fig.5).

Table 1 shows the frequency of leaf emergence in different months of the growth period for all the four open-grown species at three different positions of the tree. In a given month the plastochron was least for the main axis and increased from top to the base of the canopy in the case of early successional species. However, such a clear pattern was not observed in late successional species, where the plastochron at different canopy positions changed in different months. The plastochron for the two early successional species tended to be minimum during July-August. In the case of late successional species, plastochron was generally longer during the latter part of the growth period

Fig. 5 Changes in longevity of leaves according to the month of their emergence on main axis (hatched bars) and I order branches (open bars) *D. sonneratioides*, 5A; *A. cadamba*, 5B (Bo, open-grown and Bf, gorest-grown individuals); *D, pentagyna*, 5C; and *A. chaplasha*, 5D (Do, open-grown and Df, forest-grown individuals).

Fig. 5

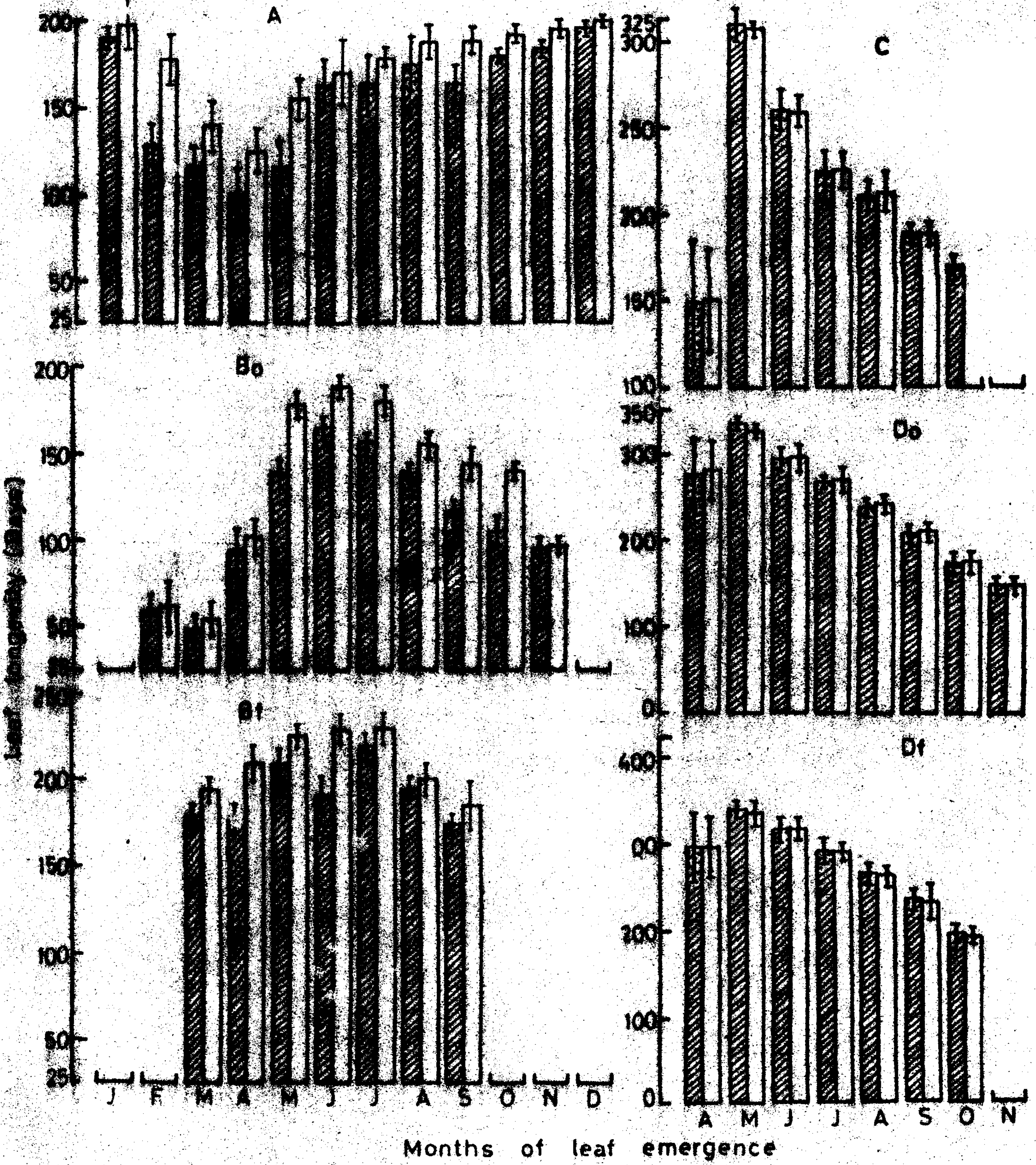

A
Bo
Bf
C
Do
Df
200
150
100
50
25
325
300
250
350
400
0
J
F
M
A
M
J
J
A
S
O
N
D
A
M
J
J
A
S
O
N
Months of leaf emergence
Leaf longevity (days)

Table 1. Plastochron intervals (in days) of different tree species growing in the open.

Species	position	Jan	F	M	A	M	J	J	A	S	O	N	D
Duabanga sonneratioides	main axis	6.2	3.5	2.8	3.3	2.3	1.9	2.8	2.2	3.3	3.4	6.0	7.8
	upper brs.	8.6 ±1.5	7.8 ±1.4	5.5 ±0.6	4.8 ±0.3	4.5 ±0.6	4.0 ±0.2	3.3 ±0.2	3.7 ±0.3	4.5 ±0.4	5.5 ±0.6	10.7 ±3.7	12.1 ±2.9
	lower brs.	13.8 ±3.0	8.6 ±1.4	6.7 ±0.9	5.7 ±0.6	7.8 ±0.7	6.5 ±0.9	4.9 ±0.4	5.9 ±0.6	6.2 ±1.3	8.6 ±1.5	11.7 ±2.9	13.8 ±3.0
Anthocephalus cadamba	main axis	-	-	23.0	16.0	17.0	19.0	11.0	13.0	20.0	24.0	28.0	-
	upper brs.	-	-	23.3 ±0.5	16.5 ±0.6	16.8 ±0.9	18.5 ±0.6	11.0 ±0.8	15.0 ±0.8	21.8 ±0.5	27.8 ±0.5	28.5 ±0.6	-
	lower brs.	-	-	28.0 ±0.8	15.5 ±1.3	18.0 ±1.4	17.0 ±0.8	12.0 ±0.8	15.8 ±0.5	21.0 ±0.8	-	-	-
Dillenia pentagyna	main axis	-	-	-	-	4.4	6.0	5.2	4.4	15.0	31.0	-	-
	upper brs.	-	-	-	-	4.7 ±0.4	5.3 ±0.6	4.7 ±0.4	8.1 ±2.1	30.0 ±0	-	-	-
	lower brs.	-	-	-	-	3.6 ±0.3	4.8 ±0.3	4.6 ±0.3	8.6 ±1.5	30.0 ±0	-	-	-
Artocarpus chaplasha	main axis	-	-	-	3.8	3.9	5.0	6.2	15.5	15.0	15.5	-	-
	upper brs.	-	-	-	3.3 ±0.4	9.5 ±1.5	4.8 ±0.4	4.7 ±1.9	20.7 ±9.0	20.0 ±8.7	31.0 ±0	-	-
	lower brs.	-	-	-	3.0 ±0.4	8.6 ±1.5	5.1 ±0.9	5.9 ±0.6	13.8 ±3.0	20.0 ±8.7	-	-	-

± standard error.

compared to the earlier part of the growing season.

A comparison of average plastochron for *A. cadamba* and *A. chaplasha* showed that the forest-grown trees of both the species had longer plastochron than that for open-grown trees at all canopy position (Table 2).

Table 3 presents the leaf area and leaf dry weight in relation to the weight of the branches bearing these leaves for open-grown trees only. This ratio was markedly higher for the two early successional species compared to the two late successional ones.

DISCUSSION

Since no sharp line can be drawn between evergreen and deciduous species of the tropics (Holttum, 1940; Koriba, 1958), Longman and Jenik (1974) recognised four distinct pattern of leafiness on the basis of relative timing of bud-break and leaf abscission. While the two early successional species, studied here, belong to continuous growth-evergreen type (*D. sonneratioides*) or periodic growth-leaf exchanging type (*A. cadamba*), both the late successional species were strictly periodic growth-deciduous type. Such a pattern of leaf presence throughout the year may have advantage to the early successional species for achieving faster growth rate, so characteristic of them.

Table 2. Average plastochron interval (in days) of two different species growing in the open as well as under the shade.

Species	light condition	main axis	upper branches	lower branches
Anthocephalus cadamba	open	19.00	19.44 ± 0.58	18.20 ± 1.40
	shade	30.86	34.06 ± 1.79	45.50 ± 2.06
Artocarpus chaplasha	open	9.26	13.41 ± 1.48	9.39 ± 0.85
	shade	13.07	19.78 ± 2.13	27.96 ± 1.40

± standard error

Table 3. Relation between source (leaf) and immediate sink (branch) of different species as 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	118.6 ± 21.60	1.22 ± 0.08

± standard error

Further, the seasonal leaf fall pattern may be related to the relative dryness of the season (Longman and Jenik, 1974) as maximum leaf fall in all these species occurred during March-April, which may help in tiding over stress conditions.

The leaf expansion was more rapid during the warmer part of the year when water availability was also maximum. Further, during this period, maximum leaf size was also attained by all the species. Similar results were obtained by other workers too (Roberts,1920; Kozlowski and Clausen, 1960).

The forest-grown early successional species had a lesser turnover of leaves compared to the open-grown ones indicating their shade intolerance (Newhouse and Madgwick, 1968). The faster growth rate of A. chaplasha compared to A. cadamba under forest conditions, further supports such a strategy where late successional species are more shade-tolerant.

The shorter life-span or longevity of leaves in ealy successional species, is of the adaptive importance for these species. It is well known that as the leaf ages, its photosynthetic efficiency decreases (Mooney, 1972; Johnson and Tieszen, 1976) which is partly physiological and partly related to the colonization of the leaf surface by epiphylls (Bentley, 1979). Thus a shorter life-span and a high turnover rate for the leaves of early successional species favour their exploitive strategy for faster growth and for the fast vertical move of the canopy to display their leaves always in a favourable light environment.

The dynamics of leaf area and production pattern of early and late successional species indicate the strategy that enable them to adapt to their ecological niche in the forest community. The early successional species, through their extended period of leaf production, are able to produce a large photosynthetic area to exploit effectively the temporary conditions of resource availability in disturbed sites (Marks and Bormann, 1972). According to Coombe and Hadfield (1962) the rapid growth of early successional species lies in their capacity for unrestricted leaf production rather than in the efficiency of energy conversion. The slower rate of leaf production of late successional species, on the other hand, may be related to their generally lower resource demand (Bazzaz, 1979; Grime, 1979).

On the basis of source-sink concept (Watson, 1956), Montenegro _et al_ (1979) worked out the ecological strategies of few shrub species considering leaf as the source and the branches as the immediate sink. As seen from the present study the early successional species tend to allocate more to the leaves than to the branches on which they are borne as compared to late successional species. This is in agreement with the exploitive strategy of early successional species discussed above.

SUMMARY

Leaf dynamics of two early successional (*Duabanga sonneratioides* Ham. and *Anthocephalus cadamba* Miq.) and two late successional (*Dillenia pentagyna* Roxb. and *Artocarpus chaplasha* Roxb.) species of a sub-tropical humid forest at Lailad has been studied here. The early successional species showed higher leaf turnover rates, reduced leaf longevity, more uniform production and fall of leaves with some fluctuation during the year and evergreen or leaf-exchanging pattern of leafiness. On the other hand, the late successional species had slower leaf turnover rates, greater leaf longevity, major peaking in leaf production and fall with deciduous habit. The leaf production pattern of forest-grown early successional *A. cadamba* was more adversely affected than that of late successional *A. chaplasha*. It is concluded that these differences in the leaf dynamics of early and late successional species are related to the successional niches they occupy in the forest community.

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CHAPTER - III

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THE NATURE AND ECOLOGICAL SIGNIFICANCE OF HETEROPHYLLY IN ARTOCARPUS CHAPLASHA ROXB.

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 and Sinnott, 1916; Brown, 1919; Ryder, 1954; Cain et al. 1956; Talbert and Holch, 1957; Jackson, 1967; and Gentry, 1969). Leaf shape variation in a single individual may be a direct consequence of morphogenetic effects of light (Heslop-Harrison, 1964) and/or other factors of the physical environment during their ontogeny (Piersall and Hanby, 1926; Milithorpe, 1959; Milthorpe and Newton, 1963; and Givnish and Vermeij, 1976). However, many plant species may have the intrinsic ability to produce different sizes and shapes of leaves in different micro-environments (Parkhurst and Loucks, 1972). *Artocarpus chaplasha* Roxb., a sub-tropical, emergent deciduous tree species, produces leaves of more than one shape and size during its life-time. This study, 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 the ecological significance of heterophylly in this species.

METHODS OF STUDY

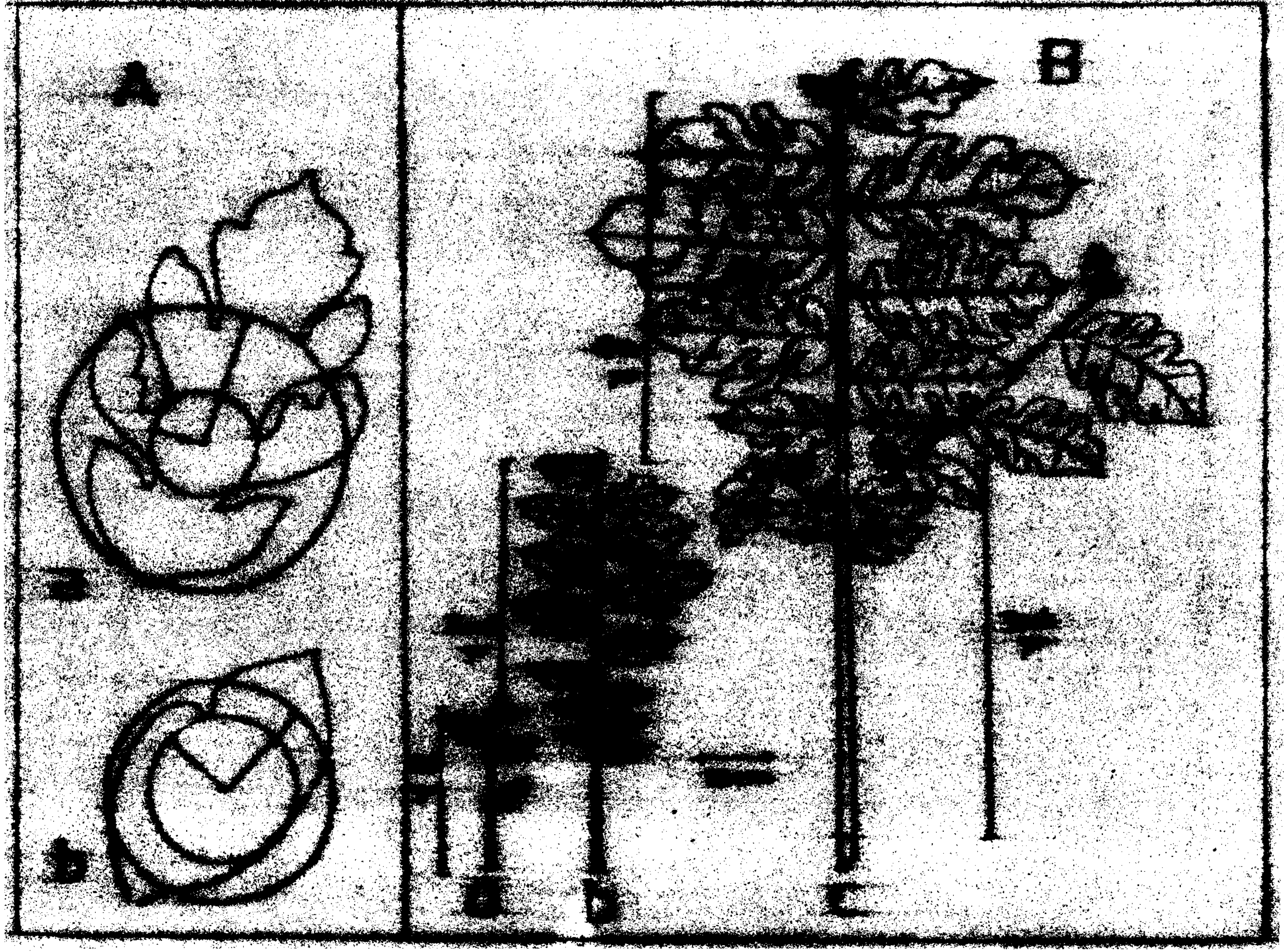
The study was carried out in a sub-tropical humid forest of north-eastern India, at Lailad. Saplings of *A. chaplasha* growing in the open (80 - 90 thousand lux) and under different degrees of shade (800 - 30,000 lux) in the forest were selected. Saplings of different age groups (1-8 yr) were available in good numbers under varying light conditions. The age of the saplings were 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 lobed and/or unlobed leaves on them. After categorizing the leave into 4 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 X breadth and leaf area was developed for each shape under each light regime and this was used to compute the leaf area of other leaves.

The depth and frequency of lobing of leaves was determined following Horn's (1971) procedure (Fig. 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.

Fig. 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 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.

1B Diagramatic sketch of growth of *A. chaplasha* upto 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 3rd year.

Fig. 4



General characteristics of growth and leaf production

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 (Fig. 1B) occurred earlier under shade. The production of lobed leaves continues on the main axis until the damage of the original main shoot tip; otherwose 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. 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 in size and may fall off soon. 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. 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 leaf 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 than those on the II and III order branches and lesser 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 upto 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.

Table 1. Leaf characteristics in 7 year 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 ± 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*.

Factors ↓ Parameters	Ratio of no. of lobed to unlobed leaves	Lobing frequency (lobe/leaf)	Area/leaf	Ratio of diam. of large to small circle (depth of lobing)	Degrees of freedom
Plant age[a]	- 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[b]	0.708**	0.898*	0.756**	0.395^{ns}	6
Light intensity	- 0.890**	- 0.918*	- 0.834**	- 0.886**	4

a. After phase change from small dentate to lobed leaves i.e. from second year of growth.

b. Only monopodial branches were considered.

* = 1% and ** = 5% level of significance and ns = not significant.

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 and 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 prevailing environmental conditions.

A. chaplasha, which establishes itself making fair growth under a forest canopy, soon overtops the other species and become 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 the 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.

SUMMARY

The qualitative and quantitative changes in leaf shape from seedling to emergent tree stage in Artocarpus chaplasha Roxb. were studied. The number of lobes 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 degree of shade, suggest its success as a mid-successional species.

Plate 4. A. Emergence of first lobed leaf in A. *chaplasha*.

B. Different shapes and sizes of leaves in A. *chaplasha*.

Plate 4

* *

CHAPTER - IV

* *

DRY MATTER ALLOCATION AND PRODUCTION PATTERN IN RELATION TO GROWTH STRATEGIES

INTRODUCTION

The allocation pattern of the available resources for various life activities is the result of various ecological and evolutionary factors related to natural selection (Cody,1966). The success of an organism in an environment can be predicted by looking at its relative apportionment of biomass or energy (MacArthur and Wilson, 1967; Gadgil and Solbrig, 1973; Abrahamson, 1975). While enough studies are available for herbaceous and shrub species, only a few attempts have been made to analyse the growth strategies of temperate forest trees in relation to their energy fixation capacity (Horn, 1971; Marks, 1975). Such an approach towards the knowledge of primary production in relation to growth strategies and successional status of tropical trees would be very rewarding in evaluation of the adaptibility and potential of different species in different tropical environment (Gomez-Pompa and Vazquez-Yanes, 1974; Ramakrishnan, 1978).

The present study involves the biomass allocation pattern and productivity in relation to growth strategies of Duabanga sonneratioides Ham., Anthocephalus cadamba Miq., Dillenia pentagyna Roxb. and Artocarpus chaplasha Roxb. which come at different stages of secondary succession after slash and burn agriculture in the sub-tropical humid forests of north-eastern India (Ramakrishnan & Toky, 1978). The former two are early successional shade-intolerant species, while D. pentagyna and A. chaplasha are late successional shade-tolerant species.

METHODS OF STUDY

Saplings or trees of different age groups (1-7 yr) were identified in the open situations in the sub-tropical forest at Lailad. Their general growth characteristics including branch and leaf fall during one year growth period were measured for the estimation of productivity. Age of the individuals was determined on the basis of growth characteristics described and discussed elsewhere. The estimations of biomass and leaf area index (LAI) were made in October when annual vegetative growth has reached its maximum. Five replicates of individuals were taken for each age category of the different species and they were excavated with intact roots. After harvest, various parameters like clean bole length, crown depth (vertical crown length from lowest branch/leaf to the top most leaf), maximum crown width, total number of branches and leaves, branch length and root length were noted. The total leaf area was computed on the basis of leaf length and breadth using correlation factors for different species, from which LAI was derived. After obtaining fresh weight of all the different components in the field, samples were dried at 80±2°C to constant weight to obtain dry weight values. The root material was sampled on the basis of their profile position in the soil as 0-10 cm, 10.1-20 cm, 20.1-30 cm, 30.1-40 cm and below 40 cm.

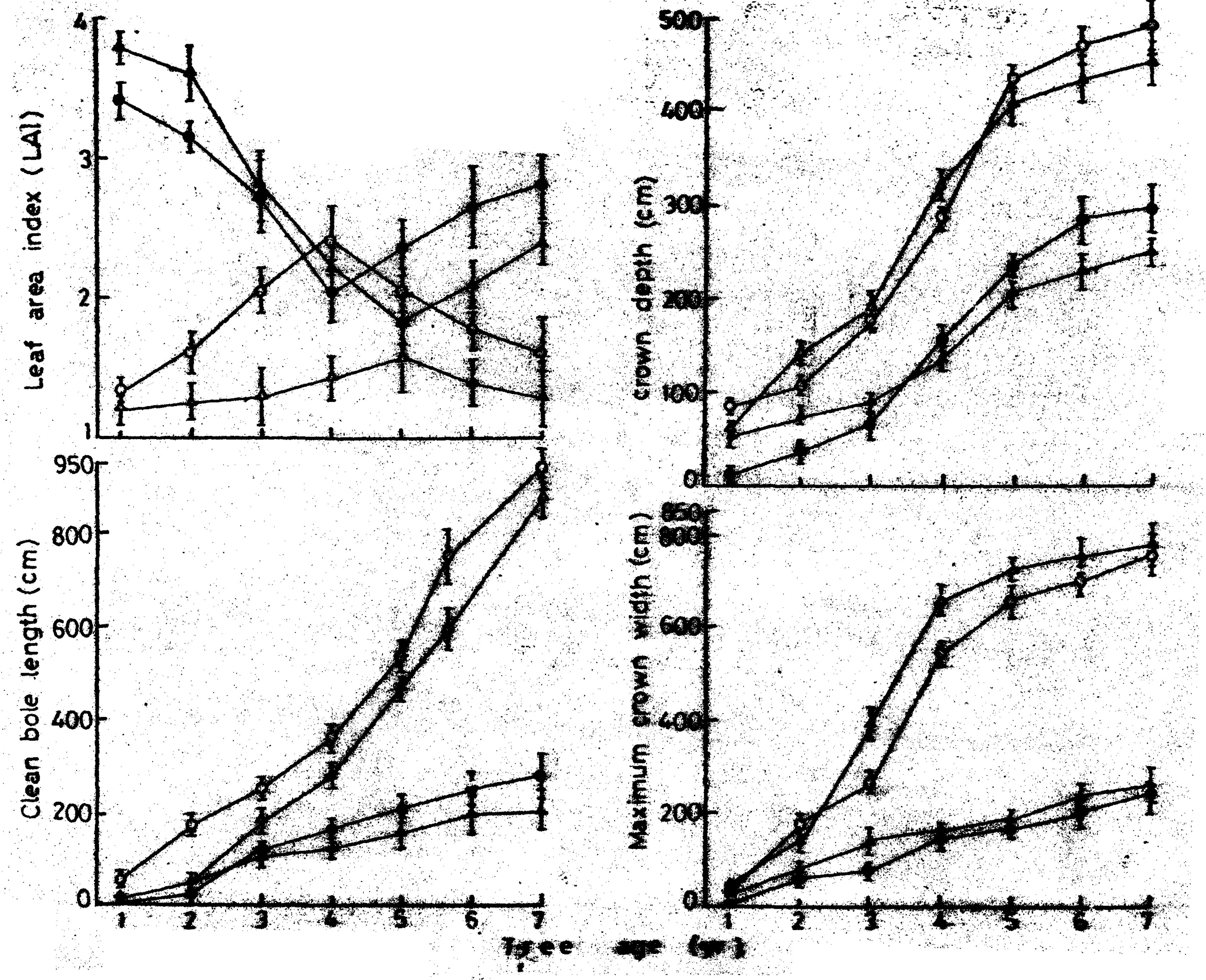
RESULTS

Fig. 1 shows the changes in leaf area index (1a), clean bole length (1b), crown depth (1c) and maximum crown width (1d) with increase in tree age of the different species. Clearcut differences were noted in the pattern of change in leaf area index (LAI) between early and late successional species. Early successionals, in general, showed lower LAI values compared to the late successional species. For the age stands considered during the present study, the late successional species showed very high LAI in the initial stages, sharply declining upto 4-5 years of age followed by an increase subsequently. On the other hand, the values for early successional species improved gradually (D. sonneratioides) or more sharply (A. cadamba), reaching a maximum in 4-5 years of age followed by gradual or sharp decline.

Clean bole length of early successional species was higher as compared to the late successional species and this became more pronounced with age. The increase in clean bole length due to age was sharper in the case of early successional species compared to the other two. The crown depth also was greater for early successional species compared to late successional ones and this became more

Fig. 1 Changes in LAI (a), clean bole length (b), crown depth (c) and maximum crown width (d) of early successional (open symbols) and late successional (closed symbols) species with tree age.
Open triangle, *D. sonneratioides*; open circle, *A. cadamba*; closed triangle, *D. pentagyna*; and closed circle, *A. chaplasha*.

Fig-1

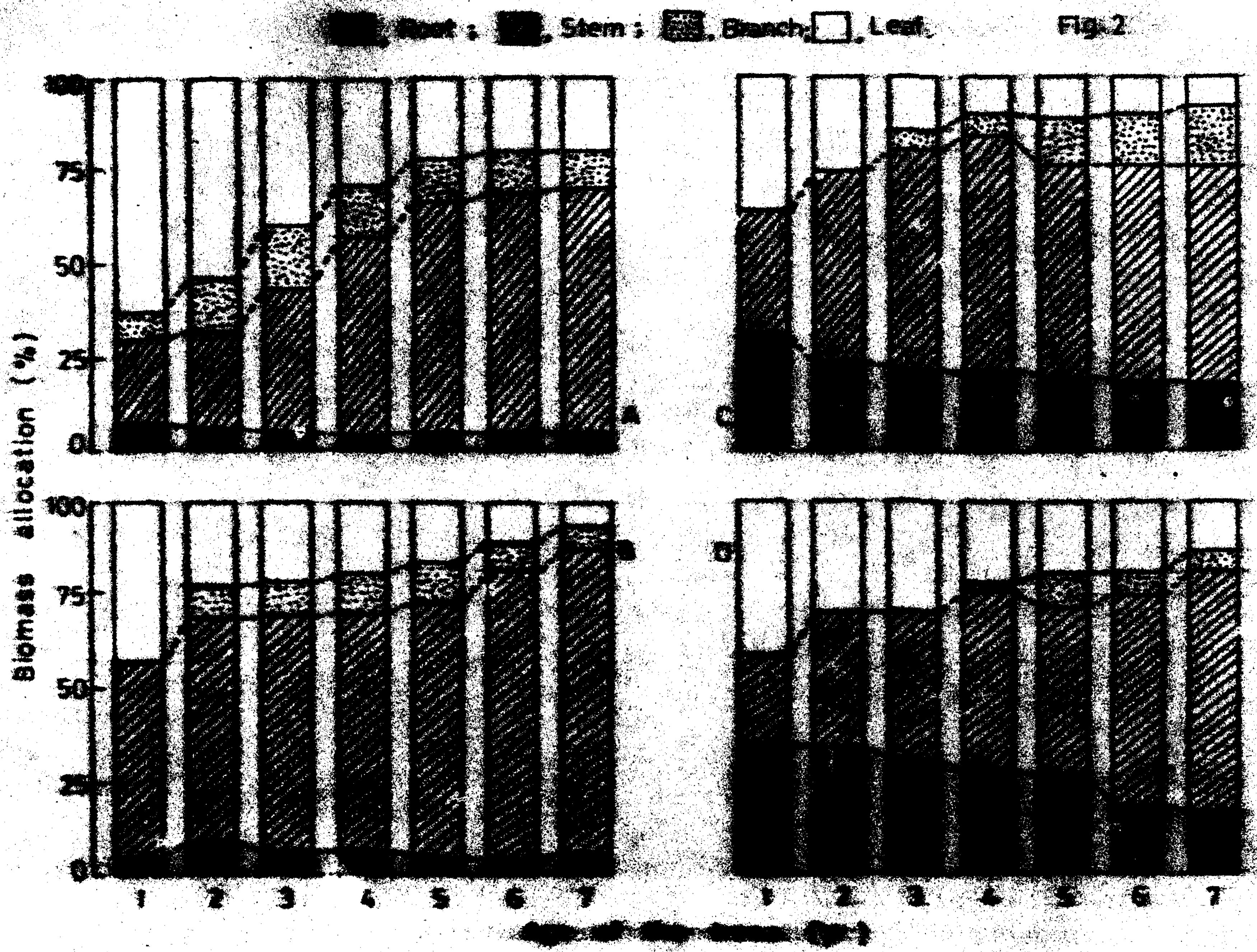

Leaf area index (LAI)
1
2
3
4
Clean bole length (cm)
0
200
400
600
800
950
crown depth (cm)
0
100
200
300
400
500
Maximum crown width (cm)
0
200
400
600
800
850
1
2
3
4
5
6
7
Tree age (yr)

pronounced with age due to sharper increase in crown depth of early successional species. For the age stands studied, the maximum crown width also followed a similar pattern as crown depth except that the difference between early and late successional species was more pronounced. The rate of increase of both the crown depth and maximum crown width slowed down after 5 years, particularly in the early successional species.

The allocation pattern of biomass in four different compartments namely root, stem, branch and leaf, expressed as the percentage of the total capital (Fig. 2) showed marked differences between early and late successional species. The allocation percentage to the root in the case of early successional species was markedly low and was in the range of 3-8%, whereas that in the case of late successional species was between 12-21%. Further, in the late successional species, the proportion allocated to the root tended to decline with age. Allocation to the branch compartment was generally more and started right from the first or second year of growth in the case of early successional species whereas it was generally low and started somewhat later in the growth of the tree of late successional species. The proportional allocation to the bole compartment was also found to be higher in the case of early successional species compared to the late successionals. As a corollary to this, allocation to the shoot by the early successional species was more than that for the late

Fig. 2 Allocation pattern of total biomass in four different compartments, viz., root, stem (bole), branch and leaf of early (A,B) and late (C,D) successional species of different age groups. A, *D. sonneratioides*; B, *A. cadamba*; C, *D. pentagyna*; and D, *A. chaplasha*.

Fig. 2


Root ; Stem ; Branch ; Leaf
Biomass allocation (%)
0
25
50
75
100
A
B
C
D
1
2
3
4
5
6
7

successional ones. Allocation to the leaf compartment declined with age in all the species with a corresponding increase to the bole compartment. This, however, was more pronounced in the case of early successional species.

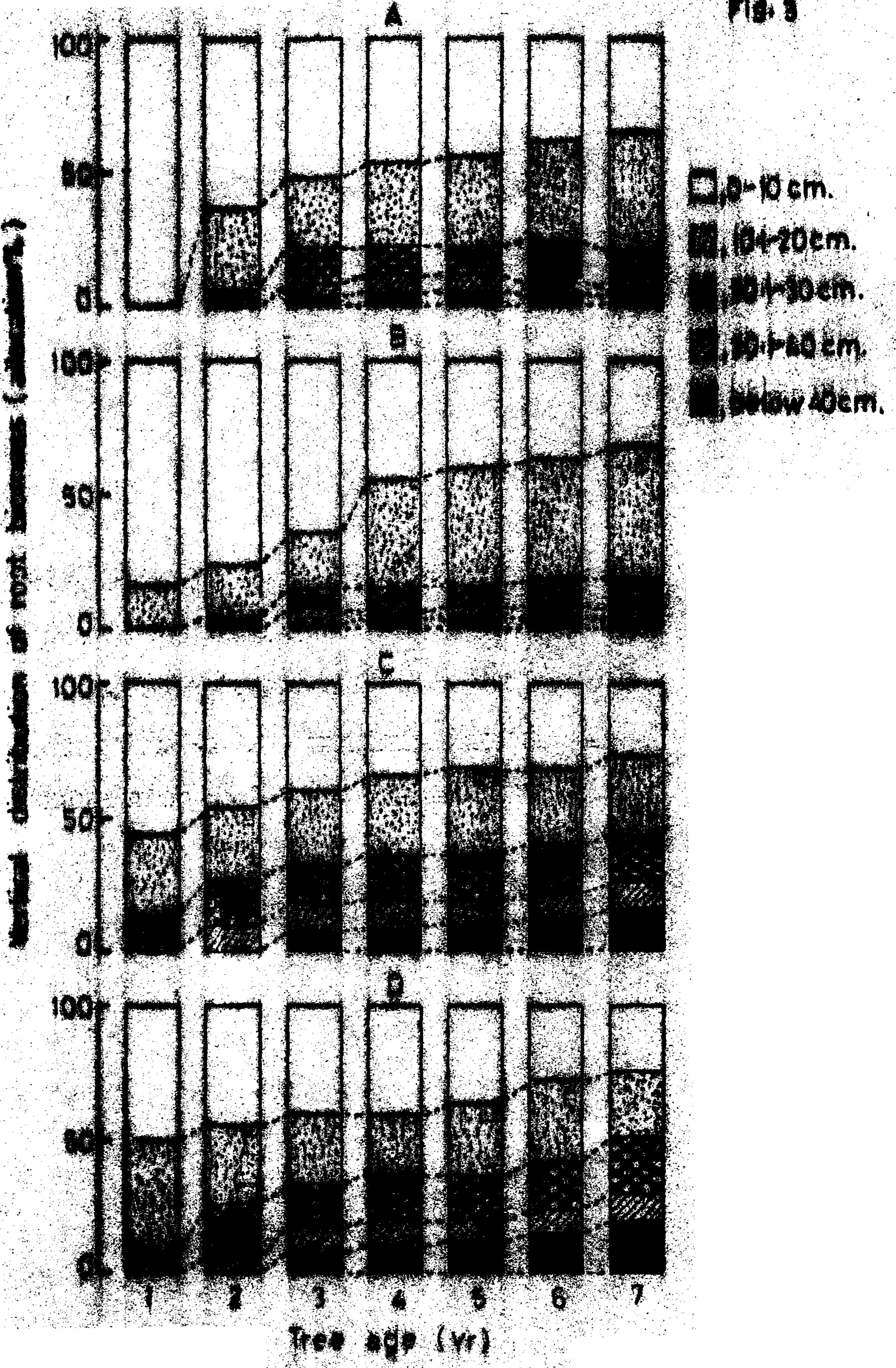
The partitioning of the root biomass down the vertical profile of its distribution in the soil also showed distinct differences between the early and late successional species (Fig. 3). For the early successional species, a higher percentage of the total root biomass was localized within the upper 20 cm of soil profile so much so that in a 7 year old tree of D. sonneratioides and A. cadamba, the roots in this zone accounted for as much as 80% of the total root biomass. In the case of the 7 year old late successionals, however, this was only 56% for D. pentagyna and 49% for A. chaplasha. In the case of early successional species, root biomass in the 0-10 cm depth declined but that in 10-20 cm depth increased with age. While this variation due to age was not so pronounced in these surface layers of the soil, the proportion of the roots below 20 cm of the soil profile markedly increased with the age in the case of the late successional species. This was particularly evident in the root system below 40 cm depth.

The shoot/root ratio for the early successionals, D. sonneratioides and A. cadamba was markedly higher in all age categories compared to the late successionals.

Fig. 3 Allocation pattern of total root biomass along the soil profiles in early (A,B) and late (C,D) successional species.

A, *D. sonneratioides*; B, *A. cadamba*;
C, *D. Pentagyna*; and D, *A. chaplasha*

Fig. 5


A
B
C
D
100
50
0
▢, 0-10 cm.
▨, 10.1-20cm.
■, 20.1-30cm.
▨, 30.1-40 cm.
■, below 40cm.
1
2
3
4
5
6
7
Tree age (yr)

D. sonneratioides showed a gradual increase in this ratio upto 4 years age followed by a decline upto 7 years, whereas no definite pattern could be detected for *A. cadamba*. Both the late successional species showed a gradual increase in this ratio with the age of the tree (Table 1).

The root production of early successional species was significantly higher ($P < 0.01$) than that of the late successional species only upto an age of 4 years. Older trees did not show any significant difference between the two categories. While the production of late successionals increased exponentially upto 7 years of growth, early successional species showed such an increase initially, followed by a slowing down in older trees (Fig. 4a).

Shoot production however, was significantly higher for early successionals in all the age classes studied. As for root production pattern, the increase in shoot production for late successional species was exponential with age while that for early successionals tended to slow down beyond 4 years (Fig. 4b).

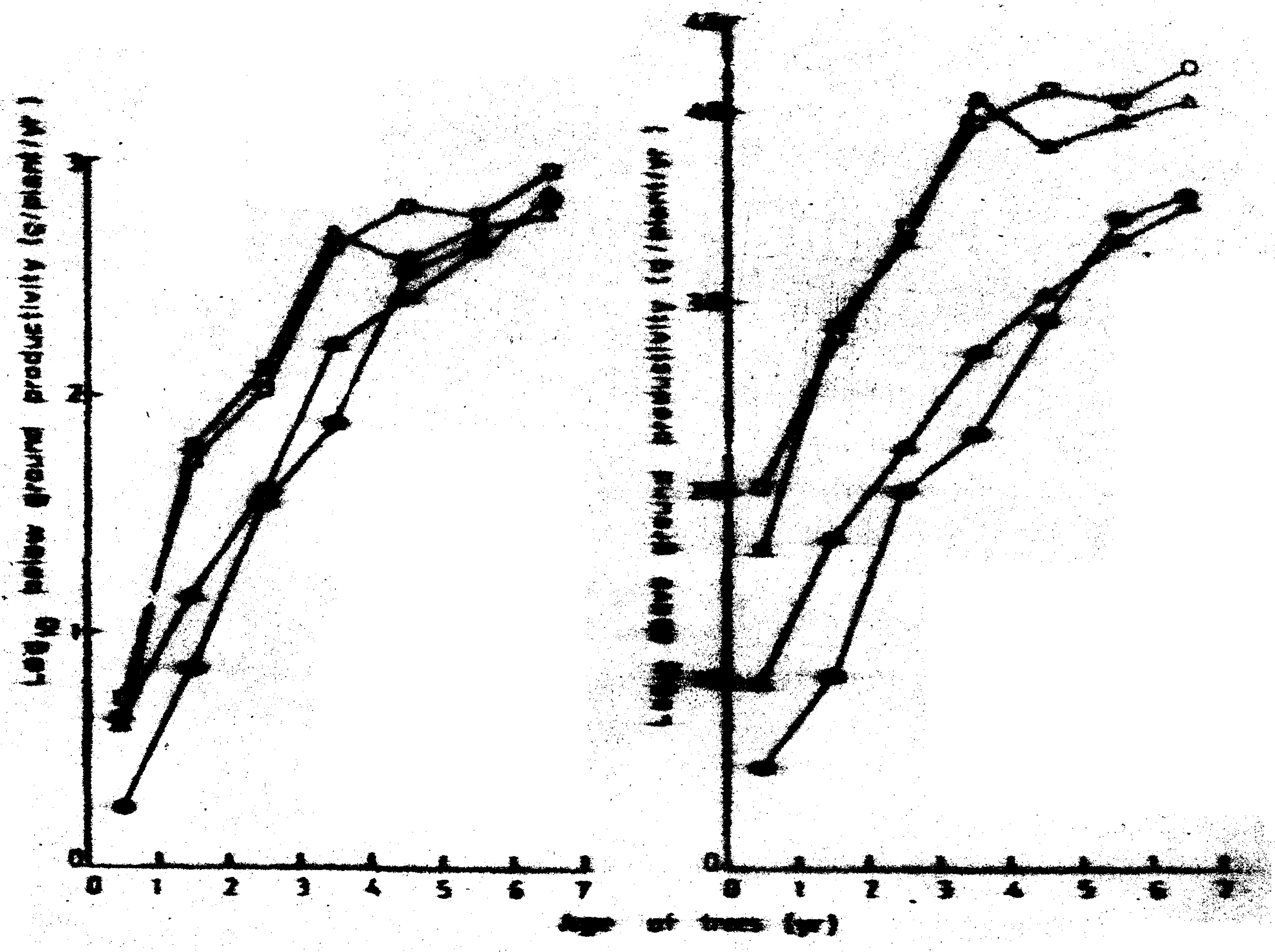
DISCUSSION

The early and late successional species studied here, show a number of significant differences with respect to allocation pattern. One of the important differences

Fig. 4 Pattern of change in below ground (A) and above ground (B) productivity of early successional (open symbols) and late successional (closed symbols) species with increase in tree age.

Open triangle, *D. sonneratioides*; open circle, *A. cadamba*; closed triangle, *D. pentagyna*; and closed circle, *A. chaplasha*.

Fig-4



Log10 below ground productivity (g/plant/yr)
0
1
2
3
0
1
2
3
4
5
6
7
Log10 above ground productivity (g/plant/yr)
0
0
1
2
3
4
5
6
7
Age of trees (yr)

Table 1. Changes in shoot/root ratio of early and late successional species with increase in tree age.

Age (yr)	Early successional		Late successional	
	Duabanga sonneratioides	Anthocephalus cadamba	Dillenia pentagyna	Artocarpus chaplasha
1	12.35	20.41	2.17	1.92
2	15.15	10.10	3.20	1.95
3	16.40	14.08	3.70	2.33
4	22.22	13.51	3.70	2.56
5	18.18	18.86	4.0	2.70
6	17.85	22.22	4.55	4.55
7	16.95	16.13	4.76	5.00

recognized, pertains to the allocation pattern to the shoot versus the root. This ratio for the early and late successional species are fairly stable with marked differences. The shoot/root ratio, often, is considered to be stable under any given set of environmental conditions for a given species (Wareing, 1970) on the basis of which Thornley (1972) developed a model to account for the partitioning of assimilates between leaf, stem and root.

The early successional species, in general, were found to allocate less to the root system compared to the late successional species. Further, the early successional species were found to have maximum distribution of their roots in the surface layer of the soil. These observations suggest firstly that, the early successional species tend to maximize allocation to the shoot system in order to put up the canopy as high as possible for exploiting the high light energy environment in early successional communities. Secondly, such a root system with most of the root biomass allocated within upper 20 cm of root length, though offering poor physical support to the shoot, would probably provide enough absorptive system to exploit the short term increase in nutrient availability and water associated with disturbed lands (Marks and Bormann, 1972; Marks, 1975). The allocation pattern of total dry matter indicates a very low percentage to root of early successional species. This is partly consistent with the remark of Watson (1971), that for maximum rate of dry matter production, 'expenditure of dry matter on the rest of the plant except leaf should be no more than is required to support the leaves in an efficient arrangement and supply sufficient nutrient and water' (Wareing, 1975). On the other hand, the allocation pattern in roots of late successional species determine comparatively uniform distribution of biomass throughout the vertical length of root system from the soil surface. The high allocation to the root compartment of late successional species suggests their conservative nature in order to draw upon the nutrients from deeper layer of the soil over a longer period of time.

Another important difference in the allocation pattern pertain to the greater proportional allocation to the bole compartment by early successionals as compared to the late successionals. This again seems to be an adaptation to put up the canopy as high as possible. This is further strengthened by the greater clean bole length of the early successional species (due to faster self-pruning of the lower branches) which help in the vertical upward movement of the crown for maximum exploitation of high light intensity. It is worthnoting here that our earlier studies suggest markedly greater extension growth for early successional species compared to the late successional ones.

Crown width and depth characteristics of a species often determine the light interception strategy of a given tree. The greater crown width of the early successional species is due to rapid extension growth of plagiotropically placed branches unlike the slow extension growth of orthotropically placed branches of these late successional species (Halle et al, 1978). Greater crown width and depth in the case of early successional species again could be considered as of adaptive significance to exploit light energy to the maximum. Rapid vertical extension growth, with leaves being distributed in many layers as indicated from the crown depth, but with loosely arranged plagiotropic branches ensure reasonably high photosynthesis even in the leaves placed down below in the canopy supporting the multilayer/monolayer concept of Horn (1971) for early/late successional species. Though LAI was higher for late successional species in the first couple of year's growth, no clearcut pattern emerged for older trees upto 7 years during the present study.

Production of both the shoot and root systems of the early successional species were generally higher than that of late successional species and this was more pronounced for the shoot production. This is related to the more favourable but transient light conditions that would prevail in an early successional community where light would soon become a limiting factor. Thus according to Horn (1971), early successional species are adapted to grow faster under light intensities between 54-100% of the full sunlight. It is also interesting to note the change in the productivity pattern with age, where the rate of this was steeper in the early age groups of early successional species followed by a slow down beyond 5 years but with an exponential growth rate throughout in the case of late successional species. This is in agreement with the results of Leburn and Gilbert (1954) who showed, while working in a tropical forest in Zaire, that the high growth rate for pioneers tended to decline within 5-8 years unlike the climax species.

SUMMARY

The growth strategies of two early successional species were compared with those of two late successional ones and related to their successional status. Apart from distinct differences in clean bole length, crown depth, maximum crown width and LAI, the former showed higher allocation to shoot particularly to the bole compartment compared to the latter which had higher allocation to the root compartment. The early successional species with a shallow root system had most of the root biomass within the upper 20 cm of the soil profile while the late successionals with deeper roots had higher proportion of root biomass below the 20 cm depth. Root production of the early successional species was significantly higher over the late successional species only upto 5 years

of age after which the differences were less marked. However, the higher production of the shoot system was consistently maintained by the early successional species.

SECTION - B

ADAPTATION OF TREES IN THE FOREST COMMUNITY

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CHAPTER - V

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PHENOLOGY OF TREES IN THE FOREST COMMUNITY

INTRODUCTION

A number of studies on phenology of different vegetation types from different climatic zones are available such as for tundra (Sorensen, 1941; Mooney and Billing, 1961), Rocky Mountains (Holway, 1965) and Rock Valley in the northern mojave desert (Shreve, 1942; Beatley, 1967) in North America. Lieth has discussed the concepts and significance of phenological studies in the understanding of ecosystem function (Lieth, 1970; Lieth and Radford, 1971). The tropical forests, however, are comparatively less understood and the investigations oriented towards the analysis and unification of periodicities of different phenophases are meagre except for a few studies like that of Boaler (1966), Janzen (1967), Holttum (1968), Croat (1969), Nevling (1971), and Daubenmire (1972). The studies of Frankie *et al* (1974) constitute one of the few detailed analysis of phenological patterns in tropical forests. Recently, Borchert (1980) has discussed the phenology of a tropical tree, *Erythrina poeppigiana*. As pointed out by several investigators, an understanding of the phenological events in a forest community may reveal the structural organisation of various types of resources in the ecosystem.

The present study was undertaken as little information is available on sub-tropical humid forests of the north-eastern India characterised by high species diversity.

THE VEGETATION

In the forest, the overstorey was chiefly composed of *Schima wallichii*, *Castanopsis indica*, *Shorea robusta*, *Tetrameles nudiflora*, *Elaeocarpus* spp., *Miliusa roxburghiana*, *Artocarpus chaplasha*, *Vitex peduncularis*, *Mesua ferrea*, *Amoora wallichii* and *Garcinia* spp. The more frequent understorey trees were *Croton oblongifolius*, *Oroxylum indicum*, *Goniothalamus Simonsii* and *Unona longifolia*. *Croton caudatus*, *Litsea lancifolia* and *Randia wallichii* were the dominant shrubs. The most important herbaceous species were *Panicum khasianum*, *Cyperus elegans*, *Fimbristylis dichotoma*, *Hedychium gracile* and *Passiflora nepalensis* with the forest opening being dominated by *Eupatorium odoratum*, *Lantana camara* and *Mikenia macarantha*.

METHODS OF STUDY

Besides, general phenological observations on tree species, a few selected trees of each species were tagged with aluminium labels for detailed observation at fortnightly/monthly intervals. Records on leaf fall, flushing, flowering activity and fruiting activity were made for 122 tree species which represented over 60% of the total tree species of the area. A species was considered to be passing through the peak of a phenophase when more than 50% of the individuals of that species were passing through that phase.

Trees were broadly divided into two categories: overstorey species consisted of canopy and subcanopy trees and the suppressed trees less than 15 m tall constituted the understorey (Croat, 1969; Frankie et al, 1974). The pattern of leafiness of the trees was classified into three groups: (i) evergreen-evergrowing type, which continually produced small quantities of new leaves showing no heavy leaf-fall at a given time, (ii) evergreen-periodic type which also never became naked as previous type but had a major leaf-fall and flushing period in a year and (iii) deciduous type which became completely naked for at least a brief period of time and showed peak leaf-fall and flushing at certain times of the year.

The general phenological features are summarized in the text and individual species characteristics are presented in the Appendix 1 and 2.

RESULTS

Leafing activity

The humid forest at Lailad maintained its green appearance throughout the year with many evergreen tree species including a few evergrowing types (Table 1). In dry months from January to March, many species dropped their leaves. Flushing and leaf production occurred during subsequent months in March to Septembar-October. About 40% of the total leaf litter of

Table 1. Types of leafing activity of tree species.

Group	Activity	Number of species	
		Overstorey	Understorey
Evergreen-evergrowing	Continuous leafing	3	1
Evergreen-periodic	Discontinuous production of leaves	28	36
Deciduous	Marked leaf fall and flushing	45	9
Total		76	46

4.3 t/ha is reported to accumulate in the drier period of February-March. In other months leaf-drop was comparatively low (Singh, 1980).

Leaf-fall:

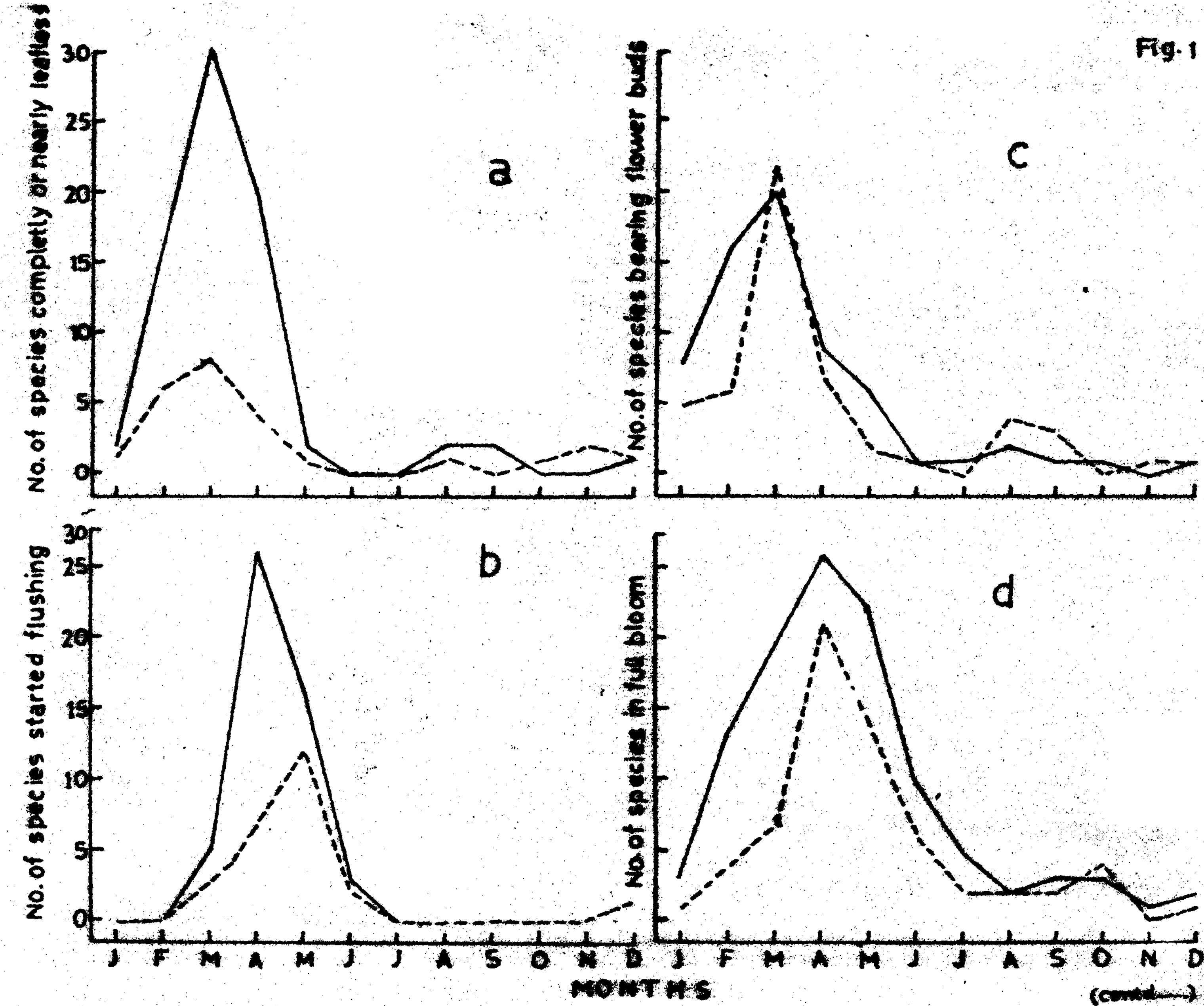
The peak of nakedness was achieved during March in both the overstorey and understorey species. None of the tree species among both the stories showed conspicuous leaf-drop during the peak monsoon period of June-July (Fig.1a). A few species like *Cedrella toona*, *Baccouria sapida*, *Elaeocarpus* spp. and *Styrax serrulatum* amongst the understorey dropped their leaves considerably during August-September. An understorey species, *Aesculus assamica* became naked during November-December.

Flushing:

Periodicity of flushing in different species as shown in Fig.1b, indicates that peak period coincided with the end of the dry season and the start of monsoon. For the overstorey species, peak flushing occurred in April whereas this was delayed by a month for the understorey species. However, the time for bud burst or first flushing extended from February-June for all the tree species observed except in the case of an understorey species, *A. assamica* which flushed during December and a few evergrowing species like *Calicarpa arborea*, *Saprosma ternatum* and *Duabanga sonneratioides* which produced some leaves throughout the year.

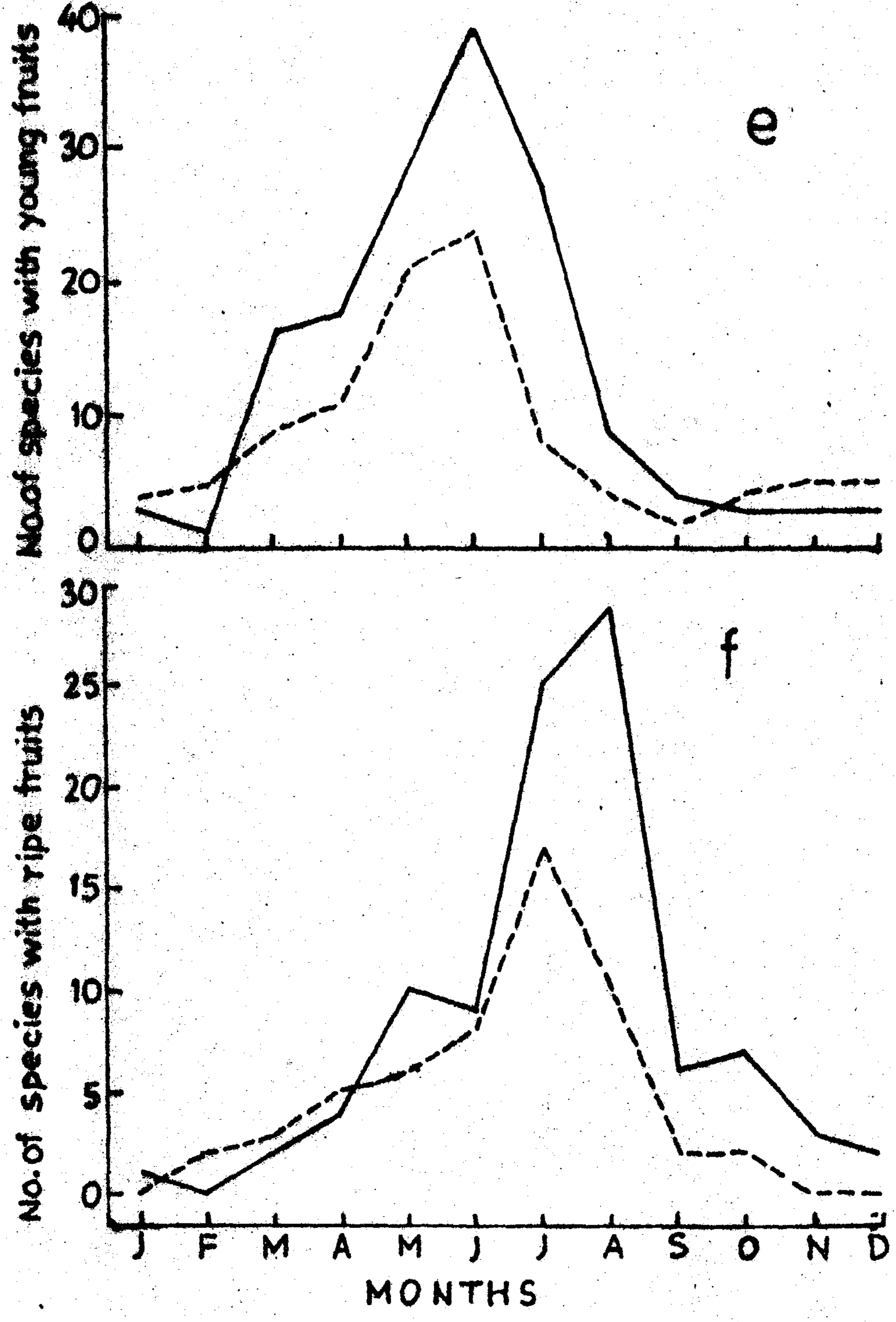
Fig. 1 Phenological periodicity of overstorey (continuous line) and understorey (broken line) tree species;
a, leaf fall; b, flushing; c, flower bud; d, flowering; e, fruit initiation and development; and f, fruit ripening and fall.

Fig. 1


a
No. of species completly or nearly leafless
0
5
10
15
20
25
30
c
No. of species bearing flower buds
b
No. of species started flushing
0
5
10
15
20
25
30
d
No. of species in full bloom
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

(contd.---)

Fig. 1


e
f
No.of species with young fruits
No. of species with ripe fruits
40
30
20
10
0
30
25
20
15
10
5
0
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

The observation on cessation of growth in a few selected over- and understorey species showed that leaf production in many of the overstorey species was over by September-October but the understorey species stopped leaf production by August-September. Thus there was a time lag of nearly a month between the growth cessation of over- and understorey species (Table 2).

Flowering activity

All the species observed, bloomed once in a year and flowering period of most of the species (seasonally-flowering) extended to about 8 weeks starting from bud inception to full bloom stage. For convenience, therefore, the flowering activity was divided into bud stage and blooming stage. Few species flowered for several months of the year covering more than one season (extended-flowering species).

Flower bud:

The period of peak for flower bud inception coincided with that of peak leaf-fall in February-March in both the overstorey and understorey species, irrespective of the fact whether they became completely naked or not. The flower bud initiation of the overstorey species started more vigorously in January-February itself though it peaked in March for both under- and overstorey species with a sharp decline in April-May. In subsequent months bud initiation was maintained at a

Table 2. Cessation of growth (leaf production)in some over- and understorey tree species.

Tree species	Growth cessation
Overstorey:	
Amoora wallichii King.	Oct. I-II
Anthocephalus cadamba Miq.	Oct. II-Nov.II
Artocarpus chaplasha Roxb.	Oct. II-Nov. I
Castanopsis indica A.DC.	Sept.III-Oct.I
Chukrassia tubularis A. Juss.	Oct. II - Oct.IV
Gmelina arborea L.	Sept.III-Oct.II
Lagerstroemia parviflora Roxb.	Sept. I - III
Mesua ferrea L.	Aug. II - Sept. I
Shorea robusta Gaert.	Aug.III - Sept.II
Sterculia villosa Roxb.	Oct. I - II
Vitex altissima L.	Sept.III - Oct. I
Understorey:	
Actinodaphne angustifolia Nees.	Aug.III - Sept. I
Bauhinia malbarica Roxb.	Sept. I - II
Lagerstroemia flos-reginae Retz.	Aug. IV - Sept.II
Oroxylum indicum Vent.	Sept. I - II
Pithecolobium longan Benth.	Aug. I - II
Premna miliflora Clarke.	Aug. II - Sept. I
Styrax serrulatum Roxb.	Aug. II - III

I II III & IV shows the different four weeks of a month.

very low level though the understorey species had a smaller peak in August-September (Fig.1c).

Flowering:

As a consequence to the pattern of flower bud development, the peak flowering among both the over- and understorey species was attained in April after which it declined sharply and was maintained at a low level beyond July (Fig.1d). A large number of overstorey species flowered during the dry season ($\frac{24}{74}$) whereas only a smaller fraction of understorey species flowered at this time ($\frac{9}{40}$). However, a larger number of understorey species flowered during the rainy season ($\frac{29}{40}$) compared to overstorey species ($\frac{48}{74}$). Considering all the species together it was seen that flowering was more during the wet season compared to the dry season flowering ($\frac{77}{114}$ vs. $\frac{33}{114}$) as shown in Table 3.

Flowering behaviour:

Most of the species like *Morus laevigata*, *Eugenia* spp. and *Pithecolobium longan* had a shorter flowering period of only about 2-7 weeks while a few species like *Duabanga sonneratioides*, *Schima wallichii*, *Calicarpa arborea* and *Aesculus assamica* showed extended flowering period of about 20-27 weeks. However, the peak flowering in *D. sonneratioides* and *Schima wallichii* was pronounced during January-February and May-June respectively but the peak of flowering in *C. arborea* and *A. assamica* extended for about 8 weeks. While no

Table 3. Number of over- and understorey species in flowering stage during dry and wet season.

	Dry season	Wet season	Extended flowerers	data incomplete
Overstorey	24	48	2	2
Understorey	9	29	2	6
Total	23	77	4	8

significant difference in flowering pattern was observed for a given species from one year to another, individuals within the species showed differences in the vigour of flowering from year to year as seen from observations over a 2 year period. Either the vigour may be more or less for an individual of a given species as in *Cedrella toona*, *Casearia glomerata* and *Anthocephalus cadamba* or the individuals that flowered in one year,may not flower at all in the next year as in *Mesua ferrea*, *Myristica linifolia*, *Mangifera indica* and *Artocarpus chaplasha*, thus showing an alternate pattern for flowering.

Fruiting activity

The fruiting period may be divided into two parts: (i) fruit development and (ii) fruit ripening and fall. The fruiting period extended over a few months both for seasonal as well as extended flowering species.

Fruit development:

A number of species of both the stories shed their flowers in March when fruit development started so that peak of fruit development occurred in June. However, developmental period for fruits of different species extended from 5 to 20 weeks. The pattern of fruit development was nearly the same in both the over- and understorey species. During the rainy season maximum number of species from both the stories had growing fruits (Fig. 1e).

Fruit ripening and fall:

The peak for fruit ripening and fall occurred in the month of July-August, though quite a few species shed their fruits in May-June as well as in September-October. Fruit ripening and shedding beyond this period was rare. (Fig.1f).

Fruiting behaviour:

All the species that showed extended flowering pattern as well as a few others like *Oroxylum indicum* and *Hydnocarpus kurtzii* bore fruits for more than 20 weeks while the rest of the species had brief fruiting periods of not more than 6-10 weeks. The proportion of tree species fruiting in dry months ($\frac{16}{118}$) was very low in comparison to those fruiting during wet months ($\frac{96}{118}$). During dry periods, fruiting in overstorey species was lesser ($\frac{9}{76}$) in comparison to understorey species ($\frac{7}{43}$) as shown in Table 4.

In the community, species producing fleshy fruits were markedly higher in number than those producing dry fruits ($\frac{72}{118}$ vs. $\frac{46}{118}$). A majority of the species produced fleshy fruits during wet months with a proportion of $\frac{65}{96}$ as compared to those yielding dry fruits ($\frac{31}{96}$). The number of species producing fleshy fruits during dry months was lesser than those producing dry fruits ($\frac{4}{16}$ vs. $\frac{12}{16}$) as clear from Table 5.

Table 4. Number of overstorey and understorey tree species bearing mature fruits during dry and wet season.

	Dry season	Wet season	Extended fruiters	Data incomplete
Overstorey	9	63	3	1
Understorey	7	33	3	3
Total	16	96	6	4

Table 5. Number of overstorey and understorey tree species producing dry and fleshy fruits during dry and wet season.

	Dry season		Wet season		Extended fruiters		Data incomplete
	D	F	D	F	D	F	
Overstorey	6	3	21	42	2	1	1
Understorey	6	1	10	23	1	2	3
Total	12	4	31	65	3	3	4

D = Dry fruits

F = Fleshy fruits

DISCUSSION

It is clear from the phenological observation of the forest and climatic characteristics of the study site that the forest community observed,is a semi-deciduous seasonal forest with a majority of the understorey and several overstorey species being evergreen. Correlation of phenological activity with naturally occurring climatic events may be best cited by the pattern of leaf-fall. The period of greatest leaf-fall coincided with the relatively xeric conditions of the dry season during the brief summer. There are several reports of maximum leaf-fall during the driest part of the year in different tropical forest types (Holttum, 1931; Beard, 1946; Taylor, 1960; Madge, 1965; Hopkins, 1966; and Frankie et al, 1974). In temperate latitudes, leaves are almost invariably dropped as days shorten and it has been demonstrated for several species that the change in photoperiod is the triggering agent (Olmsted,1951), others have implicated dryness more than photoperiod with major peaks of leaf-fall closely related with major peaks of dryness (Daubenmire,1972) as was also observed in the present study. Generally speaking, most of the emergent species shed their leaves during the early part of the dry season with species like Sterculia villosa and Tetrameles nudiflora shedding their leaves as early as January but in any case before mid-February. However, the canopy and subcanopy species like Garcinia cowa, Miliusa roxburghiana and Illex exelsa did not have peak leaf-fall until March. This may be related to the relatively xeric environment to which these species are exposed due to direct insolation or otherwise. Maximum leaf-fall occurring during the dry summer, not only helps in conservation of soil moisture but also ensures faster decomposition of the bulk of leaf litter during the following monsoon season when temperature and humidity conditions are more favourable (Singh, 1980).

Flushing and leaf production started towards the end of the dry season frequently before the onset of rains as also shown for other seasonal tropical forests (Champion, 1936; Rawitscher, 1940; Webb, 1959; Boaler, 1966; Daubenmire, 1972; and Frankie _et al_, 1974). Walter (1964) attributes the pre-rain flushing to the triggering effect of rising temperature which may be applicable to the present study but such a correlation was not observed by Daubenmire (1972) in a tropical forest in Costa Rica. Day length increase, as it occurs in the present case during March-April, may also contribute to induce flushing as suggested by Njoku (1964) and Lawton and Akpan (1968).

The induction of apical bud dormancy or cessation of growth is more often attributed to prevailing temperature regime. Cooler night temperature tended to induce bud dormancy in _Gmelina arborea_ (Longman, 1969). He showed that plants with nights of 26°C stopped their growth but none at 31° or 36°C. In the present study the delay in growth cessation of overstorey species may be attributed to the longer duration of higher temperature regimes at this level due to direct insolation compared to that at the canopy level of the understorey species. In experimental studies, however, temperature and day length are shown to interact in controlling the bud dormancy (Thimann, 1962; Njoku, 1964).

Synchronization of flowering with the dry season as observed in the present study has also been reported for many wet forests (Duke and Black, 1953; Njoku, 1963). Apart from moisture related factors, a change in photoperiod has also been assumed to trigger flowering (Njoku, 1963; Lawton and Akpan, 1968). Daubenmire (1972) suggests that in tropical deciduous forests,pollination is almost entirely by animals (mainly bees) whereas in temperate deciduous forests wind is the usual agent and more active during the dry season (Whitehead, 1969). The peak flowering coinciding with relative leaflessness of the canopy may also facilitate insect pollination by enhancing the visibility and ready access to the flower (Janzen, 1967). The timing seems to be for minimizing leaf interference for insects or even wind pollination. This alteration between flowering and leafing activity may be related to internal competition among plant organs for metabolites and/or hormones (Alvim, 1964).

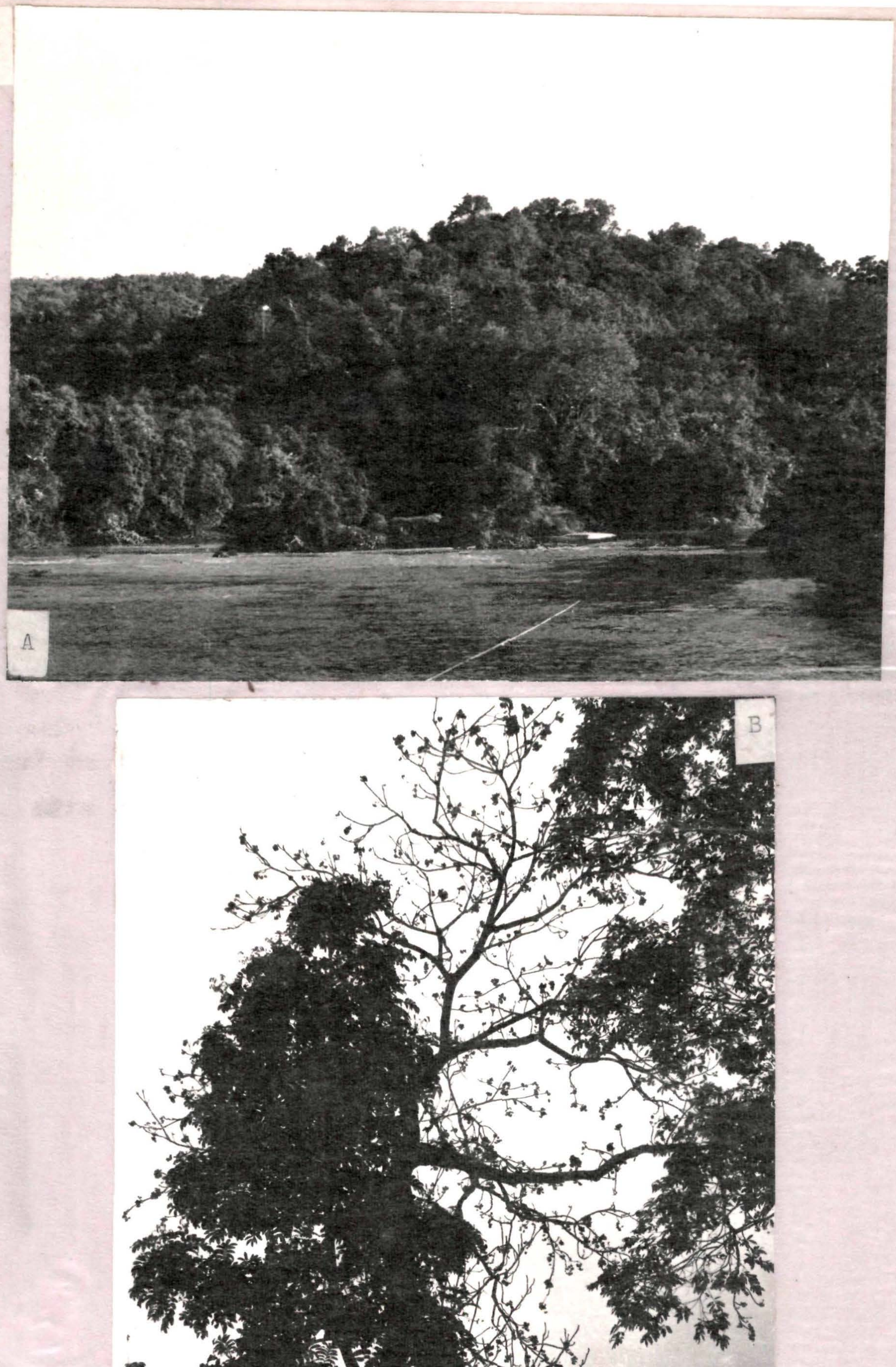
Peak fruiting in the community occurred during the wet season, most of them producing fleshy fruits with large or small seeds. The development of fleshy fruits is made possible by better moisture conditions prevailing during the wet season, These are mostly animal-dispersed often passing through their digestive tract. The need for high moisture level for proper development of fleshy fruits was shown by Zahner (1968). He showed experimentally that the shortage of soil moisture reduced the rate of enlargement and the final size of the fleshy fruits. Most of the dry season fruiters including some extended fruiters like *Duabanga sonneratioides* and *Schima wallichii* produce small winged seeds liable to be disseminated by wind during the dry period. Most of the species, producing fleshy fruits during wet season had larger fruits and seeds whose germination and early survival is possible only under better moisture conditions.

SUMMARY

Phenological observations on 122 tree species in a subtropical humid forest in north-eastern India were made. The forest had a higher proportion of evergreen compared to deciduous species. Leaf-fall of most of the tree species coincided with the dry season. Flushing in a majority of the tree species started towards the end of the dry season after different degree and period of leaflessness. Leaf production in the overstorey species extended over a

longer time period compared to the understorey species. For most of the species, flowering coincided with leaflessness. Proportionately more number of overstorey species flowered during the dry season, and wet season flowering was more for the understorey species. A majority of the species produced fruits during the wet season in which case the fruits were mostly of fleshy types. Fruits produced during the dry season were mostly of dry types. The significance of these results are discussed.

late 5



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CHAPTER - VI

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ON THE RELATION AMONG GROWTH STRATEGIES, ALLOCATION PATTERN, PRODUCTIVITY AND SUCCESSIONAL STATUS OF TREES IN THE FOREST COMMUNITY

INTRODUCTION

Species in a community differ in their growth characteristics and biomass production rate and therefore, it is necessary to consider biomass and production not only at the ecosystem level but also at the level of different species in the community (Gomez-Pompa and Vazquez-Yanes, 1974). While the studies on the productivity of temperate forest ecosystems (Lieth and Whiltaker, 1975) as well as that on tropical and sub-tropical forest to a certain extent (Farnworth and Golley, 1974) have been carried out at some depth, only few attempts have been made to understand differences existing between species at different successional status (Jordan, 1971; Farnworth and Golley, 1974). The aspect of resource allocation pattern related to the ecological niche a species may occupy, has received even lesser attention except for a few studies in temperate tree species of different successional status (Marks, 1974, 1975; Ramakrishnan *et al.*, unpublished). Such an approach of the partitioning of assimilates between root and different compartments of the shoot is of fundamental importance for understanding the adaptive strategies influencing species growth and production (Wareing and Patrick, 1975). Such a study of growth characteristics related to productivity would also form a basis for evaluation of species mixture for better forestry practices (Ramakrishnan, 1978).

The present study, therefore, deals with the general growth characteristics of different tree species in relation to production in a 50 year old sub-tropical humid forest community at Lailad, developed after slash and burn agriculture (Jhum) in north-eastern India (Ramakrishnan and Toky, 1978).

METHODS OF STUDY

The forest at Lailad has a disturbed peripheral region and an undisturbed central core (Singh, 1980). Six early successional light demanding tree species growing along the periphery of the forest, seven late successional shade-tolerant species from the central core and nine mid-successional tree species which are intermediate in their shade-tolerance, found in the transition zone, were selected for this study. Individuals of 4-6 years of age were identified for the study of general growth characteristics like root shape, extension and radial growth of the main axis, flushing pattern, leaf production and leaf longevity. The study of the biomass allocation pattern was done only in the case of 12 species where individuals of 1 to 5 years of age were available. However, all the 22 tree species were considered for the estimation of average below ground and above ground productivity. Biomass estimation was done in October-November when vegetative growth was at its maximum with maximum number of leaves on the individuals. Individuals were excavated and after obtaining fresh weight of the different components viz. root, stem, branch and leaf in the field, the samples were dried at 80±2°C to a constant weight.

RESULTS

The general growth characteristics of 22 tree species of 4-6 years age are shown in Table 1. In general, the growth period of early successional species was longer than that of mid-successional ones, the late successional species having the shortest growth period except for Saprosma ternatum which showed continuous growth throughout the year. Except for those growing throughout the year, growth was chiefly confined to the warmer parts of the year, in case of few others growth cessation occuring during September-October. The root characteristics markedly differed with the successional status of the trees. Early successional species had superficial spread of roots occurring mostly in the upper 20 cm of the soil profile, tap root being less distinct. The mid-successional species had distinct tap root but with considerable lateral spread while the late successional species showed a strong and deep tap root system with little lateral spread.

While tree height, in general, tended to be more in the case of early and mid-successional trees compared to late successional species. The annual shoot extension growth tended to be more for early successionals compared to late successional species, the mid-successional ones being more or less intermediate between the other two. A similar pattern was observed also for initial dbh as well as for annual radial increment. The early and late successional species showed continuous type of extension growth and leaf production during the growth period without any interruption. The mid-successional species showed distinct flushing separated by a rest period ranging from one month as in *Chikrassia tubularis* to over two months as in *Actinodaphnae angustifolia*. The number of flushing per year varied from one as in *Cinnamomum* sp. and *Dysoxylum procerum* to three-four as in *Amoora wallichii*, *Castanopsis indica* and *Chikrassia tubularis*. The number of leaves per flushing on the main axis varied greatly from 4-5 in *A. wallichii* to 14 in *Myristica linifolia*. This number was almost constant for each flush of a given species. The number of total leaves produced in a year, generally decreased from early to late successional types. The longevity of leaves was minimum for early successional species followed by mid-successionals and was longest for late successional species, It may be noted that the late successional species like *Cinnamomum* sp., *Goniothalamus Simonsii*, *Garcinia anomala* and *M. ferrea* bore leaves for more than one year.

Table 1. General growth characteristics of 22 tree species divided into three distinct successional status.

Species	initial age (yr)	growth period	root shape	initial ht. (cm)	annual extension (cm)	initial diam (dbh) (cm)	annual radial growth (cm)	growth type/ no.of flushes	leaves/ flush	total leaves per shoot/ yr	range of leaf longevity (week)
1	2	3	4	5	6	7	8	9	10	11	12
Early successionals:											
Sapium baccatum	4	all the year	superficial spread	469.0	116.0	3.20	1.40	continuous type	-	184	16-22
Sterculia villosa	5	Apr-Oct	thick pulpy	278.0	72.0	3.40	0.74	" "	-	24	20-24
Zanthoxylum Rhetsa	5	Mar-Oct	spreading, branched	394.0	83.5	3.20	0.54	" "	-	58	24-38
Hibiscus macrophylla	5	Mar-Oct	" "	703.0	102.5	4.60	1.14	" "	-	34	22-30
Litsea sebifera	4	Mar-Oct	" "	217.5	78.0	3.64	0.42	" "	-	35	42-48
Vitex oltissima	5	May-Aug	" "	303.0	74.5	3.80	0.82	" "	-	36	32-46
Mid-successionals:											
Amoora wallichii	4	May-Oct	tap root with many laterals	350.6	80.5	2.90	1.10	flushing type, 3 flushes	4-5	14	41-50

Table 2 (contd.)

1	2	3	4	5	6	7	8	9	10	11	12
Dysoxylum procerum	5	Apr-Oct	tap root with many laterals	365.5	65.5	2.40	0.34	1	12	12	44-50
Chikrassia tubularis	4	May-Oct	" "	351.0	87.0	2.50	0.64	4	11-13	48	34-46
Castanopsis indica	4	Apr-Oct	" "	301.0	82.0	2.65	0.42	3	10-13	36	40-50
Englehardtia spicata	6	Jun-Sep	" "	285.0	43.5	3.54	0.36	1	8	8	28-48
Elaeocarpus robustus	4	Jun-Oct	" "	265.0	57.0	2.25	0.45	1	16	16	40-52
Myristica linifolia	5	Apr-Aug	" "	280.0	73.0	2.80	0.78	1	14	14	44-53
Actinodaphnae angustifolia	4	Jun-Oct	" "	328.0	94.5	2.65	0.85	2	7-10	17	49-60
Cinnamomum sp.	6	Jun-Sep	" "	356.0	58.0	3.48	0.34	1	16	16	50-64

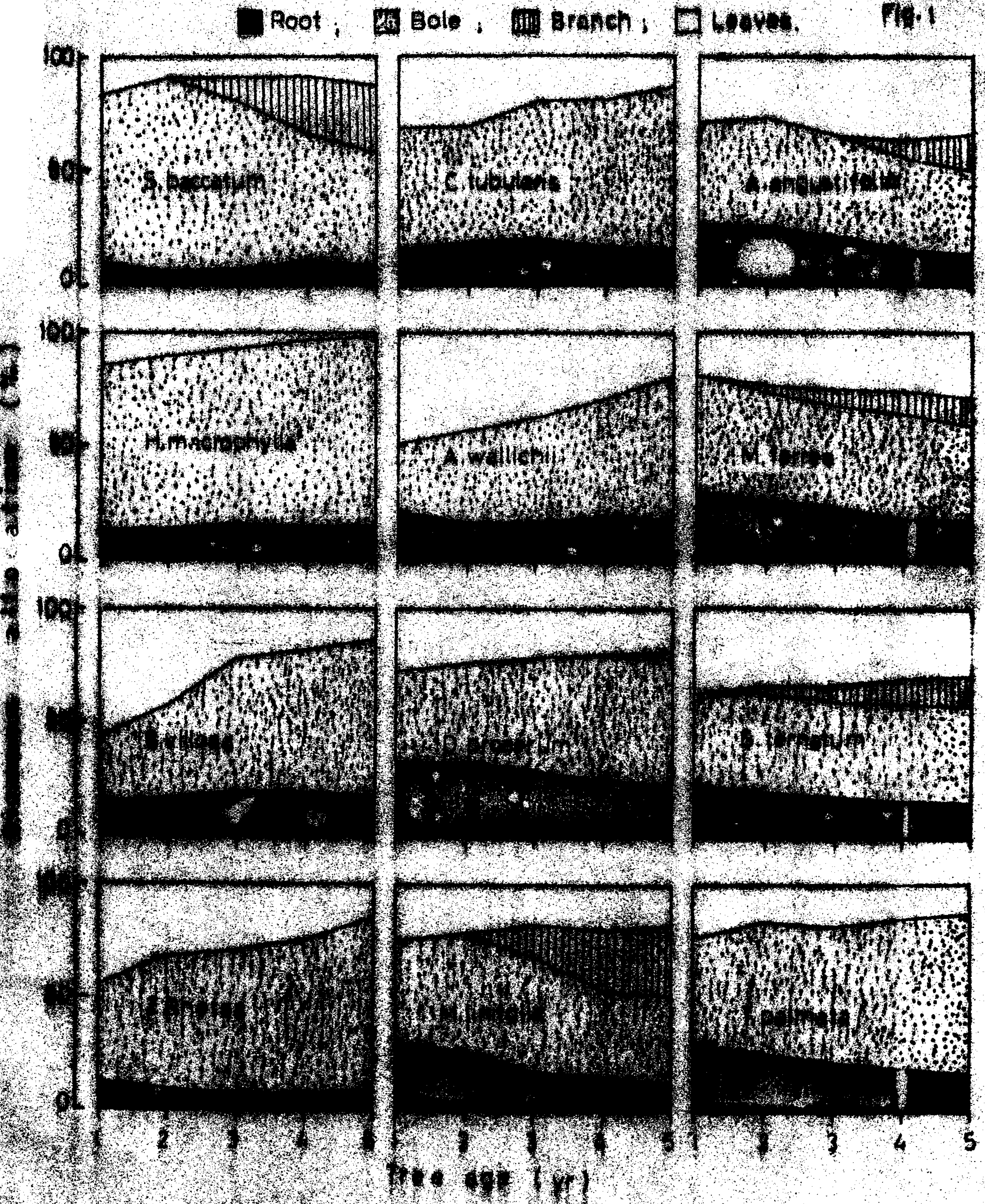
Table 1 (contd.)

1	2	3	4	5	6	7	8	9	10	11	12
Late successionals:											
Saprosma ternatum	5	all the year	tap root with few laterals	324.0	50.9	2.50	0.38	continuous type	-	18 pairs	50-62
Michelia punduana	5	May-Oct	" "	193.0	43.8	1.62	0.32	" "	-	14	42-50
Goniothalamus Simonsii	5	May-Sep	" "	255.5	46.2	3.24	0.43	" "	-	8	54-68
Garcinia anomala	6	Feb-Nov	" "	380.0	52.0	4.45	0.80	" "	-	30	50-58
Miliusa roxburghiana	6	May-Sep	" "	215.0	28.5	1.58	0.30	" "	-	25	42-48
Travesea palmata	4	May-Sep	" "	208.5	32.5	1.48	0.28	" "	-	7	46-50
Mesua ferrea	5	Jun-Sep	" "	148.0	28.0	1.20	0.24	1 flush	10 pairs	10 pairs	48-56

The allocation pattern of biomass in the four different compartments of root, stem, branch and leaf, is expressed as the percentages of total capital in each of the 12 tree species (Fig. 1). The proportional allocation to roots of early successional species (Sapium baccatum, Hibiscus macrophylla, Sterculia villosa and Zanthoxylum Rhetsa) was lower in comparison to that in mid- and late successional species. Further up to 5 years of age, the allocation percentage to roots was nearly constant with minor fluctuation for early successionals while there was a gradual decrease from 1-5 year in some of the mid-successional (Dysoxylum procerum, Myristica linifolia, Actinodaphnae angustifolia) and all the late successional species. (However, the roots of S. villosa were thicker and pulpy at the initial stages of growth and showed greater allocation as compared to other early successional species). In general, allocation to the bole (main axis) decreased from early to late successional species. The early successional species remained branchless upto 5 years except for Sapium baccatum in which the modular growth resulted in many branches after 3 years of growth. All the late successionals and M. linifolia, a mid-successional species, showed considerable allocation to branches after 3 years of growth. (Travesea palmata, a late successional species remained branchless upto 5 years). The allocation to leaves in the early successional species generally decreased with

Fig. 1 Biomass allocation pattern (%) of 12 different tree species arranged roughly in three groups. The first column is of early successional, second column mid-successional and the third column (except *A.angustifolia*, a mid-successional species) represents the late successional species.

Fig. 1



■ Root ; ▨ Bole ; ▥ Branch ; ☐ Leaves.
100
50
0
S. baccatum
C. tubularis
A. angustifolia
H. macrophylla
A. wallichii
M. ferrea
B. villosa
D. procerum
S. ternatum
palmata
1
2
3
4
5
Tree age (yr)

age but this decrease was slower in the case of late successional species.

The average below ground and above ground productivity was nearly similar for early and mid-successional species but higher than that for the late successional ones. However, the below ground productivity as compared to above ground productivity was proportionately higher for late successional species compared to that of the early successional ones. (Table 2).

DISCUSSION

The different tree species from a successional gradient which could broadly be categorized into early-, mid- and late successional species, showed a number of differences in growth characteristics of adaptive nature. A simple and uniform measure of growth is a year's elongation of the terminal twig (main axis) of saplings ($H_o$rn, 1971). This annual extension growth of the main axis of early successional species was markedly higher than that of the mid- and late successional ones. This faster growth is partly achieved due to longer duration of growth period for early successional species as compared to that for late successional ones. Thus, the former strarts growth earlier and stop much later. It may be noted here that the time of initiation of extension growth for all the species was more

Table 2. The average belowground and aboveground productivity (g/plant/year) of 22 tree species divided into three distinct successional status.

Species	belowground productivity	aboveground productivity
Early successionals:		
Sapium baccatum	82.0 ± 2.31	518.8 ± 38.46
Sterculia villosa	74.4 ± 3.16	430.8 ± 12.46
Zanthozylum Rhetsa	71.8 ± 2.08	398.4 ± 16.48
Hibiscus macrophylla	77.2 ± 3.24	539.2 ± 24.56
Litsea sebifera	86.4 ± 5.78	392.3 ± 16.45
Vitex oltissima	78.5 ± 5.24	304.0 ± 24.68
Mid-successionals:		
Amoora wallichii	83.1 ± 4.21	284.9 ± 13.24
Dysoxylum procarum	69.6 ± 5.24	265.7 ± 8.26
Chikrassia tubularis	88.3 ± 8.24	447.1 ± 28.26
Castanopsis indica	74.2 ± 3.04	398.6 ± 29.08
Englehardtia spicata	71.5 ± 3.28	308.0 ± 31.45
Elaeocarpus robustus	82.2 ± 9.25	324.0 ± 21.60
Myristica linifolia	89.5 ± 8.48	464.2 ± 36.84
Actinodaphnae angustifolia	74.5 ± 6.24	402.4 ± 24.20
Cinnamomum sp.	83.2 ± 8.04	308.5 ± 42.14
Late successionals:		
Saprosma ternatum	86.4 ± 3.01	244.4 ± 22.46
Michelia punduana	72.2 ± 5.62	234.2 ± 16.45
Goniothalamus Simonsii	66.5 ± 5.05	204.2 ± 30.18
Garcinia anomala	96.5 ± 4.62	320.0 ± 24.20
Miliusa roxburghiana	62.4 ± 4.45	184.0 ± 16.48
Travesea palmata	38.8 ± 3.68	84.8 ± 8.54
Mesua ferrea	56.8 ± 2.04	138.2 ± 12.04

± standard error

variable than the time of growth cessation unlike that in temperate trees (Kramer, 1943; Kozlowski and Ward, 1957; Marks, 1975). Differences in the time of initiation of extension growth of different species may be important ecologically as the species at different successional status and age may experience different environment of light, temperature and humidity (Marks, 1975). The growth strategy of early successional species may help in the fast vertical upward movement of their crown for maximum exploitation of high light environment, as the early successionals are adapted to grow faster than late successionals only at high light intensity i.e. between 54-100% of full sunlight (Horn, 1971).

The mid-successional species exhibited flushing type of growth pattern with fairly long intermittent rest period between two successive flushes. The rapid extension of internodes followed by periods of rest may have adaptive significance to periods of environmental stress and may permit association of diverse species on the same site with a wide range of vertical stratification (Brown, 1971). This pattern of growth, more common in temperate species, is regarded as more competitive, allowing successful association of numerous woody plants. The mid-successional species have the characteristics similar to 'gap phase species' of Watt (1947) which are best considered intermediate in successional status and extension growth characteristics. These species may also be found in climax forest but they differ from late successionals in their inability to maintain advanced regeneration beneath a closed canopy. They may maintain themselves in the climax forest by colonizing gaps in the canopy (Marks, 1975). However these gaps are not so frequent and have been calculated to occur in some tropical forests on an average of 100 years (Hartshorn, 1978). These gaps are caused by the death of mature trees or by the fall of major branches. The slower but sustained (continuous) growth of the late successional species is suited to diminished light conditions created during the later stages of succession.

The greater number of annually produced leaves and shorter leaf longevity in the case of early successional species as compared to late successional ones may be related mainly to the light conditions prevailing in the early successional environment. It has been found that the rate of leaf production and leaf abscission are faster under high light intensity (Bentley, 1979). The longer the leaves that remain on the plant, the greater are the chances of colonization of leaf surface by epiphylls which may adversely affect the primary production of a species by obscuring photosynthetic area (Bentley, 1979).

The early successional species of the community in general, were found to allocate less to the root system compared to the late successional species. These observations suggest firstly, that the early successional species tend to maximize allocation to their shoot system with higher productivity (Watson, 1971; Wareing and Patrick, 1975) in order to put up their canopy as high as possible for exploiting the high light environment. The greater allocation to the bole compartment supports this strategy. Secondly, the spreading root system mostly in the upper soil profile (20 cm) provide enough absorptive system though with poor physical support. This type of root distribution may exploit the short term increases in nutrient and water available in disturbed sites (Marks and Bormann, 1972). On the other extreme, the late successional species have higher allocation to their roots in order to draw upon the nutrient pool from deeper soil layers and exhibit deeper roots with less lateral spread. Between these two extremes are the mid-successional species which are intermediate, with a tap root system but with considerable lateral spread to exploit disturbed sites as well as to occur in more developed communities.

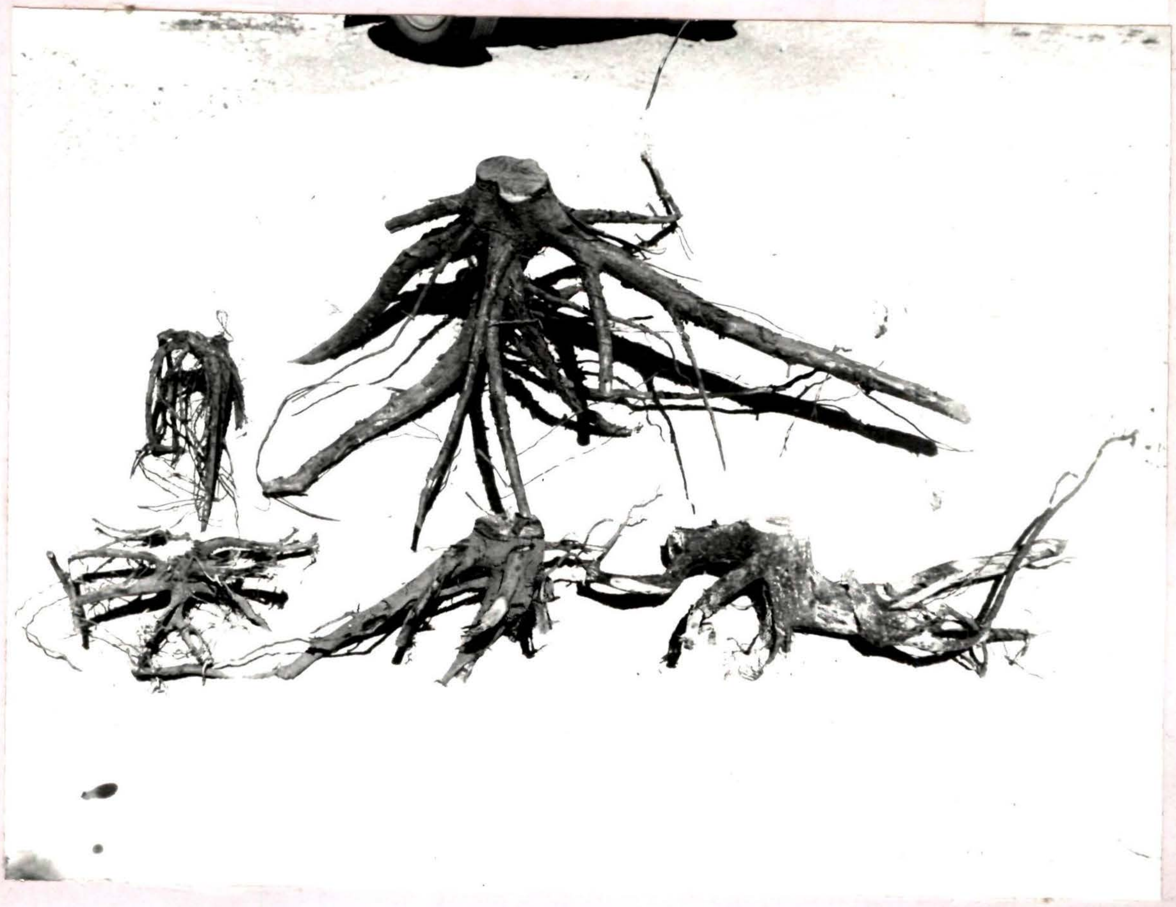
The productivity pattern could be related to the successional status which in turn is related to the growth characteristics of the trees. Root productivity of the early and mid-successional species was only slightly higher than that of the late successional species. On the other hand, the average shoot productivity was markedly higher for early successional species and least for late successional ones, the mid-successional species behaving in an intermediate manner.

SUMMARY

The present study deals with the growth characteristics, biomass allocation pattern and average productivity of 22 tree species occupying different ecological niches in a 50 year old sub-tropical humid forest in north-eastern India. The early successional species were shown to have greater shoot production as compared to late successional ones and these were related to their growth pattern. The biomass allocation pattern of early successional species showed higher allocation to the shoot than to the root as compared to the late successional ones. The root system of the early successional species were surface feeders with no conspicuous tap root system whilst the late successional species had deep penetrating tap root system with little lateral spread. The mid-successional species were intermediate in all the respect between the two extremes. These differences between the three categories of tree species are discussed in relation to the ecological niche they occupy in the community.

Plate 6

Plate 7



* * *

CHAPTER - VII

* * *

SEED GERMINATION AND SEEDLING ESTABLISHMENT OF TREES IN THE FOREST COMMUNITY

INTRODUCTION

Germination and seedling establishment are two very critical phases in life-history of a species (Ramakrishnan, 1972; Gomez-Pompa and Vazquez-Yanes, 1974; Harper and White, 1974). The duration of suitable conditions and the rate at which the seed is able to respond to these, are major factors which determine germination and establishment under field conditions. Factors like topography of the soil surface, light, temperature and moisture regime of seed bed, soil compaction and depth of burial are much discussed (Harper et al, 1965; Hett and Loucks, 1971; Sheldon, 1974; Noble and Whalley, 1978).

Not much is known about the ecology of germination and establishment of tree seedling under natural conditions (Kinnaird, 1974). Our understanding of tropical tree species in this regard is even lesser. The present study, therefore, deals with the germination and establishment of 12 important tree species of a sub-tropical forest under different conditions of topography, light and depth of burial in the soil.

METHODS OF STUDY

The germination and establishment studies were carried out in a sub-tropical forest community at Lailad.

Estimations of seed weight for all the species were made after drying the seeds at 80$\pm$2°C for 48 hours. Except for Mesua ferrea and Amoora wallichii, the seed coat contributed little to the seed weight and therefore, the seed weight was considered to be an indicator of seed reserve.

For the first experiment, sites with two different topography (level and slope of 30°angle) were selected in the open as well as under a forest canopy. At each of the four sites, 36 quadrats of 1 m^2 were marked after clearing the litter and herb layer on the soil surface. Each quadrat was divided into two-halves for germination test at two different depths. Seeds were sown at depth of 2 and 5 cm using graduated pegs and a card-board sheet with 50 uniform holes to place 50 seeds at equal distances from each other. Seed sowing was done in July, 1979 followed by monthly observations of seed germination and establishment. All treatments were replicated 3 times.

In the second experiment, 100 one-month old seedlings of Duabanga sonneratioides Ham., a shade-intolerant early successional species and Artocarpus chaplasha Roxb., a shade-tolerant late successional species, were planted in 1 m^2 quadrat at equal distances both in the open and under a forest canopy on level ground. Monthly observations were made on establishment of seedlings. The treatments were replicated 5 times.

RESULTS

Table 1 shows the average seed weight for fresh and oven dried seeds of the different species. The early successional species, generally had smaller seeds with lesser seed weight compared to mid- and late successional species except for *Dillenia pentagyna* which had light seeds with low seed reserve.

The germination percentage of early successional species like *Sterculia villosa*, *Premna miliflora* and *Lagerstroemia parviflora* was higher at 2 cm depth of seed burial as compared to that at 5 cm depth except for *Erythrina stricta* which showed the reverse behaviour. The former three species, generally showed lower germination percentage on the slope than on level ground particularly at 2 cm depth of burial but the trend was often different at 5 cm depth of burial. The germinability of seeds in the shade was either not significantly different or was less than that in the open, depending upon the species. Only rarely did the germination improve in shade. Mid-successional species like *A. wallichii* and *Bauhinia purpurea* responded little to differences in the light regime, topography or depth of seed burial with respect to seed germination and a similar behaviour was noted for the late successional species too (Table 2).

The survivorship of seedlings of different species

Table 1. Average weight/seed in fresh and oven dried conditions.

Species	fresh seed (g)	dried seed (g)
Early successional:		
Sterculia villosa	0.30	0.24
Erythrina stricta	0.22	0.14
Premna miliflora	0.02	0.008
Lagerstroemia parviflora	0.01	0.006
Mid-successional:		
Bauhinia purpurea	0.22	0.17
Amoora wallichii	12.04	9.86
Late successional:		
Dillenia pentagyna	0.22	0.01
Artocarpus chaplasha	0.64	0.42
Sterculia coccinea	0.92	0.41
Pithecolobium longan	0.74	0.58
Mesua ferrea	3.94	3.31
Garcinia cowa	0.33	0.22

Table 2. Maximum germination percentage (of total seed put in the soil) of different species in the field conditions. (Upper values, in the open; and in parenthesis, under shade of the forest canopy).

Species	depth of seed burial			
	2 cm		5 cm	
	slope 0°	slope 30°	slope 0°	slope 30°
Early successionals:				
Sterculia	87.3±3.7	74.0±2.3	43.3±5.7	54.0±3.5
villosa	(79.7±1.8)	(76.7±4.4)	(48.0±5.0)	(54.7±8.1)
Erythrina	58.3±4.4	75.0±8.7	70.0±5.7	78.3±2.2
stricta	(68.3±7.3)	(56.7±6.0)	(76.7±8.8)	(91.7±4.4)
Premna	90.0±2.9	74.2±6.8	68.3±4.4	68.3±5.1
miliflora	(81.7±3.0)	(77.5±4.3)	(41.7±6.0)	(71.7±10.9)
Lagerstroemia	35.0±5.1	36.0±3.6	30.7±3.5	26.7±5.8
parviflora	(36.0±5.5)	(34.0±3.5)	(20.0±3.5)	(29.0±3.8)
Mid-successionals:				
Bauhinia	96.0±1.2	97.3±1.8	98.7±4.3	99.3±0.7
purpurea	(93.3±0.7)	(95.3±1.8)	(100 ±0)	(98.7±1.3)
Amoora	96.7±3.4	93.3±6.6	96.7±3.4	96.7±3.4
wallichii	(93.3±3.4)	(96.3±1.9)	(96.3±1.9)	(93.3±4.2)
Late successionals:				
Dillenia	40.1±4.9	26.7±2.2	27.8±2.6	26.7±6.9
pentagyna	(34.4±5.1)	(31.1±5.9)	(16.7±3.9)	(26.7±4.8)
Artocarpus	85.3±2.2	76.6±5.8	88.7±3.4	87.8±3.4
chaplasha	(90.0±3.2)	(74.4±4.3)	(86.7±2.6)	(82.2±4.7)
Sterculia	89.2±2.2	92.5±1.4	90.0±2.9	95.8±2.2
coccinea	(95.8±1.4)	(92.5±2.5)	(98.3±2.9)	(93.3±5.2)
Pithecolobium	95.0±2.5	97.5±2.5	95.0±8.7	91.7±6.3
longan	(98.3±2.9)	(95.0±2.9)	(94.2±6.3)	(90.0±3.7)
Mesua	67.3±4.7	76.0±4.0	74.7±7.1	81.3±3.5
ferrea	(81.3±3.5)	(72.0±4.6)	(81.3±5.8)	(76.0±8.3)
Garcinia	76.0±2.0	72.7±5.0	72.7±4.4	74.0±5.3
cowa	(75.3±1.2)	(28.0±6.0)	(77.3±3.1)	(64.0±4.6)

± standard error

under two light regimes at the end of rainy season, winter and summer drought period is expressed as the percentages of total seedlings present after germination was complete (Fig. 1). The number of survivors after the rainy season declined drastically for all the early successional species except *S. villosa* under both the light conditions. Among the early successional species *S. villosa* and *L. parviflora* suffered higher seedling mortality during winter than the other two, under both the light conditions. The mid-successional and late successional species all showed very low rainy season mortality except for *A. chaplasha* and *D. pentagyna*. Mortality in winter months and during the summer drought was more pronounced in the open than in shade for the late successional species. The mid- and late successional species also showed generally high survival at the end of one year period compared to early successional species, the only exception being *D. pentagyna*.

The monthly pattern of survivorship of an early successional, *D. sonneratioides* and a late successional, *A. chaplasha* in the open and under the shade was observed using transplanted seedling (Fig. 2). *D. sonneratioides* showed steep decline in population under shade with total mortality after 8 months whereas in the open the mortality in this species was very low so that 55% of the seedlings survived at the end of one year. On the other hand, heavy mortality occurred in both the open and shade-grown seedlings

Fig. 1 Survivorship (%) and mortality (%) of seedlings growing in the open (a) and under forest canopy (b) during rainy season, winter season and drought with final establishment (%) after one year in early successional (1-4), mid-successional (5-6) and late successional (7-12) species. 1, *Sterculia villosa*; 2, *Erythrina stricta*; 3, *Premna miliflora*; 4, *Lagerstroemia parviflora*; 5, *Bauhinia purpurea*; 6, *Amoora wallichii*; 7, *Dillenia pentagyna*; 8, *Artocarpus chaplasha*; 9, *Sterculia coccinea*; 10, *Pithecolobium longan*; 11, *Mesua ferrea*; and 12, *Garcinia cowa*.

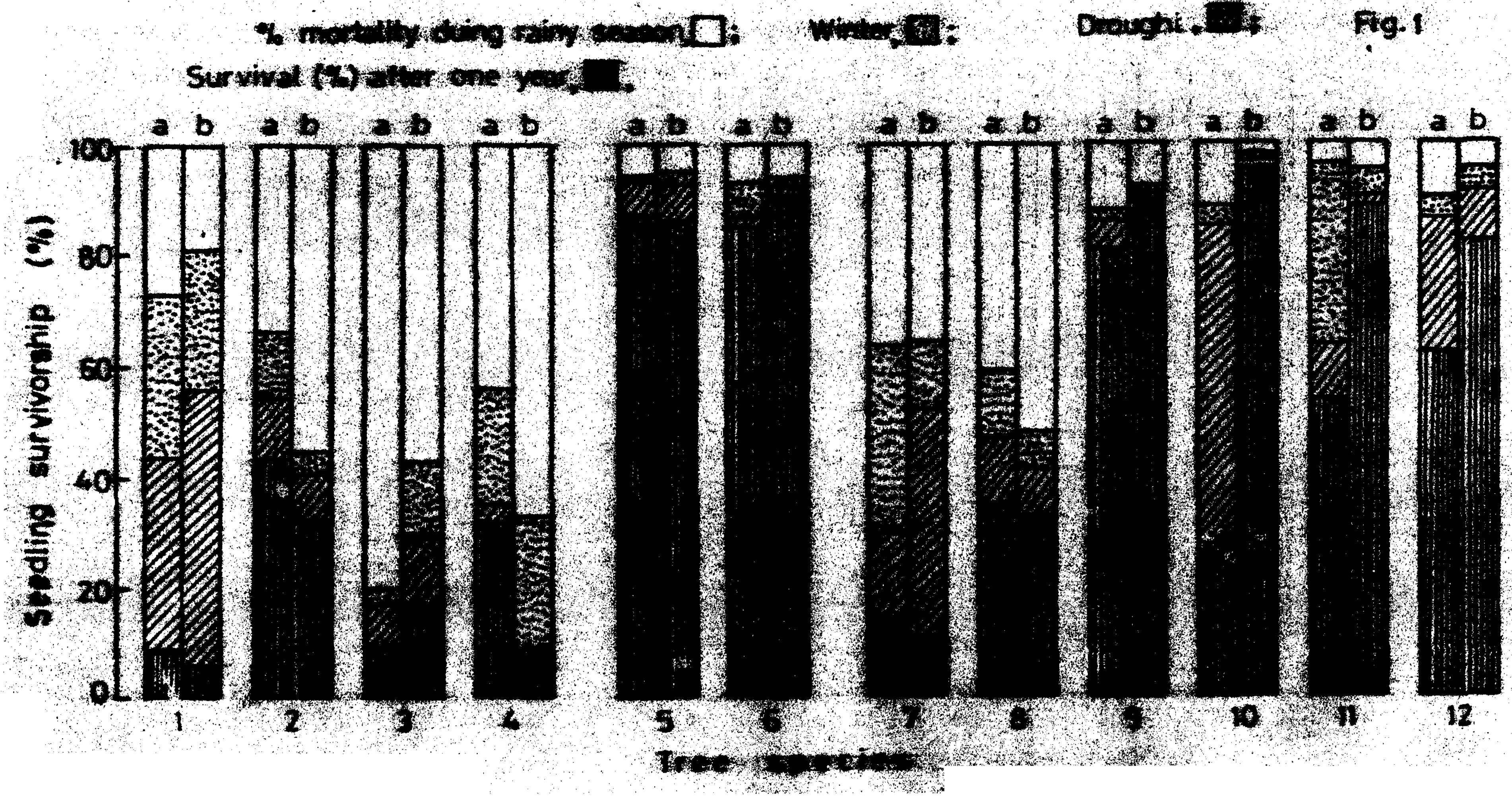
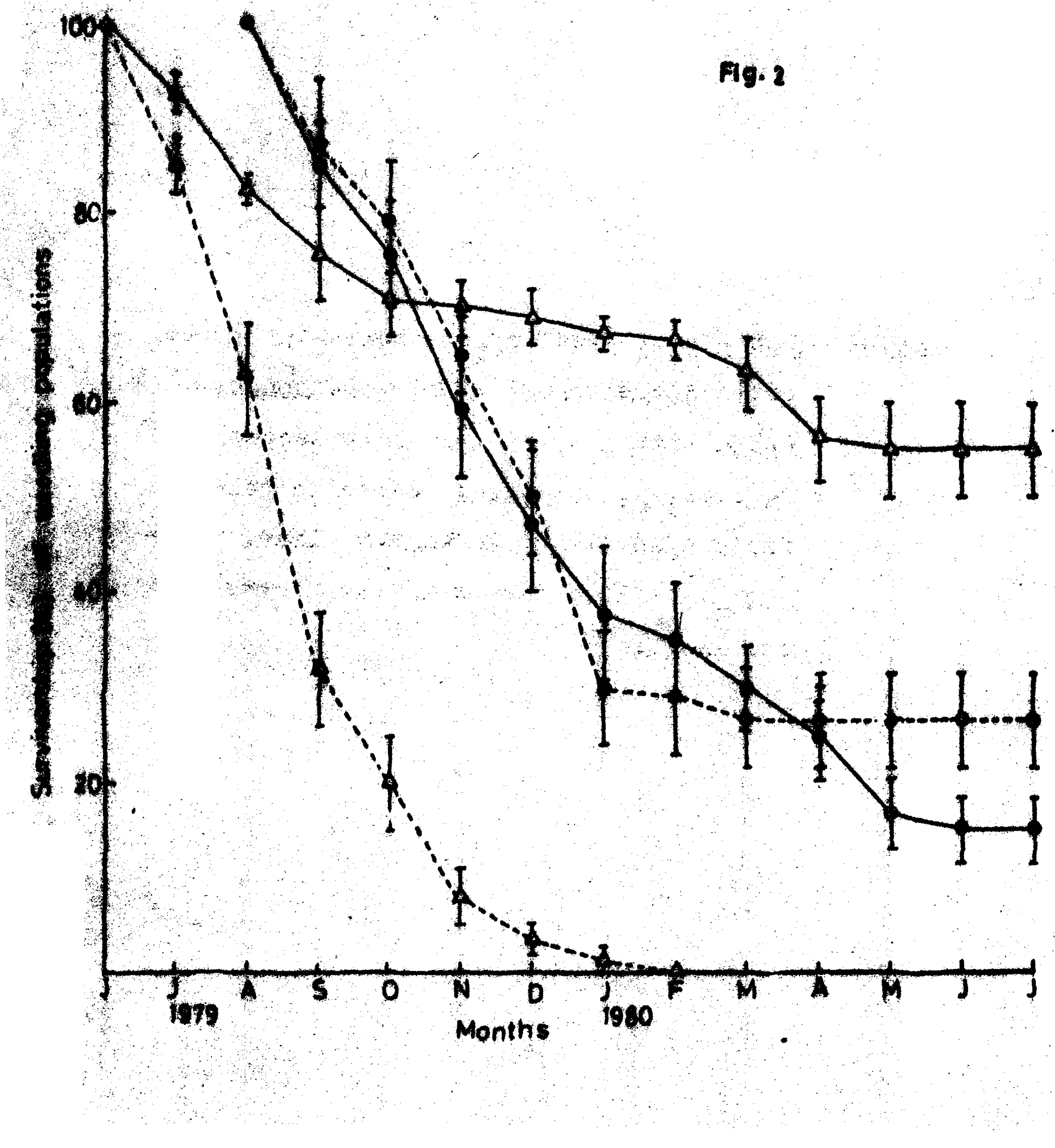

% mortality during rainy season ☐;
Winter ▨;
Drought ▨;
Survival (%) after one year ■.
Seedling survivorship (%)
0
20
40
60
80
100
a
b
1
2
3
4
5
6
7
8
9
10
11
12
Tree species

Fig. 1

Fig. 2 Pattern of seedling survivorship of one early successional species *D. sonneratioides* (open triangle) and one late successional species, *A. chaplasha* (closed circle) in field conditions. Continuous line, open-grown seedlings; broken line, forest-grown seedlings.

Fig. 2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1980
Months

of *A. chaplasha* during the first few months. However, the final survival value was higher in the shade than in the open for this species.

DISCUSSION

After its escape from predation and pathogens, the chance that a non-dormant, surface-lying seed will develop into an established seedling is dependent on its fixation in a safe-site which provides the specific condition for its germination and establishment (Harper *et al*, 1971; Sheldon, 1974; Grime, 1979). Shaw (1968) found 50% more germination from the buried acorns of *Quercus petraea* compared to surface lying ones and attributed the seed burial, a protective mechanism which is created by natural soil disturbance in the forest. In the present case, seed burial at a shallow depth was found to be more favourable for germination of the early successional species which generally have light seeds. The deep seated seeds of these species may fail to germinate because of the low potential of the seedlings due to meagre seed reserves to penetrate through the soil profile (Sheldon, 1974). The late successional species generally with heavier and larger seeds showed equally good germination at both the depths of seed burial. Further, this could also be related to light availability at these depths, as early successional species generally do better under high light regimes. However, the present studies on germination in the open and under the shade show significant reduction under shade for some of the early successional species.

The mortality pattern, in general, of the early and late successional species are quite different from one another. The generally high mortality of the early successional species at the end of the rainy season may be related to heavy washout of the soil and the consequent exposure of the superficially placed root system of this category of species (Chapter IV). This is also supported by poor establishment of early successional species on steep slopes where seed/seedling washout is likely to be severe. This is in contrast to the mid- and late successional species which are shown to have well developed deep penetrating tap root system. Further, the seedling survivorship of the late successional species, generally was more in shade than in the open, probably related to their shade-tolerant nature (Horn, 1971; Grime, 1979) which provides protection from water stress. Conversely, the drastic reduction in the survivorship of the early successional species under the shade may be due to their requirement of high light intensity (Horn, 1971). Further, the shade-intolerant species are reported to be more susceptible to fungal attack under shade compared to the shade-tolerant species (Vaartaja, 1962; Grime and Jeffrey, 1965). Such a differential pattern for early and late successional species in the open and shade has been further supported by that of D. sonneratioides belonging to the former category and A. chaplasha belonging to the latter category.

SUMMARY

Observations on seed germination and seedling establishment for 12 important tree species of different successional status were made by seed introduction at two different conditions of light, topography and depth of seed burial in a sub-tropical humid forest. The germination percentage of early successional species was higher in the open, at shallower depth (2 cm) and on the level ground while the shade, steep slope and deep burial (5 cm) adversely affected the germination percentage of these species. Mid- and late successional species responded little to differences in these condition. The survivorship of seedlings of early successional species at the end of rainy season was more adversely affected than that of mid- and late successional species. This was related to the generally lighter seeds of early successionals. The higher seedling survival of late successional species in shade than in the open and the reverse behaviour of the early successional species are related to their adaptation to different light regimes in the forest community.

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APPENDIX

Lists of species recorded and their phenological characteristics are given below. Abbreviation used in the lists are as follows:

NLD, no significant leaf-drop observed at a time.
CL, production of leaves round the year.

1. Phenological records for overstorey tree species.

Tree species 1	Leaf-drop leaflessness 2	Flushing 3	Flowering 4	Mature fruits 5
Alstonia scholaris R. Brown				
Amoora wallichii King.	Feb-Mar (NLD)	Apr	Feb-Mar	Jun
Anthocephalus cadamba Miq	Feb-Mar	Mar	May	Sep
Aperosa oblonga Muell.	Jan-Mar	Apr-May		Aug
Artocarpus chaplasha Roxb.	Mar-Apr	Apr	Apr-May	Jul
Baccouria sapida Muell.	Aug-Sep Feb-Apr	Apr	Apr-May	Jul-Aug
Beilschmiedia Roxburghiana Nees.	NLD	May	Nov-Dec	Mar-Apr
Bischoefia javanica Blumi.	Feb-Mar	Mar-Apr	May	Aug
Bombax malabaricum D.C.	Feb-Mar	Apr-May	Feb	Apr-May
Casearia glomerata Roxb.	Feb-Mar	May	Apr-May	Jul-Aug
Castanopsis indica A. DC.	Sep-Oct Feb-Mar	Mar	Jun-Jul	Sep
C. tribuloides A. DC.	Sep-Oct Feb-Mar	Mar-Apr	Jun-Jul	Sep-Oct
Cedrella toona Roxb.	Aug-Sep Feb-Mar	Apr	May	Jul-Aug
Ceiba pentandra Gaert.	Jan-Feb	Apr-May	Jan-Feb	Apr
Chrysophyllum sp. L.	Mar-Apr (NLD)	May	Apr-May	Jul-Aug

1	2	3	4	5
Chukrassia tubularis A. Juss.	Sep-Oct, Feb-Mar	Apr	Apr-May	Jul-Aug
Cordia myxa L.	Feb-Mar	Apr-May	Apr-May	Jul-Aug
Dillenia indica L.	Aug-sep, Feb-Mar (NLD)	Mar-Apr	May-Jun	Aug-Sep
D. pentagyna Roxb.	Feb	May	Apr-May	Jul
Diospyros kaki L.	Reb-Mar (NLD)	Apr-May	May-Jun	Feb-Mar
Duabanga sonneratioides Ham.	Feb-Mar (NLD)	CL	Oct-Mar	May
Dysoxylum binectiferum Hook.	Mar-Apr (NLD)	Mar-Apr	Jan-Feb	May-Jun
D. procerum Hiern.	Mar-Apr (NLD)	Mar-Apr	Feb	Jun-Jul
Elaeocarpus obtusus Blume.	Aug-Sep, (NLD) Feb-Apr (NLD)	Apr	Apr	Jul-Aug
E. robustus Roxb.	Sep-Oct, Feb-Apr (NLD)	Apr	Apr	Jul-Aug
Englehardtia spicata Blume	Feb-Mar	May-Jun	Feb-Mar	Apr-May
Erythrina stricta Roxb.	Jan-Feb	Apr-May	Feb	Mar-Apr
Eugenia aquea Burm.	Sep-Oct, Feb-Mar (NLD)	Mar-Apr	Apr	Jun-Jul
E. jambolana Lam.	NDL	Apr	Mar-Apr	Jun
E. magnifolia Wall.	NDL	Apr-May	Mar-Apr	Jul
E. munronii Wight.	Feb-Mar (NLD)	Mar-Apr	Dec-Jan	Apr-May
E. polypetala Wight.	Feb-Mar	Apr-May	Apr	Jun-Jul
Ficus altissima Blume.	Aug-Sep, Feb-Mar (NLD)	Mar-Apr	Mar-Apr	May-Jun
F. benghalensis L.	NLD	Feb-Mar	Mar	Apr-May
F. clavata Wall.	NLD	Mar-Apr	Feb-Mar	Apr-May
F. elastica Roxb.	Sep-Oct (NLD)	Mar	Apr-May	Aug-Sep

1	2	3	4	5
F. geniculata Kurz.	Feb-Mar (NLD)	Apr	Apr	May-Jun
Foramina colorata Roxb.	Jan-Feb	Apr	Feb-Mar	Jun-Jul
Garcinia anomala Planch.	Feb-Mar (NLD)	Apr-May	Mar-Apr	Jun-Jul
Garcinia cowa Roxb.	Feb-Mar (NLD)	Apr	Mar	Jul
Gmelina arborea L.	Feb-Mar	May-Jun	Apr-Jun	Jul-Aug
Hibiscus macrophyllus Roxb.	Feb-Mar	Mar	Apr-May	Jun-Jul
Hydnocarpus kurzii King.	NLD	Mar-Apr	Apr	Oct-Nov
Illex excelsa Wall.	Feb-Mar	Apr	Apr	Jun-Jul
Itea macrophylla Wall.	NLD	Apr-May	Apr	Jun-Jul
Karya arborea	Feb	Apr-May	Apr	Jun-Jul
Lagerstroemia parviflora Roxb.	Feb-Mar	Apr-May	Jun-Jul	Aug-Sep
Lannea grandis Engler	Feb	May		
Machilus khasianum Nees	Feb-Mar (NLD)	Mar-Apr	Apr-May	Jun-Jul
Mangifera indica L.	Feb-Mar (NLD)	Apr	Feb-Mar	May-Jun
Melia composita Willd.	Aug-Sep, Feb-Mar	Apr	Mar-Apr	Jun-Jul
Memecylon cerasiforme Kurz.	NLD	Apr	Apr-May	Jul-Aug
Mesua ferrea L.	NLD	Apr-May	Mar-Apr	Jul-Aug
Meliusa roxburghiana Hook.	Mar-Apr	May	Apr-May	Jul-Aug
Morus laevigata Wall	Jan-Feb	Apr	Feb-Mar	Apr-May
Myristica linifolia Roxb.	NLD	Apr-May	Feb-Mar	Jun-Jul
Phoebe angustifolia Meissn.	NLD	Apr-May	Apr-May	Jul-Aug
Psychotria sp. L.	NLD	Mar-Apr	Apr-May	Jul-Aug

1	2	3	4	5
Rubiacea	Mar-Apr (NLD)	Apr-May	May	Aug-Sep
Sapium baccatum Roxb.	Mar-Apr (NLD)	CL	Apr-May	Aug-Sep
Saprosma ternatum Hook.	NLD	CL	Apr-May	Aug-Sep
Schima wallichii Choisy	Feb-Mar	Mar-Apr	Apr-Aug	Oct-Dec
Shorea robusta Gaert.	Apr-Jun	Apr-May	Mar-Apr	Jul
Spondias mangifera Willd.	Jan-Feb	May-Jun	Mar-Apr	Jun-Jul
Sterculia villosa Roxb.	Jan-Feb	Jul-Aug	Feb-Mar	Jan-Jul
Stereospermum chelonoides DC.	Mar-Apr	Apr	Apr-May	Jul-Aug
Talauma phellocarpa King.	Feb (NLD)	Apr	Apr	Jun-Jul
Tectona grandis L.	Apr	May-Jun	Jan-Mar	May-Jul
Terminalia chebula Retz.	Jan-Feb	Apr	Jul-Aug	Nov-Dec
T. myriocarpa Heurk & Muell.	Jan-Feb	Apr	Feb-Mar	May-Jun
Tetrameles nidiflora R.Br.	Jan	May-Jun	May	Jul-Aug
Trewia nudiflora L.	Feb-Mar	Apr-May	Mar-Apr	Jul-Aug
Vitex altissima L.	Jan-Feb	Apr-May	Apr-May	Jul
V. glabrata R. Brown	Feb	Apr	Apr	Jul-Aug
V. penduncularis Wall.	Jan-Feb	May	Apr-May	Jul-Aug
Zanthoxylum Rhetsa DC.	Dec-Jan	Mar	Jul-Aug	Sep-Oct

2. Phenological records for understorey tree species.

Tree species	Leaf-drop, leaflessness	Flushing	Flowering	Mature fruits
1	2	3	4	5
Actinodaphnae angustifolia Nees.	Feb-Mar (NLD)	May	-	-
A. obovata Blume	Feb-Mar (NLD)	May	-	-
Aesculus assamica Wall.	Nov-Dec	Dec-Jun	Nov-May	Jun-Sep
Alangium lamarckii, Thwaites	Feb-Mar (NLD)	Apr	May	Jul
Antidesma acuminatum Wall.	Feb-Mar (NLD)	Apr	Apr-May	Jul-Aug
Bauhinia melabarica Roxb.	Feb-Mar (NLD)	Apr	Oct-Nov	Mar
B. purpurea L.	Feb-Mar	Apr	Sep-Oct	Mar-Apr
B. variegata L.	Feb-Mar	Apr-May	Oct	Mar-Apr
Calicarpa arborea Roxb.	Mar-Apr (NLD)	CL	May-Oct	Aug-Jan
Cassia fistula L.	Feb	May	May-Jul	Mar-Apr
Croton joufra Roxb.	Feb-Mar	Apr	Mar-Apr	Jun-Jul
C. oblongifolius Roxb.	Feb-Mar	Mar-Apr	Mar	Jul-Aug
Derris robusta Benth.	NLD	Apr	Jul-Aug	Oct-Nov
Glochidion acuminatum Muell.	NLD	Apr-May	Apr-May	Jul-Aug
G. hirsutum Muell.	NLD	Apr-May	Apr-May	Jul-Aug
Goniothalamus Simonsii Hook.	NLD	Apr-May	Apr-May	Jul-Aug
Helicia errarica Hook f.	NLD	Apr-May	-	-
Heptapleurrum hypoleucum Kurz.	NLD	Apr-May	Apr	Jun-Jul
Kydia calycina Roxb.	Jan	May-Jun	Jan-Veb	Mar-Apr
Lagerstroemia flos-reginae Ratz.	Feb	Apr-May	May-Jun	Aug-Sep
Leea aequata L.	Feb-Mar (NLD)	Jun	Jan-Feb	Apr-May

1	2	3	4	5
Litsaea sebifera Pers.	Feb (NLD)	Mar-Apr	Apr-May	Jun-Jul
L.citrata Blume	Feb-Mar (NLD)	Mar-Apr	Apr-May	Jul
L. salicifolia Roxb.	Feb (NLD)	Mar-Apr	Apr-May	Jul-Aug
Mallotus khasianum Hook f.	Mar (NLD)	Apr-May	Apr	Jun-Jul
M. phillipnensis Muell.	Feb-Mar (NLD)	Apr-May	Apr	Jun-Jul
Measa indica Wall.	Mar-Apr (NLD)	Apr-May	Apr-May	Jul-Aug
Meliosma simplicifolia Roxb.	Feb-Mar (NLD)	Apr	Jan-Feb	Apr-May
Micromelum pubescens Blume	NLD	Apr-May	-	May
Oroxylum indicum Vent.	Jan	May-Jun	Aug-Oct	Sep-Mar
Pavetta indica L.	NLD	Mar-Apr	Apr	May-Jun
Pithecolobium longan Benth.	Feb-Mar	Apr	Mar-Apr	Jun-Jul
Plectronia dallyana Blume.	Feb-Mar (NLD)	Apr-May	Apr	May-Jul
Polyalthia jenkinsii Benth.	NLD	May	May-Jun	Jul-Aug
Premna miliflora Clarke.	Feb-Mar	Mar-Apr	Apr	May-Jun
Prismetomeris albidiflora Thwaite	NLD	Mar-Apr	-	Jun-Jul
Quercus spicata Smith.	Mar (NLD)	May	Nov-Dec	Apr-May
Rhus succedanea L.	Feb-Mar (NLD)	May-Jun	-	Jun-Jul
Sauroza nepalensis DC.	Mar (NLD)	Mar-Apr	Apr-May	Jul-Aug
Sauroza punduana Wall.	Mar (NLD)	Mar-Apr	Apr-May	Jul-Aug
Semicarpus anacardium L.	Jan-Feb	May-Jun	Aug-Sep	Dec-Jan
Sterculia guttata Roxb.	NLD	May-Apr	Feb-Mar	Jul-Aug
Styrax serrulatum Roxb.	Sep-Oct	Apr-May	Apr-May	Sep-Oct
Trevesia palmata Vis.	NLD	Apr-May	Apr	Jun-Jul
Unona longiflora Roxb.	NLD	Apr-May	Apr	Jun-Jul
Vatica lanceaefolia Blume	Mar-Apr (NLD)	Apr-May	Apr	Jun-Jul

LIST OF PUBLICATIONS

1. The nature and ecological significance of heterophylly in *Artocarpus chaplasha*. *Proc. Indian Nat. Sci. Acad.* B 41,(4) pp.1-6, (1981), (In Press).
2. Adaptive significance of seed polymorphism in *Lagerstroemia parviflora* Roxb. *Curr. Sci.* (Accepted).
3. Phenology of trees in a sub-tropical humid forest in north-eastern India. *Vegetatio*. (communitated)
4. On photoblastism in seed germination of *Duabanga sonneratioides*. *Proc. Ind. Acad. Sci.* (communicated)
5. On the relation among growth strategies, allocation pattern, productivity and successional status of trees of a sub-tropical forest community. *National Symposium on Improvement of Forest Biomass*. Solon, India (communicated)
6. Dry matter allocation and productivity in relation to growth strategies of some tree species. *J. Appl. Ecol* (submitted).
7. Growth pattern analysis of some tree species of a sub-tropical humid forest. I. Architecture and shoot growth characteristics. *Biotropica* (submitted)
8. Growth pattern analysis of some tree species of a sub-tropical humid forest II. Leaf dynamics. *Biotropica*, (submitted).
9. Germination and seedling establishment of some tree species in a sub-tropical humid forest. *Trop. Ecol.* (submitted).
10. Ectomycorrhizal status and growth of Khasi pine(*Pinus kesiya* Royle ex. Gordon) in the soils of disturbed land of Cherrapunjee. *Proc. Ind. Nat. Sci. Acad.* (communited).