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

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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.

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Signature of the
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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;

Beatley, 1967) in North America. Lieth has discussed the concepts and significance of phenological studies in the understanding of productivity and ecosystem function (Lieth, 1970, 1971; Lieth and Radford, 1971). However, the dearth of plant phenological studies in tropical latitudes has been pointed out by various authors (Rees, 1964; McClure, 1966; Gibbs and Leston, 1970; Nevling, 1971). Many of the investigations of phenology of tropical forests have been carried out in markedly seasonal climates (Njoku, 1963,1964; Boaler, 1966; Jeffers and Boaler, 1966; Janzen, 1967; Croat, 1969, 1975; Hopkins, 1970; Smythe, 1970; Nevling, 1971; Daubenmire, 1972; Foster, 1973; Malaisse, 1974; Putz, 1979). Studies in more or less aseasonal climate are by Medway (1922) Holttum (1931, 1940),Corner (1952),McClure (1966),Koriba (1958),Ng (1977),in Malaysia and Singapore; Baker and Baker (1936) in New Hebrides; Brookfield (1969) in Solomon Islands; Koelmeyer (1959) in Shri Lanka; Frankie et al (1974) in Costa Rica and Jackson (1978) in Brazil.

Because trees are subject to different environmnental conditions depending upon their position in the canopy, tree species were divided into under- and overstorey by Frankie et al (1974) for a detailed comparative study. Investigators working in a variety of tropical forest-types, have observed maximum leaf fall corresponding with the relatively xeric conditions or the driest part of the year (Holttum, 1931; Baker and Baker, 1936; Taylor, 1960; Madge, 1965; Hopkins, 1966). In north-western Brazil almost all deciduous trees of 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 <u>et al</u> (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 <u>et al</u> (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 <u>et al</u>

(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 <u>Khaya grandifolia</u> 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 subseqnent 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 rythmic (with regular alteration 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 Kempfand 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°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 continuumof 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.