STUDIES ON ECOLOGICAL ADAPTATION OF SHRUB SPECIES IN SUCCESSIONAL FOREST COMMUNITIES

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I certify that the thesis entitled "STUDIES ON ECOLOGICAL ADAPTATION OF SHRUB SPECIES IN SUCCESSIONAL FOREST COMMUNITIES", submitted by Shri. U. Baruah, 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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STUDY AREA AND CLIMATE

PREFACE

Quantitative information on germination, establishment, growth, architecture, leaf dynamics, and allocation strategies of shrub components of sub-tropical humid forests is meagre, though much information from north-east India on the tree components of this ecosystem is already available through a series of studies done by Ramakrishnan and his co-workers. The present study on the shrub strata of sub-tropical humid forests over a successional gradient of environment is intended to fill this gap.

The thesis starts with a General Introduction, with an extensive survey of related literature, followed by a brief description of the study area and climate. This is followed by 7 chapters in which the results obtained during the present study on the shrub community are set. Each chapter is a self-contained unit with its own Introduction, Methods of study, Results and Discussion. They are prepared in a format that could be submitted for publication, and therefore some overlap in writing was unavoidable. The literature cited in the text is all given together at the end of the thesis.

Apart from its academic value, the results obtained here is significant from an applied angle, for complementing shrubs with trees in restoration of human impacted ecosystems, based on successional concepts. The identified and characterized shrubs, could contribute to the fodder and fuelwood needs of the people of the region. These shrubs could also be made a part of the slash and burn agriculture (jhum) system both during the cropping and the subsequent fallow phases for agroforestry practices that would help in removing the distrotions that have come about in the recent past due to rapid shortening of the jhum cycle.

GENERAL INTRODUCTION

Tropical forest is a dynamic system of a high order of organisation, in which the morphological, physiological and ecological features of individual members are linked together, creating form and function, unknown outside this forest (Longman and Jenik, 1974). In a forest ecosystem, the shrub community that comes up as an understorey community, plays a key role in the functioning of the entire ecosystem along with others, forming a part of the food chain for mammals and birds and controlling microclimate of the site. The understorey community may contribute upto 50% of the total above ground biomass (Grove, 1985).

Humid forests are charaterstic of the north - eastern hill region and show wide variations, ranging from humid sub - tropical forests at lower elevations (Singh, 1982a,b,c; Shukla and Ramakrishnan, 1982a) to humid montane forests at higher elevations (Boojh and Ramakrishnan, 1981a). Much of the region receives an annual average rainfall of 2000mm or more. Slash and burn agriculture locally called 'Jhum', is the predominant form of agriculture among the tribal people of the region (Ramakrishnan et al., 1981; Toky and Ramakrishnan, 1983a). It forms an important land use pattern. This system of cultivation involves slash and burn of the secondary communities followed by mixed cropping for a year or two. The site is then abandoned for secondary succession and is again cultivated after a fallow period. Therefore, at lower elevations in Meghalaya, the vegetation is represented by a number of seral communities ranging upto about 60 years of age (Toky and Ramakrishnan, 1983a; Singh and Ramakrishnan, 1982a).

Succession is an orderly process of ecosystem change resulting from modification of the environment by the biological community, culminating in a persistant ecosystem type (Odum, 1969). The pattern and the rapidity of with which the forest community develops during succession, depend upon the degree of destruction and the clearing of the underground propagules of the community that existed before the process started (Ramakrishnan and Toky, 1978).

The process of vegetation regeneration in the tropical forest has been given considerable attention with different approaches and interest, mostly at the community level (Kenoyert, 1929; Bodowsky, 1961; Gomez -Pompa, 1971). Though, much informations on the growth characterstics of trees are available (Honda and Fisher, 1978; Hallé and Oldeman, 1975; Hallé et al, 1978; Parkhurst and Loucks, 1972), informations regarding the adaptations of trees under varied environmental conditions are limited. A few scattered studies on these aspects from different parts of the world are also available (Kempf and Pickett, 1980; Pickett and Kempf, 1981). However, the shrub community has received little attention. The present study is an attempt to evaluate the growth behaviour and its adaptive significance as related to shrub species that come up at different stages of secondary succession. This type of study is necessary to identify some of the important species from the understorey community to meet the increasing needs ~~of~~ for fuel wood. Further, this study has ~~also~~ implications for designing vegetation strategies based on successional concepts (Ramakrishnan et al. 1982), apart from its own academic value.

SEED GERMINATION AND ESTABLISHMENT

Germination of sedd is a critical phase during plant development and ecological conditions determine the persistance and patterns of species distribution (Mc Donough, 1970; Ramakrishnan, 1972). The period between germination and initial establishment is often a time of high mortality (Harper and White, 1974). These two aspects of plant's life cycle have been related to adaptation and distribution pattern of species in space (Harper, 1965; Cohen, 1967; Ramakrishnan, 1972; Ross and Harper, 1972; Thompson, 1973) and in time (Kapoor and Ramakrishnan, 1973).

Seed germination of early successional species with small seeds is often 'epigeal' (Richards, 1952; NG, 1974). The frequency of epigeal germination declines with seed size in late successional species (NG 1974). This type of germination is adv~~e~~antageous as the cotyledons become photosynthetic soon after germination. Sheldon (1974) showed that deep seated seeds of species producing small and light seeds often fail to germinate because of the low vigour of the seedlings, due to meagre seed reserve to penetrate through the soil profile. Seed burial is favoured for larger seeds and Shaw (1968), found 50% more germination from the buried acorns of *Quercus petraea* than from surface lying seeds. This may be related to heavy predation of large seeds as was shown in *Astrocaryum maxicanum* (Sarukhan, 1978). In tropical forests, seeds and seedlings predation may be particularly very heavy (Burg~~r~~ess, 1972; Janzen, 1974; Whitmore~~s~~, 1975).

Germination requirements of different species or the population within the same species have often been related to distribution and adaptation patterns of species/ populations (Harper, 1965; Ramakrishnan, 1972; Ross and Harper, 1972; Mc Noughton, 1966; Semwall and Purohit, 1979; Okusanya, 1980; Garwood, 1982). Our earlier studies on tree species (Boojh and Ramakrishnan, 1981b; Shukla and Ramakrishnan, 1982b) suggest higher germination percentage in the open for early successional trees while mid - and late successional species germinate and establish well ~~in~~ under shade.

Initial survivorship of seedlings of late successional species has been reported to be more under shade (Kinnaird, 1974) than that of the early successional as also suggested through our studies in north - eastern India (Boojh and Ramakrishnan, 1981b; Shukla and Ramakrkshnan 1982b). Further, Vaartaja (1962) and, Grime and Jeffrey (1965) reported that shade intolerant species are more susceptible to fungal attack under shade than the shade - tolerant species themselves.

PHENOLOGY

Phenology refers to different phases of the life cycle of organisms that occurs throughout the year (Leith, 1970). It provides the background information and functional rhythm of plant and plant communities. The phenology of a particular species is classified into different phases, depending upon the different events in the life - cycle. Each event is called as a phenophase. The entire sequences of different phenophases occurring around the year is called as phenodynamics and the elaboration of the phenodynamics for each species in a community is called as the phenological spectrum.

Tropical environment vary seasonally in temperature, humidity, rainfall and wind speed (Richards 1952). All these factors alone or in combination play a key role in triggering phenological changes in tropical plants (Longman and Jenik, 1974). The climatic changes also bring about fluctuations in pollination, seed dispersal predators and competitors (Lieberman, 1982). The relation of water with different phenophases and drought deciduousness strategy of some plant species have been studied by different workers (Oppenheiman, 1951; Giliberto and Estay 1978; Reich and Borchert, 1984).

Flushing and leaf fall:

The adaptive significance of different types of leaf replacement strategies has not received much attention. Jackson (1978) has discussed the adaptive advantages of different kinds of leaf replacement activities in forests. 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. Such a strategy would result in maximum leaf fall during the optimal growing season or to a continuous level of leaf fall if new leaf growth were to be continuous. In fact, seasonal cold or drought stress is usually present and leaves must be shed to minimize the effects of this stress. Because cold stress in cold temperate forests has a relatively sudden and predictable onset, cold temperate forests normally have a pulse of leaf fall at the end of the warm season (Bray and Gorham, 1964). In most of the lowland tropical forests,

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leaf fall has been found to be maximum in the dry season of the year (Hopkins, 1966; Frankie *et al.*, 1974; Reich and Borchert, 1982). In some tropical forests the maximal leaf fall has been reported during the wet season (Edward, 1977; Jackson, 1978; Brassel *et al.*, 1980). The only forest found to have non - seasonal leaf fall are Malaysian *Diptorocarpus* (Mitchell, cited in Bray and Gorham, 1964) which are characterized by relatively uniform climate.

Flowering and fruiting :

Seasonality has profound influences on flowering and fruiting of vascular plants (Corat, 1975). Dry season flowering is a common phenomenon in tropical forests (Ducke and Black; 1953; Janzen, 1967). Frankie *et al.* (1974) found that dry season has twice the number of species in peak flowering than wet season. A little change in photoperiod is a sufficient stimulus in triggering flowering (Njoku, 1958, 1963)

Moisture content is one of the major determinant for the production of fruit (Lieberman, 1982). High moisture requirement for proper development of fleshy - fruits was suggested by Zahner (1968). Animal - dispersed fleshy fruited species largely occur during wet season and wind - dispersed dry fruits tend to be more during the dry season (Frankie et al., 1974; Lieberman, 1982, Shukla and Ramakrishnan, 1982a). Though much information is available on general phenological patterns (Janzen, 1967; Nevling, 1971; Medway, 1972; Daubenmire, 1972; Putz, 1979; Opler et al., 1980; Liberman, 1982; Reich and Borchert, 1984) of tropical forests, most of these studies are mainly on forests with seasonal changes. Only recently, attention has been paid through some of our previous studies on general phenological patterns of sub - tropical forests (Boojh and Ramakrishnan, 1981a, Shukla and Ramakrishnan, 1982a). Little is known on phenological behaviour of shrub under different climatic conditions and in different successional forest..

ECOLOGICAL STRATEGIES

Organisms have certain limited amount of energy available to expend for different life-purposes (Cody, 1966). Based on his observations on clutch-size in birds, he argued that the way in which an organism allocates its limited energy to such ends as reproduction, competition and predation avoidance is a result of its ecological and evolutionary history. Magnifying the ideas of Cody (1966), Mc Arthur and Wilson (1967) pointed out that organisms in an open envrironment are selected for greater reproductive potential (r-selection), whereas organisms in a closed environment are selected for greater competitive, ability (k - selection). Gadgil and Solbrig (1972) expanded this idea by emphasizing upon the mortality patterns rather than the fullness of the habitat, though the validity of this vewpoint has often been suspected (Hickman, 1975; Gaines et al., 1974). The central idea of r - and k- selection has been considered from a number of other features also like duration of life - cycle and ability to propagate in crowded or uncrowded environments (Fisher, 1978; Williams, 1966; Gadgil and Bossert, 1970; Pianka, 1970; Livdahl, 1979; Parry, 1981).

Grime (1974) pointed out that the plant biomass in any habitat may be limited by 'stresses' or 'disturbances'. He defined stress as any factor limiting plant growth like shortages of light, water and nutrients while 'disturbance' as any factor responsible for the partial or total loss of the biomass like herbivory, pathogenecity and human activities. Thus, Grime (1974, 1977) recognized stress tolerance as a distinct strategy evolved under intrinsically unproductive environments or under extreme resource depletion induced by the vegetation itself. In this three strategy model, ruderal and stress tolerant strategies correspond to the extremes of r - and k - selection while competitive strategy occupies an intermediate position. This model further, provides various equilibria among ruderal, competitive and stress tolerant strategies.

The architectural model of higher plants represent the standard solution to the utilization of energy offered by the environment and each of these model is more or less suited to an (r - or k - determined) life cycle. Hallé _et al_. (1978) has described briefly in each of his model description about the possible utilization of energy. In higher plants, i.e., trees there is a useful representation of distribution of energy between vegetative (k - oriented) and reproductive (r-oriented) strategies, with any defense against predators incorporated into the complex of k - oriented (competitive) factors. Because of trees immobability, physical flight from predators is possible only in the seed - phase and is then linked to the reproductive (r - oriented) behaviour of the tree.

Bormann and Likens (1979) proposed two growth strategies for tree species that enable them to occupy different stages of ecosystem development after disturbance. The two constrasting strategies are (i) exploitive strategy best adapted to conditions immediately after disturbance and suited for early successional environments where there is minimum competition and abundant natural resources, and (ii) a conservative strategy better adapted to late successional environments, of high competition and lesser resource availability. Similar patterns of plant adaptation or species strategies have been implicated or proposed in a number of other studies (Grime, 1974, 1979; Harper and White, 1974). Harper and White's (1974) concept of shade - intolerant colonizing (r-type) species, for instance, is closely related to the exploitive growth strategy. By way of contrast, shade - tolerant species possessing fewer and larger seeds and a long juvenile period could be considered representative of the conservative (k) strategy.

Investigations on biomass/energy allocation patterns (Shukla and Ramakrishnan 1984a, Saxena and Ramakrishnan 1984a) attempt to ~~ensurer~~ answer two basic questions ; (i) how different life histories like annuals and perennials differ in their allocation pattern and (ii) how the strategy of a species is influenced by various environmental factors. It has been shown that annuals devote a substantially higher proportion of their resource - budget for reproduction because of their shorter life span compared to perennials where the emphasis is given to storage of energy for future growth and development by reducing the reproductive budget (Harper and Ogden, 1970; Harper et al., 1970; Hickman, 1975; Pitelka, 1977; Peterson and Bazzaz, 1978; Clark and Burk, 1980). Similarly the differences in allocation strategy amongst the perennials with differing growth habits have also been demonstrated (Turkington and Cavers, 1975; Pitelka, 1977; Saxena and Ramakrishnan 1984a).

An important feature of the reproductive strategy of perennials pertain to the nature of sexual and vegetative reproduction. It has been shown that sexual reproductive allocation remains generally fixed under different environmental stresses, whereas vegetative reproductive allocation would show plasticity and is often reduced under stressful environments (Ogden, 1974; Thomas, 1974; Abrahmson, 1975a, b). Keeley and Keeley (1977) predicted that non - sprouting chaparral shrub such as _Arctostaphylos glauca_ should have higher reproductive allocation compared to the sprouting species, _Arctostaphylos gladulosa_. They got no clearcut differences between the two regenerative strategies and suggested that the reproductive cost here is small and may be averaged over a long period of time. However, these workers employed only the absolute biomass values instead of the more appropriate proportionate analysis given by Harper and Ogden (1970)

Most of our knowledge on resource allocation patterns are based on biomass/energy; only a few studies have considered the allocation of nutrients, which may be equally important in the evaluation, in a situation with a limited supply as suggested by Harper and Ogden (1970). Van Andel and Vera (1977) on the basis of their study on growth and allocation of biomass and nutrients showed that the annuals may suffer from severe competition during, the later part of the year due to rapid accumulation of nutrients by the perennating species.

A high efficiency of nutrients use, generally expressed as dry matter production per g nutrient (inverse of tissue concentration) has been suggested to be an adaptation to nutrient stress(Loneragan and Asher, 1967; White 1972, 1973) However, such evaluation may be sometimes misleading when there is luxury uptake and large vacuolar storage of nutrients. (Bielaski,1973; Brady,1973). Small

(1972) suggested that respiration, photosynthetic or net assimilation rates per g nutrient uptake may be a ~~more~~ stronger expression of nutrient use efficiency. In # fact, more information on these aspects is warranted.

GROWTH AND ARCHITECTURE

The architecture of a plant is a visible, morphological expression of its genetic blue print. However, categorization of architecture model in higher plants is somewhat complicated because of different architectural phases that the individual passes through from seedling to adult stage.

It is a dynamic concept distinct from shape or physiognomy which is static. Similarly, it is not synonymous to growth habit, which refers essentially to the ultimately expressed form of the organism (herb, shrub or tree) and implicates size. Architecture does not involve size, and dimunitive herbs and giant forest trees may exhibit precisely the same architecture. Hallé and Oldeman(1970) has described 23 architectural models and each model was named after a botanist who has contributed to a knowledge of the model or has done morphological research exihibiting the model. The pioneering works of Hallé and Oldeman (1970, 1975) and Hallé *et al.* (1978) on these lines have opened up new avenues of systematic researches on forest trees.

Architecture models are recognized mainly by criteria which related to primary extension growth. Radial growth from a vascular cambium which brings about secondary increase in thickness serves to stabilize the primary system., although in some trees secondary changes do influence the architecture (~~eg.~~ e.g. Koriba's model, Troll's model). Stabilization by secondary tissue is not indispensable as is shown by trees either without a cambium or with little cambial activity. Absence of cambium is chiefly expressed architecturally in a restriction of branching which is described by Hallé *et al.* (1978) in relation to monocotyledons.

Extension and radial growth :

"Growth of a tree is complex phenomenon being a result of the activities of primary apical meristems and secondary cambial meristems to both intrinsic and extrinsic forces, which are not uniform either in time or in 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 Büsgen and Münch (1931) dealing largely with temperate species. Later on, Kozlowski (1964) reviewed in detail the current state of the knowledge in shoot growth particularly of north-temperate species.

In temperate trees, two widely different patterns of shoot growth occurs. 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; Here only one type of leaves occur Kozlowski, 1958, 1963). In the other type shoots are not fully preformed in the winter bud and both early and late leaves are produced (Critchfield, 1960; Clausen and Kozlowski, 1965). Kozlowski (1972) subsequently recognised three different patterns of shoot growth in trees: predetermined, heterophyllous and recurrent flushing type. Gill (1971) studied composition and expansion of bud of Fraxinus americana and called the predetermined shoot as 'determinate' and all other extension types as 'indeterminate

Whilst sufficient information on shoot growth of temperate species are available, our understanding of the growth of tropical trees are limited. In older literature, the studies specific to tropical tree growth largely refer to comprehensive investigations of phenology (Büsgen and Münch, 1931). Some factual basis for our understanding of growth expression in tropical trees comes from a study of the method of extension o growth of woody plants mostly derived from the examination of shoot morphology (Tomlinson and Gill, 1973). Although Koriba (1958) collected much valuable information about over 500 species from Singapore, these observations are largely based upon qualitative morphological examination. They may not be meaningful in some cases where the growth types exhibit no morphological change in shoot.

However, two main patterns of extension growth in tropical trees was observed. One is rhythmic growth and the other is continuous growth. Rhythmic growth means regular alternation of growth and rest. According to Hallé and Martin (1968), rhythmic growth is that one, where shoots have marked endogenous periodicity of extension. This term is synonymous with episodic (Romberger); intermittent (Koriba, 1958); or articulate

(Tomlinson and Gill, 1973). The other one is continuous growth, where shoots have no marked endogenous periodicity of extension. This is synonymous with evergrowing (Koriba, 1958) and non-articulate (Tomlinson and Gill, 1973).

One of the most important environmental factors that influence the rate of shoot extension is light intensity. The intensity of light directly affect the rate of photosynthesis which inturn influences other metabolic processes involved in growth. Grime and Jeffrey (1965) noted an inverse correlation between growth rate and survival of tree seedlings at low light intensities and suggested that slow growth rate may play a role in adaptation to shade. The growth of woody plants in relation to water has also been studied widely (Kramer and Kozlowski, 1960; Rutter and Whitehead, 1963; Zahner, 1968). Evidence ~~of~~ accumulated suggests that growth rate may be very sensitive to temperature changes too. A number of species also grow faster under longer than under shorter day lengths (Longman, 1972).

The duration of growth per year is variable among different species and individuals of the same species of different age group. 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 frost of forest is over and is completed during a short-part of the frost - free season (Kramer, 1943; Kozlowski, 1962). In the tropics, wet and dry seasons often control the periodicity of growth (Gaertner, 1964). It has been found that there are species which may show continuous growth throughout the year (Gill and Tomlinson, 1971). But this ever - growing or continuous shoot growth is still a matter of discussion , because it implies that apical meristems undergo no "rest' period during the entire life cycle. Tomlinson and Gill (1973) refer to it as nonarticulate growth, i.e., without regular change in leaf morphology.

Cambial growth of tropical species is very diverse. In many species, xylem increment may continue during most or all through the year. Growth rings may or may not be correlated with periods of shoot growth (Kramer and Kozlowski, 1979). Daubenmire (1949) found cambial growth related to length of the day rather than to air or soil temperature. This was further supported by Fraser's (1952) findings on both growth initiation and growth cessation. The same external and internal factors which control bud break and leaf fall also control the timing of the period of cambial activity (Longman and Jenik, 1974).

Branching pattern and orientation:

Branching pattern is one of the most conspicuous features of woody plants for efficaceous leaf display at the same time giving structural strength, with important adaptive significance (Horn, 1971; Whitney, 1976; Honda and Fisher, 1978; Mc Mohan and Kronhauer, 1976). The size and form of an individual tree crown depend upon the amount of leader extxnsion growth and the number, size and disposition of the branches (Cannel, 1974). The distribution of species at different habitat is also reflected through its branching system. Species from shaded communities adapt a branching system by which they minimise shading within the crown of an individual plant. On the other hand, open, sunny habitat species adapt a different strategy by which they can minimise energy expenditure on non - photosynthetic tissue (Pickett and Kempf, 1980). Horn (1971) coined these two types of branching pattern as monolayer and multilayer branching system of plant. Through extensive studies Boojh and

Ramakrishnan (1982a) and Shukla and Ramakrishnan (1986) have shown contrasting features for branching of early successional versus late successional species, and related them to the light environment to which they are adapted.

The number of leaf - bearing units (shoots) increases by the proliferation of original seed - borne or plumular shoot meristem. The simplest mechanism for proliferation of a meristem is by its equal division into two daughter meristems of initially equal growth potential. This is called as dichotomy or terminal branching. Only in such species, the axillary or lateral branching involves the development at each node of one or more lateral meristems from the terminal meristem, which may or may not continue its activity. Axillary branches are formed by two methods. - Syllepsis or prolepsis. The definition of syllepsis was first coined by Spath (1912). According to him syllepsis is the continuous development of a lateral meristem to establish a branch, without any evident intervening, period of rest of the lateral meristem. Later on, Hallé *et al*. (1978) also started using this definition given by Spath (1912). Hallé *et al*. (1978) defined prolepsis as 'the discontinuous development of a lateral bud from a terminal meristem to establish a branch, with some intervening period of rest of the lateral meristem'.

Morphology of branch expression:

In monopodial branching, lateral branch meristems are produced (continuous or rhythemic) by a permanent terminal meristem. In sympodial branching, lateral branch meristems successfully function for a limited period as a terminal shoot and are successively evicted. Sympodial growth by substitution occurs when the terminal meristem either aborts or become reproductive and makes no further contribution to the vegetative architecture of the plant. Sympodial growth by apposition occurs when both terminal and lateral meristems of each unit is evicted into a sub - ordinate position and extension growth of the axis is continued by a vigorous lateral branch which in its turn eventually becomes abruptly erect (Koriba, 1958; Tomlinson, 1978).

The distinction between orthotropic and plagiotropic shoots mainly depend upon the combination of morphogenetic and physiologic responses (Tomlinson and Zimmermann, 1977).

Orthotropic shoots are erect, have radial symmetry and phyllotaxis is most commonly decussate or spiral. A plagiotropic shoot has a horizontal or oblique orientation (more or less diageotropic) with dorsiventral symmetry, either by virtue of a distichous phyllotaxis or if spiral or decussate, by secondary orientation(petiolar or twisting of internodes). The degree of differentiation of a meristem may be changed either by external influences or by modifications of internal correlations. Of special interest are those woody plants in which there is no inherent change of expression within a single meristem producing axes of architectural significance. Such axes are described by Hallé and Oldeman (1970) as mixed axes.

Bifurcation ratio:

Bifurcation ratio strictly a quotient is another important approach to compare the number of terminal to proximal branches (Leopold,1971). This type of ratio was first used to quantify drainage patterns of stream basins (Horton, 1945). More recently, it has been used to characterize the branch networks of biological systems, such as trees (Holland, 1969; Baker _et al_.,1973; Mc Mahon and Kronauer, 1976; Whitney, 1976; Steingraeber _et al_., 1979; Pickett and Kempf, 1980; Kempf and Pickett, 1981). Lower bifurcation ratio is associated with monolayer, while, higher ratios are associated with multilayer leaf display (Whitney, 1976).

Apart from the bifurcation ratio, other fine scale parameters like branch angle, branch length, interbranch length are important determinants because they may contribute to contrasting leaf display patterns between sun and shade positions of crowns as well as of plants (Honda, 1971).

Reiteration :

In tropical forests, the leader axis or trunk of a plant with pronounced articulation or 'bayonet' 'Joint' is a very common feature and this type of joint represents levels where the terminal meristem has been broken or aborted leading to its substitution by another trunk~~s~~. This is simply a relay mechanism involved in the building of a sympodial trunk, in conformity with the architectural model. This term reiteration (after Oldeman, 1974) is not to be confused with another general terms, regeneration. Regeneration is undoubtedly an important ecological process, especially in temperate trees where it is a major determinant of tree shape, whereas reiteration is the mechanism by which regeneration of a damaged tree takes place. Reiteration is a morphogenetic process, not necessarily implying the 'repairing' of a previously disturbed organic system. Regeneration indicates the re - establishment of something lost.

LEAF DYNAMICS

Higher plants are all organised as iterations of a basic construction of module and leaf with its axillary bud ~~is~~ as the construction unit in the shoot (Harper and White, 1974; Harper and Bell, 1979; White, 1979). As a plant grows, new modules are added to the structure and old ones die. The parts of a modular organism have their own birth and death rates; gnet has its own internal populations dynamics and the relative placement of the module units determines the forms of the organisms (Harper and Bell, 1979). The dynamic concept of architecture (Hallé et al., 1978) also interprets the plant growth in terms of the organized accumulation and flux of constructional units (buds, leaves, etc.). ?

Leaves and its axillary bud with smallest module of the organized structure in higher plants and leaves may have many properities associated with members of a population, e.g, they may increase in number exponentially in a rapidly growing plant, they have juvenile, mature and senescent phases, death rates and survivorship patterns. Bazzaz and Harper (1977) have shown that it is relatively easy and rewarding to describe the growth and reaction of plants to different environments by applying demographic procedures for the analyses of population of leaves. This approach has recently been followed for tropical tree species from early and late successional environments (Boojh and Ramakrkrishnan, 1982b; Shukla and Ramakrishnan, 1984b).

Flushing pattern :

The flushing in tropical and temperate species mostly demonstrate rhythmic 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 flushing at certain times and less at other times have been shown by different workers (Njoku, 1963; Hopkins, 1970). In evergreen seasonal forests, flushing frequently occurs in the dry season before the start of the rains (Longman and Jenik, 1974). This shows that the rainfall cannot be a triggering agent for flushing (Njoku, 1984).

Expansion and leaf size :

The expansion of leaf is potentially influenced by variability in the different environmental factors (Terry, et al.,1983). The growth rate of leaves is normally closly linked with shoot elongation and is often quite rapid during the middle part of the growing season (Longman and Jenik, 1974). The high vigour of leaves in the middle part of the growing season may also shorten the plastochron interval (Gill and Tomlinsion, 1971). However, monthly variations of an intrinsic nature has been observed in many tropical trees (Shukla and Ramakrishnan, 1984b).

Variation of leaf size and shape in relation to different climatic conditions is much discussed (Richards, 1952; Ryder, 1954; Longman and Jenik, 1974). The final leaf size and the seasonal duration of leaf expansion varies greatly among species, type of shoot and the environment (Kozlowski, 1971;Shukla and Ramakrishnan,1984b). Shading often influences the growth of leaves of Cocoa and Coffee (Murray and Nicholas, 1966). Parkhurst and Loucks (1972) developed a model of leaf size on the basis of its water use efficiency in different environment. Fedorov (1966) regarded variation of leaf size of little adaptive significance, though Hestop - Harrison (1964) considered 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. Recently Shukla and Ramakrishnan (1981) in Artocarpus chaplasha found that lobing in this species to be closely linked with light intensity, branch order, branch length and tree age. The plasticity in leaf shape characteristics and the ability of the species to grow under open as well as under different degrees of shade, suggest its success as a mid - successional species.

Retention of a large leaf surface is likely to be helpful in increasing dry matter production (Zavitowski et al., 1974). Leaf longevity is important both as a nutrient nutrient cycling process and as a specific plant adaptation (Shaver, 1981). It plays a major role in determining the nutrient turnover rates in ecosystems because a a significant portion of the nutrient capital in the ecosystem is in the leaves (Whittaker _et al._,1979; Groham _et al._,1979). Bentley (1979), from his study on leaf longevity of some understorey species of tropical forest showed that this is correlated with light intensity in the environment. On the other hand, longer retention of leaves is unfavourable for leaf production itself due to increase in epiphylls. Mooney (1972) reported that with increase in leaf age the photosynthetic efficiency of leaf decreases. Therefore it is reasonable to assume that rapid growth and productivity of a tree is related to the fast turn over of leaves of shorter leaf longevity and the consequent high leaf area exposed at a given time (Boojh and Ramakrishnan, 1982b; Shukla and Ramakrishnan, 1984b). Thus, light demanding early successional trees were shown to have a high leaf turn over rate compared to shade tolerant late successional species.

Leaf fall :

Leaf fall can be influenced by many environmental factors (Longman and Jenik, 1974). Other considerations include the age of the leaf and the extent of competition with younger leaves or other growing parts (Addicott and Lyon, 1973; Kramer and Kozlowski 1960). In tropical forests, the leaf fall occurs almost throughout the year (Boojh and Ramakrishnan, 1982b; Shukla and Ramakrishnan (1984b) Maximum and minimum leaf fall however, occur during the dry season and the wet season respectively (Boojh and Ramakrishnan, 1982b; Shukla and Ramakrishnan, 1984b). Seasonal fluctuation of leaf fall in evergreen and deciduous elements in a tropical forest have an effect both on the nutrient status of the soil and microclimate of the forest as a whole (Longman and Jenik, 1974).

In the tropics, the deciduous habit cannot be sharply demarcated from the evergreen (Holttum, 1940; Koriba, 1958). Longman and Jenik (1974), on the basis of relative timing of bud - break and leaf abscission, has recognised four different patterns of flushing : (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 occur throughout the year with little change in the appearance of the tree. The number of flushes also varies widely in different species which do not show continuous growth. Choudhary (1964), Purohit and Nanda (1968) and recently Ramakrishnan and Shukla (1983) described the flushing pattern of Indian trees and found a maximum of four flushes per year. These flushes are often intrinsic rather related to external environmental factors.

ADAPTATION OF EARLY VERSUS LATE SUCCESSIONAL SPECIES

Of several important aspects dealing with adaptive features of trees, the architectural pattern and growth co-ordination form a basis for the differences in photosynthetic or production efficiency of these giant producers (Ramakrishnan *et al.*,1982). Though enough information~~s~~ on adaptive significance of various structures in trees are available, there is still a strong need to analyse information regarding the reactions and adaptation of trees to varied environmental conditions and occupancy of successional niche. During earlier studies on seed germination and establishment pattern of at lower elevations, north - east India (Shukla and Ramakrishnan, 1982b) from different successional environments, early successional species were shown to have higher percentage of seed germination in the open at shallower depth in the soil, whereas, mid - and late successional species respond little to ~~the~~ such differences in environmental conditions. This shows light demanding nature of early successional species. The higher seedling survival of late successional species in shade compared to the open and the reverse behaviour of early successional species are related to their adaptation to different light regimes in the forest community(Ramakrishnan _et al._, 1982).

Similar to the germination and establishment pattern of seedlings in early successional species, the other growth characteristics of early successionals also show significant differences from those of late successional species(Boojh and Ramakrishnan, 1981b; Shukla and Ramakrishnan, 1982b). Early successional species generally showed a prolonged period of indeterminate growth, having shorter dormancy period, more extension and radial growth and leaf production than late successional species. The sparse branch arrangement, facilitating leaf exposure to a greater degree and longer growth period of early successional species accounted for their faster growth. On the other hand, the late successional species showed shorter growth period and densely packed canopies with peripherally placed leaves that account for survival under shade. In the early successional species, the production and the contribution of first - order branches to the total framework of branch complex was much higher than that in the late successional species. On the basis of these studies the early successional species was shown to have an 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 had a conservative strategy where the aim is to make growth, though slowly, even under shaded situations 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. Different workers have attributed different ecological charateristics of the early and the late successional species to varied physiological attributes. Thus, Coombe and Hadfield (1962) have suggested that the fast growth rate of early successional tropical tree species is not due to higher photosynthetic rate but to unrestricted capacity of leaf production, also supported by our studies (Boojh and Ramakrishnan, 1982b; Shukla and Ramakrishnan, 1984b). Others (Marks, 1975; Bormann and Likens, 1979) have shown differential leaf area index (LAI), leaf display angle and allocation patterns for early versus late successional temperate species, and elaborated for the tropical species in north-east India (Boojh and Ramakrishnan, 1982a; Shukla and Ramakrishnan, 1986).

The orientation of branches and leaves usually shape the geometry of the tree crown (Honda and Fisher, 1978) and this has been related to its adaptation for light interception (Horn, 1971). Though the branch angle increase from top to bottom in both early and late successional species, the early successionals have more acute placement of branches under forest grown conditions. The late successional species under similar situations have more horizontally oriented branches in order to maximize photosynthesis under low light regimes (Boojh and Ramakrishnan, 1982a; Shukla and Ramakrishnan, 1986).

The early successional species have generally higher bifurcation ratio (Rb) than late successional species. According to Whitney (1976) the higher bifurcation ratio of early successional species is one to the less forking in the first order branches (Strahler's ordering). The lower bifurcation ratio of forest - grown individuals in comparison to that of open - grown ones, is consistent with the contention of Steigraeber 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. However bifurcation ratio may (Shukla and Ramakrishnan, 1986) or may not (Boojh and Ramakrkshnan, 1982c; Boojh and Ramakrishnan, 1982a) have ecological value, a contention also supported by (Borchert, 1982). More work is obviously needed.

Early successional species have a greater fluxes of births and deaths of leaf population than late successional species. Thus, these species have developed a competitive attribute in the form of large size of leaf populations. This in turn is dependent upon an extended period of photosynthetic activity under conditions conducive to high productivity. In late successional species the lower flux of leaf modules especially in forest-grown situations can be attributed to their rapid adjustment in growth in response to local depletion in resources arising during competition (Ramakrishnan et al., 1982).

Early successional species have a number of differences in their production and allocation pattern of biomass from late successional species (Shukla and Ramakrishnan, 1984a) allocation to the root system compared to the late successional species suggest that the early successionals tend to maximize productivity of above ground (Markes, 1975; Shukla and Ramakrishnan, 1984a; Waering and Patrick, 1975). This would help to put up their canopy as high as possible for exploiting the high light environment. The greater allocation to the bole (Shukla and Ramakrishnan, 1984a) supports this strategy. Moreover, the early successional species have spreading root systems in the upper soil profile (20cm) which is adv~~e~~antageous to provide enough absor~~p~~btive system though with poor physical support (Shukla and Ramakrishnan, 1984a). This type of root system may exploit the short term increase in nutrient and water available in disturbed sites (Marks and Bormann, 1972). On the other extreme, the late successionals have the higher allocation to deeply placed roots in order to draw upon the nutrient pool from deeper soil layers (Shukla and Ramakrishnan, 1984a).

THE PRESENT STUDY

The earlier studies done on sub-tropical humid forests at lower elevations in north-eastern India by Ramakrishnan and his co-workers are largely related to aspects such as ecosystem function related to biomass, productivity and nutrient cycling in successional plant communities, (Toky and Ramakrishnan 1983a,b; Singh and Ramakrishnan, 1982a,b,c,). General phenological attributes of the humid tropical forest have also been discussed (Shukla and Ramakrishnan, 1982a). Detailed morphometric analysis of growth, architecture and in depth phenology of trees of early and late successional environments have also been done (Shukla and Ramakrishnan 1984a,b; 1986). However, detailed information available on shrub strata of this ecosystem is meagre. The present study, therefore, is an attempt to fill this gap.

The present work was done at Lailad at an altitude of 296 m in Meghalaya, by identifying selected shrub species of early and late successional environments in secondary successional fallows developed after slash and burn agriculture (Jhum) (Toky and Ramakrishnan, 1983a; Ramakrishnan *et al.*, 1981; Shukla and Ramakrishnan, 1984a, b ; Shukla and Ramakrishnan, 1986). A comparative morphometric analysis of architecture and leaf dynamics of these two categories of species was done on similar lines as that was completed for tree (Ramakrishnan _et al._, 1982). This was supported by a general phenological analysis of 70 shrub species from three secondary successional fallows. Growth and allocation patterns of biomass and nutrients were also done on selected, light demanding and shade tolerant shrubs over a successional gradient. Differential germination and establishment patterns of early, mid - and late successional species was done in this study area, based on 15 selected shrub species, similar to a study done by Shukla and Ramakrishnan, (1982b) on tree components.

The present study, therefore, is aimed at an evaluation of the role of shrub species in the forest ecosystem under considerations, over a successional gradient.

STUDY AREA AND CLIMATE

The study area (Fig. 1) is located at Lailad which is about 70 km towards the northern side of Shilliong city, the capital of Meghalaya in the north-eastern region of India. It lies between 25°45" - 26°0" N latitude and 91°45" - 92°0" E longitude at an elevation of about 296m. 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° to 60°. The climate is typically monsoonic with about 80% of the total annual rainfall occuring 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 Nongkyllem 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 northwest 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. To represent 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).