ECO-PHYSIOLOGICAL ATTRIBUTES OF BAMBOO FORESTS IN SUCCESSIONAL COMMUNITIES IN NORTH-EASTERN INDIA

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I certify that the thesis entitled "ECO-PHYSIOLOGICAL ATTRIBUTES OF BAMBOO FORESTS IN SUCCESSIONAL COMMUNITIES IN NORTH-EASTERN INDIA" submitted by Shri. Kottapalli Sreenivasa Rao, 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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CONTENTS

PREFACE

Bamboos constitute an interesting group of plant species because of their unique biological attributes such as their demographic strategies, growth and architectural design, flowering and fruiting behaviour. They are an imprtant plant resource with a variety of uses for the rural communities of the country and with industrial value for pulping for paper and rayon. In the north-eastern hill region, they also play an important ecological role in the slash and burn agricultural system (jhum) during the recovery phase of the ecosystem during secondary succession after cropping. Thus, earlier studies done by Ramakrishnan and his co-workers have emphasized the potassium conservatory role of one of the species, *Dendrocalamus hamiltonii* Nees and Arn. Yet, so little is known on the biology of bamboos in general, and the bamboos in India in particular, except for some taxonomic studies. In fact, this is one of the very few attempts made in an understanding of the biology/ecology of this important group of species. The present work, therefore, centres around four important species of bamboo, namely, *Dendrocalamus hamiltonii* Nees and Arn., *Neohouzeoua dulloa* A. Camus, *Bambusa tulda* Roxb. and *Bambusa khasiana* Munro. Besides, a general socio-economic analysis of this important natural resource of the region was done with particular reference to east Khasi Hills district of Meghalaya, India.

The aspects mentioned above are covered in five Chapters, each with its own Introduction, Methods of Study, Results and Discussion. The Chapters are selfcontained, and prepared in a manner that is ready for publication. The thesis starts with a Chapter on General Introduction, followed by one on Study area and Climate. Literature Cited in the text are arranged at the end of the thesis.

Being one of the very few studies of this kind on bamboo species, this has considerable academic value, and at the same time application in terms of management of this important natural resource that is being fast depleted.

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GENERAL INTRODUCTION

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Individual species attributes determine, to a large measure, the community/ ecosystem functions. During secondary succession after slash and burn agriculture in north-eastern India, bamboos form an important component of the seral communities. Their population structure and eco-physiological attributes, therefore, play a major role in determining ecosystem function during early phases of secondary succession.

DEMOGRAPHY AND POPULATION DYNAMICS

Mortality/natality patterns:

Populations of colonizing species pass through a variety of growth phases with time. Initially, the population grows exponentially till the resources become limiting. In due course of time, if natality and mortality become equal, the population size gets stabilized showing fluctuations around a mean value. During this period, growth of such populations with similar resource needs, however, brings about certain changes in the environment. This change may prove unsuitable for early colonizers resulting in local extinction due to increased mortality.

Existence and elimination of population of a species, from a given environment solely depends upon its ability to adjust with the changing environment. This change in environment may directly reflect fluctuations in population size. These fluctuations in population size are termed as 'population dynamics' by Elton (1933). According to him, it concerns with rate of increase and decrease and the influence of environmental factors on the size of the population.

Lokta (1931) and Volterra (1931) proposed separately different theoretical equations for calculating population growth rate based on birth, death, immigration and emigration rates which were confirmed by Gause (1934), Gause (1934) put forward the famous 'Gause hypothesis' which suggests that two species having identical ecological niche cannot survive together for a long time; eventually one will replace the other.

The early seedling phase of a plant's life is generally considered to be the most risky and this risk is exaggerated due to increasing density of the same or another species (Harper and White, 1974; Watkinson, 1978; Cook, 1980; Smith, 1983a; Ramakrishnan, 1972). When individuals of a species are released into a favourable environment their number increases rapidly at first and then stabilizes, thus implying, that it is the population size which itself, in some way regulates the rate of population growth (Harper and Gajic, 1961; Ramakrishnan, 1972). Individuals may respond to density in two ways: (i) a reduction in seed output or lowered rate of vegetative reproduction and (ii) a reduction in the chance of individual survival (Harper and Gajic, 1961; Ramakrishnan and Kumar, 1971). Just as in a population of single species, density stress intensifies the expression of small differences (genetic and environmental) between individuals, so too in mixed populations stress may exaggerate and exploit inter-specific differences (Ramakrishnan and Jeet, 1972). The experimental model of de Wit (1960) are superbly designed to study the behaviour of two species in a mixture. In this model the two species are grown together at varied proportions while overall density of the mixture is maintained constant.

The behaviour of two or more species growing together and interfering with each others mechanisms of population control is of great interest. An understanding of the ways in which one species succeeds at the expense of another and the ways in which plant species may co-habit within a relatively stable community without one succeeding at the expense of another, must depend on a knowledge of the manner in which populations are controlled (McNaughton and Harper, 1960a,b; Harper and McNaughton, 1962; Harper and Clatworty, 1963; Ramakrishnan and Jeet, 1972).

The populations of *Avena fatua* and *Avena barbata* have properties of self-regulating systems in which frequency dependent selections allow stable co-habitation of two species. Under experimental conditions, regulation in both species acted through a plastic response to density as opposed to a predominantly mortal response involving changes in survival rates (Marshal and Jain, 1969). The studies by Ramakrishnan and Jeet ((1972) on the competitive relationship existing between *Argemone* species indicate that *A. mexicana* reacts more sensitively to intra-specific competition than *A. ochroleuca*.

Population regulation operates via density-dependent processes of mortality and fecundity. A density-dependent mortality factor is one that relaxes as population density declines, and thereby slows or halts population decrease. When population density increases, a density-dependent mortality factor kills an increasing proportion of the population. An example is seen in the relationship between seedling survival and the original density of seeds in the Wisconsin population of *Acer Saccharum* studied by Hett (1971). Density-dependent fecundity may also regulate population size by the production of fewer seeds per plant as population density rises (Watkinson and Harper, 1978; Smith, 1983b).

As plants in a dense population become larger with age, the density of individuals in the population decreases due to mortality. As long as the relationship between mean plant weight and density is governed by a line with slope -3/2, total plant weight will increase. This is because mean plant weight is increasing faster than density is falling and is called 'self thinning'. White (1980) observed this quantitatively in about eighty species of trees and herbs.

A great deal of literature has accumulated on the mortality rates of plant populations over about two decades. Deevey (1947) on the basis of work with different populations, concluded that, in general, the individuals follow three types of death/decay pattern.

A cohort with Deevey type I survivorship has low mortality in early and middle life but a rapid change to high mortality later on. Type II survivorship is typified by a constant death risk throughout the life cycle. Type III is a pattern of high juvenile and low adult mortality by long-lived plant species. Juvenile mortality has been observed in the seedling populations of various weed species (Hett, 1971; Sharitz and McCormick, 1973; Sarukhan and Harper, 1973; Hett and Loucks, 1976). This period seems to occur at the transition stage between the dependence of seedlings on seed food reserves, and their establishment when they start independent assimilation. Seedling mortality may be due to factors such as drought (Tazaki, 1960; Peterson, 1966; Cavers and Harper, 1967; Friedman and Orshan, 1975; Marquis, 1975).

In most of the plant population studies the survivorship curves have been found to be Deevey type II which implies constant death risk throughout the life span of the population. The studies on the mortality pattern of maize done by Ramakrishnan and Kumar (1971) also showed that mortality is a continuing risk that the population has to put up with throughout its life cycle. However, in <u>Denthoria caespitosa</u>, Williams (1970) observed Deevey type III survivorship curve with heaviest mortality in the early life (seedling stage). In contrast, Canfield (1957) observed Deevey type I survivorship curve with less risk of death in young and middle period of age and high mortality risk in old age in *Trichacha catifornica* *Bautelous hirsuta* and *B. chondrosioidea*.

Demography:

A number of studies are available now on population dynamics of perennial herbs. Sarukhan and Harper (1973) made a detailed study of demography of three species of *Ranunculus* in a grassland situation which was subsequently analysed mathematically by Sarukhan and Gadgil (1974). Hawthorn and Cavers (1976) studied the demography of the perennial herb, *Plantago major* and *P. rugeli*.

Kushwaha *et al*. (1981) showed that seedling mortality increased with the age of the fallow starting with 1, 3,5, 10 and 20 years, after slash and burn agriculture, in *Eupatorium odoratum* no recruitment occurred in 10- and 20-year old fallows. Ramakrishnan and Mishra (1981) studied the population dynamics of *Eupatorium adenophorum* in fallows after slash and burn agriculture (jhum) at higher elevations in north-eastern India and observed a net population increase through both vegetative and sexual reproduction in early successional fallows upto 6 years. Mortality of seedlings was high in 1- and 3-year old fallows, low in 6-year old fallow and reached 100% in older fallows. Further, they showed that seedling mortality was maximum during monsoon although some seedlings died in winter too, as a result of drought and frost. Kushwaha _et al_. (1983) studied the population dynamics of _Imperata cylindrica_ in successional communities after slash and burn agriculture (Jhum) in different fallows of 1,3, and 5 years age and observed that the loss in population in different fallows was due to reduced light penetration and greater moisture stress in these fast developing communities, resulting in complete elimination during the seventh year of fallow regrowth. Only the 0-year old fallow, where the plant cover was sparse, had maximum recruitment. Similar results were observed by Sharma (1985) while studing the population dynamics of _Imperata cylindrica_ related to slash and burn agriculture (jhum) in north-eastern India at different altitudes. Similarly, a number of studies on the demography of forest herbs are available (Hutchings and Barkham, 1976; Ernest, 1979; Barkham, 1980 a,b; Cook, 1980; Solbrig _et al_., 1980; Holland, 1981; Solbrig, 1981; Wells, 1981; Bierzychudek, 1982 a,b; Cook and Lyons, 1983; Hutchings, 1983).

In plant populations, there are two levels of population structure: (i) the number of plants and (ii) the number of shoot units per plant. This dualism is particularly conspicuous in clone-forming plants, where not only does the plant develop from single seedling as a sub-population of parts, but some of these parts may also root and eventually become severed from the original. The result is a sub-population of wholly discrete functional units, "ramets" with the genetic identity of the single individual, "the genet". Thus, the clonal growth of a rhizomatous plant involves the continued reduplication of discrete modular units, the 'ramets' and the sum of these units representing the 'genet', which is the product of a single zygote (Harper and White, 1974). Recruitment of new genets is often rare among clonal plants, and the dynamics of their population is dominated more by the birth and death of clonal modules than of whole genets (Noble _et al._, 1979). The ability of a single genotype to form fragmented phenotypes is just one of the variants in the life-history patterns of modular organisms (Harper and Bell, 1979).

In most of the studies available on clonal perennials, ramets were treated as units of population (Sarukhan and Harper, 1973; Soane and Watkinson, 1979; Solbrig _et al._, 1981; Cook, 1983; Pitelka _et al._, 1985; Hartgerink and Bazzaz, 1984). Lovett-Doust (1981) studied the population dynamics of _Ranunculus repens_ in contrasting habitats but growing on the same substrate. She concluded that despite the presence of a large viable seed bank in the grassland soil, germination and establishment of new genets was rare in both sites. Further she observed that the birth rate of ramets per rosette was apparently density-independent, but death rate per rosette was density-dependent, particularly in summer. She also observed that woodland populations follow an opportunistic strategy for rapid spread and sampling of the environment whereas a conservative one for consolidation and slower radial spread as in the adjacent grassland. Pitelka *et al.* (1985) too found similar results, while dealing with *Clintonia borealis*. Here too no seedling recruitment was observed, while ramet mortality was found to be density-dependent.

Plant demography has been used to elucidate aspects of ecological succession (Sharitz and McCormick, 1972; Raynal, 1979; Kushwaha *et al.*, 1981; 1983; Ramakrishnan and Mishra, 1981; Cook and Lyone, 1983). Comparison of closely related species (Sarukhan and Harper, 1973; Hawthorn and Cavers, 1976; Solbrig, 1981; Yadav and Tripathi, 1981), differences between populations of the same species growing on contrasting soil types (Bishop *et al.*, 1978; Ramakrishnan, 1961) populations growing on the same substrate but in contrasting vegetation (Lovett-Doust, 1981; Ramakrishnan and Kumar, 1971) and populations growing at different altitudes (Sharma, 1985; Papiya, 1981) all have been matter for discussion.

Age Structure:

The most reliable method for estimating the age of perennial species is to follow the fate of labelled seedlings or tillers of known age in permanent quadrats. This method has been successfully used by Tamm (1956, 1972a,b). In <u>Anthoxanthum</u> <u>odoratum</u>, Antonovics (1972) observed that different populations have different longevity according to their adaptation to a particular habitat and suggested that differences in longevity of individuals of different populations may be related to environmental conditions.

Age structure of a population refers to the categorization of individuals into various groups representing different age classes in a population. Age structure of a species may largely determine its survivorship. Williams (1970) and Antonovics (1972) observed differential decay rates for the individuals recruited at different times. It also gives valuable information about the recruitment of new individuals to the population, the transition of individuals from one age-group to another age-group, the number of individuals reproducing and also the mortality rate as influenced by age (Rabotnov, 1978). Many (Richards, 1952; Emlon, 1972; Schall, 1978) have suggested that the unstable age structure of plant species observed may be due to large environmental fluctuations that may occur during critical periods in plant life.

Not much information is available on the population dynamics of bamboos in their natural environment. Kadambi (1949) observed the ramet population of Dendrocalamus strictus to survive until five to six years if human interference was excluded. Based on this data White (1980) calculated the survivorship of ramets and found them to be of Deevey type I curve.

ARCHITECTURE AND GROWTH PATTERN

Early work on growth characteristics of trees are largely confined to their north temperate representatives (Büsgen and Münch, 1929; Kozlowski, 1964). The generalizations made from such studies cannot be representative for all tree species (Tomlinson and Gill, 1973). Comparatively fewer investigations have been carried out on trees of tropical zones. Studies specific to tropical tree growth in older literature largely refer to comprehensive investigations of phenology (Büsgen and Münch, 1929). The studies of Koriba (1958) in Singapore are generalized and essentially comparative in approach. This work refers to periods during which species are visibly flushing, i.e., exhibiting a crop of new leaves usually associated with shoot extension and it has been concluded that trees exhibit endogenous rhythms in their growth.

Some specific studies which have investigated the dynamics of shoot initiation and expansion in tropical trees include those by Bond (1942, 1945), Hallé and Martin (1968), Purohit and Nanda (1968), Greathouse and Laetsch (1969), Greathouse et al. (1971), Borchert (1969), Holdsworth (1963), Taylor (1970, 1975), Scarrone (1965) Gill and Tomilson (1971), Ramakrishnan et al. (1982) Boojh and Ramakrishnan (1982a), Shukla and Ramakrishnan, (1986). The classical works of Hallé and Oldeman (1970, 1975) and Hallé et al. (1978) on the growth and dynamics of tropical trees have highlighted the value of systematic researches on the forests and trees of the tropics.

Extension growth:

Extension growth or the elongation of the branch axes of a shoot system, varies widely among tree species in its rate, phenology and underlying morphogenetic basis. A wide range of extension growth patterns have been recognized in tree species. On the onehand, there are species with a single flush of shoot growth wholly preformed in the previous year's overwintering bud ('determinate growth'), as exemplified by many north temperate species. Typically shoot elongation in such species is completed rapidly (less than eight weeks), during favourable growing conditions which include the longest photoperiod of the year. On the otherhand, there are species where more leaves are produced along the leader in a growing season than there are embryonic leaves and primordia in the winter bud. This has been referred to as 'indeterminate growth'.

These two patterns of growth have been widely recognized in temperate trees. The growth in tropical trees is more diverse than that in the temperate regions and the periodicity of shoot growth in tropical trees has been a centre of controversy. If recurrent flushes occur at regular intervals the growth has been termed as rhythmic or periodic, the same at irregular intervals has been called as episodic, intermittent or recurrent (Romberger, 1963; Zimmermann and Brown, 1971). Hallé _et al_.(1978)

have collectively placed all these under one broad category of rhythmic growth mainly in the context of tropical trees where time-lag, between different growth flushes are very small. Thus, they have distinguished two main patterns of growth:

(i) Rhythmic growth - defined by Hallé and Martin (1968) in which shoots have a marked endogenous periodicity of extension. This term may be regarded as synonymous with episodic (Romberger, 1963) or with intermittent growth (Koriba, 1958). The term 'rhythmic' may imply a regular cycle, though this is not intended in the definition by Hallé et al., (1978).

After a period fo dormancy, flushing in tropical trees or bud burst in temperate trees, most strikingly demonstrate rhythmic growth. Flushing largely indicates rapid expansion of preformed leaves. In many trees with essentially rhythmic growth, expansion is less rapid and less obvious, so that the rhythm may have limited application.

The morphological indication of rhythmic growth in the mature shoot is a more or less pronounced segmentation of the axes (referred to by Tomlinson and Gill (1973) as 'articulate growth'). In trees which develop bud scales, there may be a series of short internodes or small leaves. For many trees with rhythmic growth the most conspicuous feature is the development of groups or tier of branches, and this periodic production of branches in relation to rhythmic growth has been referred to as 'rhythmic branching'.

(ii) Continuous growth - in which shoots have no marked endogenous periodicity or extension. It implies that the apical meristem undergoes no 'rest' or in the more precise usage of Rombrger (1963) 'quiescence'. The trees in the tropics which have been described as evergrowing by Koriba (1958), come in this category. As little is known about the physiology of dormancy, the continuous growth is distinguished by the absence of pronounced morphological segmentation. A more or less continuous process of leaf production is involved in continuous growth. This is implicit in Koriba's (1958) description and in the type of shoot referred to as 'non-articulate' by Tomlinson and Gill (1973).

Shukla and Ramakrishnan (1986) suggested that rhythmicity may not often have morphological expression, as implied by Hallé <u>et</u> <u>al</u>.(1978). The phenomenon of continuous vs. rhythmic growth studied by them is an example which illustrates this. The species which show a morphological rhythm, such as *Duabanga sonneratoides*, in reality had no seasonal bud dormancy in north-eastern India, unlike the same species studied in Malaysia by Hallé *et al*. (1978). On the otherhand, species considered to have continuous growth on the basis of morphology (e.g. *Anthocephalus cadamba*) in reality had a distinct period of seasonal bud dormancy.

The usage of various terms such as intermittent (Koriba, 1958), episodic (Romberger, 1963) articulate (Tomlinson and Gill, 1973) for discontinuous growth of tropical trees has caused considerable confusion. Basically in tropical trees three distinct categories of growth pattern were identified by Shukla and Ramakrishnan (1986). They are: (i) indeterminate - evergrowing, with no dormant phase, (ii) indeterminate-periodic, with a dormant phase and (iii) determinate, with leaf production and extension growth restricted to pre-determined leaves from an earlier dormant-bud phase. Such species may have only one flush per year as in *Engelhardia spicata*, *Mesua ferrea* and *Myristica linifolia* or two flushes, as in *Actinodaphne augustifolia*; three flushes as in *Castonopsis indica* or even four as in *Chikrasia tubularis* (Ramakrishnan and Shukla, 1982).

Tree architecture:

Organization in trees reflects the precisely controlled genetic programme which determines their development. This has been comprehensively described by the pioneer works of Hallé and Oldeman (1970, 1975) through the concept of architecture, which has permitted a typological categorization of growth models. The visible morphological expression of the genetic blueprint of a tree at any one time is referred to as its architecture. For a tree, the growth programme which determines the successive architectural phases is called as its architectural model or shorter, its model (Hallé *et al.*, 1978).

Architecture is a dynamic concept distinct from shape or physiognomy which is static. Similarly, it is not synomymous 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; dimunitive herbs and giant forest trees may exhibit precisely the same architecture. Hallé and Oldman(1970) has described 23 architectural models. Each model is named after a botanist who has contributed to a knowledge of the model or has done morphological research exhibiting the model. Architectural models have been recognized mainly by criteria which relate to primary extension growth. Bamboos being a distinct group have been described under the McClures' model (Hallé *et al.*, 1978).

Branching and axis differentiation:

Unbranched trees are those like single stemmed palm of which the coconut is a familiar example, remain vegetatively unbranched because they lack lateral meristems completely. A number of dicotyledons, of which *Carica papaya* is a familiar example are architecturally unbranched and belong to the same model (Corner's) (Hallé *et al.*, 1978).

Branched trees have two modes of branching. 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 one architectural model (Schout's) has been accounted for such trees.

Though qualitative approach followed by Hallé *et al.* (1978) have helped in a systematic organisation of tree growth forms, there is no relationship between these architectural models and the successional status of the tree species. In fact, quantitative differences in tree architecture are more significant ecologically than qualitative differences represented by these models (Ramakrishnan et al., 1982; Boojh and Ramakrishnan, 1982a; Shukla and Ramakrishnan, 1986). Thus Duabanga sonerationides and Anthocephalus cadamba, one an early successional species and the other a late successional one, both belong to Raux' model and yet differ with respect to growth pattern (Shukla and Ramakrishnan, 1986). According to them, a dynamic and quantitative approach to growth analysis is essential in order to understand the architecture and growth strategies of trees.

Morphology of branch expression:

The exillary 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 Spath (1912) as restated by Hallé et al.(1978) for syllepsis is 'the continuous development of a lateral meristem to establish a branch, without an evident intervening period or rest of the lateral meristem.

Hallé et al. (1978) define 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'.

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

An orthotropic shoot has an erect orientation (negatively geotropic), radial symmetry and phyllotaxy, most commonly decussate or spiral. A plagiotropic shoot has a horizontal or oblique orientation (more or less diageotropic) and dorsiventral symmetry either by virtue of a distichous phyllotaxy or of spiral or decussate by secondary orientation (petiolar twisting of internodes). The degree of differentiation of a meristem may be changed either by external influence 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 Oldemann (1970) as mixed axes. Among the several possibilities, the most distinctive type are those axes in which an initial orthotropic phase shows a pronounced distal curvature, the site of a future branch complex.

Reiteration:

The concept of reiteration of the tree model exists as an ecological extension of the architectural concept (oldeman, 1974). At the beginning of tree's life after germination, it produces the initial model, which is one of those described by Hallé and Oldeman (1970). Later and under propitious ecological conditions, meristems which do not initiate any growth during the model's development, may copy all or part of the model. This copy should not be confused with ramification and is called 'reiteration'. Thus, the process of reiteration is a mechanism of architectural adjustment by which the damaged tree accommodates itself to its environment.

In each structural ensemble in the forest, the different points where bigger reiterations occur, constitute an irregular space which is called the inversion surface. The levels of those surfaces correlate with different storeys where the tendency to produce always bigger organs such as stems, reverses and becomes a tendency to produce smaller organs such as little branches around the crown. This architectural inversion involves the regulation of vertical gradients of light and humidity which change to a lower or higher degree than in the average gradient.

Branch and leaf orientation:

Branching pattern is one of the most conspicuous features of woody plants. Efficacious leaf-display, minimization of non-photosynthetic tissue (Horn, 1971; Whitney, 1976; Honda and Fisher, 1978; Boojh and Ramakrishnan, 1982b; Shukla and Ramakrishnan, 1984a;) structural strength (McMahon and Krohaur, 1976) and optimization of translocation (Leopold, 1971; Leigh, 1975) are the potential adaptive functions of branching design of trees. Species growing in different environments have adapted different branching patterns and leaf display characteristics. Whitney (1976) suggested that the species of closed forests growing under canopy shade are selected to favour minimization of shading within the crown and this was quantified through comparative studies in early versus late successional trees in northeast India (Ramakrishnan et al., 1982; Boojh and Ramakrishnan, 1982c) Horn (1971) categorized this type of leaf display as a non-random, highly structured monolayer. In contrast to this, trees adapted to open situations would be expected to approach a multilayer state, having a number of small overlapping leaves randomly distributed through the crown (Horn, 1971).

The geometry of photosynthetic apparatus is an important feature in the adaptive mechanism of trees and has been related to their strategy for light interception (Horn, 1971; Douglas and Ramsaden, 1973; Lang, 1973; Monsi et al., 1973). Generally, the orientation of leaves in sun positions of the crown or the leaves of the upper canopy is such as to enhance photosynthesis and promote leaf cooling during high solar radiation. In shade positions, leaves orient to maximize the individual leaf photosynthesis by displaying themselves in horizontal monolayers (Horn, 1971; Baker et al., 1973; Honda and Fisher, 1978; McMillan and McClendon, 1979; Pickett and Kempf, 1980).

Bifurcation ratio:

Differences in branching in trees are demonstrated by bifurcation or branching ratio, which is the ratio of number of distal to proximal branches. This type of ratio was first used to quantify the 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; Leopold, 1971; Oohata and Shdei, 1971; Baker *et al.*, 1973; McMahon and Kroneuer, 1976; Whitney, 1976; Thornley, 1977; Niklas, 1978; Steingraeber *et al.*, 1979; Pickett and Kempf, 1980; Kempf and Pickett, 1981; Boojh and Ramakrishnan, 1982a; Ramakrishnan *et al.* 1982; Shukla and Ramakrishnan, 1986).

Oohata and Shidei (1971) subjected seedling of *Quercus phullyraloides* to different planting densities and levels of light intensity and found that bifurcation ratio was insensitive to changes in light environment. Whiteny (1976) compared bifurcation ratios of open and shade grown *Fraxinus americana* and similarly concluded that bifurcation ratio values approach a species specific constant. Whitney (1976) further suggested that bifurcation ratio is a measure of morphological adaptation to a particular successional status. Thus, the lower bifurcation ratios are associated with the monolayer late successionals, while higher ratios are associated with multilayer display of leaves, characteristic of early successional species. Recently, Steingraber *et al.* (1979) and Pickett and Kempf (1980) have shown that bifurcation ratio varies within a single species growing under different environments. Thus, they found that individuals from exposed habitats had higher branching ratios and in addition also possessed longer terminal branches than those beneath the canopy.

However, bifurcation ratio, is considered to be a relatively crude index of tree architecture, while branch angle and branch length have been found to have a major effect on the architecture (Honda and Fisher, 1978; Steingraber *et al.*, 1979; Pickett and Kempf, 1980; Kempf and Pickett, 1981; Nelson *et al.*, 1981). Recently, the ecological implication of bifurcation ratio has been evaluated through a series of studies by Ramakrishnan and his coworkers (Shukla and Ramakrishnan, 1986; Boojh and Ramakrishnan, 1982a,c; Ramakrishnan *et al.*, 1982).

LEAF DYNAMICS

Higher plants are all organised as iterations of a basic construction module or leaf with its axillary bud 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; a genet has its own internal population dynamics and the relative placement of the modular units determines the forms of the organism. Form is a consequence of dynamics (Harper and Bell, 1979), and the dynamic concept of architecture interprete plant growth in terms of the organized accumulation and flux of specific constructional units (buds, leaves etc.) as the blueprint.

Leaf and its axillary bud are the smallest module of the organized structure in higher plants and leaves may have many properties associated with members of populations, e.g. they may increase in number exponentially in a rapidly growing plant, they have juvenile, mature and senescent phases, death-rates and survivorship curves. 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 analysis of populations of leaves.

Though some aspects of leaf demography of tree species have been worked out like census (Büsgen and Münch, 1929), longevity (Gill and Tomlinson, 1971), age-structure (Kinerson et al., 1971) or abcission strategies (Kozlowski, 1973; Addicott, 1978), very few (Boojh and Ramakrishnan, 1982b; Shukla and Ramakrishnan, 1984a) studies are available on the leaf dynamics of plants in successional environments and in relation to their adaptive value.

Leaf production:

Leaf production estimates have been of interest to foresters and horticulturists (usually as a part of wider studies on productivity). The early studies on leaf production estimates have been reviewed by Büsgen and Münch (1929). With the increased emphasis on the role of leaf biomass in ecosystem studies and primary productivity (Baskerville, 1965; Satoo, 1970), later investigations were carried out on changes in leaf production over time in mono-specific stands (Rennie, 1955; Ovington and Heitkamp, 1960; Switzer et al., 1967; Wiegert and Monk, 1972; Marks, 1974) and mixed species forests (Covington and Aber, 1980), and adaptive leaf population flux (Boojh and Ramakrishnan, 1982b; Shukla and Ramakrishnan, 1984a).

Leaf longevity:

Most leaves are determinate in growth (though a few are not and retain a functioning apical meristem, Hallé et al., 1978) and have a determinate life span. Within a species this life span may be environmentally determined. Leaf populations undergo mortality over a time period. Survivorship curves best represent this pattern and have been constructed for various species: Abies veitchii (Kinerson et al., 1974); Actinodaphne longifolia (Yuwaka et al., 1977); Ledum groenlandicum, Kalmia polifolia, Chamaedaphne calyculata (Reader, 1978); Linum usitatissimum (Bazzaz and Harper, 1977); Viola sororia (Solbrig et al., 1980). Without exception they all show Deevey type I survivorship curve (Deevey, 1947), where there is an initial period of constant low probability of death followed by a rapidly increasing risk. Recently, Boojh and Ramakrishnan (1982b) have shown differential survivorship curve patterns for early versus late successional trees in a sub-tropical montane forest in north-east India.

In plants that carry cohort of leaves for more than one year an age structure may develop if successive annual cohorts overlap. Studies on leaf age-structure exist for certain species since the physiological significance of leaves of different age classes affect tree productivity (Linson, 1958; Woodman, 1971; Kinerson et.al., 1974). The studies done on early versus late successional tree species show that the former bear a larger population of younger leaves than the latter.

The adaptive significance of different types of leaf replacement strategies have not received the kind of analysis that Janzen (1967) provided for flowering and fruiting phenology. Jackson (1978) has discussed the adaptive advantages of different kinds of leaf replacement activities in forests. He has proposed that the most advantageous strategy of leaf replacement in a perennial plant in a seasonal 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. In the lowland tropical forests, leaf fall has been found to be maximum in the dry season particularly at the end of the season (Hopkins, 1966; Fittkau and Klinge, 1973; Frankie *et al.*, 1974; Boojh and Ramakrishnan, 1982; Shukla and Ramakrishnan, 1982). In some tropical forests the maximal leaf fall has been reported during the wet season (Cornforth, 1970; Edwards, 1977; Jackson, 1978; Brassel *et al.*, 1980).Khiewtam (1986) has shown a second significant peaking in wet season leaf fall in a sacred grove at Cherrapunji. The only forests found to have non-seasonal leaf fall are Malaysian Dipterocarps (Bray and Gorham, 1964), which are characterized by relatively uniform climate.

SECONDARY SUCCESSIONAL PATTERNS

The pattern of secondary succession and the rapidity with which a forested community develops depends upon the degree of destruction and the clearing of the under-ground propagules of the community that existed prior to this operation. In north-east India the length of the slash and burn agriculture (jhum) cycle (intervening fallow phase between two successive croppings at the same site was shown to play an important role in determining the pattern of vegetation development (Ramakrishnan et al., 1981). The pattern of secondary succession in the fallows during the first few years when weedy species dominate, varies considerably depending upon the jhum cycle and the intensity and duration of cropping. Thus, Toky and Ramakrishnan (1983a) reported four types of early succession where herbaceous communities dominate. This phase is then replaced gradually by bamboo and shrubs and trees. If the jhum cycle is very short, succession would be arrested indefinitely at the pioneer weed stage (Saxena and Ramakrishnan, 1984b). This was also noted under 'Lua' forest in Thailand where Eupatorium odoratum is a predominant weed (Zinke et al., 1978).

Clements (1916) and Odum (1969) proposing a 'relay floristic model' pointed out that here each set of species makes the environment less favourable for itself and more favourable for the following set of species. Such a replacement continues until community reaches its climax stage. Egler (1954) proposed 'initial floristic composition' dominates the subsequent stages of succession after a major perturbation. Saxena and Ramakrishnan (1984b) found that the early stages of secondary succession following the burning tended to confirm closely to the initial floristic composition model, under shorter jhum cycles of 4 and 6 years, but followed the relay floristics model under longer jhum cycles of 10 and 20 years. Further, the studies of Toky and Ramakrishnan (1983a) and Mishra and Ramakrishnan (1983c) showed that species diversity increased while dominance decreased during secondary succession.

In the recent past, attempts have been made to understand the processes of vegetation succession in terms of the properties and evolutionary strageties of the individual species. Succession was explained as a displacement of r-strategists adapted to dispersing and colonizing unoccupied sites by K-strategists, emphasizing on the efficient exploitation of the site (Loucks, 1970; Pickett, 1976). The strategies of early colonizing annual (Saxena and Ramakrishnan, 1984c) and perennial (Saxena and Ramakrishnan, 1984b) herbs during secondary succession after slash and burn agriculture has been worked out and two reproductive pathways, one a heavy seed production strategy and another a high allocation to vegetative propagation have been suggested.

Pickett (1976) stated that amelioration of the environmental extremes takes place during vegetation development and thus succession is a temporal gradient from high stress to low stress taking into consideration other plant interactions like allelopathy, nitrogen fixation and herbivore-predator effects. Grime (1974; 1977) described three primary strategies in plants which are related to their ability to withstand disturbance, competition and stress. According to him, 'stress' is any factor that reduces the biomass, including shading and nutrient depletion, except competition. He, explained that succession to be a process leading to a more stressful environment rather than amelioration of the environment as envisaged by Pickett (1976). Grime (1977) described succession as the replacement of species essentially with ruderal strategy by species with increasing stress tolerance. As the productivity of the site increases during succession, the shift is towards a competitive strategy.

Cornell and Slatyer (1977) proposed three distinct successional pathways: (i) facilitation pathway, similar to classical relay floristic pathway that operates in primary successions (Lawrence et al., 1967; Reiners et al., 1971); (ii) tolerance pathway which assumes that later successional species to be successful, whether or not early successional species have preceeded them. However, this has not received evidence so far (Noble *et al.*, 1979); (iii) inhibition pathway describes situations where later species cannot grow to maturity in the presence of earlier ones (Keever, 1950; Parenti and Rice, 1969).

Whittaker and Lavine (1977) described four types of vegetation succession: (i) replacement succession which is similar to the relay floristic model, (ii) direct succession that assumes reestablishment of the pre-existing species after disturbance as in deserts and tundra, (iii) cyclic succession that refers to the cycles observed in chapparal due to recurrent fires, and (iv) mosaic succession that refers to the localized changes during vegetation succession.

Noble and Slatyer (1977) identified a variety of vital attributes, that determine:(i) method of arrival or persistance of the species at a site during and after the disturbance (ii) ability to establish and attain maturity in a developing community and (iii) time taken for the species to reach critical stages in the life history. They emphasized that vital attributes may form the basis of evolutionary trends during succession.

PLANT STRATEGY ANALYSIS

Growth and nutrition:

Light has been recognised as a major factor influencing the replacement of species during secondary succession (Marks, 1974; Bazzaz, 1979). In general, competition for light and nutrients increases through succession. During early succession rapid growth, which depends upon abundant resources, is advantageous. Later in succession such resources may be less available, and those plants with inherent high growth rates and resource requirements may not survive.

Grime (1977) suggested that shade adapted climax tree species may have slower growth rate than the sun adapted early successional ones. Such a differential strategy for early vs. late successional trees have been shown by Ramakrishnan and co-workers through a series of studies (Ramakrishnan *et al*., 1982; Boojh and Ramakrishnan, 1982a; Shukla and Ramakrishnan 1986). Ruderal and competitive species have higher relative growth rates compared to stress tolerant species (Grime, 1977). This indicates slower relative growth rate in late succession, both due to the high expenditure of carbon in maintenance of living but non-productive tissues and decreased mineral availability to support further growth. Late successional species seldom exhibit high relative growth rate of early invaders. Their low relative growth rate puts them at a disadvantage in early succession, but because of their higher tolerance limits of low annual resources these species maintain a positive relative growth rate even in late succession and eventually become dominant (Grime, 1977; Connell and Slatyer, 1977; Ramakrishnan *et al.*, 1982).

Nutrient requirement of secondary successional species is important to predict the successional changes specifically in nutrient poor soils in fields abandoned after cultivation. Such species are expected to have efficient system to withstand the lower nutrient availability in the soil (Vazques-Yanes and Gomez-pompa, 1974). Kellman (1969) suggested low nutrient requirements for early successional species and an increase in the resources apparently did not affect the course of succession. A similar conclusion was also made by Hartcombe (1972) through his studies on *Cercopia obtusifolia*. West and Chileote (1968) explained that the disappearance of *Senecio sylvaticus* in the second year after slash and burn of douglas fir areas was due to its high mutrient requirement, and decrease in nutrient availability particularly of nitrogen and phosphorus, in soils after one year of vegetation development.

Chapin (1980) stated that plants with high relative growth rates have high nutrient requirement to support new tissue production and rapid root production and leaf turnover. At the opposite extreme, infertile soils are most successfully exploited by stress tolerant species whose inherently low growth rates can be adequately maintained by their low capacities for photosynthesis and nutrient absorption. Fast growing tree species such as <u>Pinus kesiya</u> in nutrient poor soils however, adopt a strategy for rapid nutrient turnover rates so that a high flux of soil nutrient pool is maintained (Ramakrishnan and Das, 1983; Das and Ramakrishnan, 1985).

A high efficiency of nutrient use, generally expressed as dry matter production per gram nutrient (inverse of tissue concentration) has been suggested to be an adaptation to nutrient stress (Lonergan and Asher, 1967; Jefferey, 1968; White, 1972; Garten, 1978). However, such an evaluation may be sometimes misleading when there is luxury uptake and large vacuolar storage of nutrients (Bieleski, 1973; Haynes and Goh, 1978). Small (1972) suggested that respiration, photosynthetic or net assimilation rates per gram nutrient uptake may be a more strong expression of nutrient use efficiency. In-fact, information on these aspects are meagre. Recently through a series of studies on nutrient uptake and use efficiencies of species, Ramakrishnan and co-workers (Sexena and Ramakrishnan, 1983a, 1984a, 1986) drew attention to the adaptive value of this parameter over a successional gradient of environment.

Resource allocation and reproductive strategy:

Cody (1966) put forth a concept based on the principle of allocation, which says that organisms have certain limited energy available to spend for different life purposes. Harper and Ogden (1970) applied it for the first time to Senecio vulgaris, and pointed out that the proportion of allocation of biomass may reflect the pattern of energy allocation provided there is strong correlation between total biomass and total calories. This was later supported by others (Hickman and Pitelka, 1975). Harper and Ogden (1970) also suggested certain major patterns of energy allocation in annual, biennial and perennial plants based on quantitative analysis. In annual plant species much of the energy is devoted to reproductive structures whereas in perennials emphasis is given on storage of energy for future growth and development, at the expense of the reproductive budget (Hickman, 1975; Peterson and Bazzaz, 1978; Bell _et al._, 1979).

McArthur and Wilson (1967) pointed out that organisms in an open environment are selected for greater reproductive potential (r-selection) where as organisms in a closed environment are selected for greater competitive ability (k-selection). Gadgil and Solbrig (1972) expanded the concept of r- and k-selection in plants and tired to formulate them more rigorously. They emphasized on the r-strategy by invoking patterns of mortality rather than 'fullness' of habitat. The central idea of r- and k-selection has been considered from a number of other aspects like duration of life cycle and propagation ability in a crowded or uncrowded environment (Fischer, 1958; Williams, 1966; Gadgil and Bossert, 1970; Pinaka, 1970; Wilber _et al._, 1974). Abrahamson and Gadgil (1973) suggested that the reproductive effort should decrease under shaded conditions, as more emphasis is given for vegetative growth, for survival of the plants here. Similar resource allocation patterns have also been shown by a number of other workers (Abrahamson and Gadgil, 1973; Gaines *et al.*, 1974; Roos and Quinn, 1977; Saxena and Ramakrishnan, 1984a).

The importance of stress and disturbed condition in the allocation of biomass was considered by Grime (1974). 'Disturbance' was defined by him as any factor that limits and cause destruction of biomass like herbivory, pathogenicity and human activities. Thus, Grime (1974, 1977) recognised stress tolerance as a strategy of plants under unproductive environments.

While considerable work has been done on the allocation of biomass or energy to different life purposes, very few studies are available on the allocation of nutrients which is also equally important in the evolution of reproductive strategy, particularly in situations with limited supply of nutrients (Harper and Ogden, 1970; Van Andel and Vera, 1977). Saxena and Ramakrishnan (1983a) studied the growth allocation pattern and nutritional status of some dominant annual weeds under successional environment and observed differences in their biomass and nutrient allocation pattern. Reproductive allocation of nitrogen and phosphorus was higher than that of biomass and potassium in these annuals. They further showed that allocation of biomass and nutrients to leaves decreased during growth and this was more pronounced at the time of reproduction. Saxena and Ramakrishnan (1983b) also studied the growth and allocation pattern of dry matter and nutrients in four important perennial weeds. They observed that the perennials often tend to allocate more to vegetative reproductive organs compared to the allocation to sexual reproduction. Further, C_4 perennials such as <u>Imperata cylindrica</u> and <u>Thysonolenna maxima</u> were shown to be adapted to survive under nutrient poor microsites of a heterogenous soil as opposed to C_3 species which were often confined to nutrient rich microsites (Saxena and Ramakrishnan, 1984c). This is because of the high nutrient use efficiency of C_4 species particularly with respect to nitrogen compared with C_3 species.

PRODUCTIVITY AND NUTRIENT CYCLING UNDER EARLY SUCCESSIONAL ENVIRONMENT

A sharp increase in the above ground biomass occurs during secondary succession. According to Lugo

(1973) maximum biomass value for tropical forests is approached in about 30 years at a level of 250 t/ha, whereas for temperate forests it was about 490 t/ha is about 170 years only (Bormann and Likens,(1979). Thus, a steady-state for biomass is reached over a shorter time period in the tropical than in the temperate forests.

The rate of accumulation of biomass is faster in the early stages of succession but may decline in the subsequent years. The rate also depends upon the type of initial vegetation established and other environmental conditions (Uhl and Jordan, 1984; Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983c).

During development of vegetation, a part of the nutrient pool is stored in the vegetation and part is returned to the surface soil by rain, wash-out from leaves and twigs, through litter and twig fall, and in the form of dead roots and root exudates. The soil humus also increases during fallow period, chiefly as a result of litter fall. High litter production during secondary successional stages compared to the mature stage was reported by many workers (Ewel, 1976; Toky and Ramakrishnan, 1983b; Mishra and Ramakrishnan, 1983c; Uhl and Jordan, 1983).

A large body of information is available on nutrient cycling in forested ecosystems (Laudelot and Meyer, 1954; Greenland and Kowal, 1960; Odum, 1970; Stark, 1970; Golley *et al*., 1977; Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983c). Some patterns are suggested for tropical forests: (i) the uptake and return of nutrients may be greater per year in tropical forests than in other types of vegetation, (ii) a larger proportion of the entire chemical inventory of the system is held in the vegetation, (iii) in tropical forests the percentage of the vegetation in green parts, the proportion lost per year as litter, and the rate of decomposition of the litter are greater than in temperate forests and (iv) the rate of uptake is strongly influenced by the rate of evapo-transpiration.

Mineral cycling pattern varies with the nutrient supply to the system, with the time available for the system to develop on the site, and also the environmental conditions. The accumulation of nutrients and their release through litter fall increases with the age of the fallow and become stabilised in mature forests (Stark, 1971a,b; Toky and Ramakrishnan, 1983b; Mishra and Ramakrishnan, 1983c).

The role of rapidly growing successional species in the restoration of disturbed ecosystems has recently become a problem of considerable interest. In general, rapid revegetation of a disturbed site decreases nutrient losses by an interaction of several factors (Marks and Bormann, 1972). The channelling of water into evapotranspiration cuts down on losses of nutrients in runoff and erosion. Shading decrease soil temperature, which results in lowered decomposition and nitrification rates and reduced supply of water-soluble ions available for removal of drinage water. Growing vegetation also reduces nutrient losses by incorporating nutrients into developing biomass (Vitousek and Reiners, 1975). This reduction of nutrient losses by developing plant biomass has important consequences for ecosystem stability. Ecosystems that recover nutrient cycling capability more rapidly (i.e. nutrient uptake equivalent to potential losser) can be considered more resilient and thus more stable. Marks (1974) investigated functional role of a successional species such as pin cherry (Prunus pensylvanica) in disturbed areas of northern hardwood forests. Pin cherry is a rapidly growing species which often occurs in dense stands in disturbed sites. It appears to be effective in preventing nutrient loss by the rapid accretion of elements into its biomass. Marks concluded that pin cherry 'promotes ecosystem stability by biotic regulation of ecosystem functions'. In another study Harcombe' (1977a,b) experimentally analysed the role of successional vegetation in retaining nutrients within disturbed tropical forest ecosystem. Further, Foster et al. (19~~9~~80) studied the effect of ragweed (Ambrosia artemissifolia) on nutrient cycling in a one year old field and showed its conservatory role of nutrients. In north-eastern India Toky and Ramakrishnan (1982) analysed the role of Dendrocalamus hamiltonii, a bamboo in nutrient conservation during secondary succession after slash and burn agriculture (jhum) and showed that this species has the ability to conserve an important element such as potassium. Similarly, the early successional weeds under slash and burn agriculture system drastically check run-off and infiltration losses of nutrients and sediment losses in the very first year of the fallow phase after cropping (Toky and Ramakrishnan, 1981b; Mishra and Ramakrishnan, 1983a; Ramakrishnan et al., 1981).

Nutrient budget analysis under slash and burn agriculture:

The long term success of slash and burn agriculture depends upon the recovery and maintenance of soil fertility (Ramakrishnan et al., 1981; Ramakrishnan, 1984b). If the nutrient lost or displaced during the short period of cultivation are approximately balanced by those replaced during the fallow period, the system could continue indefinitely (Mishra and Ramakrishnan, 1983b; 1984). The maintenance of soil fertility in hot, humid and high rainfall area is a serious problem and is more severe in situations where the cycle has become shorter, due to poor recovery of soil fertility and increased intensity of weed competition. This is in turn results in reduced crop yield under short cycles (Nye and Greenland, 1960; Waters, 1971; Toky and Ramakrishnan, 1981a; Mishra and Ramakrishnan, 1983b).

When the forests are cleared and the debris is burnt, all the cations are released on the surface soil as ash. Heavy losses of carbon, nitrogen and sulphur occur due to volatilization during the burn (Nye and Greenland, 1960; De las Sales and Folster, 1976; Ramakrishnan and Toky, 1981; Mishra and Ramakrishnan, 1983b; 1984). For phosphorus, though there are no obvious mechanisms of volatilization, losses are reported through convection via particulates to the atmosphere (Freedman, 1981). There are conflicting reports on addition of phosphorus through fire, (Nye and Greenland, 1960; Stark, 1971; Stromgaard, 1984) and others suggesting some losses for phosphorus through fire and this was corroborated by Swamy (1986) in a slash and burn agriculture system.

Carbon and nitrogen losses occurred from the slash and burn agriculture system during and after a year of cropping period (Nye and Greenland, 1960; Zinke et al., 1978; Ramakrishnan and Toky, 1981; Mishra and Ramakrishnan, 1983d). Similar to carbon losses, there is also a net loss of nitrogen after cropping compared to that of the pre-burn soil pool. Nitrification after the burn is shown to be accelerated due to high microbial activity, due to rise in pH and temperature of the surface soil (Griffith, 1949; Moore and Joyebo, 1963; Ahlgrên and Ahlgren, 1965). This increase is attributed partially to the removal of chemical inhibitors (Reed, 1951; Smith et al., 1968; Rice, 1974; Saxena and Ramakrishnan, 1984b). Deforestation for shifting agriculture or other needs has a major impact on both the amount and relative proportions of water, dissolved substances and particulate matter lost from the system. Moreover, the total concentration of cations in the soil solutions depends upon the concentration of anions. A high level ~~of nit~~ of nitrate ion due to increased 'biological activity' (Ahlgren and Ahlgren, 1960; Wells, 1971) after burning balances a corresponding concentration of cations in the soil solution and therefore heavy losses through water occurs (Bormann et al., 1968; Lewis Jr. 1974). The loss of water, nutrients and sediment gets reduced as crop and weed cover ~~is~~ establishes (Toky and Ramakrishnan, 1981a; Mishra and Ramakrishnan, 1983d), with a transfer of nutrients from soil to the plant biomass.

STATE OF KNOWLEDGE OF BAMBOO STUDIES

Taxonomy:

Bamboos of the old world have received taxonomic attention since the comprehensive treatment of 1839 by Ruprecht in Leningrad, based on herbarium specimens and the literature upto his time. This was followed in 1868 by the more extensive work of colonal Munro whose excellent descriptions, notes, and system of classification have been a basis for subsequent studies. In the same period, Sulpiz Kurz was travelling in Java ~~and came~~ and came to know and study bamboos in the field. His treatment of bamboo and its uses (1876) contains a storehouse of field observations on those of the Indian subcontinent and Malayan archipelago. Further attention was paid to Asiatic bamboos in the monograph by Gamble (1896) who treated those of Burma, India, and Malaya. Additional treatments of bamboos of this region were prepared by Bor (1938, 1940) for Assam, by Rhind (1945) for Burma, and by Holttum (1958) for the Malay Peninsula. The bamboos of Java were covered by Backer and van den Brink (1968), but those of the remainder of this large assemblage of islands, including such bamboo rich areas as Borneo and Sumatra, have not been treated. Holttum (1967), however, prepared an account of the bamboos of New Guinea. Lin (1961, 1968) has written brief treatments on those of Thailand and Taiwan. The Philippine bamboos, although not revised as a group, have been covered by Merill (1923-25) and Brown (1951).

Taxonomic accounts of the bamboos of China appear in the many publications of F.A. McClure (1973) who spent most of the years between 1919 and 1940 in Canton where he developed a lifelong interest in these plants, Besides McClure, Keng Yi-li and Keng Pai-chieh, have studied the bamboos of China and published descriptions of many new species, and keys to the Chinese species appear in publications by Keng Yi-li (1933); and Keng Pai-chieh (1948).

In Japan, where bamboos are so important, both economically and culturally, the literature is voluminous. Among these are the papers by Makino and Shibata (1901) on the genus Sasa; numerous publications by Nakai (1925; 1942), and the comprehensive monograph by Takenouchi (1932). The most common species were recently treated by Ohwi (1965). The older studies of Japanese bamboos are widely revised by Muroi (1956) and others.

The bamboos of Africa are treated in scattered publications such as those by de Wildeman (1920), Alvino (1950), Robyna (1955), and Clayton (1970). Those of the Malagasy Republic have been treated in various publications by Lin (1967).

McClure (1973) published a paper on the genera of new world bamboos, those of the austral part of the American continent are covered in the publications of Parodi (1936, 1941, 1945) that deal with the genera and species of Argentina and Chile. McClure and Smith (1967) presented a revision of bamboo genera and species of the Brazilian state of Santa Catarina.

Ecological attributes:

There are many accounts in Asia of the spread of bamboo into disturbed habitats. Forests of Vietnam destroyed by deliberate firing and warfare in the present century have resulted in clearings where bamboos have been able to take hold. A recent report by Drew (1974) states pure bamboo populations taking over where forests are destroyed, provided they are present in the area as in Thailand where colonies of the bamboo species Thyrsostachys invade the land cleared of teak forests. In Laos, extensive tracts of giant bamboos now cover areas that many years ago were cleared for cultivation (Soderstrom and Vidal, 1975). The typical kind of information available for bamboos of the old world is provided by Troup (1921) for Melocanna bambusoides Trin. This "is a typically gregarious bamboo, and occupies extensive tracts of country in the Chittagong and Arakan Hills, where the destruction of tree-growth by shifting agriculture has over considerable areas produced a veritable sea of bamboo resulting from culms which have sprung from rhizomes remaining alive in the ground after the tree-growth has been destroyed". Haig et al.(1958) also mention that as a result of shifting agriculture, huge expanses of grass and bamboo forests are established in Asia. In the north-eastern region of India bamboos form a major component in communities developed after slash and burn agriculture (jhum) (Ramakrishnan _et al_., 1981; Toky and Ramakrishnan, 1983a).

Because of bamboo's economic importance in that country, Japan has taken the lead in ecological studies. These studies and have dealth with species of temperate or warm-temperate genera such as _Sasa_ and _Phyllostachyus_. Like most temperate species, these have rhizomes of the running type which permit the plants to spread over wide areas quickly. The tropical bamboos, such as those found in Amazonia, are adapted to much warmer conditions, and have abbreviated rhizomes that form bamboos of the clump type. It is probable that the ecological studies carried out on these bamboos in Japan will not be applicable, except in general terms, to the tropical species, because both habit and habitat are so different.

In tropical America the native Indians lived in harmony with the forest, and large-scale clearings and destruction did not come about until after the proliferation of European settlements (Meggers, 1971). Where civilizations did develop in the New World, they centered around another grass, maize. Native bamboos, of course, have been and still are utilized by the native people, but they have never become a dominant feature of the vegetation as they have in Asia. This is doubtless because, they are kept in balance with the natural unaltered forest ecosystems. Scanty as it is, the knowledge of bamboo ecology was brought into focus with publication of a book, "Ecology of Grasslands and Bamboolands of the world", edited by Numata (1979).

Studies on the role of bamboo in forest succession are, however, rare. Some accounts on the productivity of bamboo was carried out by Hozumi *et al.*~~,~~ (1969) in Cambodia. Biomass studies of pure bamboo stands in Laos were made by Soderstrom and Vidal (1975). Huberman (1950) and Ueda (1960) estimated the dry-matter yields of some managed bamboo stands. Oshima (1961) reported aboveground biomass of 14.1-114 t ha^{-1} for four Japanese species of *Sasa* bamboos. Aboveground biomass of *Arundinaria alpina* K. Schum which attains maximum heights of 20 m in highland Kenya, is approximately 100 t ha^{-1} (Wimbush, 1945). Dry matter production of two *Chusquea* species in South-Central Chile was estimated by Vablen *et al.* (1980).

Natural propagation of bamboo mainly takes place asexually through extensive rhizomes. Uchimura (1980) on the basis of this extensive studies on bamboo implicated rainfall and nutrient availability as two major factors determines shoot elongation in bamboo.

The flowering of bamboo has been a matter of special interest and it varies depending upon the species of bamboos which some species of bamboos show periodical flowering. The bamboo culm may die after flowering in some species, whereas in others they may not die even though the culm is defoliated and weakened temporarily. Several theories were formulated about flowering of bamboo; (i) Pathological theory, destruction of bamboos through casual organisms like nematodes, fungi, insect pests and parasites brings about flowering (Koide, 1882; Shirai, 1908), (ii) Periodical theory, a cycle of bamboo regeneration through asexual method through rhizome and culm elongation, reaching maturity and then resulting in flowering (Kawamura, 1927; Masumura, 1971; Katayama, 1978), (iii) Mutation theory, bamboo regeneration through any methods of asexual propoagation is considered as mutation, resulting in flowering of bamboos (Kasahara <u>et al</u>., 1969), (iv) Nutrition theory, Flowering and fruiting are usually the results of a physiological disturbance arising chiefly from the poor growth of the vegetative cells, brought about by an imbalance of carbon-nitrogen ratio (Muroi, 1962; Ueda, 1960),

(v) Man-made theory, clear cutting and fire are man-made practices that can induce bamboo flowering (Uchimura, 1980).

All these theories are only observations and in order to determine which of the theories are profitable for each of different species, there is a need to know the meteorological factors or conditions that induce flowering. In conclusion, it may be noted that our knowledge on bamboo flowering is meagre.

PRESENT STUDY

Slash and burn agriculture popularly called 'jhum' in India and also in the north-east, and variously termed locally in the country (Tekenglu in Nagaland, Dawar or Dipa in Madhya Pradesh, Kumri in Western ghat region or podu in Orissa) is a common land use practice in the humid tropics throughout the world (known as Milpa in Central America, Zande in Africa, Chena in Sri Lanka, Kaingin in Philippines and Tsembaga in Papua New Guinea). It involves slash and burn of the vegetation followed by mixed cropping for a year or two before the land is abandoned for natural regeneration for a few years and before coming back to the same site for cropping. This fallow period between two successive croppings at the same site representing one cycle was fairly long in north-east India (20-30 years) in the past. However, in the recent past, it has come down to 4-5 years due to increased population pressure and reduced acreage. This has often resulted in an arrested succession at the weed stage (Saxena and Ramakrishnan, 1984b), which in turn has drastically degraded the quality of environment in terms of vegetational cover and soil fertility (Ramakrishnan and Toky, 1981). This was critically reviewed by Ramakrishnan (1985a) based on over a decade's research of his group. In another review (Ramakrishnan, 1984b) he also focussed upon the science behind the rotational bush fallow agriculture (jhum) and its value for an integrated development of the tribal areas of the north-east India.

As a result of perturbation to the forest ecosystem by man or by natural means, such as fire drastic changes occur in the environment in the tropics and subtropics, due to their fragile nature. Considerable attention has been given to study the processes involved in the recovery pattern through a descriptive approach (Kenoyer, 1929; Budowsky, 1961), evolutionary approach (Gomez-Pompa, 1971).

population approach (Sarukhan, 1964) or an ecosystem approach (Franforth and Golley, 1974; Ramakrishnan *et al.*, 1981). However, our knowledge of the adaptive strategy of individual species under varied environments after perturbaration is more important for better understanding of the vegetation recovery process. The need for such studies was emphasized by many workers (Gomez-Pompa and Vazquez-Yanes, 1974; Golley and Medina, 1975; Bazzaz, 1979; Toky and Ramakrishnan, 1982; Saxena and Ramakrishnan, 1984c).

Bamboos form an important component of secondary successional fallows upto about 30 years and fallow regrowth after slash and burn agriculture in north-eastern India. The present study deals with demography and population dynamics, growth and architectural strategies, and leaf population dynamics of two important species of bamboo, namely *Dendrocalamus hamiltonii* Nees and Arn. and *Neohonzeoua dulloa* A. Camus. An attempt has also been made to value the role of bamboo in the socio-cultural life of the one of the tribes of the region, namely, the Khasi in east Khasi Hills district.