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

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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 cohabitation 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 Denthoria caespitosa, 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; [illegible]akrishnan and Mishra, 1981; Cook and Lyons, 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 Anthoxanthum odoratum, 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 of 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 *et al.* (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 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; 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 soneratioides 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. Whitemy (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 bifurca-

tion 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 interprets 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., 1987; 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 nutrient 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 Pinus kesiya 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 Imperata cylindrica and Thysonolenna maxima 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 (Borman 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, 1983).

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, 1983; 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 run-off 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. (1980) 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 succession 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 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; Ahlgrën 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 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 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 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), Robyns (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 have dealt 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 Veblen 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 et al., 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 petturbation 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 perturbation 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 Neohouzeoua dullooa 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.

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STUDY AREA AND CLIMATE

****

Fig. 1. Location of study area in north-eastern India. 1. Lailad; 2. Umpri; 3. Umroi; 4. Machipani and 5. Chenkii.

Fig.i

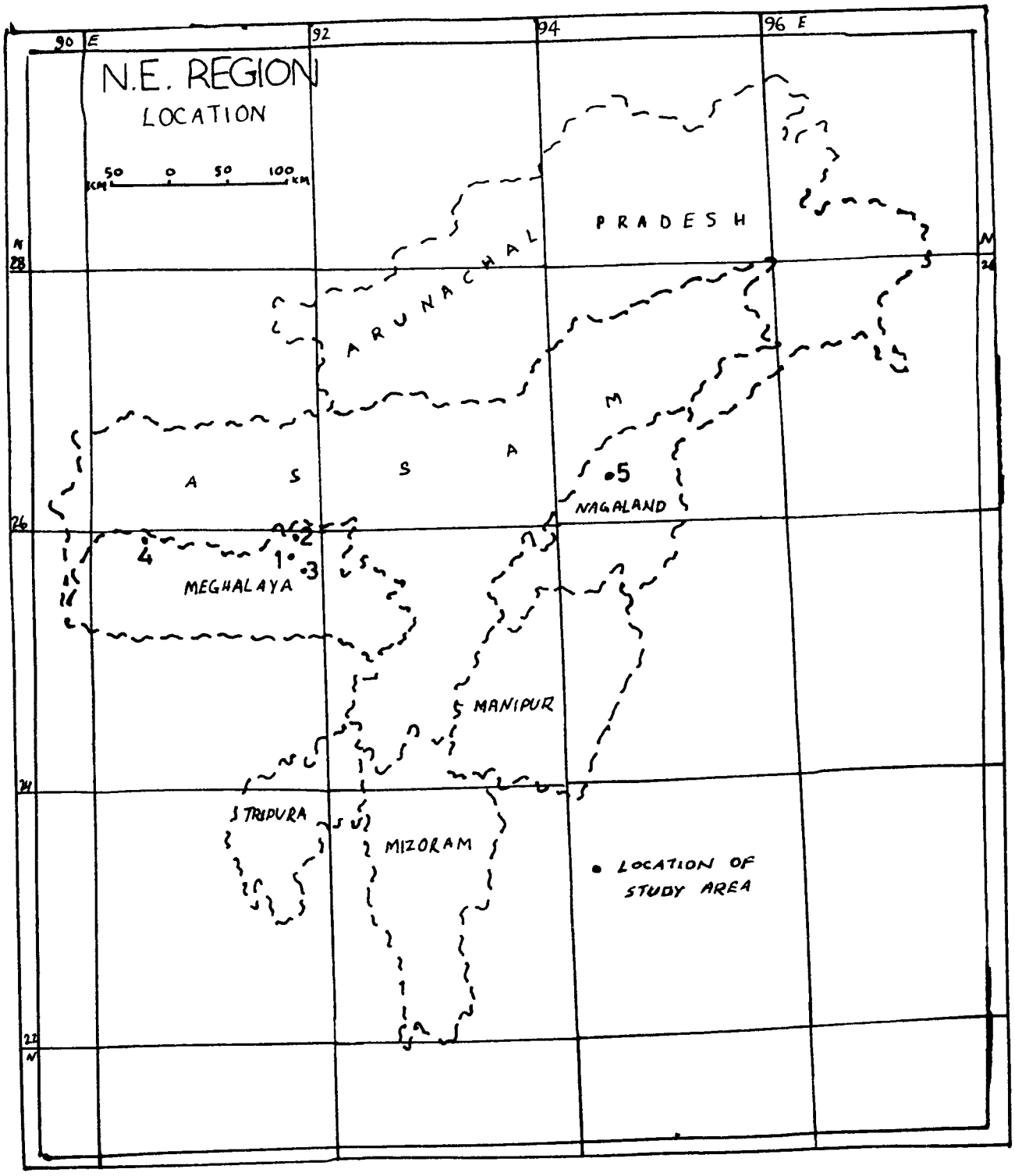
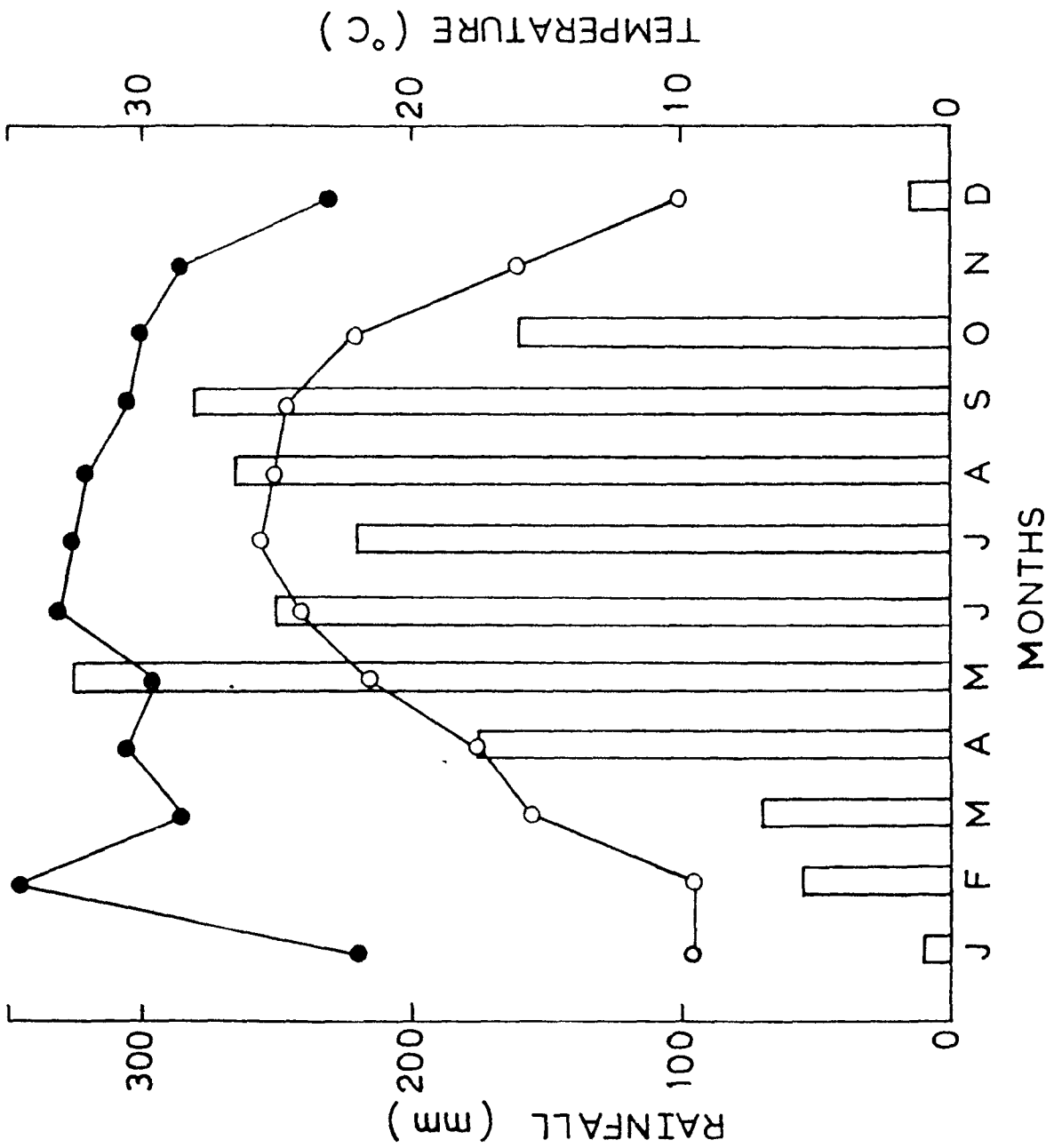

N.E. REGION
LOCATION
50 0 50 100 KM
90 E
92
94
96 E
28 N
26
24
22 N
PRADESH
ARUNACHAL
ASSAM
NAGALAND
MEGHALAYA
MANIPUR
TRIPURA
MIZORAM
1
2
3
4
5
LOCATION OF STUDY AREA

Fig. ii. Ombrothermic diagram of the study area (Lailad) 1983. Closed circle, mean monthly maximum temperature; Open circle, mean monthly minimum temperature; Bars represent monthly rainfall.

Fig. ii


TEMPERATURE (°C)
30
20
10
0
RAINFALL (mm)
300
200
100
0
J F M A M J J A S O N D
MONTHS

The present study was done at the lower elevations of north-eastern hill region of India. While detailed analysis of demography and population dynamics, studies pertaining Architectural analysis and adaptive strategies were done at Lailad, in Khasi Hills, for role of bamboos in shifting agriculture and socio-economic analysis studies, Machipani in Garo Hills, Chankii in Naga Hills, Umpri and Umroi in East Khasi Hills district of Meghalaya were selected (Fig.i). The pre-cambrian rocks are represented by gneiss, schists and granites. The soil is a red sandy loam of laterite origin, with pH 5-7. The angle of the slope generally ranged from 20^{o} to 40^{o}.

As all the study sites have similar climatic conditions the details of Lailad climate is given here (Fig. ii). The climate has three distinct seasons: (i) a brief summer extending from mid-February to May, (ii) a rainy season from May to September and (iii) a mild and relatively dry winter from October to mid-February. The average maximum temperature during the summer period was $30.7^{o}C$ and the average minimum was $14.4^{o}C$. 73% of the annual rainfall of 1800 mm occurred

during the rainy season. The average maximum temperature during the rainy season was 31.4°C and the average minimum was 24.1°C, whilst that for winter months were 26.5°C and 10.8°C respectively.

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CHAPTER 1

COMPARATIVE ANALYSIS OF THE POPULATION DYNAMICS OF TWO BAMBOO SPECIES, *DENDROCALAMUS HAMILTONII* NEES AND ARN. AND *NEOHOUZEOUA DULLOA* A. CAMUS IN SUCCESSIONAL ENVIRONMENTS IN NORTH-EASTERN INDIA.

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INTRODUCTION

During early phases of secondary succession after slash and burn agriculture (Jhum) in north-east India, bamboos form an important component of the plant community (Ramakrishnan et al., 1981; Toky and Ramakrishnan, 1983a). After a fallow period of 5-6 years dominated by herbaceous weeds (Saxena and Ramakrishnan, 1984b), bamboos form an important component of the next phase in plant succession alongwith shrubs and tree saplings. While some species such as Dendrocalamus hamiltonii that are strictly light demanding get eliminated as light availability in the community declines after a period of about 25 years of fallow regrowth, others such Neohouzeoua dulloa which can tolerate shade but prefer a high light environment may continue even in older communities. However, vast areas under weed communities and bamboo forests in the north-east, as elsewhere, are a consequence of large scale disturbance through slash and burn agriculture (Drew, 1974; Haig et al., 1988; Soderstorm and Vidal, 1975; Saxena and Ramakrishnan, 1984b).

Neohouzeoua dulloa A. camus (Syn. Teinostachyum dulloa Gamble ex. Munro) is an evergreen bamboo of the lower elevations upto an altitude of 1200 m in north-

eastern hill region of India. The records available with the village headman in the study area and published report (Janzen, 1976) show that this species flowered gragariously in 1968. However, flowering elsewhere in the north-east, in Cachar Hills of Assam, was also recorded earlier in 1951 (Gupta, 1972). On this basis, Janzen (1976) predicted another gragarious flowering in 1985, though this did not happen. In early successional communities of upto 25-years of fallow regrowth this species is vigorous. The clumps (genets) established through seedlings here, are generally more than 1 m^2 but have vigorous vegetative reproduction through culms (ramets) established from a close knit but extensively branched underground rhizome system. The number of ramets may be about 50 under more favourable environmental conditions. In older fallows, this species grows as an understorey component but the genet size is much less with only about half the number of ramets per genet. The ramets with a height of 4 to 5 meters and a diameter of 3 to 6 cm is used extensively for basket making, handicrafts and for hut construction. The young sprouts are also consumed as food by the tribal farmer.

Dendrocalamus hamiltonii Nees and Arn. Ex. Munro is a deciduous bamboo species occuring at an altitude of upto 1200 m with sporadic and gregarious flowering habits with an intermast period of 30-40 years for the latter (Cavendish, 1905; Gupta, 1972; Janzen, 1976; Varmah and Bahadur, 1980). The number of ramets per genet may be upto 60, each ramet being 16-18 meters long and 12-25 cm in diameter. They are extensively used as firewood and for hut construction, handicrafts and exported for pulping. The young tender shoots are edible. The present study deals with a comparative analysis of the population dynamics of these two species over successional environment.

METHODS OF STUDY

Three replicate fallows of 1-, 5-, 10-, 15-, 20-, 25- and 60-years were identified on the basis of our observations and also based on the records available with the village headman and Forest Department. Care was taken to ensure similar topography, slope (average 30^{o} angle), exposure and soil type. Phytosociological studies were based on thirty 1 m^2 quadrats for herbaceous vegetation and thirty 100 m^2 quadrats for shrubs and trees. The importance value indices (IVI) based on relative frequency, relative dominance

and relative basal cover were calculated following Misra (1968) and Kershaw (1971).

Five replicates of 100 m^2 permanent quadrats were laid at each site to study the dynamics of ramets (vegetative culms) during a one year period starting from June 1983 for D. hamiltonii and from April 1983 for N. dullooa. All individual ramets present at the beginning of the study period were considered to be more than one year old and classified as old population. Any individual ramet appearing above the soil surface was counted as gains (births) and those lost through natural causes as losses (deaths). Ramets appearing in a given month were marked as a cohort.

Growth index of a stand in a unit area was calculated as the ratio of the number of new ramets produced during the one year study period to the number of ramets originally present. The genets (clump of ramets) in terms of genet area and the number of ramets were analysed at each site at the end of one year study period.

Since flowering in D. hamiltonii occured only in fallows of 5 to 25 years, the number of genets that flowered were analysed for seed reproductive potential

Table 1.1. Importance value indices (IVI) of the vegetation of 1- to 60-year old successional fallows.

Species	Fallow age(years)						
	1	5	10	15	20	25	60
Herbs:							
Ageratum conyzoides L.	60.02	36.11	35.03	10.84			
Arundinella bengalensis (spreng) Druce	32.60	4.60	19.78	14.58			
Borretia hispida (L.) K. Schum	24.52	9.98	9.60				
Carex Cruciata vahl	4.83	6.62	25.98	30.36	18.78	8.30	
Cymbopogon khasianum (Hack.) Stapf.ex Bor.	11.87	1.93	4.50	7.92			
Cyperus globosus Retz	0.04	4.18	11.03	6.65	7.32	8.96	10.09
Desmodium triquetrum (L.) DC	11.75	10.89	10.84	5.98			
Eupaterium odoratum L.	21.90	67.59	16.64	4.86			
Ficus hispida L.	3.32	2.62	3.21				
Fimbristylis dichotoma(L) vahl	6.37	1.58					

Grewia elastica heyle	9.08	0.93					
Hedychium cornonarium Koenig				5.14	11.19	18.18	31.05
Hedychium gracile Roxb			2.73	8.12	10.33	17.76	40.05
Imperata cylindrica (L.) P. Beauv.	9.12	41.28					
Mikania micrantha H.B.K.	9.64	44.24					
Panicum khasianum Munro	6.14	3.96	18.09	13.90	16.39	8.73	12.09
Panicum maximum Jacq.	8.62	7.54	27.61	20.19	4.58		
Passiflora nepalensis wall.				10.71	22.86	13.25	15.58
Setaria glauca Beauv.	9.11						
Scleria tessellata willd.	11.98	2.60	8.76				
Thysanolaena maxima (Roxb.) O.ktze	13.40	6.05	6.96	3.88			
Shrubs:							
Cinnamomum sp.	2.38	2.91	3.36	4.11	3.47	2.05	
Combretum decandrum Roxb.	1.16	1.15	1.31	1.29	1.73	2.06	2.12

Croton oblongifolius Roxb.				1.19	2.87	2,86	4.67
Euria acuminata DC	1.22	1.77	2.06	2.56	1.80		
Gnetum sp.					1.69	2.28	4.04
Lees Sp.						2.04	4.23
Litsaea khasiana Meissn.			1.02	1.22	1.69	2.28	3.26
Maesa indica (Roxb.) wall.	2.55	2.03	1.36				
Mallotus philippensis (Lour.)Muell.			1.01	1.58			
Melastoma malabthricum L.	3.65	2.02	1.29				
Melia azadrach L.	1.95	0.88	0.98				
Mesua ferrea L.				1.20	1.69	1.92	4.73
Musaenda sp.			0.99	1.57	1.17		
Osbeckia crinta Benth				1.21	1.67	4.09	8.19
Sterculia villosa Roxb					1.67	2.24	9.94
Trees:							
Albizia lebbeck (L.) Bent		0.61	1.01	1.62	3.30	2.83	1.16

Albizia chinensis (osb.) Merr.	0.31	0.88	1.32	2.15	3.51	3.69	0.99
Alnus nepalensis D. Don		0.26	0.70	0.86	1.63	1.97	
Amoora Wallichii king	1.07	1.50	2.32	3.34	4.43	3.36	
Anthocephalus cadamba (Roxb.) Miq		0.61	1.30	1.62	2.78	0.73	
Artocarpus chaplasha Roxb		0.26	0.29	0.85	2.10	3.30	4.84
Bauhinia variegata L.	0.97	1.14	1.68	2.43	2.77	20.5	0.72
Bombax ceiba L.		0.26	0.70	1.25	1.95	2.39	13.50
Callicarpa arborea Roxb.	1.55	1.49	1.99	2.46	2.13	2.05	12.32
Careya arborea Roxb.	0.75	0.88	1.31	1.65	1.20		
Castanopsis indica A. Dc			0.29	0.38	1.64	3.34	15.03
Cedrela toona Roxb.				0.38	2.09	4.46	12.03
Duabanga soneratoides Ham		0.61	1.68	2.86	3.44	2.20	1.96
Dillenia indica L.		0.61	2.00	2.46	3.43	4.17	14.07
Dendrocalamus hamiltonii (Nees & Arn) Ex. Munro	6.27	13.06	37.94	78.87	108.23	125.68	4.19

Eugenia communis wight		0.26	0.70	1.21	1.19	0.62	
Garcinia paniculata (G.Don) Roxb.				0.50	2.12	3.33	9.71
Gmelina arborea Roxb		0.26	0.71	1.24	2.17	3.32	12.31
Lagerstroemia indica L.			0.30	1.20	2.17	3.33	14.03
Macaranga denticulata Muell.	3.49	3.54	2.74	2.69	3.35	0.64	
Machillus khasiana Meissn			0.30	1.27	1.92	3.05	9.63
Micromelum glaberrinum (Roxb) Roem.		1.14	1.72	2.50	1.29		
Miliusa roxburghiana (wall)H.K.F.2TH			0.34	0.97	2.01	2.98	5.64
Neohouzeua dülloa A. camus	6.01	6.81	12.32	16.69	19.49	13.89	5.12
Sapium baccatum Roxb	2.76	2.64	2.32	2.26	1.56	1.32	
Schima wallichi (D.C.) korth	3.38	3.26	3.76	3.23	4.21	4.58	1.97
Terminalia bellirica (W&A) Bedd			0.31	1.04	1.71	2.63	2.57
Vitex peduncularis R. Br.	1.33	1.15	1.73	1.29	0.56		
Vitex glabrata R. Br.	1.35	1.76	1.74	1.28	1.20		

of this species. Seedling recruitment and establishment was followed in these fallows using twenty randomly laid 1 m^2 permanent quadrats in each fallow plot, in half of which the litter layer on the soil was removed. Seedling studies started in May 1983 was followed for a one year period.

RESULTS

Vegetation analysis:

The early stages of secondary succession was dominated by herbaceous species (Table 1.1), the more important ones being Ageratum conyzoides, Arundinella bengalensis, Eupatorium odoratum, Imperata cylindrica and Mikania micrantha. After a period of about five years of fallow regrowth a number of shrubs and trees come up. Shrubs such as Eurya acuminata, Litsaea assamica, Mallotus philippensis and Combretum decandrum and trees such as Amoora wallichii, Anthocephalus cadamba, Duabanga sonneratoides, Dillenia indica, Sapium baccatum and Schima wallichii were important components during 5 to 25 years of fallow regrowth. Species of bamboo, Dendrocalamus hamiltonii and Neohauzeoua dulloa were also abundant at this stage, the former being more dominant. D. hemiltonii reached its peak growth in

Table 1.2: Population flux of *N. dulloa* ramets in 1- to 60-year old successional fallows

	Fallow age (years)						
	1	5	10	15	20	25	60
a) Number of ramets ha^{-1} at the beginning of study(April,83)	400	2000	5200	4600	5000	3300	3000
b) Number of ramets produced ha^{-1} during study period	1100	1600	2100	2300	2300	1500	1200
c) Number of ramets lost ha^{-1} during study period	400	800	1100	700	700	300	300
d) Number of ramets ha^{-1} at the end of study (April, 84)	1100	2800	6200	6000	6000	4600	3900
e) Number of ramets ha^{-1} recorded during the study period	1500	3600	7300	6900	7300	4800	4200
f) Net change (d-a)	700	800	1000	1400	1000	1300	900
g) Rate of change(d/a)	1.8	1.4	1.2	1.3	1.2	1.4	1.3
h) Percentage annaul mortality (c/e x 100)	26.7	22.2	15.1	10.1	9.6	6.3	7.1
i) Growth index of population (b/a)	2.8	0.8	0.4	0.5	0.5	0.5	0.4

20- to 25-year old fallows. In a 60-year old fallow this species was confined only to the peripheral open areas. N. dulloa, however, reached its peak growth in 15- to 20-year old fallows,,but also occured in a 60-year old fallow as an understorey species. 60-year old fallow was a mixed forest with trees such as Castanopsis indica, Cedrela toona, Gmelina arborea and Lagerstomia indica.

Ramet population dynamics of N. dulloa:

The number of ramets present at the beginning of the study period and that recruited during the year increased with fallow age, reaching a maximum in 10- to 20-year old fallows and with a sharp decline in older ones (Table 1.2). The number of new ramets lost during the study period was more in 5- to 20-year old fallows. However, the percentage annual mortality was maximum in a 1-year old fallow, declining with fallow age. The rate of change remained more or less constant in all the fallows except in a 1-year old fallow; this was also reflected to some extent in the growth index of the population which was highest in a 1-year old fallow.

Table 1.3: Recruitment of N. dulloa ramets through each monthly cohort in 1- to 60-year old successional fallow (expressed as a percentage of the total recruitment)

Monthly cohort	Fallow age (years)						
	1	5	10	15	25	35	60
May	27.3(27.3)	56.3(17.9)	42.9(12.9)	39.1(8.1)	47.8(12.9)	46.2(13.0)	55.6(12.8)
June	45.5(18.2)	25.0(7.1)	33.3(6.5)	34.8(8.1)	30.4(8.1)	38.5(10.4)	22.2(5.1)
July	27.3(18.2)	18.8(3.6)	14.3(3.2)	17.4(4.8)	13.0(1.6)	15.4(4.3)	28.2(5.1)
August	0.0(0.0)	0.0(00.0)	9.5(3.2)	8.7(1.6)	8.7(3.2)	0.0(0.0)	0.0(0.0)

Percentage contrinution to the ramet population, by different cohorts is indicated in parentheses.

Table 1.4: Genet size and structure of *N. dullos* in 1- to 60-year old successional fallows

Fallow age (years)	Number of genets Ha^{-1}	Number of ramets $genet^{-1}$	Genet area (m^2)
1	197	5	0.11
5	199	19	0.41
10	203	48	1.01
15	193	51	1.21
20	196	49	1.23
25	199	42	0.61
60	191	29	0.30

Table 1.5. Population flux of D. hamiltonii ramets in 1- to 60-year old successional fallows

	Fallow age (years)						
	1	5	10	15	20	25	60
a) Number of ramets ha^{-1} at the beginning of study (May,83)	1000	2200	5500	6000	6900	7300	150
b) Number of ramets produced ha^{-1} during study period	700	1900	2900	3100	4000	1800	26
c) Number of ramets lost ha^{-1} during study period	200	800	1400	1400	2100	1100	16
d) Number of ramets ha^{-1} at the end of study (May 84)	1500	3300	7300	7700	8800	8000	160
e) Number of ramets ha^{-1} recorded during study period	1700	4100	8400	9100	10900	9100	176
f) Net change (d-a)	500	1100	1800	1700	1900	700	10
g) Rate of change (d/a)	1.5	1.5	1.33	1.28	1.1	1.1	1.1
h) Percentage annual mortality (e/e x 100)	11.77	19.51	16.67	15.39	19.27	12.09	9.09
i) Growth index of population (b/a)	0.70	0.86	0.53	0.52	0.58	0.25	0.17

10- to 20-year old fallows produced four cohorts in a year whilst all others produced only three (Table 1.3). Much of the recruitment occurred during May to July. Generally speaking recruitment of N. dulloa through a first cohort was more than through subsequent cohorts in except for 1-year old fallow. The older ramets prior to the study period had maximum contribution to the total population, in all the fallows. The contribution by the first cohort of the current year was markedly higher than that by the subsequent cohorts. The last cohort produced during the season had the least contribution to the total population size.

Though the genet number per unit area did not show much variation in different fallows, the area occupied by individual genets was maximal in 10- to 20-year old fallows with sharp decline in younger and older fallows (Table 1.4). The number of ramets per genet was maximal in 10- to 25-year old fallows with a sharp decline in 1- and 60-year old ones.

Ramet population dynamics of D. hamiltonii:

The ramet population already present in the fallows reached its maximum in a 25-year old fallow with a drastic decline in a 60-year old one (Table 1.5). However,

Table 1.6: Recruitment of D. hamiltonii ramets through each monthly cohort in 1- to 60-year old successional fallows (expressed as a percentage of the total recruitment)

Monthly cohort	Fallow age (years)						
	1	5	10	15	20	25	60
June	28.57	31.58	27.59	21.62	32.50	44.44	42,31
July	42.86	26.32	27.59	21.62	27.50	27.78	30.77
August	14.29	26.32	20.69	18.92	20.00	16.67	26.92
September	14.29	15.79	17.24	13.51	12.50	11.11	0.00
October	0.00	0.00	6.90	8.11	7.50	0.00	0.00

Table 1.7: Genet size and structure of *D. hamiltonii* in 1- to 60-year old successional fallows.

Fallow age (years)	Number of genets ha^{-1}	Number of ramets $genet^{-1}$	Genet area (m^2)
1	113	2	0.77
5	115	32	1.16
10	115	52	1.90
15	115	63	2.27
20	116	64	2.44
25	115	63	2.53
60	6	30	2.17

the number recorded during the study period, their birth during the year and the survivors out of it all reached peak values in a 20-year old fallow and drastically declined in a 60-year old one. Rate of change in population structure declined with the age of the fallow. Growth index for the ramet population was higher in 1- and 5-year old fallows; in 25- and 60-year old fallows it dropped markedly.

Ramet production in 10- to 20-year old fallows occurred over a period of five months from June-October; in others it occurred for four months except in a 60-year old fallow, where it was confined to three months only (Table 1.6). Major recruitment occurred in June to July declining in subsequent months.

The genet number was more or less the same in all the fallows excdpt in a 60-year old one. Where there was a drastic decline (Table 1.7). Number of ramets per genet reached a maximum in 15- to 25-year old fallow but declined in a 60-year old one.

Seedling population dynamics of D. hamiltonii:

Seedling recruitment was very high when the litter layer was undistrubed than when the litter was removed

Fig. 1.1 Cumulative gains and losses (a) and net population change (b) of D. hamiltonii seedlings during the study period. Closed circle, 5-year; Open circle, 10-year; closed triangle, 20-year and open triangle, 25-year old fallows. _____, with litter cover on the ground; - - - -, without litter cover on the ground.

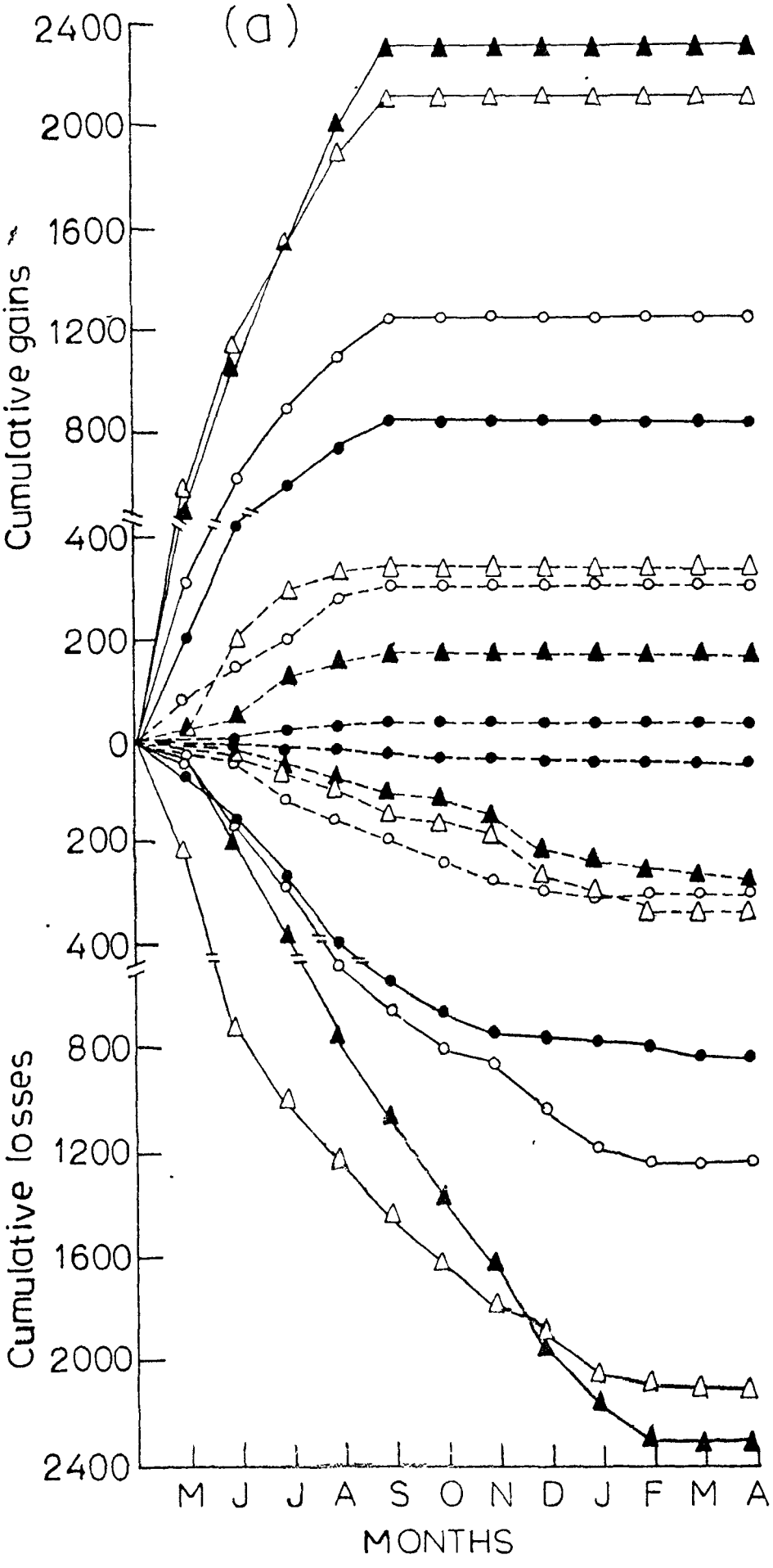
(a)
2400
2000
1600
1200
800
400
200
0
200
400
800
1200
1600
2000
2400
Cumulative gains
Cumulative losses
M J J A S O N D J F M A
MONTHS

Fig. 1.1

Fig. 1.1

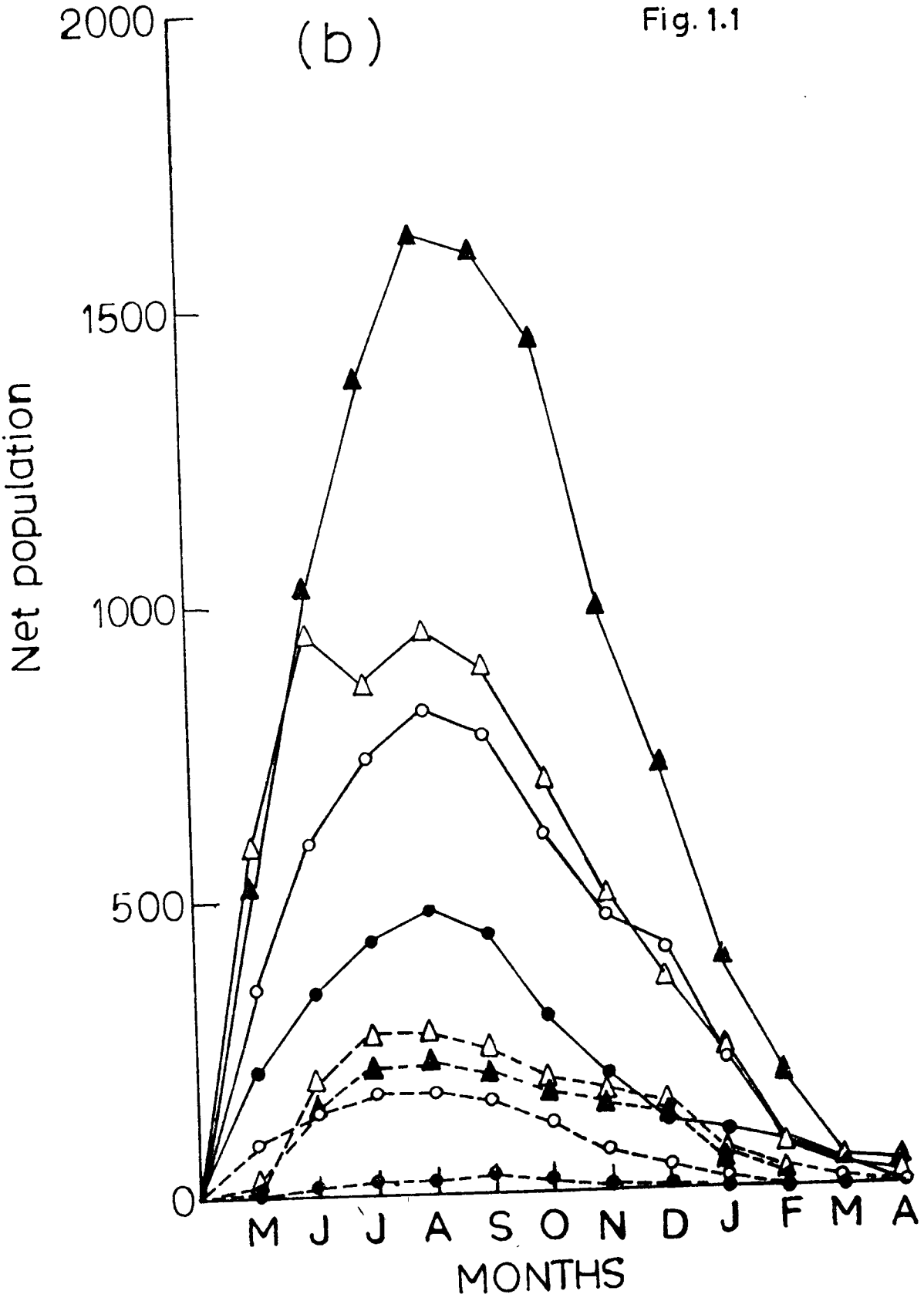

Fig. 1.2. Percentage contribution to the net population surviving at the end of first year (a) and second year (b) by different monthly seedling recruitments of D. hamiltonii. Dark column, with litter cover on the ground; open column, without litter cover on the ground.

Fig. 1.2

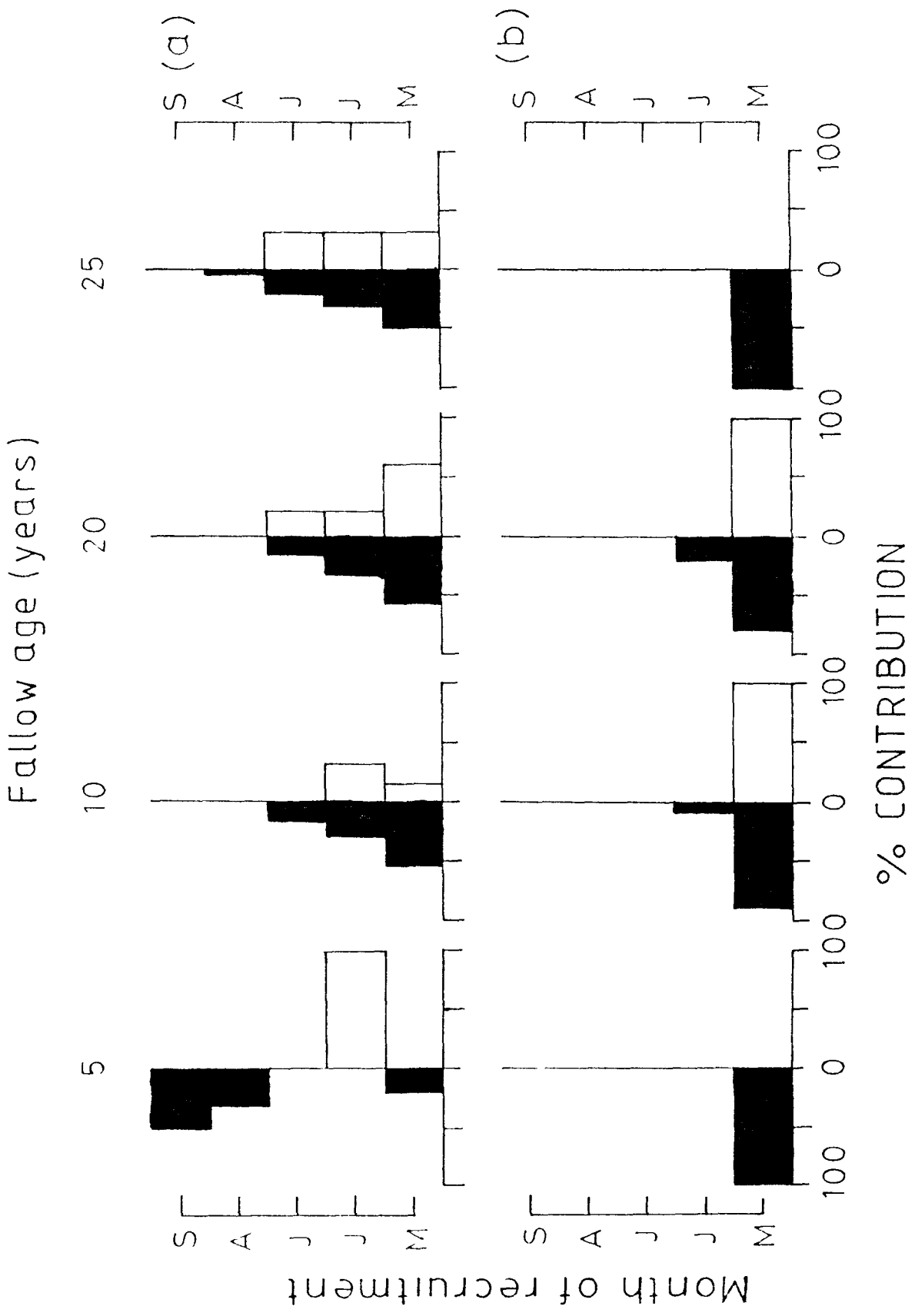
(a)
(b)
S A J J M
Month of recruitment
Fallow age (years)
5
10
20
25
100 0 100
% CONTRIBUTION

Table 1.8: Population flux of *D. hamiltonii* seedlings in 5- to 25-year old successional fallows (values within the parentheses are for plots without lifer cover)

	Fallow age (years)			
	5	10	20	25
a) Number of seedlings m^{-2} at the beginning of study (May 1983)	212(5)	346(89)	528(34)	599(13)
b) Number of seedlings recorded m^{-2} (produced) during study period	810(36)	1221(296)	2276(263)	2088(321)
c) Number of seedlings lost m^{-2} during study period	804(35)	1208(293)	2251(258)	2071(318)
d) Number of seedlings m^{-2} at the end of study (May 1984)	6(1)	13(3)	25(5)	17(3)
e) Net change (d-a)	-206(-4)	-333(-86)	-503(-29)	-582(-10)
f) Rate of change (d/a)	0.03(0.2)	0.04(0.03)	0.05(0.15)	0.03(0.23)
g) Percentage annual mortality (c/b x 100)	99.26(97.22)	98.94(98.99)	98.90(98.10)	99.19(99.07)

(Table 1.8). In plots where litter was not disturbed maximum recruitment occurred in a 20-year old fallow, whilst in plots without litter recruitment was maximum in a 25-year old fallow. Mortality was very severe and was more than 97% and was not affected by the litter layer. Seedling establishment was more in a 20-year old fallow with decline in younger and older fallows. Seedling regeneration did not occur in a 60-year old fallow.

The cumulative gain and losses, alongwith net population size in different months are shown in Fig. 1.1 a&b. Seedling recruitment occurred between May to September but mortality continued upto the following February to March. The population flux was much more pronounced where litter was left undisturbed compared to the treatment where litter was removed. Net population size peaked in August to September.

The survival at the end of the first year period of the seedling recruited in a given year is shown in Fig. 1.2a and the survival of the same at the end of second year is shown in Fig. 1.2b. On plots with litter, survival at the end of the first year period was generally more for those produced earlier in the season, except in

Table 1.9: Reproductive output of *D. hamiltonii* in 5- to 25-year old successional fallows

	Fallow age (years)			
	5	10	20	25
a) Genets ha^{-1}	115	115	116	115
b) Percentage fertile genets ha^{-1}	4.39	5.26	3.45	3.95
c) Number of ramets $genet^{-1}$	12	29	31	31
d) Number of inflorescence $ramet^{-1}$	346	461	489	501
e) Seeds $inflorascence^{-1}$	15	58	68	73
f) Seeds $ramet^{-1}$	5347	25632	33532	36623
g) Seed production Kg $genet^{-1}$	1.6	8.0	10	11
h) Seeds ha^{-1}	26994	155048	134195	166360

a 5-year old fallow. Such a pattern was not obvious on plots without litter. However, at the end of the second year period the seedlings survived were largely from the seedling cohort produced in May. In 5- and 25-year old plots without litter no seedlings from the previous year survived.

Though the proportion of fertile genets in the population was not very different in different fallows (Table 1.9), the seed production parameters such as inflorescence per ramet, seeds per ramet or a genet all increased with fallow age. Seed production per hectare was low in a 5-year old fallow compared to older ones.

DISCUSSION

Neohouzeoua dulloa being a species that flowers gregariously once during its life span, the population dynamics of this species related to successional environment had to be based exclusively on clonal reproduction. However, with sporadic flowering occurring in Dendrocalamus hamiltonii the population dynamics is based on both clonal and seedling studies; gregarious flowering reported in this species (Varmah and Bahadur, 1980) was not observed during the study period.

Being an important component of early successional environments after slash and burn agriculture (jhum) in north-east India (Ramakrishnan *et al.*, 1981; Toky and Ramakrishnan, 1983a), these bamboo species are subjected to considerable fluctuations related to soil and micro-environment. Apart from changes in pH, moisture and nutrient status of the soil as related to litter accumulation and decomposition (Ramakrishnan and Toky, 1981; Toky and Ramakrishnan 1983a), increased potential evapo-transpiration and reduced light availability are related to a change from an open to a closed community. Though the species are light demanders, as is evident from their relative dominance in 10- to 25-year old fallows, *N. dullooa* showed a remarkable plasticity for survival even in a more closed forest environment of 60 years of age. On the other hand, in a 60-year old forest, *D. hamiltonii* was confined only to its disturbed peripheral part, where light availability was higher (Singh and Ramakrishnan, 1982). Thus *N. dullooa* with greater plasticity (Chapter 2) is exposed to more diverse ecologic situations during its establishment and development, compared to *D. hamiltonii*.

Ramet dynamics in the two species:

Starting with a low recruitment of ramets in a 1-year old fallow for both the species, ultimate population size improved upto 20 or 25 years of fallow age in the case of N. dulloa; the population size of N. dulloa in a 60-year old fallow was not very much altered compared to 25-year old fallow, but sharply declined in D. hamiltonii. However, the vigour of population was low in a 60-year old fallow for both the species as seen from the number of ramets per genet and the genet area. The low vigour in a 1-year old fallow may be a consequence of a high degree of disturbance in the site during the preceeding slash and burn operation followed by cropping for one year (Toky and Ramakrishnan, 1981a). The increment in the number of ramets per unit area with fallow age upto 20 or 25 years may be related to the age of the stand as shown under plantation conditions in Japan (Ueda, 1960).

In the case of the light demanding herbaceous species such as Eupatorium odoratum (Kushwaha et al., 1981; Kushwaha and Ramakrishnan, 1982), Eupatorium adenophorum (Ramakrishnan and Mishra, 1981) and Imperata cylindrica (Kushwaha et al., 1983), light as

a factor was implicated as responsible for the restriction of these species from late successional environments. The low vigour of the two species in a 60-year old fallow may be because of shade stress to which these light demanding species are subjected. N. dulloa is more shade tolerant compared to D. hamiltonii as seen from the relatively unaffected ramet recruitment in a closed 60-year old forest.

The production of more monthly cohorts in 10- to 20-year old fallows when compared with younger and older ones suggests of the greater vigour of growth of these species at these sites. Generally speaking, the larger recruitment of ramets through the first cohort in N. dulloa alone, which incidentally also had least mortality of individuals gave extended favourable time period for population compared to the subsequent cohorts. This again is also reflected in the percentage contribution to the population structure which was more through the first cohort of N. dulloa, though only next to the pre-existing population. The absence of such a pattern in the sporadically flowering D. hamiltonii suggests that this feature is perhaps of greater value to a more predominantly colonal species such as N. dulloa. Lovett-Doust (1981) reported that a clonal species such as

Ranunculus repens also had larger contribution to its population through the first monthly cohort.

Our observations suggest that natural mortality in ramet populations largely occur during the Juvenile phase. Grazing of young sprouts by animals such as pigs and monkeys and insect attack are the chief causes for this. Though in the study area human interference was excluded, young sprouts are also harvested for food, more often in D. hamiltonii, than in N. dulloa. The older ramets of both the species are also harvested for hut construction, D. hamiltonii being harvested also for export for pulping.

While the ramet population size showed differences in different fallows, the genet population size of N. dulloa was not very much altered upto 60-years of fallow age. In D. hamiltonii genet population size was drastically reduced only in a 60-year old fallow. In N. dulloa, recruitment of new genets is not only rare (Noble et al., 1979) but happens only once during the life cycle after gregarious flowering and mast seeding and the population dynamics is largely dominated by birth and death of clonal modules rather than whole genets. Though the intermast phase for D. hamiltonii has been recorded as 30 to 40 years, the age at which sporadic

flowering (Janzen, 1976) in a genet is initiated is not clear. This is an aspect that needs more study as many gregarious flowering bamboos such as Dendrocalamus strictus and Bambusa tulda have been shown to flower within a brief time period under cultivation (Banik, 1980).

The differences in ramet reproductive plasticity in D. hamiltonii and N. dulloa have implications for bamboo forest management. Both the species are light demanders and D. hamiltonii obviously is more demanding than the other.

Seedling dynamics in D. hamiltonii:

The contribution through seedling recruitment in D. hamiltonii is very low (1 to 2% only). Though it is difficult to identify a genet that would flower in a given year, our observations over a four year period suggest that those genets conserve their resources for seed production by not producing any ramets for a year prior to flowering, or sometimes for two years as in Dendrocalamus strictus (Troup, 1921). One of the factors respónsible for poor seedling recruitment is the heavy predation by Jungle fowl, other migratory birds and red ants. The low production of seeds during sporadic flowering may not offer sufficient attraction for other larger animals reported

for mast seeding species (Janzen, 1971, 1976). However, flowering resulted in the total death of both aboveground and belowground parts unlike that reported by Numata et al., (1984) for Phyllostachyus bambusoides from Japan, where the post-flowering phase may have a few slender ramets produced from a few of the live nodes of the mostly dead rhizomes.

Increase in seed production upto 25 years of fallow regrowth, though the genet number remained essentially the same is due to increased production of ramets and their larger biomass related to longer growth period in older fallows. Increase in seedling recruitment upto 20 years of fallow regrowth followed by a decline in a 25-year old fallow and no seedling recruitment at all in 60-year old fallow agrees with the earlier observation of ours, suggesting that the peak growth of this species during secondary succession is between 10 to 20 years (Ramakrishnan et al., 1981; Toky and Ramakrishnan, 1983a). While seedling recruitment occurred during the monsoon period from May to September, seedling mortality was a continuing event through the first and second years after production. It may be noted that the seedlings produced at the beginning in May had greater chance to reach adulthood compared to those produced in the subsequent months. This may be partly related to few

predators at this time and longer duration of favourable growth period for these seedlings.

Though presence of litter enhances seedling germination, the establishment of seedlings on soil surface with litter is hampered because of the physical hindrance offered by the litter for the roots to reach the mineral soil. On the other hand, the seedling establishment on the soil surface from where litter has been removed is subjected to both heavy predation and desiccation due to exposure causing equally high mortality. Appropriate management of mulching on the soil surface may be an important technique that could be used for optimizing seedling establishment and management of bamboo forests under natural conditions.

SUMMARY

A comparative analysis of the population dynamics of two bamboo species, Dendrocalamus hamiltonii Nees and Arn. and Neohouzeoua dulloa A. camus, with varying degrees of plasticity in a successional environment was studied. N. dulloa with more plasticity was a clonally reproducing species, gregariously flowering followed by seed reproduction occurring only once in 14-17 years. D. hamiltonii also had sporadic flowering and therefore

had both clonal and seed reproduction simultaneously. Clonal reproduction in D. hamiltonii was optimal in fallows of 10 to 20 years of age with a drastic decline in a 60-year old fallow. N. dulloa, on the otherhand, showed a decline in vigour of the genets and ramets in a 60-year old fallow, but with lesser effect on population size. Seedling recruitment in D. hamiltonii is poor but offers possibility of better management through manipulation of surface mulching techniques. Population recruitment in successional environments have implications in bamboo forest management.

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CHAPTER 2

ARCHITECTURAL PLASTICITY OF TWO BAMBOO SPECIES (*NEOHOUZEOUA DULLOA* A. CAMUS AND *DENDROCALAMUS HAMILTONII* NEES AND ARN.) IN SUCCESSIONAL ENVIRONMENTS IN NORTH-EASTERN INDIA.

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INTRODUCTION

During secondary succession after slash and burn agriculture in north-east India, edaphic (Ramakrishnan and Toky, 1981; Toky and Ramakrishnan, 1983b) and micro-environmental changes such as reduction in light availability occur with the development of a closed community (Toky and Ramakrishnan, 1983a; Singh and Ramakrishnan, 1982). Species occurring in the early successional environment show varying degree of plasticity for survival in such fast changing situations. Canopy architecture is particularly important for capitalizing upon changing light environment during succession (Boojh and Ramakrishnan, 1982a,b; Shukla and Ramakrishnan, 1984a, 1986) and, therefore, determine to a large extent the success of woody species in transient environments (Schulze, 1983). Much of the work on canopy architecture in relation to succession pertains to temperate broad-leaved tree species (Brunig, 1976; Nelson et al., 1981; Borchert and Slade, 1981; Kramer and Kozlowski, 1979). It is only in recent times that tropical woody species have started receiving some attention (Ramakrishnan & Shukla, 1982; Shukla and Ramakrishnan, 1984a, 1986). However, all these studies refer to different species over a successional gradient

and no information is available on architectural plasticity of the same species in such a gradient. Further, the only information available on the architectural attributes of bamboos pertain just to a brief qualitative description given by Hallé et al. (1978) who placed all of them under McClure's model.

The success of an organism in a given environment is because of a favourable allocation of the limited available resources (biomass and nutrients) to the diverse life purpose such as maintenance, growth and reproduction (Schaffer et al., 1982; Vincent and Pullium, 1980; Paltridge and Denholm, 1974; Cohen, 1976; Abrahamson and Caswell, 1982). In the rapidly changing early successional environments, the strategy adopted by a given species is likely to change over a time period as shown by us in a perennial weed Eupatorium odoratum (Saxena and Ramakrishnan, 1984a). Whilst much of the allocation strategy studies pertain to herbs, woody species have started receiving attention only recently (Ramakrishnan and Shukla, 1982; Shukla and Ramakrishnan, 1984b). As far as we know, there is no information available on the allocation strategies of bamboo species, which stand apart from broad-leaved woody shrubs and trees in their growth characteristics.

The present paper, therefore, deals with the plasticity in the architectural design and allocation strategies of two early successional bamboo species, Neohouzeoua dulloa A. Camus and Dendrocalamus hamiltonii Nees & Arn. The former is more plastic occurring in successional fallows of upto 60 years whilst the latter is restricted to the first 25 years only, after slash and burn agriculture (Ramakrishnan et al., 1981; Toky and Ramakrishnan, 1983a) at lower elevations in Meghalaya in north-east India.

METHODS OF STUDY

1-, 5-, 15-, 25- and 60 year old fallows were identified based on our own observations and the records available with the village headman and the Forest Department. Care was taken to ensure similar topography, soil type, exposure and slope.

Architectural Studies:

Ten replicate ramets (culms) from randomly selected genets (clumps), produced during the monsoon period in 1982 were marked in February, 1983. Further, ten replicate ramets recruited in April 1983, in case of N. dulloa and June 1983, in case of D. hamiltonii were

also identified. The observations in a 60-year old fallow were restricted to N. dulloa only. Regular weekly/ monthly observations were made on these individual ramets from a platform erected around each of them.

Allocation studies:

N. dulloa is a gregariously flowering bamboo species, that flowered last in 1968, before total extinction, in the study area. Therefore, the population under observation have the same stock age of about 15 years. D. hamiltonii apart from its sporadic flowering behaviour exhibits gregarious flowering too. It flowered gregariously, last in 1956, in the study area. The stock age of this species is, therefore, less than 30 years. In the present study the age of a genet was measured as regeneration age which was equivalent to fallow age upto 15 years in N. dulloa and upto 25 years in D. hamiltonii. The population of N. dulloa present in 25- and 60-year old fallows, however, had the same stock/regeneration age, namely 15 years. Since the stock age-regeneration age was the same for N. dulloa population in a given fallow (because this species regenerated after gregarious flowering in 1968) the genets were all of the same size in that fallow. This

permitted random selection of genets. On the otherhand, D. hamiltonii with both gregarious and sporadic flowering had genets of different sizes and therefore selection was done taking care to ensure similar size for all genets in a given fallow.

Ten replicate genets of both species, selected from each site were harvested in August, 1984. The aboveground parts were separated into bole (zero-order branch or main axis), branches (all orders except zero-order branch) and leaves. Belowground parts (rhizome and roots) were carefully excavated, washed thoroughly and weighed. Samples were dried at 80°C and dry weights computed.

All the samples were ground and passed through a 0.5 mm sieve and analysed for elemental composition after acid digestion using methods suggested by Allen et al. (1974). Nitrogen by Kjeldhal method, phosphorous calorimetrically by ammonium molybdate blue method, potassium by flame-photometry and calcium and magnesium by EDTA-titration method were determined.

RESULTS

Architectural studies:

Neohouzeoua dulloa and *Dendrocalamus hamiltonii* have sympodially branched underground rhizome systems. Each rhizome branch, which may vary from 9 to 14 cm in *N. dulloa* and from 12 to 24 cm in *D. hamiltonii* has a narrow 'neck' which broadens out into a thick 'base' (Fig. 2.1d). Two of the lateral buds of the 'base' would produce two rhizome branches. If, however, either of them are damaged, two branches are ensured by activation of one or two other lateral buds. The apical bud at the 'base', however, would give rise to the aboveground shoot system. Since the rhizome is thicker in *D. hamiltonii* than in *N. dulloa* and since the aerial branch diameter is also lesser in the latter species the genets (clumps) are loosely organised in *N. dulloa* than in *D. hamiltonii*. The number of ramets (culms) in a genet is highly variable.

The crown shape of *D. hamiltonii* is highly variable. In a 5-year old fallow, where the other species are predominantly herbs, better light availability results in a broad crown form for the lower half of the canopy, sharply narrowing above (Fig. 2.1a). The first-order

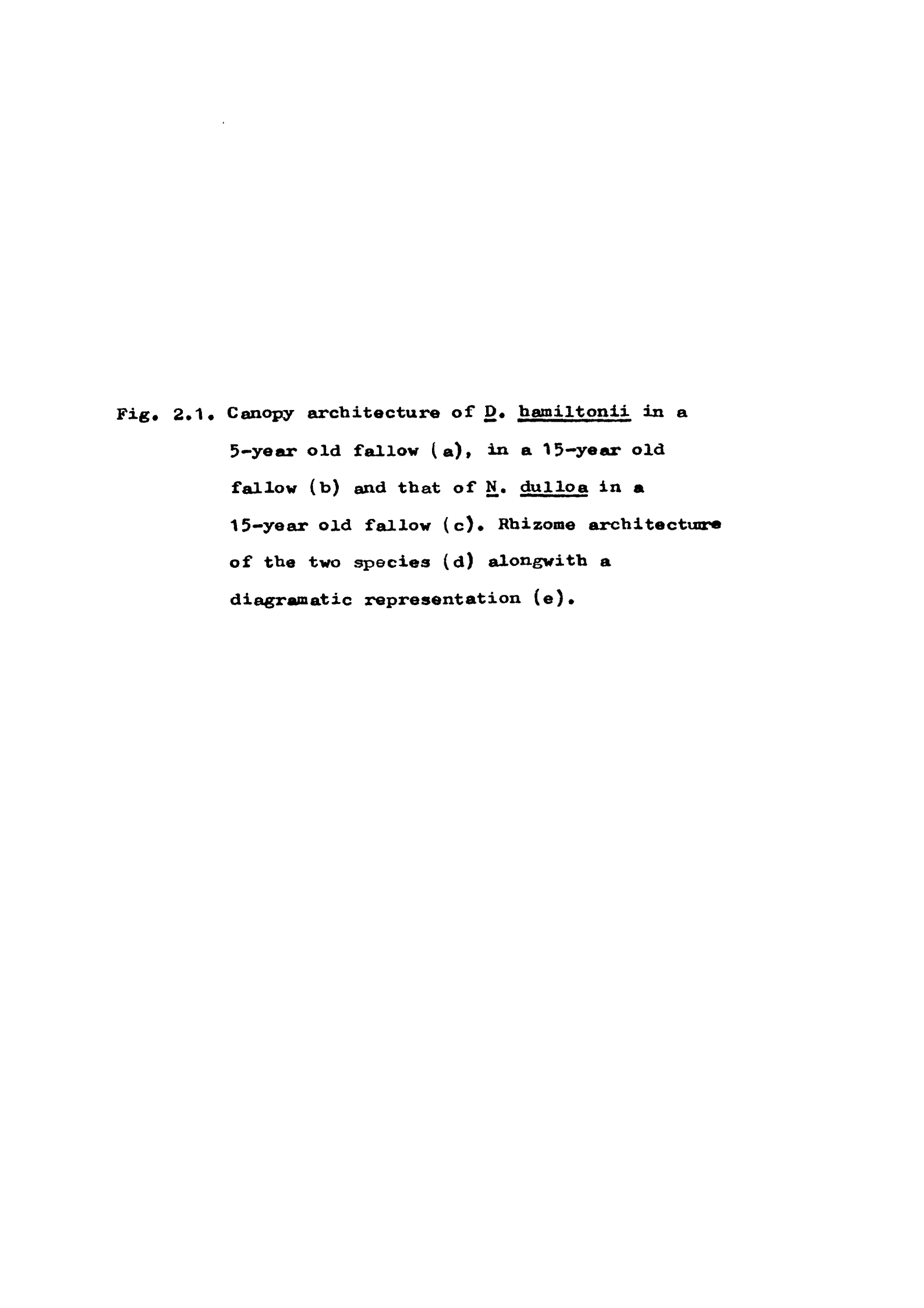
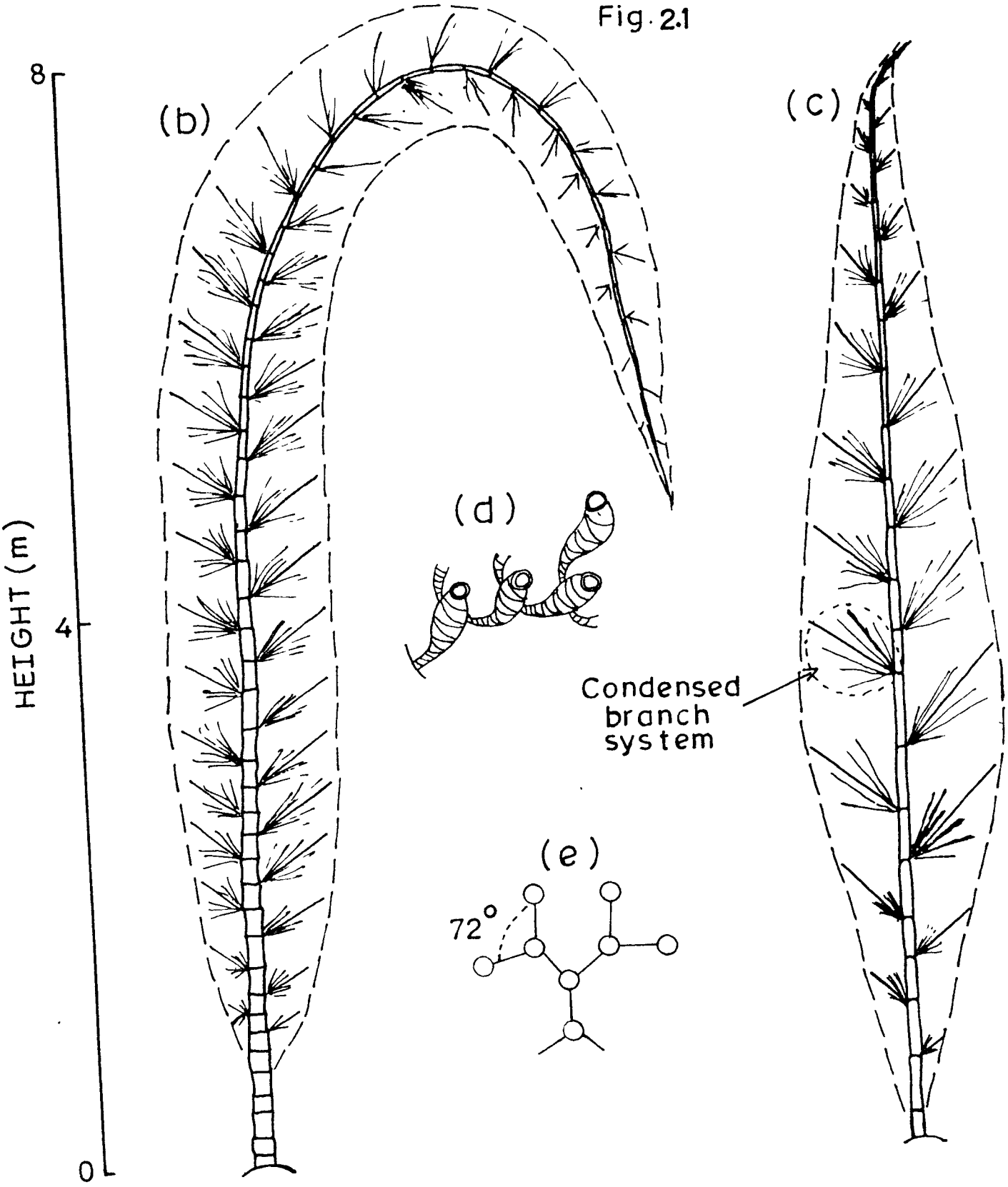


Fig. 2.1. Canopy architecture of D. hamiltonii in a 5-year old fallow (a), in a 15-year old fallow (b) and that of N. dulloa in a 15-year old fallow (c). Rhizome architecture of the two species (d) alongwith a diagramatic representation (e).

Fig. 2.1

Fig. 2.1

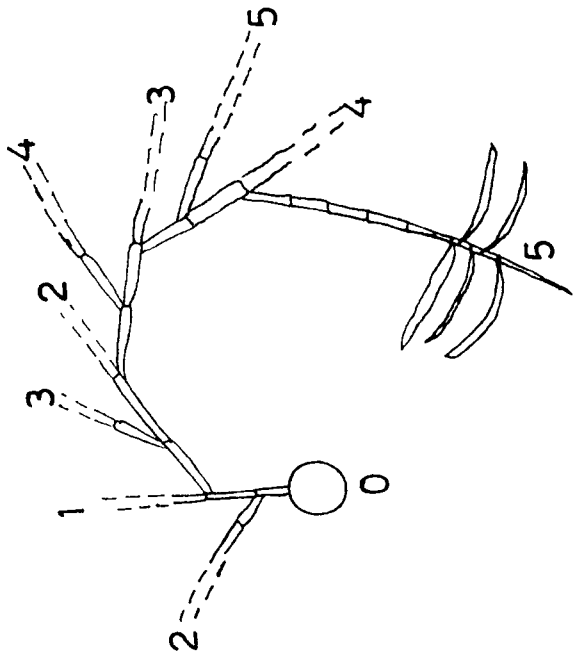


branch system in the broader region of the crown alone are extremely long compared to the subsequent branch orders, where as the different branch orders are more or less of the same length in the narrow part of the canopy. In older fallows, however, where trees and shrubs compete with D. homiltonii for space and for light availability, the crown form of this species is very narrow, somewhat cylindrical in shape with a whip like tip (Fig. 2.1b). Here the first-order branches and the subsequent ones are more or less of the same length. In N. dulloa, since the first-order branches are somewhat longer than the subsequent branch orders in the mid-canopy position the crown is broader in the middle, tapering on either side (Fig. 2.1c).

All the branch orders show determinate growth due to high degree of preformation. The orthotrophic zero-order branches of a ramet completes its elongation in both the species over a period of 90-120 days, after which branch production is initiated in the same year (Syllepsis) in N. dulloa and in the following year only (prolepsis) in D. hamiltonii. Reiteration (Hallé et al., 1978) of the zero-order branch occurs in D. hamiltonii, but not in N. dulloa. In the latter case, apical damage to the

Fig. 2.2. Diagramatic representation of the organization of branch orders in a branch complement in the two bamboo species. Zero to fifth-order branches are shown alongwith the leafy shoots viewing on branch orders first to fifth.

Fig. 2.2



zero-order axis would arrest its further growth. In both the species, all the branch orders are produced at the same time and elongation is completed simultaneously. N. dulloa, however, normally produce only upto the fourth-order branch system, except in a 15-year old fallow where the fifth-order branch production may occur but in the following year only. D. hamiltonii may produce branch systems upto the fifth-order.

The pattern of branch production is shown in Fig. 2.2. Both the species consistently had continuous first order branch production at all nodes of the zero-order branch system, except for D. hamiltonii in a 5-year old fallow. In a 5-year old fallow, however, first-order branch production in D. hamiltonii was diffuse (brahcnes arising from some of the nodes on the zero-order branch system only).

From the axillary buds of the two basal nodes of the first-order branch would arise two second-order branches, from the axillary buds on the two basal nodes of the second-order branch would arise two third-order branches and so on, so that a set of upto 31 branches may be produced in a condensed form (Figs. 2.1b, 2.2). However, branch production may stop with one unit only

at the first-order stage, with three units at the second-order stage, with seven units at the third-order stage, or with fifteen units at the fourth-order stage. Thus, as a rule, two branches would always arise at every stage of branch production, starting with the second order branch system.

The two species conform to the McClure's model as described by Hallé *et al.* (1978). The essential features of the model are that all the aerial parts are vegetatively determinant in their growth. They consider the determinant axis and the branch systems as a very large determinant organ, something like an elaborate compound leaf.

The rhizome branch dimensions of the current year growth of *N. dulloa* reached a maximum in a 15-year old fallow with a decline in older fallows (Table 2.1). The values for *D. hamiltonii*, however, reached its maximum in a 25-year old fallow.

The number of individuals per unit area in *N. dulloa* reached a maximum in a 15-year old fallow, with decline in 25- and 60-year old fallows. However, the number of individuals in *D. hamiltonii* reached a maximum in a 25-year old fallow (Table 2.2). All growth parameters

Fig. 2.3. Change in internodal length in relation to internode number, with fallow age in N. dulloa (- - - -) and D. hamiltonii (_____). Closed circle, 5-year; open circle, 15-year; closed triangle, 25-year and open triangle, 60-year old fallows. Inset figure shows elongation rate of the zero-order branch of N. dulloa (- - -) and D. hamiltonii (———) in a 15-year old fallow (open circle).

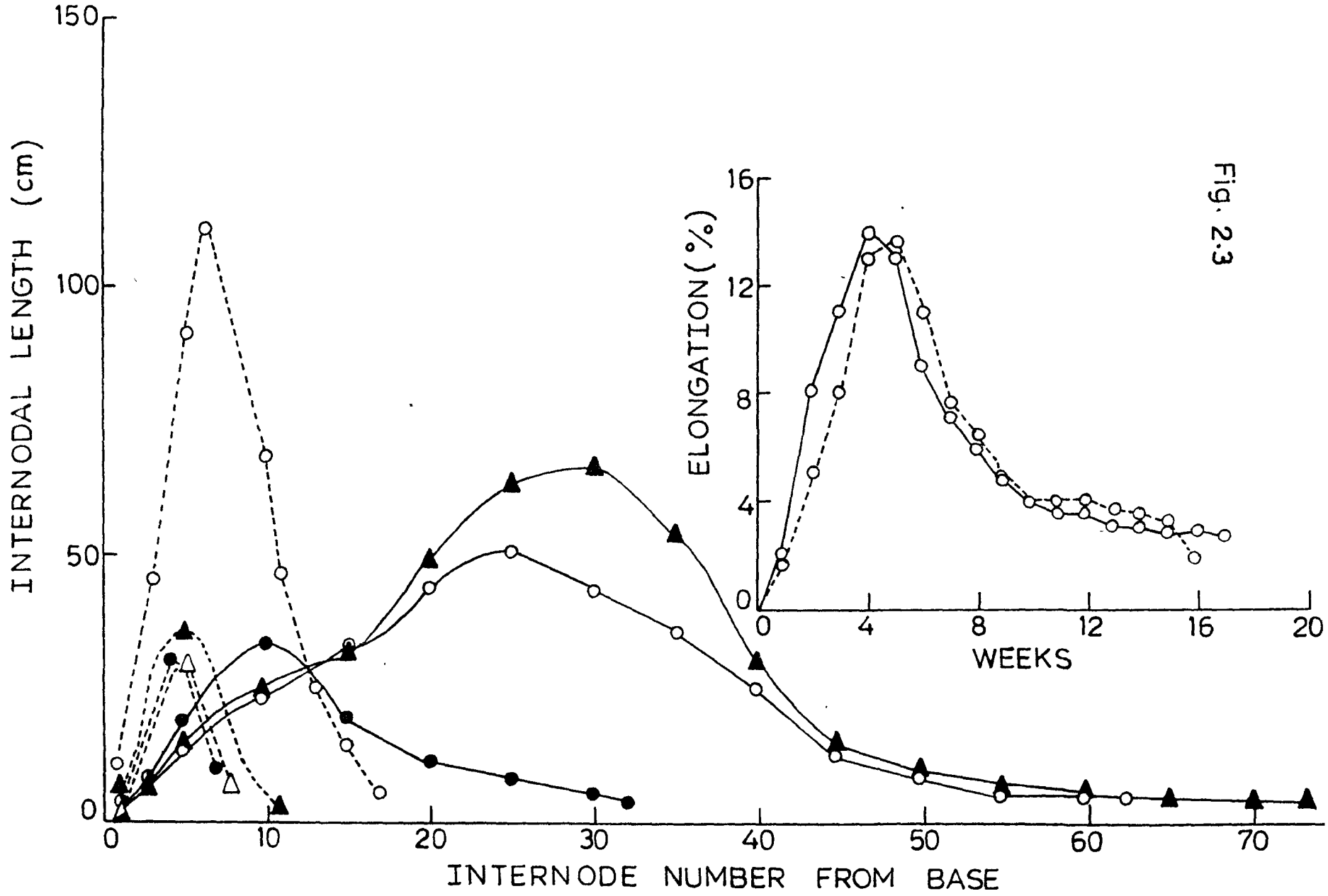

INTERNODAL LENGTH (cm)
150
100
50
0
0
10
20
30
40
50
60
70
INTERNODE NUMBER FROM BASE
ELONGATION (%)
16
12
8
4
0
0
4
8
12
16
20
WEEKS

Fig. 2.3

Fig. 2.4. Variation in the dormancy of buds (%) on the current year's ramet (zero-order branch) of N. dulloa (a) and last year's ramet of D. hamiltonii (b), with fallow age. Dorment buds, Dark column, Active buds, open column.

Fig. 2.4

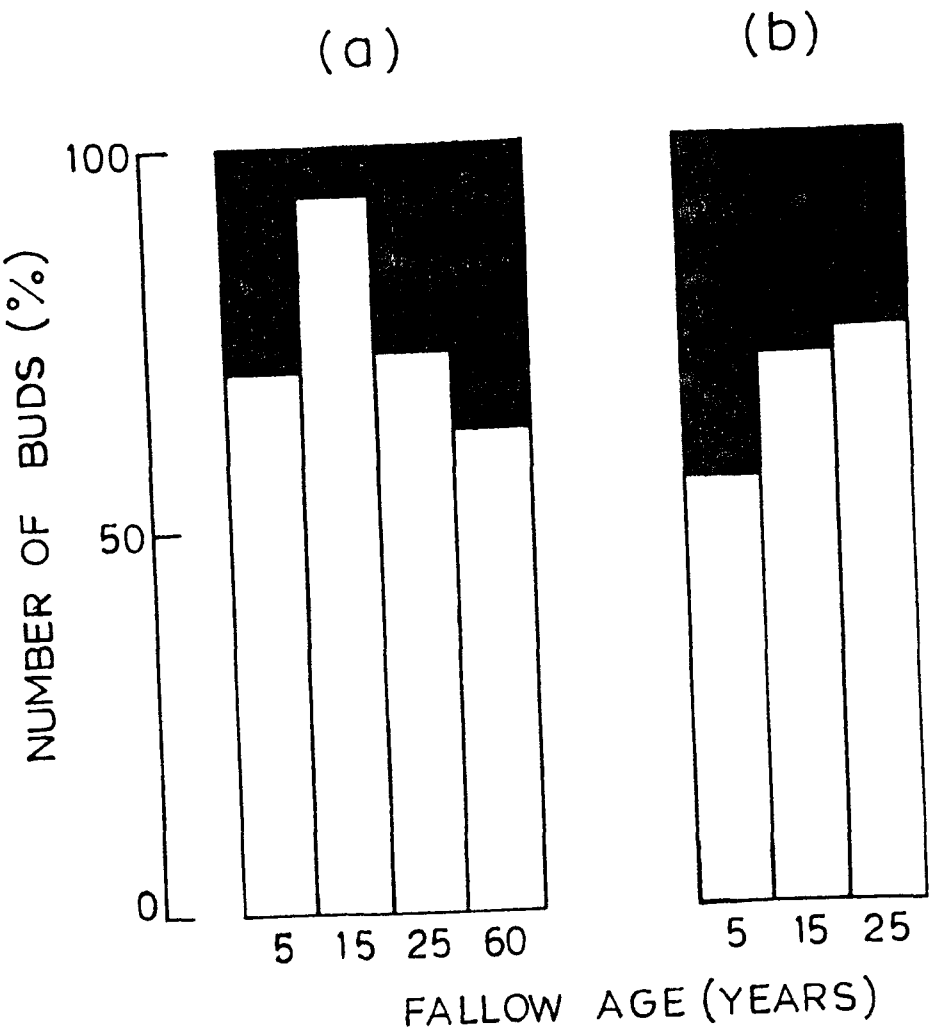


Table 2.1: Variation in current year's rhizome branches of bamboos (mean ± S.E.), in 5- to 60-year old successional fallows (Values within parentheses are for *D. hamiltonii*)

Fallow age (years)	Branch length (cm)	Diameter at neck (cm)	Diameter at base (cm)
5	9.7 ± 0.63	2.1 ± 0.51	3.3 ± 0.32
	(12.7 ± 1.14)	(4.7 ± 0.47)	(6.8 ± 0.66)
15	13.5 ± 1.23	5.4 ± 0.47	6.9 ± 0.69
	(21.5 ± 1.77)	(9.6 ± 0.66)	(18.2 ± 1.30)
25	11.2 ± 0.82	3.0 ± 0.35	3.5 ± 0.28
	(23.6 ± 1.93)	(9.9 ± 0.70)	(18.3 ± 1.36)
60	9.5 ± 0.92	2.3 ± 0.22	2.9 ± 0.25

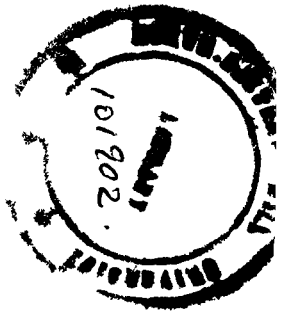


Table 2.2: Important characteristics of N. dullea and D. hamiltonii in 5- to 60- year old successional fallows (values within parentheses are for D. hamiltonii)

Parameters	Fallow age (years)			
	5	15	25	60
a) Genet area (cm^2)	0.41 ± 0.03 (1.16 ± 0.11)	1.21 ± 0.11 (2.27 ± 0.17)	0.61 ± 0.05 (2.53 ± 0.21)	0.30 ± 0.03
b) Number of ramets $genet^{-1}$	19 ± 1.30 (32 ± 2.85)	51 ± 3.20 (63 ± 4.11)	42 ± 2.9 (63 ± 2.53)	29 ± 1.9
c) Number of ramets ha^{-1}	2000 (2200)	4600 (6000)	3300 (7300)	3000
d) Length of ramet (m)	1.35 ± 0.12 (3.80 ± 0.35)	8.30 ± 0.82 (13.70 ± 1.23)	2.90 ± 0.21 (16.90 ± 1.68)	2.05 ± 0.16
e) Diameter of ramet at 10 cm from base(cm)	2.5 ± 0.20 (5.9 ± 0.58)	5.2 ± 0.38 (14.2 ± 1.14)	2.9 ± 0.21 (16.8 ± 1.36)	2.5 ± 0.16
f) Annual elongation in current year's ramet (cm)	185 ± 12.9) (400±28.6)	835 ± 50.8 (1420 ± 73.8)	300 ± 25.8 (1750 ±101.3)	215 ± 17.9
g) Total height to crown width ratio	1.69 (0.91)	6.91 (10.60)	3.22 (13.00)	2.56
h) Leafing behaviour	Evergreen leaf exchange type (Deciduous)			

for

in N. dulloa reached a maximum in a 15-year old fallow with decline in older fallows. Growth parameters of D. hamiltonii increased with fallow age upto 25 years.

The number of internodes of the zero-order branch of the ramet of N. dulloa reached a maximum in a 15-year old fallow whilst it was highest in a 25-year old fallow for D. hamiltonii (Fig. 2.3). In these fallows, the internodal length generally was more than in others. Where elongation was more vigorous (15-year old fallow for N. dulloa and 25-year old fallow for D. hamiltonii). there was a shift in the position of the longest internode from the base upwards. Since, in all the fallows, for both the species, the weekly elongation pattern was essentially the same, that for a 15-year old fallow alone is given in the inset Fig. 2.3. Maximum elongation occurred 4-5 weeks after initiation and by the tenth week more than 80% of the elongation was completed.

First-order branch production in N. dulloa was sylleptic but in D. hamiltonii it was proleptic. The bud dynamics of N. dulloa during the current year of its production (Fig. 2.4a) and that of D. hamiltonii for the following year of its production (Fig. 2.4b), indicate that in the former, but dormancy was minimal (6% only)

in a 15-year old fallow. In D. homiltonii on the other hand, dormancy in the one-year old buds declined with fallow age.

In both N. dulloa and D. hamiltonii the elongation declined with increase in the order of the branches (Table 2.3). The elongation shown for N. dulloa on the last year's ramet represents an apical portion of a few condensed nodes with tightly packed leaf sheaths ranging from 10 to 13, that fell off in the first year itself and replaced in the second year. In D. hamiltonii, however, this replacement would occur in the third year only, and is not presented here. Elongation of first-order branches in N. dulloa was maximal in 15-year old fallow with decline in others, where as subsequent order branch systems had maximum elongation in a 25-year old fallow, Fifth-order branch production in N. dulloa occurred proleptically in a 15-year old fallow alone.

Since first-order branch elongation varied with canopy position in D. hamiltonii, this is given in Table 2.4. From the base of the canopy elongation of the first-order branches increased sharply at nodes 10 to 20, more markedly so in a 5-year old fallow. A sharp decline in elongation occured at nodes 20 to 30 in a

Table 2.3.: Variation in shoot elongation (cm) (mean ± S.E.) of bamboos in 5- to 60-year old successional fallows (leafy shoot exchanged during the second year is given in parentheses).

Fallow age (years)	Species	Branch order				
		First	Second	Third	Fourth	Fifth
5	N. dulloa	40.1 ± 3.57 (10.2 ± 0.66)	26.3 ± 1.86 (7.6 ± 0.35)	23.4 ± 2.4 (6.9 ± 0.29)	20.3 ± 1.33 (6.3 ± 0.19)	
	D. hamiltonii	71.3 ± 20.50	30.4 ± 2.18	21.7 ± 2.18	18.3 ± 0.51	18.1 ± 0.60
15	N. dulloa	65.3 ± 4.0 (13.9 ± 0.4)	30.3 ± 0.89 (7.9 ± 0.29)	26.7 ± 2.11 (7.3 ± 0.25)	23.3 ± 1.14 (7.1 ± 0.29)	20.6 ± 1.23
	D.hamiltonii	65.7 ± 9.60	51.1 ± 1.49	50.4 ± 2.25	48.6 ± 0.92	46.7 ± 1.45
25	N. dulloa	35.2 ± 3.07 (11.2 ± 0.38)	32.6 ± 1.23 (7.3 ± 0.19)	30.3 ± 3.03 (7.6 ± 0.22	29.3 ± 1.30 (7.3 ± 0.13	
	D.hamiltonii	60.3 ± 9.70	50.5 ± 1.49	48.7 ± 2.56	48.7 ± 2.12	47.3 ± 1.01
60	N. dulloa	30.9 ± 3.00 (10.6 ± 0.29)	28.6 ± 0.60 (4.5 ± 0.13)	27.9 ± 0.60 (4.5 ± 0.19)	23.6 ± 0.73 (4.5 ± 0.13)	

Table 2.4: Variation in elongation (cm) (mean ± S.E.) in first-order branches of *D. hamiltonii* at different positions on zero-order branch in 5- to 25-year old successional fallows

Fallow age (years)	Branch position (node number from base)			
	0-10	10-20	20-30	<30
5	14.3 ± 0.92	254.1 ± 10.7	25.3 ± 2.6	
15	13.9 ± 0.98	75.3 ± 4.2	51.6 ± 4.7	18.7 ± 1.6
25	12.6 ± 0.81	73.9 ± 5.6	59.2 ± 2.9	23.6 ± 1.8

Fig. 2.5. (a) Standing biomass (kg genet^{-1}) of N. dulloa (closed circle) and D. hamiltonii (open circle) in successional fallows. (b) Biomass accumulation rates (kg genet^{-1} yr^{-1}) in aboveground (- - - -) and belowground (————) components of N. dulloa (closed circle) and D. hamiltonii (open circle) in successional fallows.

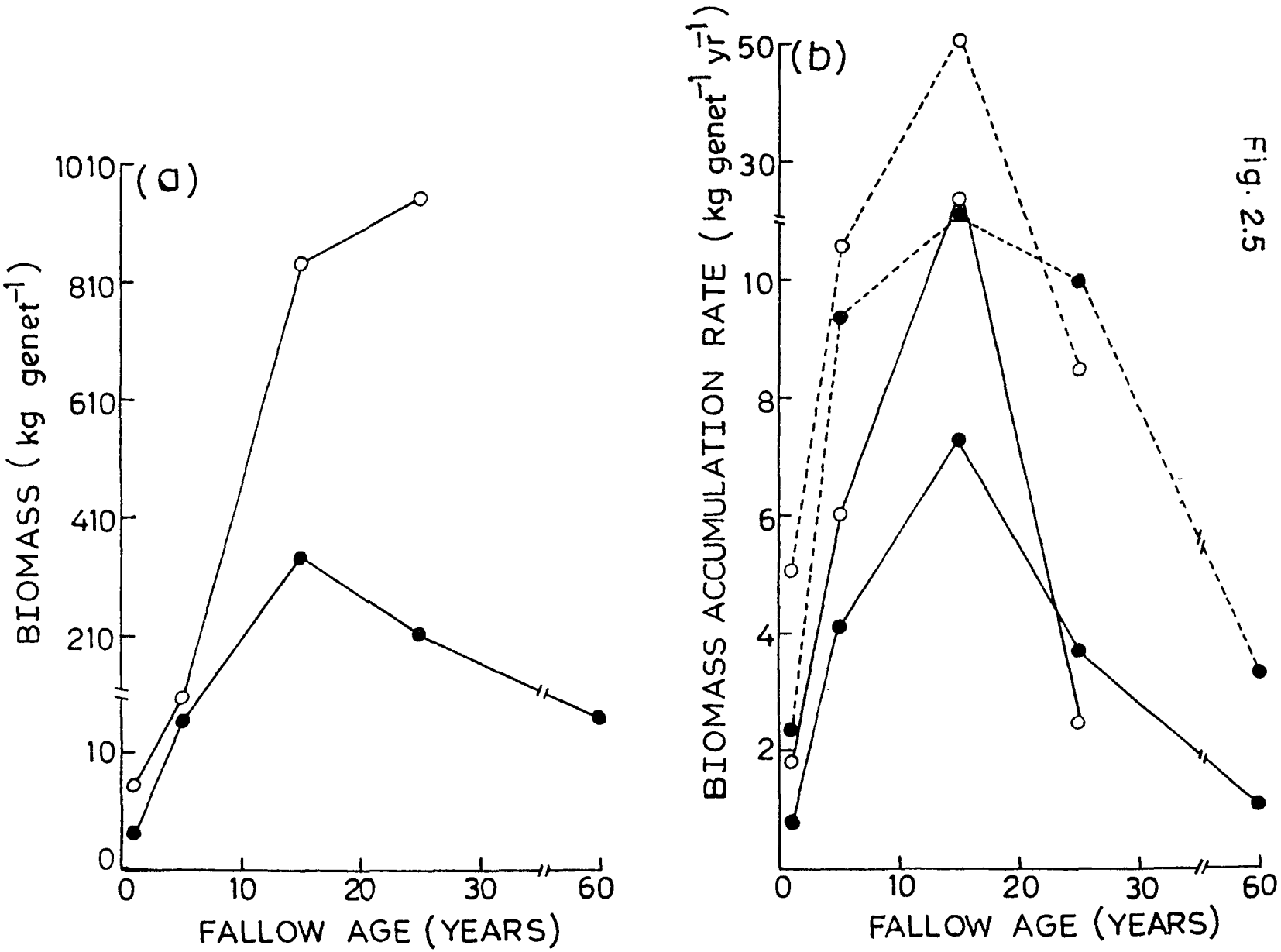

(a)
BIOMASS (kg genet^{-1})
1010
810
610
410
210
10
0
0
10
20
30
60
FALLOW AGE (YEARS)
(b)
BIOMASS ACCUMULATION RATE (kg genet^{-1} yr^{-1})
50
30
10
8
6
4
2
0
10
20
30
60
FALLOW AGE (YEARS)

Fig. 2.5

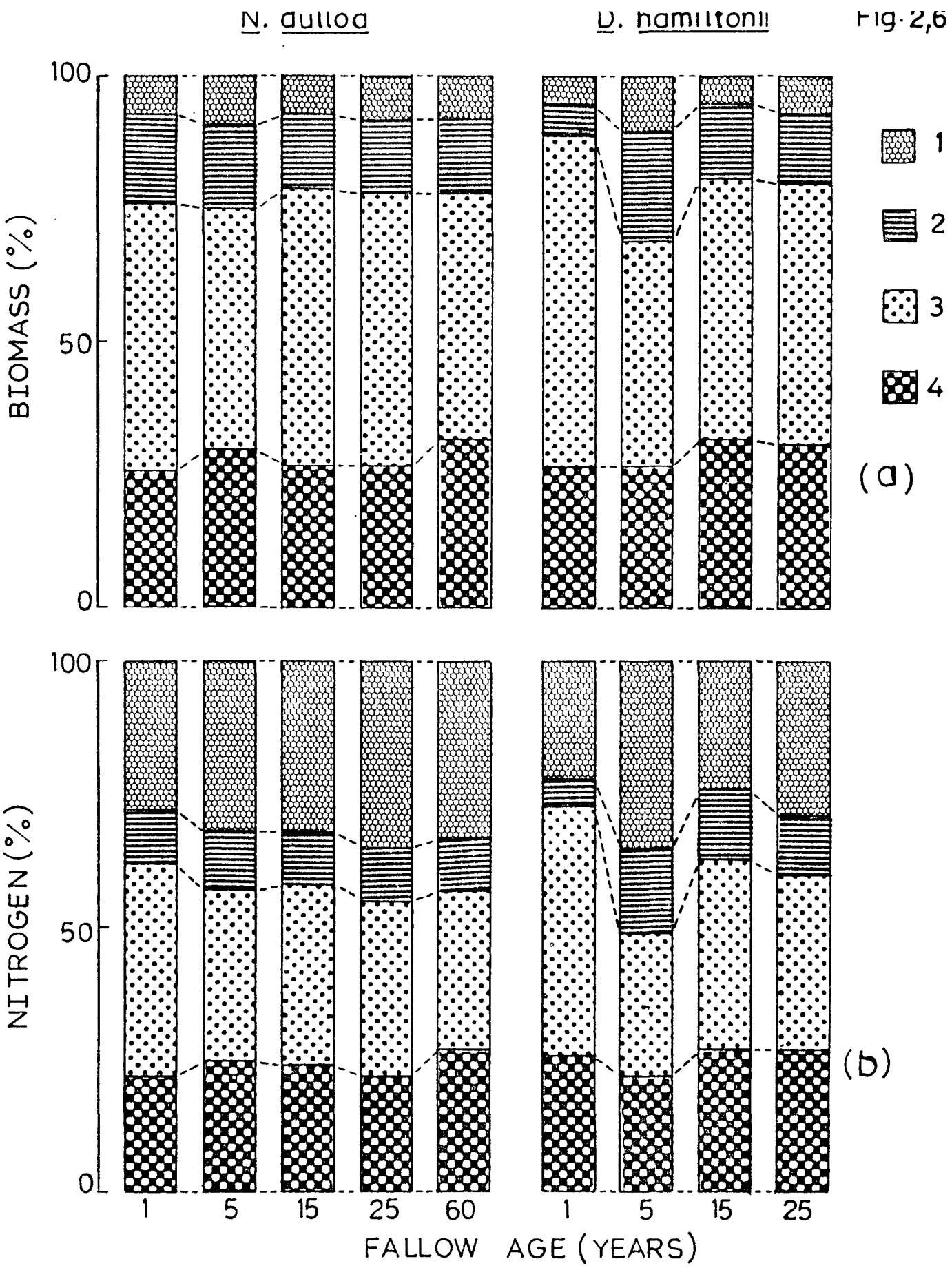
5-year old fallow; but the decline in other fallows was gradual at this position but sharper at nodes < 30.

Allocation studies:

The standing biomass per genet was maximal in a 15-year old fallow for N. dulloa with decline in both younger and older fallows (Fig. 2.5a). D. hamiltonii however, showed increase in standing biomass with fallow age upto 25 years. The rate of accumulation in belowground and aboveground parts was maximal in a 15-year old fallow for both the species (Figs.2.5b). It may be noted that the rate of accumulation of both aboveground and belowground parts of N. dulloa in 25- and 60-year old fallows, was calculated on the basis that the age of the genet was 15 years only. The rate of accumulation of both aboveground and belowground biomass in D. hamiltonii declined in a 25-year old fallow.

The aboveground/belowground ratio of N. dulloa markedly declined in a 5-year old fallow (Table 2.5) with significantly ($P = < 0.05$) higher values in 1- and 15-year old fallows. Compared to a 15-year old fallow, the aboveground/belowground ratio declined sharply in a 60-year old one. For D. hamiltonii this ratio declined sharply ($P = < 0.05$) in 15- and 25-year old fallows.

Fig. 2.6. Allocation pattern (%) of biomass (a), nitrogen (b), phosphorus (c), potassium (d), calcium (e) and magnesium (f) to different organs in *N. dulloa* and *D. hamiltonii* in successional fallows. Symbols used here are indicated in (a). 1, leaves; 2, bole; 3, branches; and 4, belowground parts.


N. dulloa
D. hamiltonii
Fig·2,6
BIOMASS (%)
NITROGEN (%)
100
50
0
1
2
3
4
(a)
(b)
1
5
15
25
60
FALLOW AGE (YEARS)

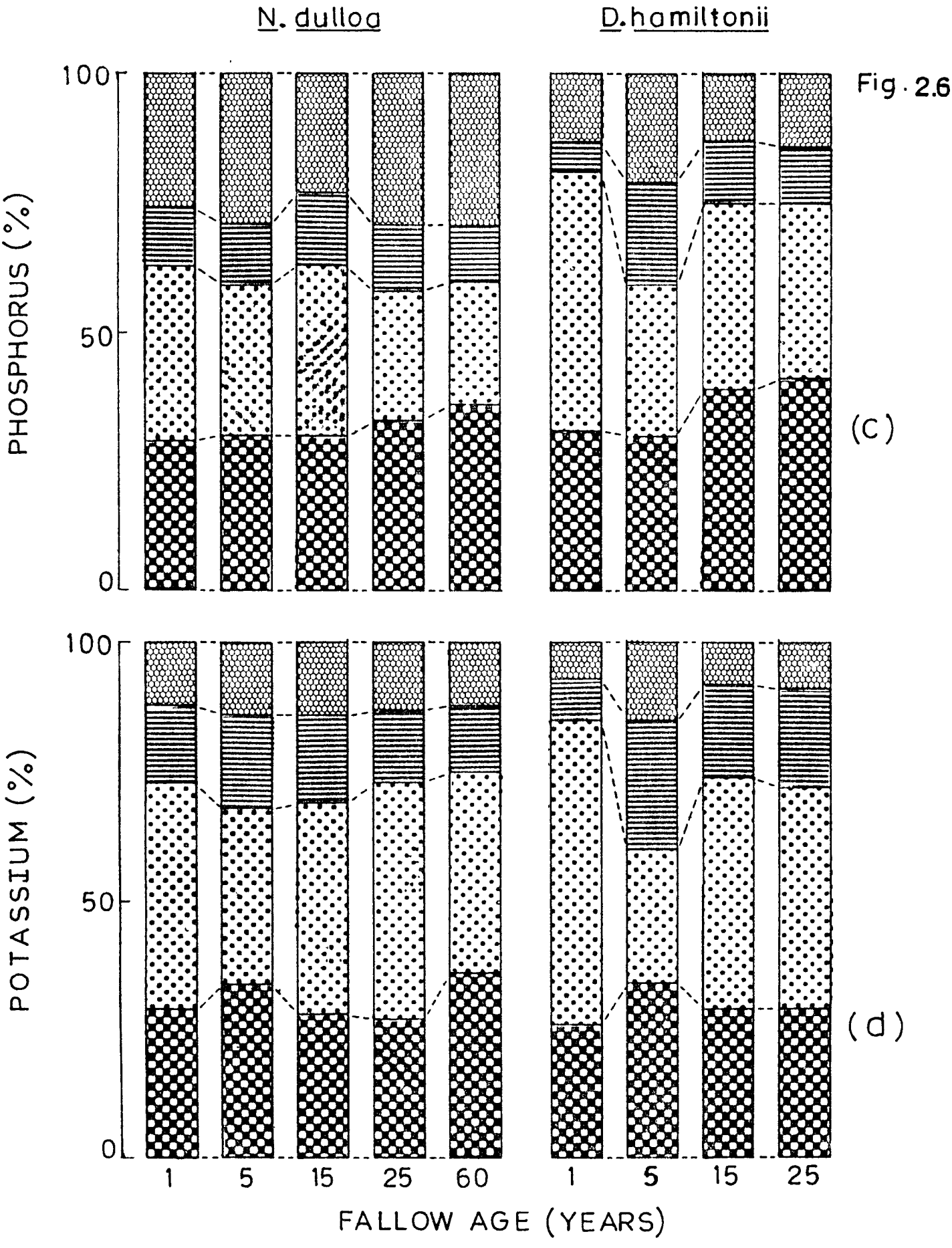

N. dulloa
D. hamiltonii
PHOSPHORUS (%)
100
50
0
(C)
POTASSIUM (%)
100
50
0
(d)
1
5
15
25
60
1
5
15
25
FALLOW AGE (YEARS)

Fig. 2.6

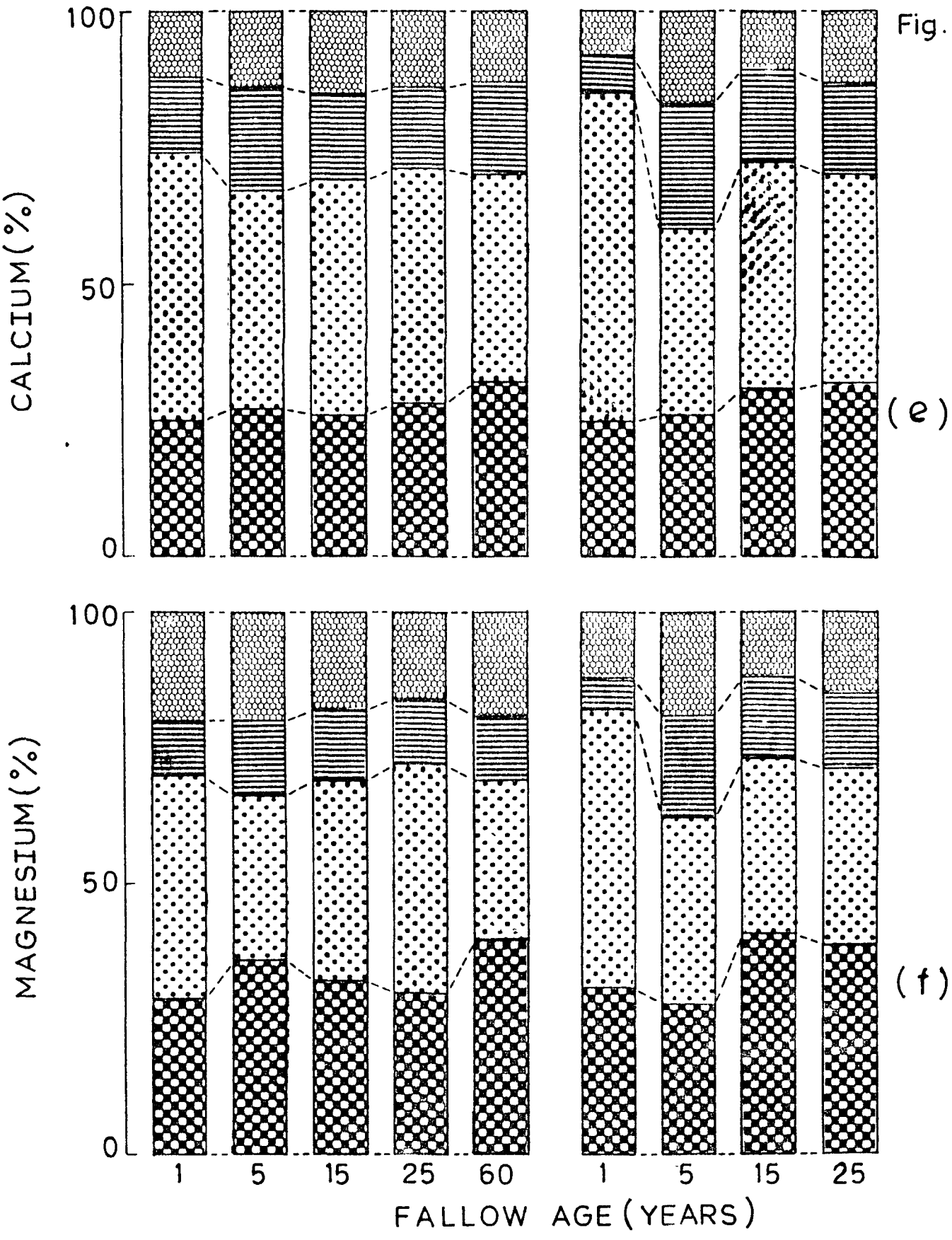

N. dulloa
D. hamiltonii
100
50
0
CALCIUM (%)
(e)
MAGNESIUM (%)
(f)
1
5
15
25
60
FALLOW AGE (YEARS)

Fig. 2.6

Table 2.5: Above-ground/below-ground ratio of bamboos in 5- to 60-year old successional fallows

Fallow age (years)	N. dulloa	D. hamiltonii
1	2.89	2.76
5	2.34	2.69
15	2.77	2.13
25	2.75	2.24
60	2.15	

Though there was not much of variation in the allocation pattern of biomass of N. dulloa to different components in different fallows, the belowground allocation was higher in 5- and 60-year old fallows (Fig. 2.6a). In D. hamiltonii, 1-year old fallow had maximum allocation of biomass to the zero-order branch where as it was for the other branch order in a 5-year old fallow.

Nitrogen allocation to the leaf component in N. dulloa increased with fallow age but reverse was the case for the zero-order branch (Fig. 2.6b). Allocation of nitrogen to the zero-order branch was minimal in D. hamiltonii in a 5-year old fallow, but that to the leaf component was maximal. Allocation of nitrogen to the leaf component was generally higher compared to biomass allocation.

The percentage phosphorus allocation to belowground parts of both the species increased in older fallows, whilst it tended to decrease in the zero-order branches (Fig. 2.6c). The leaves of N. dulloa had more phosphorus than the leaves of D. hamiltonii.

Generally speaking, the allocation of potassium, calcium and magnesium showed pattern similar to biomass allocation (Fig. 2.6d-f).

DISCUSSION

Architectural studies:

Hallé *et al*.(1978) established McClure's model to accommodate the basic architecture of bamboos. There are differentiated axes of two kinds; first "sigmoid" trunk axes which are essentially mixed, originate by basel branching and bear, second, plagiotropic leafy branches; both kinds show determinate growth due to a high degree of preformation. Takemouchi (1931) and McClure (1966), however, differentiated both the below-ground and aboveground parts as solid (internodes filled) and hallow (internodes empty) axes respectively. Based on this difference and also based on the fact that the zero-order branch of Hallé *et al*. (1978) is in fact a number of branch systems that are sympodially produced, ordering was done, for the present study, with respect to above ground branches alone, the aboveground main axis being designated as the zero-order branch.

The canopy architecture of *D. hamiltonii* showed plasticity depending upon the fallow age. In a 5-year old fallow with shorter internodes and longer first-order branches placed below, which gradually shorten towards the upper canopy positions the ramet assumes

a conical shape. This is related to greater space and light availability in this fallow. In older fallows, the variation in the length of the first-order branches at different canopy positions is less pronounced so that the ramet assumes a cylindrical form.

Over a successional gradient, N. dulloa showed greater plasticity occurring in fallows of upto 60 years, preferably as an emergent upto 15 years of fallow regrowth and as a ground layer shrub in a 25-year old fallow and in the closed broad-leaved 60-year old forest. On the other hand, D. hamiltonii has a range only upto 25-years as an emergent, without any ability to withstand shade. In this species, growth is optimum in 15-and 25-year old fallows. Partly because light is a limiting factor in fallows older than 25 years of age, due to rapid growth of broad-leaved trees in older fallows, and partly because the intermast phase for D. hamiltonii is 30-40 years depending upon the geographical zone (Varmah and Bahadur, 1980; Janzen, 1976), this species is eliminated during succession after 25 years. N. dulloa with a reported intermast phase of 15-17 years (Janzen, 1976) is, however, able to regenerate through seeds even in fallows as old as 25-35 years and survive upto 60 years of fallow age because of its shade

tolerance. However, the vigour of this species in a 60-year old fallow is restricted.

Unlike trees where extension and radial growth are continuous activities through out the life cycle of the species, in bamboos, these activities occur just once in the initial phase of ramet procution; extension growth occurs through more elongation of the zero-order branch, whilst radial growth is through cell enlargement and thickening of preformed tissue. Since successive generations of zero-order branches within a given genet tend to be thicker than the earlier ones (Hallé et al., 1978) it should be expected that the ramets produced in older fallows would be generally thicker, as the stock/ regeneration age would increase though upto a point. However, such an indefinite increase in diameter size of the zero-order branch is constrained by species plasticity. Thus in D. hamiltonii maximum diameter for the zero-order branch is attained in a 25-year old fallow, since this light demanding species has optimum light availability upto this stage. On the other hand, N. dullooa being favoured by high light regime in the environment, for this species of a relatively smaller size, light availability is maximum only upto 15 years of fallow regrowth (after which it occurs only as an

under-growth). Therefore, maximum dimension for the zero-order branch is attained in a 15-year old fallow. Zero-order branch thickness in 25- and 60-year old fallows declined even though the stock and regeneration age of the population was the same as in a 15-year old fallow.

With increase in total number of nodes in a given ramet which increased in N. dulloa only upto 15 years and in D. hamiltonii upto 25 years, there was an upward shift in the position of the longest internode of the zero-order branch. It may be noted that the number of days taken for elongation to be completed is more or less constant at 90-120 days irrespective of fallow age. Since internode elongation is from base upward and since peak elongation occurs during a definite time period, i.e., fifth week after elongation starts, as observed here and reported by others (Ueda, 1960; McClure, 1966), such a shift in the position of the longest internode (Takenouchi, 1932; McClure, 1966) is understandable.

With lesser storage capacity in the belowground rhizome of N. dulloa, sylleptic branch production upto the fourth-order (fifth-order brahch production is

proleptic if it occurs as in a 15-year old fallow), with simultaneous leaf production may be advantageous to this species for quick growth. On the other hand, proleptic branch production in D. hamiltonii would not adversely affect its quick growth, as there is a greater availability of stored food in the belowground rhizome of this species. In other words, N. dulloa is more dependent upon immediate photosynthetic activity for rapid growth and branch production unlike D. hamiltonii which can make use of reserve food in the first year when a ramet is initiated.

In agreement with the plasticity behaviour of these two species, least dormancy accompanied with maximum branch production occurred in a 15-year old fallow for N. dulloa and in a 25-year old fallow for D. hamiltonii. Further, with greater space and light availability in a 5-year old fallow, D. hamiltonii had better developed first-order branch systems with diffuse lower order branches on them (cf. fig. 2a). In older fallows the lower branch orders on the first-order branch originate from the basal node of the latter but appear as if they arise from the zero-order branch itself because of a high degree of condensation (Figs. 2b, 3). Diffused branch organization in a 5-year old fallow would thus

ensure better display of the lower branch orders and consequently a better display of leaves to maximize production under a high light regime.

Being light demanders, the two species show a high degree of sloughing-off of branches as the light availability to the lower canopy branches decreases. Such a rapid drop-off of lower branches [illegible]enable rapid upward canopy shift was also a general feature of early successional trees (Boojh and Ramakrishnan, 1982a; Shukla and Ramakrishnan, 1986). The sympodially produced leafy shoots born on the branch systems other than the zero-order branch also loose their vigour as light availability at lower canopy positions of the two species decreased, again suggesting the light demanding nature of the two species.

Allocation studies:

In keeping with the adaptive growth strategies discussed earlier for the two species, biomass of D. hamiltonii increased with fallow age upto 25 years where as that for N. dulloa declined sharply in fallows older than 15 years, perhaps, due to decreased light availability. However, the biomass accumulation rate in both the species peaked in a 15-year old fallow suggesting that

growth conditions are most favourable here compared to other fallows. Apart fr m decr-ased light availability, competition for space and nutrients may also explain such a patt-rn.

During the first 15 years, there is considerable fluctuation in aboveground/belowground ratio of N. dulloa. During the first year, shoot growth is active with rapid transfer of resources from belowground to aboveground compartment. With greater photosynthetic activity of the above ground parts, there is a retransfer of resources again to the belowground organs resulting in a lower ratio. Subsequently the shoot growth is further accelerated partly by an upward transfer of resources from the belowground parts resulting in a higher ratio in a 15-year old fallow. The lowest aboveground/belowground ratio attained in N. dulloa in a 60-year old fallow may be an adaptation for survival through vegetative growth during the subsequent slash and burn operation. Such a survival strategy has been observed in many rhizomatous species such as Imperata cylindrica developed in successional fallows after slash and burn agriculture (Saxena and Ramakrishnan, 1983a). Such a shift in aboveground/belowground ratio is more pronounced in D. hamiltonii where it declined with

increasing fallow age. A useful strategy for any species arising after slash and burn of a forested ecosystem as in the north-eastern Hill region of India should be, to capitalize upon the resources of an enriched substratum, which is transient, and make adequate growth as quickly as possible. The species establishing in such environments could have two contransting sets of stragegies: (i) establishment from seed vs. establishment from vegetative sprouts and (ii) C_3 vs C_4 photosynthetic pathway (Saxena and Ramakrishnan, 1983). The two bamboo species are predominantly clonal, flowering once during the life cycle with an intermast phase of 30-40 years in D. hamiltonii (Varmah and Bahadur, 1980; Janzen, 1976) and 15-17 years in N. dulloa (Janzen, 1976). Therefore, with greater allocation of resources to the belowground organs of reproduction (Keeley and Keeley, 1977), these species represent an extreme stage in vegetative vs. reproductive strategy. With vegetative reproduction being advantageous under frequent disturbances (Gill, 1975; Saxena and Ramakrishnan, 1983a) as in the slash and burn agriculture system and sexual reproduction occurring sporadically in D. hamiltonii and gregeriously in both the species, the failure rate of seed reproduction is very high (Willson, 1971). This is partly due to

predation and partly because of the high mortality of the weaker seedlings derived from very light and small seeds.

Much of the biomass, as much as 25-32%, is allocated to the belowground organs of reproduction, also observed in other bamboo species (Gadgil and Prasad 1984). A tendency in both the species to allocate more biomass and nutrients to the belowground parts in the older fallows is understandable as a strategy for survival and regeneration after a subsequent disturbance. Greater allocation of biomass and nutrients to the branches in a 5-year old fallow is related to the broader canopy design of the species which is different here from the other fallows. It is also interesting to note that the proportional allocation of phosphorus to the belowground parts was much higher for both the species. A more effective redistribution of this element compared to many others for vegetative reproduction in Ixia polystachya (Hocking, 1984) and in Solidago species (Abrahamson and Caswell, 1982) is also reported. Higher allocation of nitrogen to the leafy component of both the species may be related to photosynthetic efficiency, since leaf nitrogen content is shown to be positively related to photosynthetic rate (Terry and Ulrich, 1973; Nátr, 1975; Murata, 1969; Field, 1983).

Such different allocation strategies of biomass and nutrients suggest that it is often difficult to establish a connection between fitness and resources allocation based on any one currency, and emphasises the importance of nutrient allocation in such studies (Van Andel and Vera, 1977; Williams and Bell, 1981; Chaplin, 1980; Abrahamson and Caswell, 1982; Saxena and Ramakrishnan, 1983a).

The growth strategy and architectural design of bamboo species are thus geared to capitalize upon the high light regime available in an early successional environment and make quick growth before light becomes limiting in a mixed broad-leaved forest that develops subsequently (Toky and Ramakrishnan, 1983a). Further, the highly developed clonal reproduction and emphasis on this in allocation of resources, particularly in older fallows is a strategy for survival in an environment of constant disturbance through slash and burn agriculture.

SUMMARY

The two bamboo species, Neohouzeoua dulloa A.camus and Dendrocalamus hamiltonii Nees & Arn. show plasticity in architectural design and in biomass and nutrient allocation strategies over a successional gradient of upto 60 years for the former and 25 years for the latter. However, optimal biomass accumulation rate was attained in a 15-year old fallow for both the species. Maximum elongation and thickness for the zero-order branch is attained in a 15-year old fallow for N. dulloa and in a 25-year old fallow for D. hamiltonii. The lower order branches produced on the zero-order branch of N. dulloa is sylleptic (except the fifth-order branch produced only in a 15-year old fallow which is proleptic) and that of D. hamiltonii is always proleptic. Least bud dormancy with maximum branch production on the zero-order branch occurred in a 15-year fallow for N. dulloa and in a 25-year old fallow for D. hamiltonii. D. hamiltonii in a 5-year old fallow had better developed first-order branch system with diffusely placed lower order branch clusters appearing as if born on the first-order branch, unlike in older fallows where first-order branch production was continuous and

lower order branch clusters appeared as if born on the zero-order branch itself. In older ramets lower branch systems are dropped off due to reduced light availability. Further, the sympodially produced leafy shoots also become less vigorous. In older fallows both the species tend to allocate more biomass and nutrients to the belowground rhizomatous component which is an adaptation for survival and regeneration after a slash and burn distrubance. With a highly restricted sexual reproductive ability (occuring only once during the life cycle) clonal reproduction is emphasised in both the species. The biomass and nutrient allocation strategies to different plant components differ. The growth stretegy and architectural design of these two species are generally geared to capitalize upon the high light regime of the early successional environment, but with a limited ability by N. dulloa to tolerate shade.

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CHAPTER 3

LEAF DYNAMICS OF TWO BAMBOO SPECIES (*NEOHOUZEOUA DULLOA* A. CAMUS AND *DENDROCALAMUS HAMILTONII* NEES AND ARN.) IN SUCCESSIONAL ENVIRONMENTS IN NORTH-EASTERN INDIA.

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INTRODUCTION

Leaf area available for photosynthesis plays a crucial role in biomass production and the change in total leaf area being primarily determined by the patterns of production and fall, and the longevity of leaves (Watson, 1956; Newhouse and Madgwick, 1968). The leaf with its axillary bud, is the smallest module of organized structure in higher plants, and leaves have many of the properties associated with members of a population. Though individual trees have been considered as aggregates of repeating and somewhat independent units in the pipe model theory of Shinozaki et al. (1964), other authors have considered branches as individual (Oldeman, 1974; Gill and Tomlinson, 1971) or dealt with leaf characteristics such as census (Büsgen and Münch, 1929), longevity (Gill and Tomilson, 1971), age-structure (Kinerson et al., 1974) or abcission rates (Kozlowski, 1973; Addicott, 1978). Much little is known on the leaf dynamics of tropical tree species (Boojh and Ramakrishnan, 1982b; Shukla and Ramakrishnan, 1984a), but no attempts have been made to study the leaf dynamics of tree grasses (bamboos), which colonize disturbed sites.

The present study deals with the leaf population dynamics of two bamboo species of successional environments at lower elevations of north-east India. While Dendrocalamus hamiltonii Nees and Arn. is confined to early successional fallows upto 25 years, Neohouzeoug dulloa A. camus is more plastic occurring in fallows upto 60 years of age, developed after slash and burn agriculture (Ramakrishnan et al., 1981; Toky and Ramakrishnan, 1983a). However, both the species are light demanders but with different degrees of shade tolerance.

METHODS OF STUDY

One year old ramets of D. hamiltonii and N. dulloa and current year's ramets of the latter species were identified in 5-, 15-, 25-, and 60-year old secondary successional fallows developed after slash and burn agriculture (jhum) in north-east India. In a 60-year old fallow D. hamiltonii was not studied as they occur only under disturbed situations along the periphery of the forest (Singh and Ramakrishnan, 1982). Identified ramets were protected from herbivory by fencing. All observations are based on five replicates.

All the existing leaves (only in N. dulloa) and

the newly forming ones were tagged with small and light weight colour-coded aluminium tags. Detailed observations, at monthly intervals, on emergence, fall and area were obtained for individual leaves on the first to the fifth order branches, starting from April, 1983 and continued for a one-year period. Leaf area was calculated on the basis of 150 leaves harvested from other ramets and using regression equation developed relating blade length and breadth and leaf area for each fallow.

RESULTS

Leafing pattern:

Both the species of bamboo bear leaves on a sympodial leafy shoot produced at the tip of each of the serial branch orders, except the zero-order branch. These sympodial leafy shoots of Neohouzeoua dulloa are produced on the sylleptically produced branch system (by the continued growth of lateral buds laid during the current year's growth), and are subsequently exchanged with new sympodial leafy shoots, starting from the second year of the production of the ramet. In Dendrocalamus hamiltonii on the other hand leafy shoots are produced on the proleptically produced branch system

Fig. 3.1. Variation in monthly leaf production (%) in current year's and last year's ramets of *N. dulloa* (a) and last year's ramets of *D. hamiltonii* (b) in successional fallows. Current year's ramet, - - - -; last year's ramet, ———; closed circle, 5-year; open circle, 15-year; closed triangle, 25-year and open triangle, 60-year old fallows.

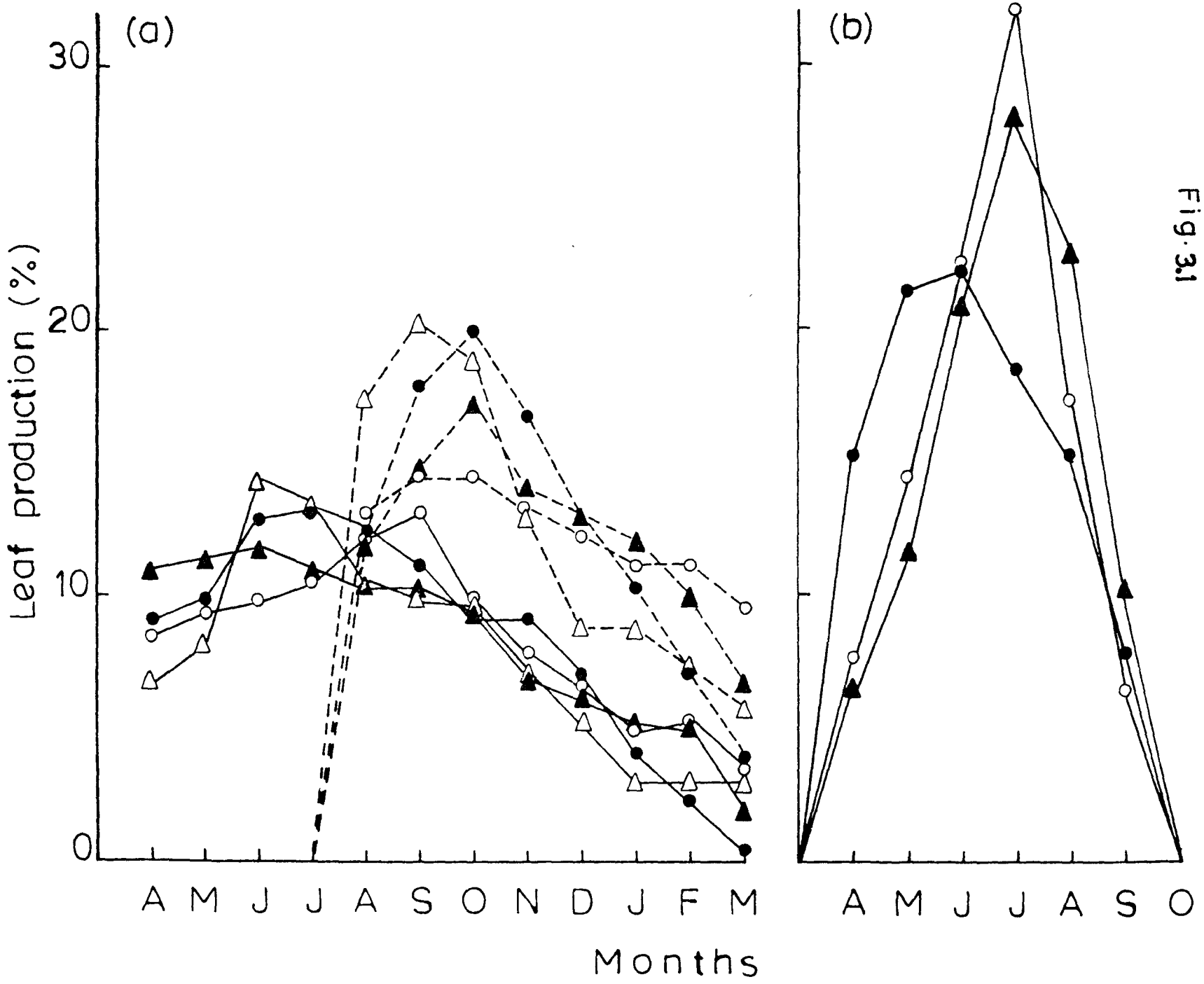


Fig. 3.1

Table 3.1: Important leafing characteristics in current year's and last year's ramets of bamboos in successional fallows. Values within parentheses are for last year's ramet

Parameters	*N. dullooa*	*D. hamiltonii*
a) Leafy shoot:		
Initiation	August-September	April - June
Exchange/replacement	April - June	April - June
b) Termination of leaf emergence	Continuous	October - November
c) Leaf production period (days)	245 (365)	- (180-210)
d) Leafing behaviour	Evergreen	Deciduous

(by the activation and growth of lateral buds laid during the previous year's growth) and are subsequently replaced (after a deciduous naked phase) with new sympodial leafy shoots starting from the third year of the production of the ramet. In D. hamiltonii, the leafy shoot for the first time is produced in April-June itself but in N. dulloa it happens in August-September (Table 3.1). This delay in N. dulloa is because, the leafy shoots appear only after the production of the sylleptic branch system is completed. Therefore, leaf production on the currently produced ramets of N. dulloa occurs only for 245 days. In subsequent years, however, leaf production in this species is continuous throughout the year. The replacement of the leafy shoots of both the species occur in April-June. N. dulloa is an evergreen species of leaf exchanging type, whilst D. hamiltonii is deciduous with a naked phase of 1-2 months and with leaf production restricted to 6-7 months.

Leaf production and fall:

In D. hamiltonii (Fig. 3.1a) leaf production peaked in June-July. On the branch system produced in the current year in N. dulloa, leaf production (Fig. 3.1.b) peaked in September-October. However, leaf production on the

Table 3.2: Annual leaf area ($x10^3$ cm^2) of bamboos (mean ± S.E.) in successional fallows.

Bamboo species	Fallow age (Years) 5	16	25	60
N. dullooa				
Current year's ramet	5.4 ± 0.5	17.7 ± 1.7	7.1 ± 0.6	2.4 ± 0.2
Last year's ramet	12.6 ± 1.0	75.7 ± 4.3	16.5 ± 1.3	4.9 ± 0.5
D. hamiltonii				
Last year's ramet	108.8 ± 5.4	998.8 ± 30.0	862.6 ± 25.7	-

Fig. 3.2. Monthly variation in leaf area in current year's ramets (- - - -) and last year's ramets (————) of *N. dulloa* and that of D. hamiltonii (—— . ——. ——— .) in successional fallows. Closed circle, 5-year; open circle, 15-year; closed triangle, 25-year and open triangle, 60-year old fallows.

Fig·3.2

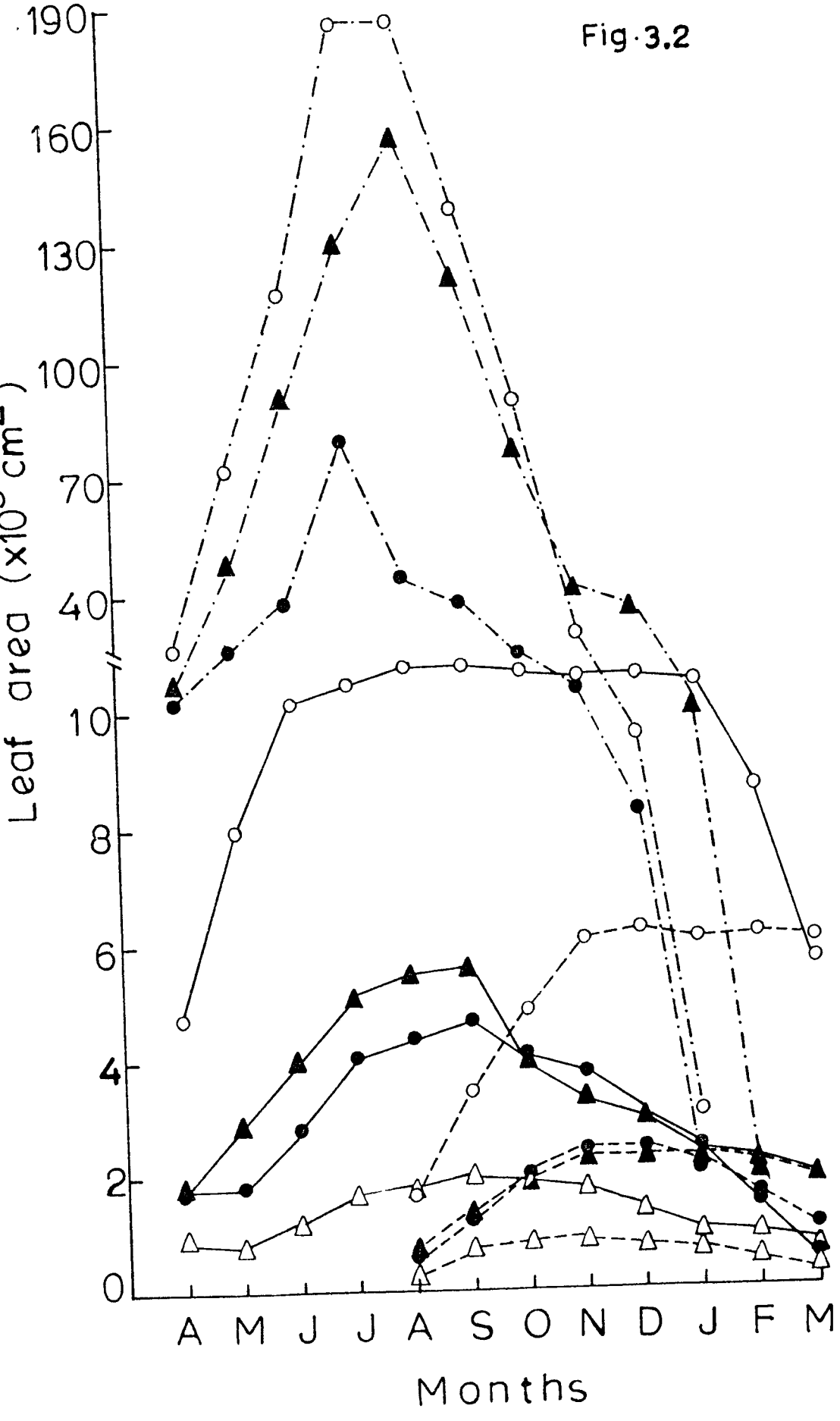
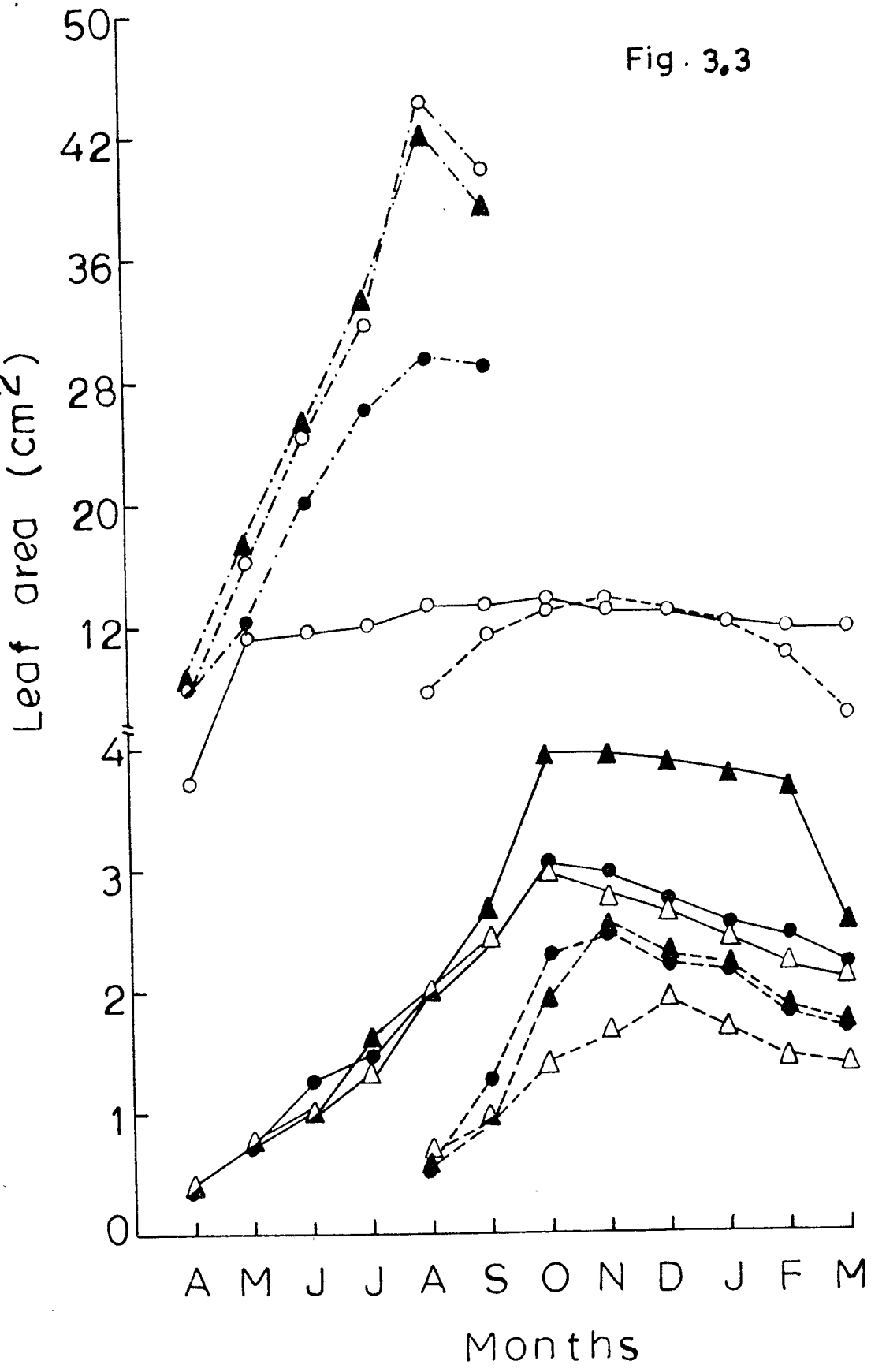

190
160
130
100
70
40
10
8
6
4
2
0
Leaf area (x10³ cm²)
A M J J A S O N D J F M
Months

Fig. 3.3. Variation in individual leaf area on current year's ramets (- - - -) and last years's ramets (————) of N. dulloa and that of D. hamiltonii (——·——·——·——) in successional fallows. Closed circle, 5-year; open circle, 15-year; closed triangle, 25-year and open triangle, 60-year old fallows.

Fig. 3.3



branch system of N. dulloa, produced in the previous year, peaking occurred in June-July in all the fallows except in a 15-year old one, where peaking was in September.

Annual leaf area achieved in N. dulloa was generally higher on the last year's ramet compared to the current year's ramet (Table 3.2). With the fallow age, leaf area attained by both the species increased reaching a maximum in a 15-year old fallow.

In D. hamiltonii maximum leaf area was attained in July-August with decline on either side and total loss in January-February (Fig. 3.2). Leaf area of N. dulloa on the last year's ramet reached a maximum in September, where as in current year's ramet it peaked in November with a decline on either side; the exception to this was leaf area of the current year's ramet in a 15-year old fallow, where it stabilized at the maximum after November.

Largest individual leaf area was attained in a 15-year old fallow in both the species (Fig. 3.2). In D. hamiltonii, individual leaf area increased reaching a maximum in August, whereas in N. dulloa individual leaf area peaked in October-December.

Fig. 3.4. Variation in the longevity of leaves recruited in different months on current year's ramets (a) and last year's ramets (b) of N. dulloa and that of D. hamiltonii in a 5-year old fallow.

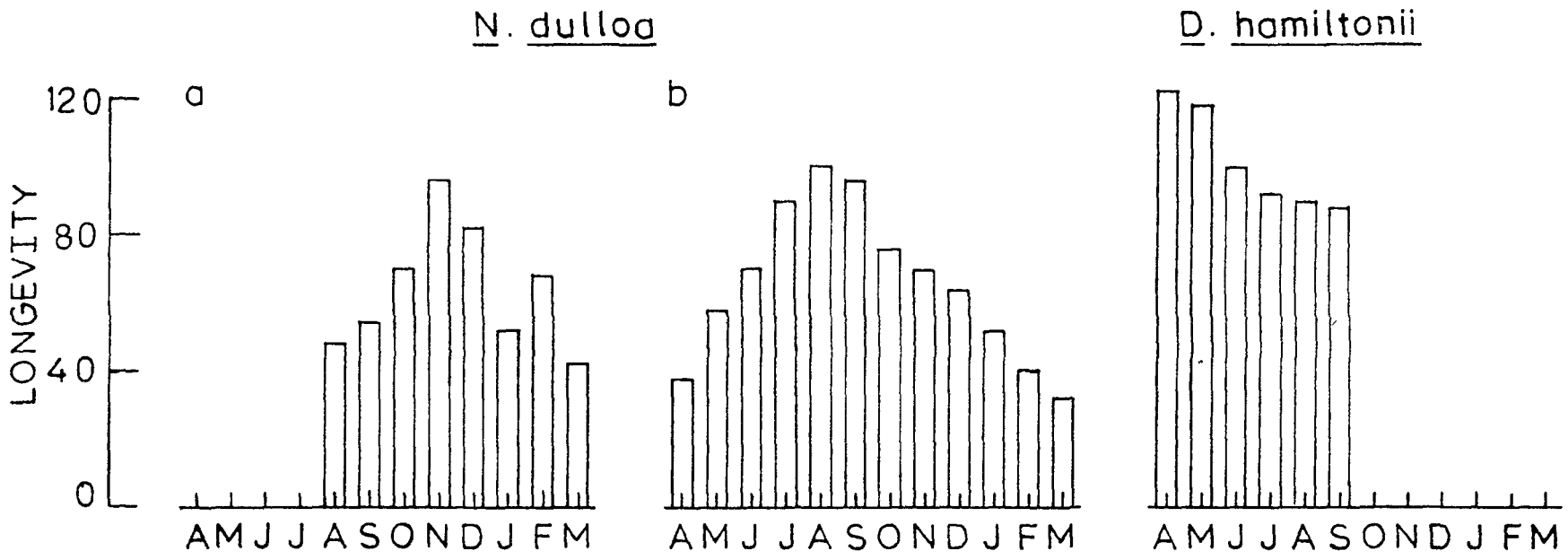

N. dulloa
D. hamiltonii
a
b
120
80
40
0
LONGEVITY
A M J J A S O N D J F M
A M J J A S O N D J F M
A M J J A S O N D J F M
MONTHS

Fig. 3.4

Fig. 3.5. Monthly leaf fall pattern in current year's and last years ramets of N. dulloa (a) and last year's ramets of D. hamiltonii (b) in successional fallows. Current year's ramet, - - - - ; last year's ramet, ———; closed circle, 5-year; open circle, 15-year; closed triangle, 25-year and open triangle, 60-year old fallows.

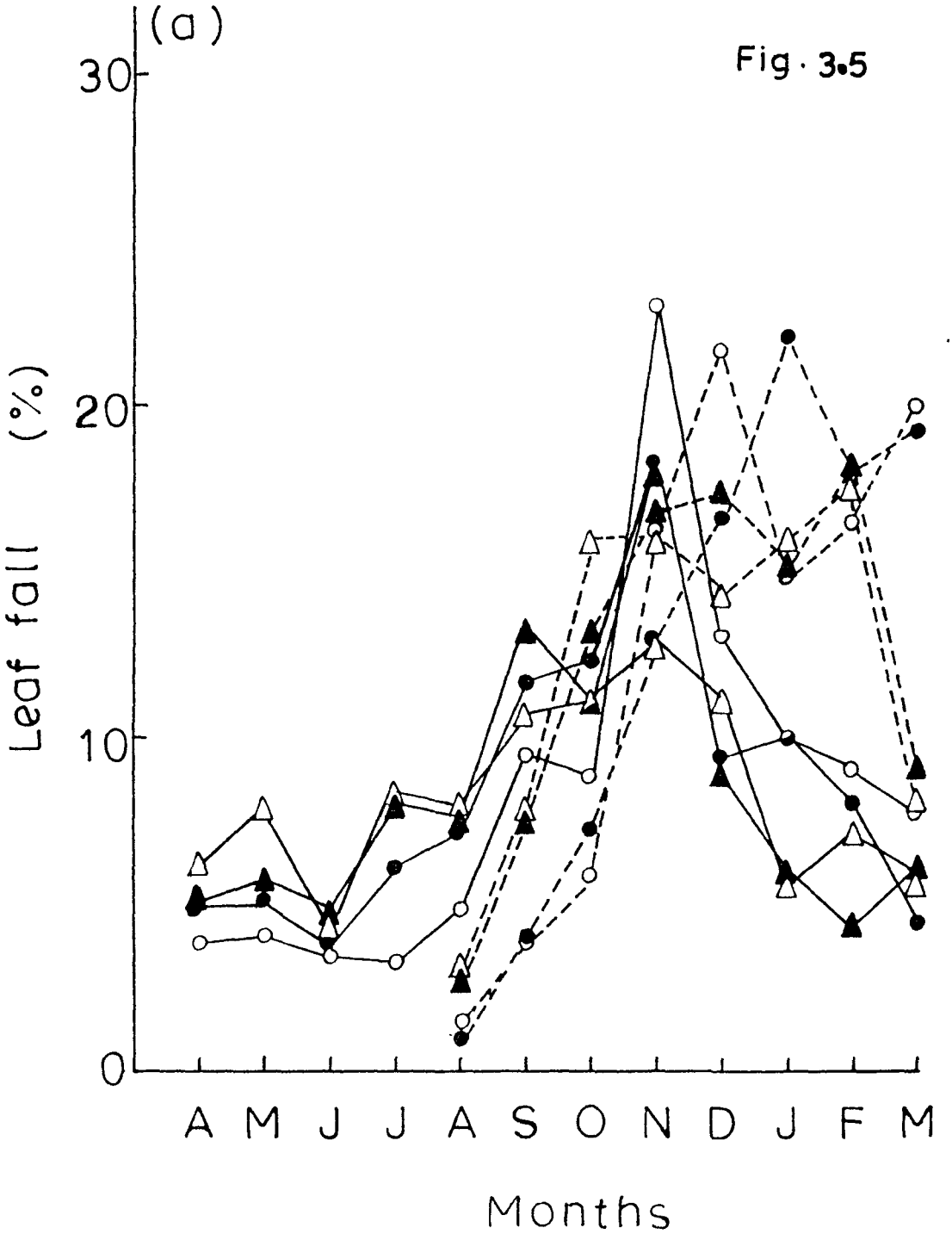


Fig. 3.5

Fig·3.5

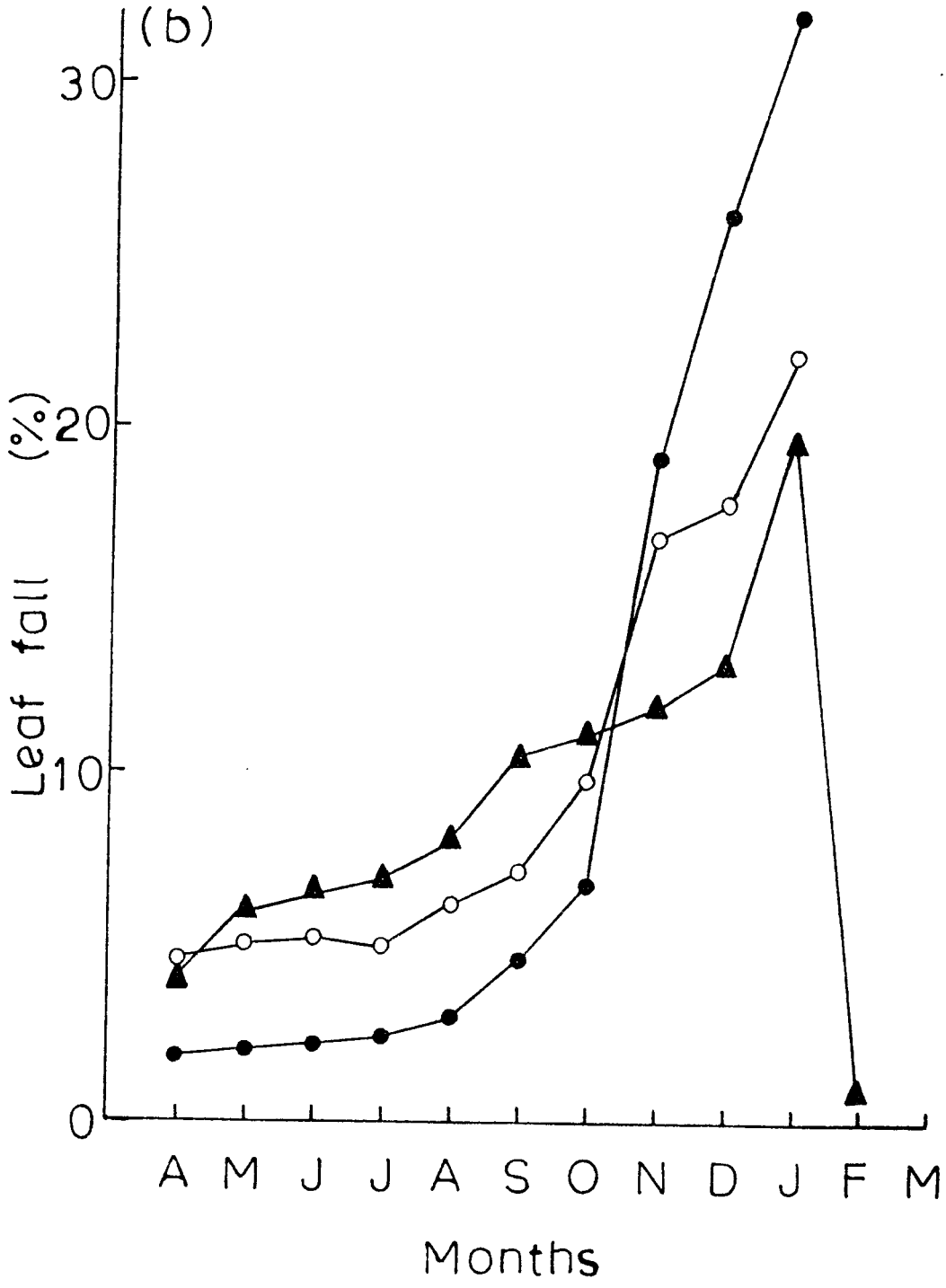


Table 3.3: Leaf population flux on current year's and last year's ramets of *N. dulloa* in 5- to 60-year old successional fallows. Values within the parentheses are for current year's ramet

Parameters	Fallow age(years) 5	10	25	60
a) Number of leaves ramet^{-1} at the beginning of study	90(0)	169(0)	65(0)	33(0)
b) Number of leaves produced ramet^{-1} during study period	411(191)	1853(456)	531(228)	170(90)
c) Number of leaves lost ramet^{-1} during study period	482(127)	1943(281)	562(144)	189(62)
d) Number of leaves ramet^{-1} at the end of study period	19(64)	200(175)	82(84)	26(28)
e) Total number of leaves ramet^{-1} recorded during study period	501(191)	2022(456)	596(228)	203(90)
f) Net change (d-a)	-71(64)	37(178)	17(84)	-7(28)
g) Rate of change (d/a)	0.21	1.18	1.26	0.77
h) Number of leaves survived in (a) at the end of study period	0	0	0	0
i) Expected time for complete turnover(years)(1/100-hx100)	1	1	1	1
j) Percentage annual mortality (c/e x 100)	96.2(66.5)	96.0(81.6)	94.3(63.2)	93.1(68.9)

Leaf longevity pattern of both the species in different fallows are not different and therefore that for a 5-year old fallow alone is shown here (Fig. 3.4). In the current year's ramet of N. dulloa, leaves produced during November-December had maximum longevity, whilst on the previous year's ramet, maximum longevity was for the leaves produced during August. There was a gradual decline in longevity of the leaves produced earlier or later. A gradual decline in the leaf longevity of D. hamiltonii occurred during the leaf production period starting from April to September.

Leaf fall in N. dulloa increased starting from April, reached a maximum in November for the last year's ramets and in December-January for the current year's ramet and declined subsequently (Fig. 3.5a). However, in D. hamiltonii, leaf fall increased starting from April and was completed by January-February (Fig. 3.5b).

Leaf population flux:

Leaf production and loss was maximum in a 15-year old fallow for N. dulloa (Table 3.3). In a 5- and 60-year old fallows there was a negative net change in the leaf population of the last year's ramet of N. dulloa,

Table 3.4: Leaf population flux on last year's ramets of *D. hamiltonii* in 5- to 25-year old successional fallows

Parameters	Fallow age(years)		
	5	16	25
a) Number of leaves ramet^{-1} at the beginning of study	415	864	611
b) Number of leaves produced ramet^{-1} during study period	2507	10586	8503
c) Number of leaves lost ramet^{-1} during study period	2507	10586	8503
d) Number of leaves ramet^{-1} at the end of study	100	871	589
e) Total Number of leaves ramet^{-1} recorded during study period	2507	10586	8503
f) Net change (d-a)	- 22	7	- 22
g) Rate of change (d/a)	0.95	1.01	0.96
h) Number of leaves survived in 'a' at the end of study period	0	0	0
i) Expected time for complete turnover (years) (1/100-h x 100)	1	1	1
j) Percentage annual mortality(c/e x100)	100	100	100

where as in all other cases there was a positive net change, at the end of one year period of observation. Rate of change for leaves on the last year's ramet of N. dulloa reached a maximum in a 25-year old fallow. The leaf population on the last year's ramet had more than 93% mortality, whereas in the case of the current year's ramet about 30-40% of the leaves were carried over to the next year. However, complete turnover of the leaf population occurred within a year. Leaf production and loss in D. hamiltonii also was maximum in a 15-year old fallow (Table 3.4).

DISCUSSION

There is much genet to genet variation in the time of leafy shoot initiation and the termination time for leaf emergence. More than one factor may be involved in individuals of a given species leafing out at different times at the same site. In clonal populations of herbaceous species, Brown et al.(1965) have implicated ramet size with phenological behaviour. On the otherhand, Lechowich (1984) has derived striking correlations between leafing phenology and the organisation of water conducting tissues in the trunk and branches. Thus the early leafing

broad-leaved temperate trees are shown to have more narrow vessels that are more efficient in water transport compared to situations where there are large vessels that are relatively inefficient. This is an aspect which need further study for bamboos.

The early successional tree species have been shown to have unrestricted leaf production and this rather than the efficiency of energy conversion is considered to be important for faster growth of species and for exploiting high light environment (Coombe and Hadfield, 1962). However, the two bamboo species follow two distinct strategies for exploiting high light regimes. N. dulloa has unrestricted leaf expansion occurring throughout the year, though the total leaf area attained is much lesser than in D. hamiltonii. The latter has restricted leaf expansion period confined to just six months in a year but at a much faster rate with total leaf area attained being many-fold than that of N. dulloa.

Much variation exist in the leaf population flux in fallows of different ages. N. dulloa is more plastic with ability to withstand shade but with limited adverse effect on leaf population dynamics. However,

the faster growth rate attained in both the species occur in 5- to 15-year old fallows (Chapter 1). This is reflected in the high birth and death rates of leaves in both the species occurring in a 15-year old fallow. It may be noted that maximum total leaf area and individual leaf area both occur in a 15-year old fallow. With broad basal canopy in a 5-year old fallow that tapers rapidly towards the upper part, and the narrow but some what cylindrical canopy design in an 15-year old fallow, D. hamiltonii is adapted for optimal leaf display under environments where light availability decreases with fallow age. If cumulative leaf area is considered in both the species, 50% leaf area production is completed in the early part of the growing season, by July in D. hamiltonii and by September-October in N. dulloa.

Further the elongation of all the branch systems of a ramet of both the species are also completed just within a month, during April itself. These are strategies advantageous to C_4 species, such as these, for maximum production during the more favourable early environments of high temperature regimes. Thus, Saxena and Ramakrishnan (1984c) have found distinct patterns of photo-

synthate production of the C_3/C_4 photosynthetic groups with more effective dry matter production by C_4 species occurring during the early part of the growing season when solar radiation would be more intense, accompanied by warmer temperature. C_3 plants, on the otherhand, had peak growth during the latter part of the growing season (October-December) when solar radiation would be less intense coupled with cool temperatures, with definite advantage to this category of species (Ehleringer and Bjorkman, 1977).

Unlike in tree species of this area where leaf fall peaked during March-April (Shukla and Ramakrishnan, 1984) in the bamboo species under consideration here, maximum leaf fall occurred in November-December for N. dulloa and in January for D. hamiltonii. This may partly be related to lower temperature conditions prevailing during the winter months and partly to the dryness of the seasons (Longman and Jenik, 1974).

Since no sharp line can be drawn between evergreen and deciduous species of the tropics (Holtum, 1940; Koriba, 1958). Longman and Jenik (1974) recognised four distinct patterns of leafiness on the basis on relative

timings of bud-break and leaf abscission. With growth and elongation of the different branch orders being confined to a very brief period of the year, all bamboos are periodic in their growth pattern while N. dulloa belongs to the 'periodic growth - evergreen type', D. hamiltonii belongs to the 'periodic growth - deciduous type'. As discussed earlier, evergreen habit is of a definite advantage to early successional tree species (Shukla and Ramakrishnan, 1984a; 1986). Though evergreenness of woody species is a common feature for many of the species of the early successional environment, deciduous species too occur. It is suggested that evergreen is of a definite advantage to exploit high light regime of early successional environments. In D. hamiltonii, the deciduous habit of the species is compensated to a large extent by the faster rate at which leaf production occurs with more than 50% leaf production right in the very early part of the growing season, by July itself.

SUMMARY

Both Neohouzeoua dulloa A. camus and Dendrocalamus hamiltonii Nees and Arn. are light demanders of early

successional environments, the former species exhibiting a greater degree of shade tolerance. N. dulloa belongs to 'periodic growth - evergreen type' whereas D. hamiltonii belongs to 'periodic growth - deciduous type'. The deciduousness of D. hamiltonii is compensated to a large extent by faster production of a larger total leaf area in the early part of the growing season, when compared with N. dulloa leaf production reached its maximum in both the species in a 15-year old fallow. The two C_4 species showed maximum growth during the very early part of the growing season itself when temperature conditions are higher.

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CHAPTER 4

ROLE OF BAMBOOS IN SLASH AND BURN AGRICULTURE (JHUM) IN NORTH-EASTERN INDIA WITH PARTICULAR REFERENCE TO NUTRIENT CONSERVATION.

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INTRODUCTION

Subsequent to slash and burn agriculture (jhum) at lower elevations in north-eastern India, the secondary succession passes from an initial herbaceous weedy community to a bamboo forest with a few broad-leaved trees and shrubs (Toky and Ramakrishnan, 1983a). Bamboos are eventually replaced by broad-leaved mixed forests (Shukla and Ramakrishnan, 1982; Singh and Ramakrishnan, 1982; Ramakrishnan et al., 1981; Toky and Ramakrishnan, 1983a). Thus, bamboos contribute significantly to ecosystem function of successional communities upto about 35 to 47 years of fallow regrowth after slash and burn agriculture. As far as we know, there is little information on the role of bamboo in ecosystem function of tropical humid forests. In fact, the biology of bamboo species are least understood (Numata, 1965; 1970; Janzen, 1976). The present study, therefore, was undertaken to assess the role of bamboo in the shifting agriculture system of north-eastern India, considering different jhum cycles (5, 10 and 15 years) at three locations at lower elevations (200 to 300 m) in Khasi and Garo Hills of Meghalaya and in Naga Hills.

METHODS OF STUDY

Three replicates each of 5-, 10- and 15-year old jhum fallows in Garo Hills, 10- and 15-year old jhum fallows in Khasi Hills and Naga Hills that are about to be slashed for jhum were identified. While selecting the replicate plots care was taken to ensure similar topography, exposure and soil conditions. Slashing of the vegetation in these fallows was done by the local tribal community in October-November.

Density and basal area measurements of bamboo are based on thirty 10 x 10 m quadrats in each replicate plot. The bamboo population from 10 quadrats of 10 x 10 m area was harvested and separated species-wise into leaf, branch and bole components. Trees and shrubs were classified species-wise into a different diameter classes and sample trees in each diameter class were harvested and separated into different components. The biomass of shrubs and trees were then calculated on the basis of a linear regression developed between different size classes and the measured biomass, and using density values. Herbaceous vegetation was harvested from 10 quadrats of 1 x 1 m size.

Plant samples were dried at 80°C for 24 hours, ground and passed through a 0.05 mm sieve, soil samples were collected from 10 random points upto 40 cm depth using a soil sampler. Air dried soil samples were ground and passed through a 0.02 mm sieve.

The elemental content of plant and soil samples was analysed following the methods suggested by Allen et al. (1974). Plant samples were analysed after acid digestion. Soil cations were estimated after extraction with 1 M ammonium acetate at pH 7. Nitrogen was determined by micro-kjaldahl method. Phosphorus was determined colorimetrically using ammonium molybdate blue method. Potassium was measured by flame-photometry and calcium and magnesium by EDTA-titration method.

For each element, the annual turnover was calculated by dividing the weight that left the compartment by the weight held in that compartment and expressed as a percentage (Reiners and Reiners, 1970). The enrichment ratio was calculated for each element as the quotient of the weight of a given element in the vegetation divided by its rate of uptake by the vegetation (Woodwell et al., 1975).

Table 4.1: Concentration and density of elements (kg ha^{-1}) (in parantheses) in the soil upto a depth of 40 cm in jhum plots of north-eastern India just before slashing

Site	Fallow age (years)	Nitrogen (%)	Phosphorus (mg $100^{-1}g$)	Potassium (meq.$100^{-1}g$)	Calcium (meq.$100^{-1}g$)	Magnesium (meq.$100^{-1}g$)
Garo Hills	5	0.19 (11932)	0.15 (9)	0.32 (630)	0.93 (793)	1.9 (1060)
	10	0.18 (10396)	0.32 (19)	0.21 (293)	1.10 (897)	1.6 (693)
	15	0.15 (8321)	0.41 (23)	0.51 (769)	1.30 (1037)	1.9 (1147)
Khasi Hills	10	0.21 (13671)	0.32 (21)	0.27 (301)	0.96 (1127)	1.6 (706)
	15	0.17 (11372)	0.36 (26)	0.48 (969)	1.10 (1096)	1.8 (1099)
Naga Hills	10	0.18 (10396)	0.27 (267)	0.23 (927)	0.88 (732)	1.7
	15	0.19 (9792)	0.36 (19)	0.46 (821)	0.95 (1121)	2.1 (1263)

Table 4.2: Density and basal area of bamboo species under different fallows before slashing for jhum in north-eastern India

Bamboo at different sites		Fallow age (years)									
		5		10		15		20		25	
		Density	Basal area	Density	Basal area	Density	Basal area	Density	Basal area	Density	Basal area
Garo Hills	D. hamiltonii	0.3	30.0	0.5	75.0	0.7	80.0	0.7	99.7	0.7	121.8
	B. tulda	0.7	70.0	0.7	75,5	0.8	83.0	0.8	107.3	0.7	105.3
Khasi Hills	D. hamiltonii	0.2	28.7	0.6	74.3	0.6	87.1	0.7	112.5	0.7	134.2
	N. dulloa	0.2	5.8	0.5	9.0	0.5	11.0	0.5	12.4	0.3	7.0
Naga Hills	D. hamiltonii	0.4	43.0	0.8	90.1	0.9	101.2	0.9	121.4	0.9	135.7
	B. khasiana	0.2	35.0	0.5	55.0	0.5	79.6	0.5	91.7	0.5	100.2

Table 4.3: Biomass of the vegetation slashed (kg ha^{-1}) in different jhum fallows in north-eastern India

Biomass components	Fallow age (years)						
	Garo Hills			Khasi hills		Naga hills	
	5	10	15	10	15	10	15
Bamboos	796 (40.5)	2825 (55.5)	4925 (50.9)	3500 (57.9)	6200 (57.5)	3200 (52.5)	5765 (51.0)
Trees and shrubs	757 (38.5)	2200 (43.2)	4715 (48.7)	2500 (41.4)	4550 (42.2)	2850 (46.7)	5500 (48.7)
Herbs	413 (21.0)	65 (1.3)	35 (0.4)	45 (0.7)	32 (0.3)	50 (0.8)	35 (0.3)
Total	1965	5090	9675	6045	10782	6100	11300

Table 4.4: Biomass contribution (kg ha^{-1}) by bamboo species to the slash in different jhum fallows in north-eastern India

Bamboo species	Fallow age (years)						
	Garo hills			Khasi hills		Naga hills	
	5	10	15	10	15	10	15
D. hamiltonii	438 (55)	1737 (62)	3211 (65)	2044 (58)	3565 (58)	1648 (52)	3084 (54)
The other bamboo species[1]	358 (45)	1088 (39)	1714 (35)	1456 (42)	2635 (43)	1552 (49)	2681 (47)
Total	796	2825	4925	3500	6200	3200	5765

[1] B. tulda at Garo Hills, N. Dullooa at Khasi Hills and B. khasiana at Naga Hills.

RESULTS

The elements present in the soil after slashing but before the burn are shown in Table 4.1. Whilst the amount of nitrogen present declined in older fallows compared with younger ones, in general, the reverse was found for all other elements.

Dendrocalamus hamiltonii was found at all sites (Table 4.2). It had higher density and basal area in khasi and Naga Hills. In Garo Hills, however, it had lesser density and basal area compared to Bambusa tulda. The density and basal area of Bambusa tulda, Bambusa Khasiana increased with fallow age upto 25 years at all sites. However, the population of N. dulloa declined in a 25-year old fallow.

In all the jhum fallows, the biomass contributed through bamboo was maximum as compared to that through rest of the species (Table 4.3). The contribution by bamboo species and by trees and shrubs increased in older fallows, whilst reverse was the case in the contribution through herbaceous vegetation.

Species-wise contribution of biomass was maximum for D. hamiltonii in all the jhum plots (Table 4.4.), at all sites. In Garo Hills, the difference between the

Table 4.5: Concentration (%) of elements in different components of D. hamiltonii and the other bamboo[1] (values in parentheses) in a 10-year old jhum fallow in north-eastern India

Element	Garo Hills			Khasi Hills			Naga Hills		
	Bole	Branch	Leaf	Bole	Branch	Leaf	Bole	Branch	Leaf
Nitrogen	0.46 (0.22)	0.50 (0.31)	3.30 (2.30)	0.45 (0.64)	0.51 (0.63)	3.00 (3.50)	0.42 (0.38)	0.53 (0.46)	3.30 (2.10)
Phosphorus	0.16 (0.09)	0.17 (0.13)	0.42 (0.33)	0.17 (0.18)	0.19 (0.29)	0.51 (0.73)	0.13 (0.10)	0.19 (0.12)	0.48 (0.27)
Potassium	2.0 (1.1)	2.6 (1.8)	3.1 (2.3)	2.1 (1.3)	2.4 (1.7)	3.1 (2.5)	1.9 (1.2)	2.5 (1.8)	3.0 (2.3)
Calcium	0.16 (0.19)	0.20 (0.23)	0.33 (0.37)	0.23 (0.23)	0.25 (0.28)	0.36 (0.41)	0.19 (0.18)	0.24 (0.26)	0.36 (0.37)
Magnesium	0.14 (0.13)	0.16 (0.15)	0.34 (0.37)	0.16 (0.10)	0.17 (0.12)	0.39 (0.33)	0.11 (0.09)	0.16 (0.12)	0.32 (0.29)

[1] B. tulda at Garo Hills, N. Dullooa at Khasi Hills and B. khasiana at Naga Hills.

Table 4.6:- Concentration (%) of elements in different components of trees and shrubs in a 10-year old fallow in north-eastern India

Elements	Garo Hills			Khasi Hills			Naga Hills		
	Bole	Branch	Leaf	Bole	Branch	Leaf	Bole	Branch	Leaf
Nitrogen	0.39	0.43	1.46	0.52	0.61	1.41	0.37	0.52	1.47
Phosphorus	0.05	0.09	0.13	0.06	0.12	0.13	0.09	0.10	0.13
Potassium	1.23	1.46	1.53	1.07	1.21	1.47	0.99	1.20	1.43
Calcium	0.51	0.66	0.93	0.47	0.60	0.83	0.39	0.61	1.01
Magnesium	0.28	0.20	0.47	0.30	0.25	0.42	0.21	0.28	0.38

Table 4.7: Density of elements (kg ha^{-1}) in the vegetation slashed in different jhum fallows in Garo Hills

Fallow age (years)	Element	Components					
		Bamboos			Trees and shrubs	Herbs	Total
		D. hamiltonii	B. tulda	Sub-Total			
5	Nitrogen	27.0	21.4	48.5 (64.3)	20.6 (27.3)	6.3 (8.4)	75.4
	Phosphorus	8.8	6.8	15.5 (49.8)	6.7 (21.4)	8.9 (28.6)	31.1
	Potassium	100.9	74.4	175.4 (62.3)	96.4 (34.3)	9.6 (3.4)	281.3
	Calcium	10.7	7.7	18.4 (16.3)	90.8 (80.4)	3.7 (3.3)	112.9
	Magnesium	7.1	5.6	12.7 (16.3)	60.4 (77.6)	4.8 (6.2)	77 .8
10	Nitrogen	94.1	61.4	155.6 (59.1)	106.8 (40.5)	1.0 (0.4)	263.3
	Phosphorus	25.0	16.4	41.3 (62.8)	23.2 (35.3)	1.3 (2.0)	65.9
	Potassium	326.1	160.9	487.0 (61.2)	307.8 (38.7)	.0.9 (0.1)	795.7
	Calcium	31.6	20.3	51.9 (14.9)	296.8 (85.0)	0.6 (0.2)	349.3
	Magnesium	23.9	17.5	41.3 (23.0)	137.7 (16.6)	0.8 (0.4)	179.9
15	Nitrogen	141.8	75.4	217.2 (61.9)	133.2 (37.9)	0.7 (0.2)	351.1
	Phosphorus	42.9	20.2	63.1 (61.0)	39.3 (38.0)	1.0 (1.0)	103.5
	Potassium	525.9	246.6	772.5 (62.0)	369.4 (29.7)	0.9 (0.1)	1246.3
	Calcium	54.5	30.9	85.4 (21.8)	306.1 (78.3)	0.4 (0.1)	391.9
	Magnesium	42.7	23.0	65.7 (32.3)	137.3 (67.5)	0.4 (0.2)	203.4

twp bamboo species was least in a 5-year old fallow, increasing with fallow age. Between 10- and 15-year old jhum fallows, in Khasi Hills and Naga Hills, the individual species contribution remained more or less the same.

A comparison of nutrient concentration in bamboo species versus shrub and tree components (Table 4.5, 4.6) suggest that the former category of species have generally higher nitrogen, phosphorus and potassium compared to the latter category of species. The reverse was the case for calcium and magnesium. While D. hamiltonii had higher concentrations of nitrogen, phosphorus and potassium compared to B. tulda in Garo Hills and B. Khasiana in Naga Hills, N. dulloa in Khasi Hills showed higher levels compared to D. hamiltonii. Such a clear-cut difference between species could not be observed for calcium and magnesium.

The density of elements in different components of the slash in Garo Hills increased with fallow age except for the herbaceous component (Table 4.7). In all the fallows, the contribution of nitrogen, phosphorus and potassium by bamboo was much more in comparison to trees and shrubs, were as reverse was true for calcium and

Table 4.8: Density of elements (kg ha^{-1}) in the vegetation slashed in different jhum fallows in Khasi Hills

Fallow age (years)	Elements	Components					
		Bamboos			Trees and shrubs	Herbs	Total
		D. hamiltonii	N. dulloa	Sub-Total			
10	Nitrogen	102.4	100.7	203.1 (61.6)	126.0 (38.2)	0.9 (0.3)	330.0
	Phosphorus	30.5	32.0	62.5 (73.0)	22.0 (25.7)	1.1 (1.3)	85.6
	Potassium	338.7	158.8	497.5 (59.6)	337.0 (40.3)	1.0 (0.1)	835.5
	Calcium	38.7	33.8	72.5 (19.4)	301.5 (80.5)	0.5 (0.1)	374.5
	Magnesium	31.0	17.0	48.0 (22.8)	161.5 (76.7)	1.0 (0.5)	210.5
15	Nitrogen	149.4	128.1	277.5 (59.0)	192.5 (40.9)	0.6 (0.1)	470.6
	Phosphorus	37.5	51.5	89.0 (73.3)	31.5 (25.9)	1.0 (0.8)	1121.5
	Potassium	541.8	234.7	776.5 (56.4)	399.5 (43.5)	1.0 (0.1)	1377.0
	Calcium	92.3	51.7	144.0 (24.0)	456.0 (76.0)	0.3 (0.1)	600.0
	Magnesium	42.5	28.5	71.0 (23.2)	235.0 (76.7)	0.3 (0.1)	306.3

Table 4.9: Density of elements (kg ha^{-1}) in the vegetation slashed in different jhum fallows in Naga Hills.

Fallow age (years)	Element	Components: Bamboos: *D. hamiltonii*	Bamboos: *B. khasiana*	Bamboos: Sub-total	Trees and Shrubs	Herbs	Total
10	Nitrogen	100.1	93.9	194.0 (59.6)	130.7 (40.2)	0.6 (0.2)	325.3
	Phosphorus	26.1	24.4	50.5 (62.3)	29.6 (36.6)	0.9 (1.1)	81.0
	Potassium	290.6	304.4	595.0 (58.5)	421.5 (41.4)	1.0 (0.1)	1017.5
	Calcium	31.5	20.3	51.8 (12.4)	365.5 (87.5)	0.4 (0.1)	417.7
	Magnesium	27.5	19.1	46.6 (14.3)	278.0 (85.5)	0.6 (0.2)	325.2
15	Nitrogen	150.3	136.7	287.0 (58.1)	206.6 (41.8)	0.4 (0.1)	494.0
	Phosphorus	51.0	34.6	85.6 (70.8)	34.5 (28.5)	0.8 (0.7)	120.9
	Potassium	481.8	404.3	886.1 (60.9)	567.7 (39.0)	1.0 (0.1)	1454.8
	Calcium	47.8	41.8	89.6 (15.2)	498.1 (84.7)	0.3 (0.1)	588.0
	Magnesium	36.2	33.8	70.0 (19.1)	296.0 (80.8)	0.4 (0.1)	366.4

Table 4.10: Inventory of nitrogen and phosphorus in the total vegetation and in the bamboo component (parentheses) in different jhum fallows before slashing of the vegetation for jhum in north-eastern India

	Fallow age (years)						
	Garo Hills			Khasi Hills		Naga Hills	
	5	10	15	10	15	10	15
Nitrogen:							
Aboveground biomass ($kg\ ha^{-1}$)	75.4 (48.5)	263.3 (155.6)	351.1 (271.2)	330.0 (203.1)	470.6 (277.5)	325.3 (194.0)	494.0 (287.0)
Release through litter ($kg\ ha^{-1}$)	36.7 (17.1)	77.2 (47.5)	88.9 (74.9)	91.0 (56.5)	127.0 (97.7)	85.6 (65.5)	114.7 (101.8)
% annual turnover	48.6 (35.2)	29.3 (30.5)	25.3 (34.5)	27.6 (27.8)	27.0 (35.2)	26.3 (33.8)	23.2 (35.5)
Annual nutrient accumulation ($kg\ ha^{-1}$)	12.0 (6.3)	20.7 (15.8)	17.4 (6.8)	26.3 (14.7)	19.9 (6.7)	26.6 (12.9)	25.2 (11.3)
Enrichment ratio	6.3 (7.7)	12.8 (9.9)	20.2 (31.8)	12.6 (13.9)	23.7 (41.7)	12.2 (15.1)	19.6 (25.4)
Phosphorus:							
Aboveground biomass ($kg\ ha^{-1}$)	31.1 (15.6)	65.6 (41.3)	103.5 (63.1)	85.6 (62.5)	121.5 (89.0)	81.0 (50.5)	120.9 (85.6)
Release through litter ($kg\ ha^{-1}$)	16.6 (3.3)	13.0 (5.9)	24.9 (11.2)	14.0 (11.0)	24.7 (14.7)	15.0 (9.9)	29.4 (14.0)
% annual turnover	53.2 (21.0)	19.7 (14.2)	24.0 (17.7)	16.3 (17.6)	20.4 (16.6)	18.5 (19.5)	24.3 (16.4)

Annual nutrient accumulation (kg ha^{-1})	0.7 (0.3)	5.2 (4.6)	6.8 (3.3)	5.8 (5.2)	7.6 (4.5)	5.9 (4.1)	7.5 (6.2)
Enrichment ratio	45.3 (62.3)	12.7 (8.9)	15.2 (19.1)	14.9 (12.1)	16.0 (19.7)	13.8 (12.4)	16.1 (13.9)

magnesium. Amongst the two species of bamboo, the contribution by D. hamiltonii was higher over B. tulda.

In Khasi Hills, the density of elements in different components was generally higher in a 15-year old fallow than in a 10-year old one (Table 4.8); the exception to this was the herbs which showed a reverse trend. Whilst the contribution of nitrogen, phosphorus and potassium by bamboo was higher than that by trees and shrubs, the reverse was the case for calcium and magnesium. Between the two species of bamboo, the contribution by D. hamiltonii was somewhat higher than that by N. dulloa except for phosphorus contribution, which was more through N. dulloa.

A similar trend was observed at Naga Hills for the different components in 10- and 15-year old fallows (Table 4.9). Trees and shrubs contributed more calcium and magnesium compared to bamboo species, and reverse was the case for other elements. Between the two bamboo species, D. hamiltonii generally contributed more of all the elements except potassium in a 10-year fallow.

Inventory of nitrogen and phosphorus in the total vegetation and in the bamboo component of it, before the fallow was slashed is given in Table 4.10. Nitrogen and

phosphorus held in the aboveground biomass of the total vegetation and the bamboo component of it, and that released through litter, improved in older fallows. While the percentage annual turnover of nitrogen for the total vegetation consistently declined with fallow age, that for phosphorus declined from 5- to 10-year old fallow at Garo Hills, but improved subsequently in a 15-year old fallow at all sites. Percentage annual turnover for nitrogen in bamboos declined from 5- to 10-year old fallows but subsequently improved. A similar change in 5- to 10-year was also observed for phosphorus, with a decline in a 15-year old fallow, only at Khasi Hills and Naga Hills but not at Garo Hills. While annual nutrient accumulation for the total vegetation generally tended to improve in older fallows, it showed some variation depending upon the site. In the case of bamboos in Garo Hills, annual nutrient accumulation improved from 5- to 10-year old fallow, followed by a decline in a 15-year old fallow here and at Khasi Hills, but not at Naga Hills. While nitrogen enrichment ratio of the total vegetation improved in older fallows, phosphorus values either declined, remained more or less the same or even somewhat improved in older fallows. Nitrogen enrichment ratio for bamboos markedly improved in older

Table 4.11: Inventory of potassium, calcium, and magnesium in the total vegetation and in the bamboo component (parantheses) in different jhum fallows before slashing of the vegetation for jhum in north-eastern India

	Fallow age (years)						
	Garo Hills			Khasi Hills		Naga Hills	
	5	10	15	10	15	10	15
Potassium:							
Aboveground biomass ($kg\ ha^{-1}$)	281.3 (175.4)	795.7 (487.0)	1246.3 (772.5)	835.5 (497.5)	1377.0 (776.5)	1017.5 (595.0)	1454.8 (886.1)
Release through litter ($kg\ ha^{-1}$)	45.4 (20.4)	69.3 (58.8)	102.9 (82.7)	70.9 (53.9)	95.5 (81.6)	93.6 (71.6)	139.3 (108.2)
% annual turnover	16.1 (11.7)	8.7 (12.1)	8.3 (10.7)	8.5 (10.8)	6.9 (10.5)	6.8 (12.0)	9.6 (12.2)
Annual nutrient accumulation ($kg\ ha^{-1}$)	53.6 (31.0)	118.2 (54.7)	133.7 (52.3)	75.5 (44.4)	105.0 (50.2)	99.5 (52.3)	91.4 (50.9)
Enrichment ratio	5.3 (5.7)	6.7 (8.9)	9.3 (14.8)	11.1 (11.2)	13.2 (15.5)	10.2 (11.4)	15.9 (17.4)
Calcium:							
Aboveground biomass ($kg\ ha^{-1}$)	112.9 (18.4)	349.3 (51.9)	391.9 (85.4)	374.5 (72.5)	600.0 (144.0)	417.7 (51.8)	588.0 (89.6)
Release through litter ($kg\ ha^{-1}$)	39.2 (2.5)	49.9 (8.1)	55.3 (13.4)	37.0 (8.9)	41.0 (15.9)	48.3 (8.8)	56.2 (15.4)

% annual turnover	34.7 (13.7)	14.3 (15.77)	14.1 (15.7)	9.9 (12.3)	6.8 (11.0)	11.6 (17.1)	9.6 (19.2)
Annual nutrient accumulation(kg ha^{-1})	3.8 (0.3)	17.8 (5.7)	30.8 (5.7)	28.7 (6.4)	41.6 (12.9)	25.7 (5.2)	30.3 (4.3)
Enrichment ratio	30.2 (57.6)	19.7 (9.1)	12.7 (15.1)	13.0 (11.4)	14.4 (11.1)	16.3 (9.9)	19.4 (20.7)
Magnesium:							
Aboveground biomass (kg ha^{-1})	77.8 (12.7)	179.9 (41.3)	203.4 (65.7)	210.5 (48.0)	306.3 (71.0)	225.2 (46.6)	366.4 (70.0)
Release through litter (kg ha^{-1})	21.4 (2.7)	21.6 (7.7)	26.8 (12.6)	27.2 (8.1)	29.0 (13.6)	33.7 (8.8)	39.7 (15.0)
% annual turnover	27.5 (21.0)	12.0 (18.6)	13.2 (19.2)	13.0 (16.8)	9.5 (19.1)	10.4 (19.0)	10.8 (21.4)
Annual nutrient accumulation (kg ha^{-1})	1.6 (0.2)	2.8 (0.5)	2.8 (0.7)	16.5 (4.1)	22.3 (4.3)	24.5 (4.6)	13.7 (1.8)
Enrichment ratio	50.4 (63.4)	63.8 (87.9)	72.2 (91.3)	12.2 (11.8)	13.7 (21.4)	13.3 (10.1)	26.8 (39.1)

Table 4.12: Removal of slash (kg ha^{-1}) from plots under different jhum cycles. Values in parantheses is that component as a percentage of the total slash removed

Biomass component	Jhum cycle at						
	Garo Hills			Khasi Hills		Naga Hills	
	5	10	15	10	15	10	15
Bamboos	30.0 (100.0)	50 (5.3)	50 (4.4)	50 (13.5)	50 (10.9)	50 (11.1)	50 (10.0)
Trees and shrubs:							
Timber	0	590 (62.8)	665 (58.6)	190 (51.4)	160 (34.8)	0	0
Firewood	0	300 (31.9)	420 (37.0)	130 (35.1)	250 (54.4)	400 (88.9)	450 (90.0)
Total	30	940	1135	370	460	450	500
Percentage slash removed out of the system	1.5	18.5	11.7	6.1	4.3	7.4	4.4

fallows at all sites while phosphorus values declined sharply from 5- to 10-year old fallows followed by an increase between 10 and 15 years.

Potassium, calcium and magnesium held in the aboveground biomass and that released through litter improved sharply in older fallows, both for the total vegetation and for the bamboo components (Table 4.11). The percentage annual turnover of all three elements declined in older fallows except for potassium and magnesium in Naga Hills. However, percentage annual turnover of all the elements in bamboos remained more or less the same or slightly improved in older fallows. Annual nutrient accumulation improved for the total vegetation in older fallows except for magnesium in Naga Hills. Annual nutrient accumulation in bamboos improved or remained same in older fallows depending upon the nutrient and site conditions. While enrichment ratio for the three elements in the total vegetation and in bamboo component largely improved in older fallows, some variation was noticed depending upon site conditions.

The slash removed out of the jhum system varied considerably and do not show a definite pattern (Table 4.12). The contribution by bamboo to the total slash

Table 4.13: Density of elements (kg ha^{-1}) in the slash removed from jhum plots under 10- and 15-year jhum cycle in north-eastern India

Jhum cycle (years)	Element	Garo Hills			Khasi Hills			Naga Hills		
		Bamboo	Trees and shrubs	Total	Bamboo	Trees and shrubs	Total	Bamboo	Trees and shrubs	Total
10	Nitrogen	2.7	63.6	66.3	2.8	16.1	18.9	2.6	18.3	20.9
	Phosphorus	0.3	13.8	14.1	0.3	2.8	3.1	0.2	4.1	4.3
	Potassium	3.0	183.3	186.3	3.1	43.1	46.2	2.7	34.7	37.4
	Calcium	0.1	176.7	176.8	0.3	38.5	38.8	0.2	30.1	30.3
	Magnesium	0.2	82.0	82.2	0.2	20.6	20.8	0.3	18.8	19.1
15	Nitrogen	2.9	30.7	33.6	3.1	17.3	20.4	2.9	16.9	19.8
	Phosphorus	0.4	9.1	9.4	0.4	2.8	3.2	0.3	2.8	3.1
	Potassium	3.7	85.0	88.7	3.6	54.0	57.6	3.4	46.4	49.8
	Calcium	0.3	70.4	70.8	0.3	41.1	41.4	0.4	40.8	41.1
	Magnesium	0.3	31.6	31.9	0.3	21.2	21.5	0.4	24.2	24.5

removed out of the system was relatively less compared to trees and shrubs, except in a 5-year old jhum fallow slashed at Garo Hills.

The density of elements removed out of the system through slash of trees and shrubs was generally higher when compared with bamboo species (Table 4.13). The nutrients removed from the jhum system through slash, expressed as a percentage of the total slash produced ranged between 4.0 and 25.2 for nitrogen, 2.6 and 21.4 for phosphorus, 3.4 and 23.4 for potassium, 6.9 and 50.6 for calcium, 5.9 and 45.7 for magnesium, depending upon the jhum cycle.

DISCUSSION

Slash and burn agriculture is a system mainly dependent upon nutrient inputs through ash fertilization (Ramakrishnan and Toky, 1981). The length of the jhum cycle is a major factor in determining the amount of nutrients added, which in turn partly determine crop yield (Toky and Ramakrishnan, 1981a; Mishra and Ramakrishnan, 1981). The fallow regrowth during secondary succession after cropping in north-eastern hill region of India is characterized by weedy communities upto about 5 years (Toky and Ramakrishnan, 1983a; Ramakrishnan

and Mishra, 1981; Kushwaha and Ramakrishnan, 1982; Saxena and Ramakrishnan, 1983b; 1984b), but bamboos form a major component of the successional stages of vegetation after the weed phase and may continue upto about 25 years as in Dendrocalamus hamiltonii or upto 35 to 47 years depending upon the intermast period for flowering of the species concerned (Varmah and Bahadur, 1980). But, a species such as Neohouzeoua dulloa may even continue though with reduced vigour upto 60 years of forest regrowth as an understorey species (Chapter 2).

The three bamboo species of larger size, Dendrocalamus hamiltonii, Bambusa tulda and Bambusa khasiana are strictly light demanders and therefore these species do not continue in the successional environment beyond 25 years as in D. hamiltonii (Toky and Ramakrishnan, 1983a; Ramakrishnan et al., 1981) or beyond 35 to 47 years which is the intermast period for B. tulda and B. khasiana respectively (Varmah and Bahadur, 1980). On the other hand, N. dulloa which is a smaller variety of bamboo, though a light demander, has the ability to survive under shade (Chapter 1). Therefore it is reasonable to find that the population size of this species increases only upto 10 years of fallow regrowth after which, as an undergrowth species its population declined.

Though the total slash biomass of bamboo increased in older fallows upto 15 years, which is related to fallow age and the consequent rapid vegetative multiplication of bamboo when light conditions are still favourable for its growth (Chapter 2), a similar increase with fallow age was also noticed for the total slash produced as observed earlier in the north-eastern region (Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983c) and by others for slash and burn agriculture systems elsewhere (Nye and Hutton, 1957; Bortholomew et al., 1953; Snedaker, 1970; Golley et al., 1976; Edward and Grubb, 1977; Ewel, 1971; Uhl and Jorden, 1984; Stormgaard, 1984). However, the proportional contribution of biomass by bamboo was either unaltered or even declined. This is related to rapid takeover of fallows by broad-leaved shrubs and trees resulting in eventual elemination of bamboo by taller tree species (Toky and Ramakrishnan, 1983a; Singh and Ramakrishnan, 1982). The proportional contribution of different species of bamboos to the total bamboo biomass, however, varied depending upon the site. It may also be noted that the slash added through weed biomass declined drastically in 10- and 15-year old fallows which is due to natural

suppression of weeds in fallows older than 5 years (Saxena and Ramakrishnan, 1984b; Swamy and Ramakrishnan, 1987).

While bamboo species are chiefly used only for hut construction for living, the amount so used is only a small fraction of about 4 to 14% of the total slash removed from the system. When under a 5-year jhum cycle, however, bamboo production is very low and a greater proportion of this commodity is removed for hut building. While in Garo Hills, in general, natural forest resources are still relatively better preserved because of lesser population pressure on the land (Ramakrishnan, 1984a), in Khasi and Jaintia Hills of Meghalaya, 5-year jhum cycles are more frequent and in many areas the cycle has come further down leading to site desertification (Ramakrishnan, 1985; Ramakrishnan, 1984b; Ramakrishnan et al., 1981). Therefore, the availability of bamboo has become more acute. The ecological implications of this lies in the fact that, as the cycle gets shortened as has been happening in the recent past, due to population pressure and reduced land availability for cropping (Ramakrishnan et al., 1981; Ramakrishnan, 1985a), bamboo production is adversely affected.

As far as we are aware there is no information available on the nutrient budgeting of bamboos in ecosystems except for the studies done by Ramakrishnan and co-workers on sub-tropical humid forests of north-eastern India (Toky and Ramakrishnan, 1982; 1983b; Chapter 2). An important point that emerges out of the present study is that bamboos generally accumulated more of nitrogen, phosphorus and potassium in the system compared to calcium and magnesium. Amongst the three bamboo species, N. dulloa was more efficient in nutrient conservation than D. hamiltonii, as is evident from tissue concentration of these elements though the latter had larger biomass and therefore higher elemental densities. The last two elements, in the all three sites, are largely located in trees and shrubs rather than in bamboos. While the physiological basis for such selective uptakes of nitrogen, phosphorus and potassium by all bamboo species in general, is a matter that needs to be investigated, the ecological implications of this is obvious. Bamboos play an important nutrient conservation role in these ecological systems of the humid tropics, particularly under a wide range of jhum cycles of 5 to 30 years.

Nitrogen, phosphorus and potassium are more critical elements in tropical soils. After burn, nitrogen is a major casualty because of rapid volatilization (Allen, 1964; Knight, 1966; Debell and Ralston, 1970) and the recovery of the lost nitrogen takes atleast 10 to 15 years (Saxena and Ramakrishnan, 1986; Mishra and Ramakrishnan, 1984). Phosphorus is another nutrient often in short supply. Earlier studies on jhum system (Mishra and Ramakrishnan, 1983b) and more recent studies too (Swamy, 1986) suggest large-scale volatilization of phosphorus as also reported by Llyod (1971), though the mechanism for volatilization is not clear. Further phosphorus fixation into unavailable forms is reported in their clay fraction for tropical soils that are rich in sesquioxides of iron and aluminium (Gebhardt and Coleman, 1974; Tinker, 1977; Parfitt and Lee, 1979; Mishra and Ramakrishnan, 1983d). Losses of potassium through runoff and percolation water in the jhum system was always found to be much heavier than that of divalent cations (Mishra and Ramakrishnan, 1983a; Toky and Ramakrishnan, 1981b). This confirms the findings of others (Allen, 1964; Llyod, 1971) who have shown that potassium was much more readily dissolved

than calcium and magnesium ions following a burn. Therefore, conservation through bamboo of all these three critical elements is of particular significance from the point of view of fertility maintenance under jhum.

Preferential uptake of phosphorus by early successional weedy communities has been suggested earlier (Toky and Ramakrishnan, 1983b). A generally higher density for phosphorus compared to that of other elements found for herbaceous communities at all sites is in agreement with this observation. Similarly, N. dulloa a bamboo from Khasi Hills, has also the ability to accumulate more of phosphorus compared to other bamboo species, an observation also confirmed by our studies on nutrient allocation strategies (Chapter 2).

In general the biomass of slash removed by the jhum farmer from the jhum system for other purposes such as hut construction, timber and fuelwood is many-fold more through shrubs and trees than through bamboos. Consequently the amount of nutrients lost out of the system is also similarly affected. With a high

capacity for conservation of nutrients such as nitrogen, phosphorus and potassium by bamboo discussed above, the losses from the system to that extent is minimized, than would otherwise happen if a larger proportion of the bamboo biomass is removed out of the system.

A general increase in nutrient density in the biomass and in the release through litter in older fallows is to be expected because of the general increase in vigour of the bamboo species with fallow age upto a certain point of time as recorded for D. hamiltonii (Chapter 1) and suggested for B. tulda and B. khasiana based upon their 35 to 47 years' intermast period (Varmah and Bahadur, 1980). The exception to this is N. dulloa which being a smaller sized bamboo soon is reduced to an understorey species in a 20-year old fallow with consequent decrease in nutrient density in aboveground biomass and that released through litter. This was seen by us on the basis of individual species analysed out of the gross data presented in Table 4.10 and 4.11.

Lower turnover rates for calcium and magnesium is to be expected for bamboos because of lesser accumulation

of these elements compared with nitrogen, phosphorus and potassium. However, annual turnover rates of potassium is low, perhaps as a consequence of a larger quantity of this element being rapidly accumulated by bamboos, and locked up in the biomass; the release through litter itself is low. The turnover rates of elements and enrichment ratio calculated for bamboos and the vegetation as a whole is dependent upon the specific bamboo species, the element concerned and site conditions. However, an important point that emerges is that, bamboos, has a critical role in the nutrients cycling of the vegetation where it dominates as in 10- and 15-year old fallows that slashed for jhum. Obvicusly more studies are required on the role of this important component of many tropical forest ecosystems.

SUMMARY

This study considers the role of bamboo species under different slash and burn agriculture (jhum) cycles of upto 15 years at three locations, at lower elevations in Khasi and Garo Hills in Meghalaya and in Naga Hills. While Dendrocalamus hamiltonii Nees and Arn. is a species common to all sites, three

others are site specific: Neohouzeoua dulloa A. Camus in Khasi Hills, Bambusa tulda Roxb. in Garo Hills and Bambusa khasiana Munro in Naga Hills. Under all the jhum cycles considered here, bamboo is an important component of the fallows slashed for jhum, contributing upto 40 to 58% of the total slash biomass and a much higher proportion (49 to 73%) of nitrogen, phosphorus and potassium, but much lesser calcium and magnesium (12 ro 32%). Apparently, bamboo has a significant role in conservation of nitrogen, phosphorus and potassium. These elements are highly labile (nitrogen and potassium) or are often immobilised in tropical soils, into an unavilable state in the clay fraction (phosphorus) due to fire. Calcium and magnesium, on the other hand, are largely held in tree and shrub components of the fallows slashed for jhum. It is concluded that bamboos play a significant role in nutrient conservation in the jhum system in north-eastern India.

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CHAPTER 5

SOCIO-ECONOMIC ANALYSIS OF BAMBOO RESOURCES IN EAST KHASI HILLS DISTRICT OF MEGHALAYA IN NORTH-EASTERN INDIA.

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INTRODUCTION

Bamboo is an important natural resource for the people of the north-eastern region of India. Not only does it play an important role in the village economy, because of its use as fuelwood, as water pipe or as material for hut construction, but also is important as part of the slash and burn agriculture (jhum) system because of its important role in conservation of nitrogen, phosphorus, potassium (Chapter 4). This important resource of this region is declining at a rapid rate because of the shortening of the jhum cycle in the recent past (Ramakrishnan, et al., 1981; Ramakrishnan, 1985b) and the consequent takeover by weeds (Saxena and Ramakrishnan, 1984b) and eventual desertification (Ramakrishnan, 1985d; 1985c). Further the giant paper mills established in the region will further accentuate the shortage of bamboo in the region. The present study is an attempt to evaluate the present utilisation pattern of this resources in one of the district, namely, the east Khasi hills district of Meghalaya.

METHODS OF STUDY

Though detailed analysis of bamboo resources available and utilisation patterns are based on the three

villages, a more generalized analysis of the utilization pattern was also done on thirty villages selected at random in east Khasi Hills district. The families in the villages were classified into categories based upon income and the dependence and utilization of bamboo resources. The consumption pattern of each category was then observed over a one-year period.

Bamboo used as firewood collected by the villagers and that exported outside the village boundary is usually cut into smaller pieces of about 75 cm long. Actual field measurements were made for the three villages, also with random observations on thirty villages. In those villages, where bamboo is also raised in plantations within the village boundary, the amount extracted from them by the few families who own them and the manner in which the extracted bamboos are disposed were observed over a one-year period.

New bamboo shoots consumed as food was calculated on the basis of observations over a one-year period on families selected at random. Bamboo shoots exported were calculated on the basis of those sold in the market, on the basis of weekly observations, since they are sold in weekly markets. Fodder consumption by cattle was based on observations of weekly harvests done by the villagers

Table 5.1: Village community structure of the three villages of east Khasi Hills district

	Villages		
	Umpri	Umroi	Lallad
Village built area (ha)	50	14	34
Number of house holds	79	63	42
Population:			
Adult males	161 (50.5)	86 (45.5)	66 (45.5)
Adult females	106 (33.2)	73 (38.6)	59 (40.7)
Children (below 12 years)	52 (16.3)	30 (15.9)	20 (13.8)
Total	319	189	145
Male/female ratio	1.31	1.03	1.07
Work force:			
Agriculturists	97 (30.4)	86 (45.5)	53 (36.6)
Traders	8 (2.5)	2 (1.1)	4 (2.8)
Govt. employees	11 (3.5)	2 (1.1)	6 (4.1)
Labourers	138 (43.3)	61 (32.3)	69 (47.6)
Dependents and part time workers	65 (20.4)	38 (20.2)	13 (9.0)

and the size of the cattle population. The food and fodder values in terms of crude protein and total sugars were analysed by indophenol blue method and anthron method respectively, following Allen et al., (1974).

Industrial export for pulping is exclusively through contractors who operate in demarcated forest areas leased out for a 5-year period at Lailad and Umpri, since 1981. Calculation on the export is based upon number of truck loads taken out on a monthly basis.

RESULTS AND DISCUSSION

Bamboo utilization pattern in selected villages:

Though the number of families was the second highest at Umroi, the area covered by the house holds is least compared to Lailad and Umpri (Table 5.1). Umpri, however, had the highest number of households. With a mixed population of different communities, Umpri and Lailad had some degree of segregation in household organization, whereas the compactness of Umroi is because it is a single community (Khasi) village. About 14 4o 16% of the population were children below 12 years. While Umroi and Lailad had approximately

Table 5.2: Land use pattern in the three villages of east Khasi Hills district

	Villages		
	Umpri	Umroi	Lallad
Area under cultivation (ha):			
Valley cultivation	93.7 (58.2)	4.9 (5.0)	11.2 (21.4)
Jhum cultivation	67.3 (41.8)	93.5 (95.0)	41.2 (78.6)
Total	161.0	98.4	52.4
Area (ha) under natural vegetation within 1 km radius of the village			
Broad-leaved forest	92.0 (29.3)	0	107.7 (34.3)
Bamboo fallows	139.4 (44.4)	0	163.1 (52.0)
Area under plantations(ha):			
Bamboo	1.3	1.7	0
Pine (*Pinus kesiya*)	0	265.0	0
Pineapple and lemongrass (*Cymbopogan* sp.)	14.3	31.7	4.7
Total	15.6	298.4	4.7

equal proportions of males and females, this ratio was weighted towards males at Umpri because of migrant male population. Umroi had a larger percentage of people involved in agriculture, followed by labourers, whereas Umpri and Lailad had more labourforce closely followed by agriculturists. The labourers at these two latter villages are employed by timber contractors.

Umpri being closer to Assam plains has a large area under valley cultivation (Table 5.2). Lailad and Umroi had large area under slash and burn agriculture (jhum), with least valley land in Umroi. Bamboo forests are more than broad-leaved forests both at Umpri and Lailad located at lower elevations, where at higher elevations of Umroi pine plantations are managed by the Meghalaya Forest Department (1/3 area) and the village community (2/3 area). A relatively small area is also under bamboo plantation done by villagers. Plantation crops such as pineapple and lemon grass (Cymbopogan sp.) introduced by Meghalaya phytochemicals are also cultivated. The yield of bamboo through different species at Umpri and Umroi is given in Table 5.3. Umroi had Bambusa khasiana whilst Umpri had Bambusa tulda and Melocanna bambusoides. Since M. bambusoides is a thinner variety but with high culm yield,

Table 5.3: Area under bamboo plantation in two villages of east Khasi Hills district and extraction pattern.

	Villages	
	Umori	Umroi
Bamboo plantation area (ha)		
Bambusa khasiana	0	1.70
Bambusa tulda	0.95	0
Melocanna bambusoides	0.35	0
Total	1.30	1.70
Extraction per ha:		
Number of culms	300	180
Biomass(kg x 10^3)	5.0	3.20
Bole	4.0	2.30
Branches	0.79	0.49
Leaves	0.21	0.17

Table 5.4: Consumption and export pattern of bamboo from 1 km radius of villages in east Khasi Hills district

	Villages		
	Umpri	Umroi	Lailad
Domestic (Kg yr^{-1}):			
Fencing	150 (15)	20 (7)	110(18)
Repairing	650 (65)	0	450(75)
Water pipes	50	0	80
Firewood (Kg x 10^3 yr^{-1})			
Within-village consumption	18 (0.23)	0	16.5(0.34)
Consumption total(Kgx10^3 Yr^{-1})	18.85	0.02	17.14
Firewood exported outside village boundary(kg x 10^3 yr^{-1})	33.9	0	0
Industrial export (Kg x 10^3 Yr^{-1})	300.0	0	500.0
Export total	339.9	0	500.0
Total extraction (Kg x 10^3 Yr^{-1})	358.75	0.02	517.14

Values in parentheses represent individual family consumption

the production of culms is much higher at Umpri inspite of reduced land area under plantation, in contrast to B. khasiana which is larger variety with fewer culms. B. tulda is a larger bamboo variety compared even to B. khasiana and this would partly account for higher biomass of the bamboo plantation at Umpri.

Consumption pattern of bamboo by the three villages are given in Table 5.4. Bamboo as firewood is consumed and also exported in large quantities both at Umpri and Lailad but not at Umroi. A recurring consumption is related to fencing and house repair. Though large quantities of bamboo was exported out for industrial use, the extraction of this at a stretch is done for 5 years only, followed by a gap of 10 years for regeneration. New house construction is done on the average after 20 to 40 years being the life span of a house, this is not accounted here. In the two villages at lower elevations, some bamboo is also used for water transportation from streams.

During the rainy season, bamboo shoots form an important food source (Table 5.5). While D. hamiltonii is the chief source at the two lower elevation villages

Table 5.5: Bamboo shoot consumption and export pattern in the three villages of east Khasi Hills district with food values

	Villages		
	Umri	Umroi	Lailad
Availability period	June-October (150 days)	June-August (90 days)	June-October (150 days)
Dry weight of shoots consumed (kg yr^{-1})			
Within-village consumption	96(1.2)	15(0.2)	80(1.9)
Export outside village	104	0	0
Total	200	15	80
Food value			
Crude protein (%)	0.235	0.195	0.235
Total sugars (%)	0.260	0.240	0.260

Per family consumption in parentheses

Table 5.6: Fodder consumption pattern in the three villages of east Khasi Hills district with fodder values

	Villages		
	Umpri	Umroi	Lailad
Availability period	April-October	April-October	April-October
Dry weight of leaves consumed (kg yr^{-1})	130(10	35(3)	125(7)
Fooder value:			
Crude protein(%)	0.23	0.20	0.23
Total sugars (%)	0.27	0.25	0.27

Numbers of families rearing cattle in parentheses

Table 5.7: Income (Rupees yr^{-1}) from the bamboo at the three villages in east Khasi Hills district

	Villages		
	Umpri	Umroi	Lallad
Firewood	8475(126)	0	0
Food (new shoots)	624 (75)	450(225)	0
Bamboos from plantation	600(100)	800(400)	0
Total	9699	1250	0

Monetary return (Rupees yr^{-1}) through export earnings per family in parentheses.

chiefly harvested from natural bamboo forests, at Umroi B. khasiana from plantation is the chief source. Bamboo shoot consumption is much higher at lower elevation villages than at Umroi. Further, export of shoots outside the village boundary is done only in few villages. Only Nepalis maintain cattle, and bamboo fodder consumption by them alone is restricted during the rainy season (Table 5.6)

The monetory returns through export of bamboo is given in Table 5.7. Firewood and bamboo shoot as food are sold only by a few families. Plantation being raised in jhum plots by a few families, only 4 to 6 families derive benefit from it. Individual culms are sold at the rate of Rs 1.25/- for M. bambusoides, Rs 2.50/- for B. tulda and Rs 4.50/- for B. khasiana. With 6 families owning 1.3 hectares of plantation in Umpri in contrast to two families owning 1.7 hectares of bamboo plantation at Umroi; income per family is higher in the latter case. These farmers sell a small fraction of the bamboo to the rest of the villagers and over 90% is exported out of the village boundary.

Fig. 5.1. Topographic map showing village distribution pattern in east Khasi Hills district.

Fig. 5.1

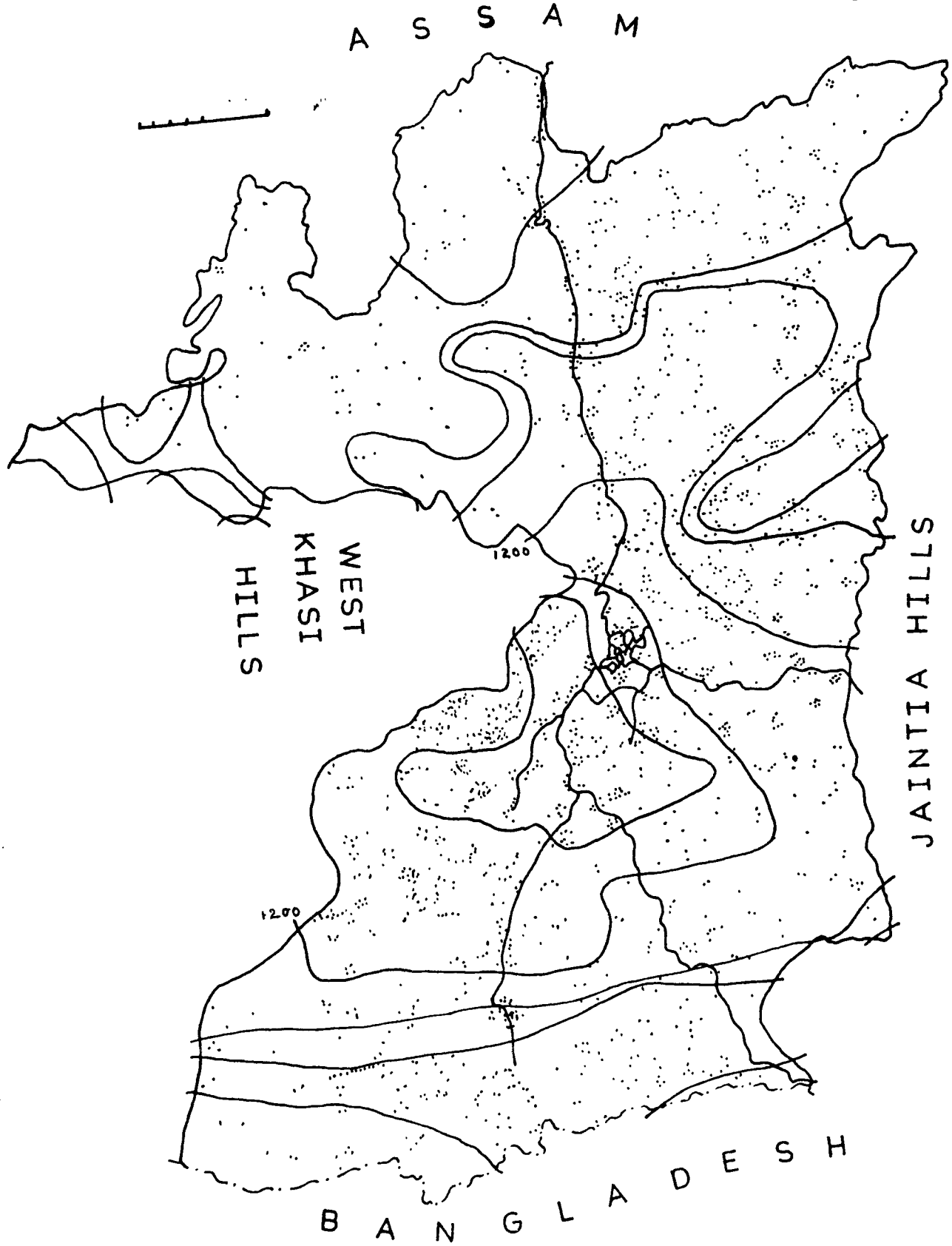

Fig. 5.2. Altitudinal succession of vegetation indicating bamboo zone in east Khasi Hills district.

Fig.5.2

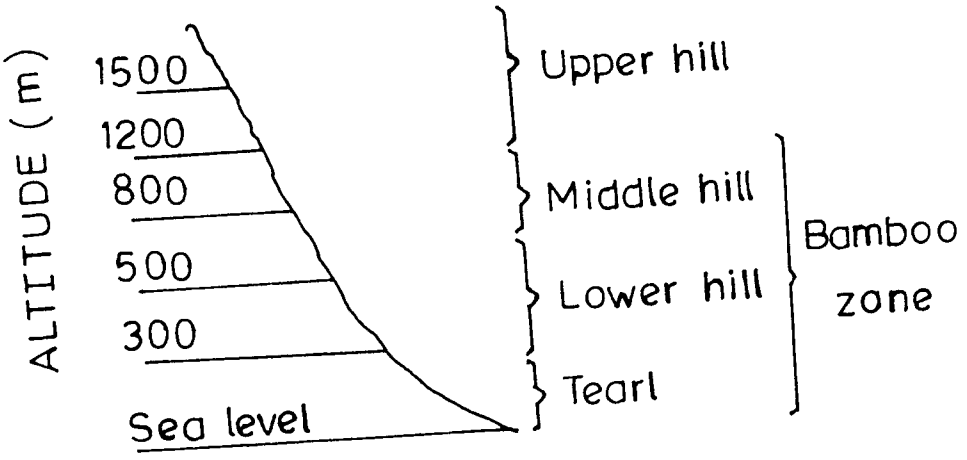
ALTITUDE (m)
1500
1200
800
500
300
Sea level
Upper hill
Middle hill
Lower hill
Tearl
Bamboo zone

Table 5.8: Land use statistics of east Khasi Hills district (1981-82)[1]

	Area (ha)	Percentage of the total
Forest	220503	37.46
Barren land	82035	13.94
Land under non-agricultural uses	17009	2.89
Cultivable waste land	155775	26.47
Land under miscellanious tree crops and groves	50477	8.58
Permanent pastures and other grazing lands	6117	1.04
Current jhum fallows	5486	0.93
Old jhum fallows	5747	0.98
Net area sown	45468	7.73
Area sown more than once	9463	1.61
Total cropped area	54931	9.33
Total geographical area	588615	100.00
Net/gross irrigated area	8371	1.42

[1]Data from District Statistical Abstract, east Khasi Hills District, 1981-82

Utilization pattern in the bamboo zone of east Khasi Hills district:

East Khasi Hills district has about 6000 villages (Fig. 5.1) of which around 2500 are in the bamboo available zone. Bamboo consumption zone, it may be noted is at an altitude range of 90 to 1200 m (Fig. 5.2). Of these 567 are villages with heavy consumption. Villages are classified on the basis that they extract an average of 100 x 10^3 kg per family. Whilst low consumption villages are 1533 and they on the average extract 0.4 x 10^3 kg per family.

The census data for the east Khasi Hills district (Table 5.8) show that land use statistics, but this is only of a limited value in assessing bamboo resources in the district. Thus, even though 37.5% is shown as under forest, much of this is a bamboo forest of not more than 20 to 25 years, rather than mixed broad-leaved ones of older age. Similarly, it is suspected that cultivable waste lands and current jhum fallows may have at least a small percentage under bamboo. Further, it seems likely that old jhum fallows are all bamboo forests (Toky and Ramakrishnan, 1983a), since there are not many forested

Table 5.9: Bamboo consumption pattern in the two categories of villages in east Khasi Hills district

	Category of villages	
	Heavy-consumption	Low-consumption
Fencing (Kg)	170	120
Repairing (Kg)	490	460
Water pipes (Kg)	90	63
Firewood (Kg x 10^3)	48	19
Food (Kg)	135	80
Fodder (Kg)	85	65
Total (Kg x 10^3)	49	19.8
Export (Kg x 10^3)	34	0
Grand total (Kg x 10^3)	83.9	19.8
Industrial (Kg x 10^3)	800	0
Number of villages	567	1533
Average villages size (number of families)	60	55

Table 5.10: Dry weight consumption/export of bamboo resources from bamboo zone villages of east Khasi Hills district

	Amount ($m \times 10^3$)
Fencing	280
Repairing	983
Water pipes	148
Firewood	19500
Export (Industrial)	800
[illegible]	50911
Food (bamboo shoot)	199
Fodder (bamboo leaves)	255
Grand Total	21365

fallows older than 25 to 30 years in east Khasi Hills district (Ramakrishnan, 1985c). Therefore a correct assessment of bamboo resources of the area, through techniques such as remote sensing is important.

The bamboo extraction pattern per village in 567 high-consumption and 1533 low-consumption villages is shown for an average village with 55 to 60 families per village (Table 5.9). In the high-consumption category total extraction is 2.5-fold more than in the low-consumption category. Much of the consumption is ag fuelwood. However, bamboo has a variety of uses in the village ecosystem.

The total utilization pattern shown (Table 5-10) here for east Khasi Hills district suggests 83.9 x 10^3 kg for high-consumption villages and 19.9 x 10^3 kg for low-cunsumption villages. Out of 34 x 10^3 kg exported outside the high-consumption villages, about ½ goes outside east Khasi Hills district chiefly to the Assam plains, exclusively for firewood. 800 x 10^3 kg goes through contractors for industrial use, chiefly for pulping in the paper mills located in Assam. It is interesting to note that consumption in the region itself is only a small fraction (though significant from the point of village economy) compared to export.

Table 5.11: Income (Rupees yr^{-1}) from bamboo exported from east Khasi Hills district

	Amount
New shoots	353808 (624)
Firewood	3855600 (6800)
Indistrial	100000
Total income to the region	4309408

Per village income within paranthe ses

The export income through bamboo from villages in the east Khasi Hills district region (Table 5.11) is exclusively from high-consumption units only. Of the total income from bamboo of ₹ 4309 x 10^3, a major component is through fuel-wood export, industrial export and export of bamboo shoots form only a small fraction of the income.

CONCLUSION

In the east Khasi Hills district low-consumption villages out number high-consumption villages. It appears that low-consumption villages are a consequence of a general decline in bamboo resources in the district. In other words, it is suspected that with passage of time more villages are likely to be added on to the low-consumption category. Though industrial export is only from a restricted area, the amount in relation to the total consumption in the village itself is very high, this pattern will be exaggerated with new paper mills going into production in the near future. Yet, there is no planning what so ever for scientific management of bamboo forests in the district or in the region as a whole. It is also interesting that much of bamboo is burnt as fuelwood within the district and even a larger amount is exported to the plains for this purpose. The

situation as far as sustainable yield of bamboo for the future is concerned is alarming; there is an urgent need for scientific management of this important resources.

SUMMARY

A general survey of bamboo utilization pattern in thirty randomly selected villages of east Khasi Hills district was done, alongwith intensive studies on three selected villages. A major use of bamboo is as firewood for local consumption and even more so for to export to Assam plains. Much bamboo, though from a restricted area is also exported for industrial purposes. Bamboo shoot is an important food source during the rainy season. A majority of villages are classified as low-consumption units because severe local shortage of this resource and it is suggested that many are being added to this from the high-consumption category.

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PLATES

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PLATE I: a) A view of slash and burn agriculture plot with mixed cropping; b) A view of 0-year old fallow.

PLATE II: a) A view of 5-year old jhum fallow with left-over trees in the background;
b) A view of 10-year old jhum fallow.

PLATE III: a) A view of 60-year old fallow at Lailad;
b) inside view of the 60-year old fallow.

PLATE V: a) A view of village market; b) Truckload of bamboo for industrial export.