ECO-PHYSIOLOGICAL AND DEMOGRAPHIC STUDIES OF WEEDS OF SUCCESSIONAL ENVIRONMENTS AFTER SLASH AND BURN AGRICULTURE IN NORTH-EASTERN INDIA

P. SUDHAKAR SWAMY

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SCHOOL OF LIFE SCIENCES

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DEDICATED

TO

MY PARENTS

Gram : JAYENU

Phone : Off. 652282
Res :

Jawaharlal Nehru University

P. S. Ramakrishnan
M. Sc., Ph. D., F.N.A., F.A.Sc. F.N.A.Sc.
Professor of Ecology

SCHOOL OF ENVIRONMENTAL SCIENCES
NEW DELHI - 110067

I certify that the thesis entitled " ECO-PHYSIOLOGICAL AND DEMOGRAPHIC STUDIES OF WEEDS OF SUCCESSIONAL ENVIRONMENTS AFTER SLASH AND BURN AGRICULTURE IN NORTH-EASTERN INDIA" submitted by Shri. P. Sudhakar Swamy, for the degree of Doctor of Philosophy of the North-Eastern Hill University, Shillong embodies the record of original investigation carried out by him under my supervision. He has been duly registered and the thesis presented is worthy of being considered for the award of Ph. D. degree. This work has not been submitted for any degree of any other University.

Date: 15 July, 1986.

Place: New Delhi.

Signature of the Supervisor

P.R. Mishra

HEAD
Centre For Eco- Development
NORTH- EASTERN HILL UNIVERSITY
Shillong- 793014.

Forwarded
1/9/86.

R. S. TRIPATHI
Professor & Head
Department of Botany
N. E. Hill University
Shillong-793014, India.

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P. Sudhakar Swamy

(P.S. SWAMY)

Centre for Eco-Development
School of Life Sciences
North-Eastern Hill University,
Shillong.

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CHAPTERS:

PREFACE

Traditional farming such as that under slash and burn agriculture (jhum) in north-east India is based upon a close inter-linkage between agriculture, weed potential and forestry sub-systems. This agroecosystem is based upon the natural soil fertility recovery processes operating during the secondary successional fallow phase, involving weed communities of the early phases and forests of bamboo and broad-leaved shrubs and trees of the later phases. Depending upon the length of the fallow phase, the weed potential is altered with increased weed potential under shorter cycles, accompanied with poor soil fertility recovery of the system, the crop yield is adversely affected. Site degradation and desertification are some of the long-term consequences of successive imposition of shorter cycles. While increased weed potential in this agroecosystem has adverse ecologic and economic consequences, this agro-forestry system is based upon sound management of weeds as part of the crop system where, traditionally, the jhum farmer retain about 20% of the weed biomass as part of the agroecosystem. The remaining 80% weed biomass is also recycled into the agroecosystem during the cropping phase itself. This 'non-weed' concept provides one of the basis for designing new management strategies for tropical agriculture.

The present study, therefore, considers two major aspects of this traditional slash and burn agriculture (jhum) system at lower elevations of Meghalaya in north-east India: (i) the ecology of an important exotic weed such as Mikania micrantha Humbold, Bonapald, Kunth, during the early secondary successional fallow phase and (ii) the agroecosystem function under a 5- and 20-year jhum cycle with respect to the 'non-weed' concept and nutrient budgeting.

The thesis starts with a 'General Introduction' surveying the literature pertaining to the topics of investigation, followed by a description of the study area and climate. Each of the subsequent nine chapters deal with one aspect of the study done on the slash and burn agriculture system. These nine chapters are organized in a crisp and condensed form meant for simultaneous publication in scientific journals. One of them, namely, weed potential of Mikania micrantha H.B.K., and its control in fallows after shifting agriculture (jhum) in north-east India in Agriculture, Ecosystem and Environment. Vol.16 : (1986). Besides the results presented, each chapter has its own brief introduction, methods of study, discussion and summary. Therefore, some amount of repetition (though minimal) was unavoidable. The literature cited in the text, however, has all been put together at the end of the thesis.

The results presented here, apart from its academic value, has applied implications from the point of view of weed management and possible improvement of the traditional agroecosystem so as to remove the recent distortions that have come about due to rapid shortening of the jhum cycle.

GENERAL INTRODUCTION

Fire, which occurs frequently in some plant communities plays an important role in the regulation of population of many plant species. A fire of mild intensity may stimulate high seedling establishment and growth by raising the soil temperature and nutrient status and by removal of plant litter and vegetation cover (Buell and Cantlon, 1953; Kelting, 1957; Lemon, 1967; Old, 1969; Sharp, 1970; Whelan and Nain, 1979). Toky and Ramakrishnan, (1983a), and Saxena and Ramakrishnan, (1984b) also observed stimulatory effect of fire on the early phase of secondary succession after slash and burn agriculture (Jhum) in north-eastern India. Kushwaha *et al.* (1983) observed that fire had promotary effect on flowering of an early successional grass, *Imperata cylindrica*.

Slash and burn agricultural system (Jhum) in north-east India involves the management of fire for temporary improvement of soil fertility for mixed cropping (Ramakrishnan and Toky, 1981a; Mishra and Ramakrishnan, 1983b), before the land is abandoned for natural regeneration of plant communities through secondary succession. The pattern and processes involved during secondary succession, therefore, is dependent upon the perturbation due to fire and due to cropping procedures.

Both frequency and intensity of the burn and the cropping practices also determine to a large degree the pattern of the early phase of secondary succession (Toky and Ramakrishnan, 1983a).

Secondary successional patterns:

The pattern of secondary succession and the rapidity with which 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. The length of the jhum cycle (intervening fallow phase between two successive croppings at the same site) also determines the pattern of vegetation development. 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 community 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) in 'relay floristic model' pointed out that 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. While, Egler (1954) proposed 'initial florestic 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 florestics model under the 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 strategies 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~~t~~, 1976). 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 reduce 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 and operates in primary succession (Lawrence *et al.*, 1967; Reiners *et al.*, 1971), (ii) tolerance pathway which assumes that later successional species to be successful, whether or not early successional species have preceded them. However, this has not received evidence so far (Noble and Slatyer, 1977), (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 florestic model, (ii) direct succession that assumes re-establishment 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. These authors emphasized that vital attributes may form the basis of evolutionary trends during succession.

DEMOGRAPHY AND POPULATION DYNAMICS

Mortality/natality patterns:

The 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 the environmental factors on the size of the population.

Lotka (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 niches cannot survive together for a long time; eventually one will replace the other.

The early seedling phase of a plants life is generally considered the most risky and this risk in exaggerated due to increasing density of the same or another species (Harper and White, 1974; Cook, 1979; Smith, 1984). 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). 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. The experimental model of deWit (1961) ~~are~~ is superbly designed to study the behaviour of two species in 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 mechanism 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 with in 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, 1960; Ramakrishnan and Jeet, 1972).

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

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

As plants in a dense population become larger with age, the density of individuals in the population decreases due to mortality. For, 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 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 patterns.

A cohort with Deevey type I survivorship has low mortality in early and middle life but a rapid change to high mortality latter on. Type II survivorship is typified by a constant death risk through out 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). 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 Cavers and Harper 1967; Friedman and Graham, 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 Kumar and Ramakrishnan (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 young 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 catifornia, Bautelous hirsuta and B. chondrosioides.

Demography:

The life history of annual plants is unique because the actively growing fraction of the popalation must be derived each year entirely from the seed bank. Annual plant species are excluded from habitats where there is dense cover of perennial species, and they occur mainly on sites where disturbance or physical stress inhibits the formation of a dense community of perennials (Harper, 1977; Grime, 1979; Hickman, 1979).

Annuals commonly colonize temporarily available habitats such as recently disturbed fields. Annuals growing on these habitats exhibit a variety of demographic patterns negatively skewed (Deevey, 1947, Type I) survivorship among individuals following germination comparatively low seed production and few seeds that survive in the soil for more than 9 months (Mack, 1976; Watkinson and Harper, 1978; Leverich and Levin, 1979). In contrast, other species are characterized by high seedling mortality (Deevey Type II and III), have higher fecundity, or have a substantial proportion of seeds that survive in the soil for at least one year (Beatley, 1967; Naylor, 1972; Sharitz and McCormick, 1973; Symonides, 1974; Hickman, 1975; 1977; Jefferies, et al., 1981). Kelmow and Raynal (1983) suggested that survival and percentage reproduction of plant that emerged in the spring varied markedly depending upon rainfall. Deevey survivorship curves, Type I, II and III were observed in cohorts from a year with abundant rainfall or a year with intermittent rainfall. Zimmerman and Weis (1984) suggested that in a beach population of Xanthium strumarium, seedling survival was largely density independent, while growth and fruit production declined significantly with increased density. He further suggested that soil moisture and the date of seedling emergence to be important to the recruitment of seedlings in a natural population.

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~~l~~ (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 at higher elevations of north-eastern India and observed a net population increase through both vegetative and sexual reproduction in early successional fallows up to 6-years. Mortality of seedlings was high in 1- and 3-year fallows, low in 6-year fallow and reached 100% in older fallows. Further, they showed that seedling mortality was maximum during monsoon although some seedlings dies 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 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 elemination 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 studying the population dynamics of Imperata cylindrica related to slash and burn agriculture in north-eastern India at different altitudes. Similarly, a number of studies on the demography of forest herbs are available (Hutchings and Barkham, 1976; Ernst, 1979; Barkham, 1980;

Cook, 1980; Solbrig et al., 1980; Holland, 1981; Solbrig, 1981; Wells, 1981; Bierzychudek, 1982a; Cook and Lyons, 1983; Hutchings, 1983).

In plant populations, there are two levels of population behaviour: the number of plants and 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 rhizomatous plant involves the continued reduplication of discrete modular units, the 'ramets' the sum of these units representing the 'genet' or product of 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. The ability of 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; Solbrig et al., 1981; Cook 1983; Pitelka et al., 1985; Harnett and Bazzaz, 1985). 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 large viable seed bank in the grassland soil, germination and establishment of new genets was rare in both sites. Further she stated 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 woodland populations follow an opportunistic strategy for rapid spread and sampling of the environment where as the conservative one for consolidation and slower radial spread as in the adjacent grassland. Pitelka *et al.* (1985) too found similar results, while dealing with *Clintonia borealis*. Here too no seedling recruitment was observed, while ramet mortality was found to be density-dependent.

Plant demography has been used to elucidate aspects of ecological succession (Sharitz and McCormick, 1972; Raynal, 1979; Kushwaha *et al.*, 1981; 1983; Mishra and Ramakrishnan, 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) populations growing on the same substrate but in contrasting vegetation (Lovett-Doust, 1981) and populations growing at different altitudes (Sharma, 1985).

Age structure:

The most reliable method for estimating the age of perennial species is to follow the fate of labelled seedling or tillers of known age in permanent quadrats. This method has been successfully used by Tamm (1956). 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 give 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).

PLANT STRATEGY ANALYSIS

Growth and nutrition:

Light has been recognized as a major factor influencing the replacement of species during secondary succession (Kushwaha and Ramakrishnan 1982; Bormann et al., 1968; Marks, 1974; Bazzaz, 1979). Competition for light and nutrients increases through succession, in general. In early succession rapid growth, which depends upon abundant resources, is advantageous. Later in succession such resources may be less available, and those plants with inherently high growth rates and resource requirements may not survive.

Grime (1976) suggested that shade adapted climax tree species may have lower growth rate than the sun adapted early successional ones. Such a differential strategy for early vs. late successional trees have been shown by Ramakrishnan *et al.* (1982) through a series of studies. Ruderal and competitive species have higher relative growth rates compared to stress tolerant species (Grime, 1976). 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 to 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 soil 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 secondary species and an increase in the resource apparently did not affect the course of succession. A similar conclusion was also made by Harcombe (1972) through his studies on _Cercopia_ _obtusifolia._ West and Chilcote (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 but 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 rate 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, adapt a strategy for rapid nutrient turnover rates so that a high flux of soil nutrient pool is maintained (Ramakrishnan and ~~Kumar~~ Das, 1983; ~~Kumar~~ Das and Ramakrishnan, 1985).

A high efficiency of nutrient use, generally expressed as drymatter production per gram nutrient (inverse of tissue concentration) has been suggested to be an adaptation to nutrient stress (Loneragan and Asher, 1967; Jefferey, 1968; White, 1972; 1973; Garten, 1978). However, such evolution may be sometimes misleading when there is luxury uptake and large vacuolar storage of nutrients (Bieleski 1973; Brady, 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. Infact, information on these aspects are meagre. Recently through a series of studies on nutrient uptake and use efficiencies of species, Ramakrishnan and co-workers (Saxena and Ramakrishnan, 1984; Ramakrishnan, 1985) drew attention to the adaptive value of this parameter over a successional gradient of environment. [illegible]

Resource allocation and reproductive Strategy:

Cody (1966) put forth a concept based on the principle 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 (Gadgil, 1973; 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 tried 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 of 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 condition as more emphasis is given for vegetative grwoth, 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 them as any factor that limits and cause destruction of biomass like herbivory, pathogenicity and human activities. Thus, Grime (1974, 1979) recognized 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 drymatter and nutrients in four important perennial weeds. They observed that the perennials often tend to allocate more to vegetative reproductive organs compared 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 micro-sites of a heterogenous soil as opposed to C_3 species which were often confined to nutrient rich micro-sites. 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 aboveground 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^{-1}, where for temperat forests it was about 490 t. ha^{-1} is about 170 years only (Borman and Likens; 1979). Thus, a steady-state for biomass is reached over a shorter time period in the tropics 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, 1983; Toky and Ramakrishnan, 1983; 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 wast from leaves and twigs, by litter and twig fall, and in the form of dead roots and root exudates. The soil humus is increased 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, 1983a; Mishra and Ramakrishnan, 1983c; Uhl and Jordan, 1983).

A large body of information is available on nutrient cycling in forested ecosystems (Laudelot and Meyer 1954; Greenland and Kowal, 1960; Odum, 1970; Stark, 1970; Golley *et al.*, 1977; Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983c). Though the information is limited, some patterns are suggested: (i) the uptake and return of nutrients may be greater per year in tropical forests than in other type 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 evapotranspiration.

Mineral cycling probably 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 stabilized in mature forests (Stark, 1971a,b; Toky and Ramakrishnan, 1983a; 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 decreases soil temperature, which results in lowered decomposition and nitrification rates and reduced supply of water-soluble ions available for removal of drainage water. Growing vegetation also reduces nitrient 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 losses) can be considered more resilient and this 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 systems in a tropical forest ecosystem. Further, Foster *et al.*(1980)

studied the effect of ragweed (Ambrosia artemissifolia) on nutrient cycling in a 1st year old field and showed its conservatory role of nutrients. 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., 1981a).

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. 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 indefinetly. 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 becomes short, due to poor recovery of soil fertility and increased intensity of weed competition. This in turn resulted in reduced crop yield under short cycles(Nye and Greenland, 1960; Watters, 1971; Toky and Ramakrishnan, 1981a; Mishra and Ramakrishnan, 1981).

When the forests are cleared and the debris is burnt, all the cations are released on the surface soil as ash.

Heavey 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, 1981b; 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 from the system (Harwood and Jackson, 1975; Ashton, 1976; Mishra and Ramakrishnan, 1983). Llyod (1971) reported massive losses for phosphorus through fire.

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 <u>et al</u>. 1978; Ramakrishnan and Toky, 1981; Mishra and Ramakrishnan, 1983b). 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 Jaiyebo, 1963; Ahlgren and Ahlgren, 1965). This increase is attributed partially to the removal of chemical inhibitors (Reed, 1951; Smith <u>et al</u>., 1968; Rice, 1974; Saxena and Ramakrishnan, 1986).

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; Weels, 1971) after burning balances the corresponding concentration of cations in the soil solution and therefore heavy losses through water occurs (Bormann et al., 1968; Lewis Jr. 1974). The loss of water, nutrients and sediment gets reduced as crop and weed cover is establish (Toky and Ramakrishnan, 1981b; Mishra and Ramakrishnan, 1983a), with a transfer from soil to the plant biomass.

At the end of the cropping period during slash and burn agriculture at higher elevations of Meghalaya, Mishra and Ramakrishnan (1984) estimated nitrogen losses from the agroecosystems to be about 640 Kg ha^{-1}. Information on nutrient budgeting in agroecosystem also meagre. Agroecosystems are open systems in which biogeochemical functions consists of inputs from various sources, outputs to various sinks and a variable degree of internal cycling.

WEEDS UNDER SHIFTING AGRICULTURE

Weed potential:

Weeds are the major cause of declining yield under slash and burn agriculture in many parts of the world and include

Eupatorium odoratum in Thailand (Zinke *et al.*, 1978) and *Imperata cylindrica* in Sarwak (Freeman, 1955). Cutting *et al.* (1959) reported that the yield of maize in Nyasaland was 4284 Kg ha^{-1} when weeded four weeks after germination, but attained only 3217 Kg ha^{-1} when weeded six weeks after germination. Emerson (1953), describes the influence of weeds on the 'milpa' system in tropical America, in which successive crops of maize, mixed with beans, are grown. The second crop yielded less than the first, probably because it was more weedy and therefore farmers like to clear a fresh land than to continue cropping on the old plot. Toky and Ramakrishnan (1981) and Mishra and Ramakrishnan (1981) reported that under shorter jhum cycles the weed problem was severe due to arrested succession by exotic weeds in north-eastern India.

Conklin (1957) estimated that a Hanunoo farmer in the Philippines spends about 300 man-hours per hectare in weeding the first year land cleared from primary forest and about 600 man-hours on land cleared from secondary forest about 20 years old. Mishra and Ramakrishnan (1981) reported that weeding is one of the energy consuming tasks performed by women folk. They further indicated that this task is more energy consuming under shorter cycles under slash and burn agriculture in north-eastern India, also confirmed by Toky and Ramakrishnan (1982).

The non-weed concept:

Recently weeds have been viewed as an useful component in agroecosystems and may pay an important role in agricultural management of the future. Studies by Chacon and Gliessman (1982), Saxena and Ramakrishnan (1984), Mishra and Ramakrishnan (1984) suggested that the non-weed concept where, weeds have a useful role to play, is an essential ingredient of traditional agroecosystems in different parts of the world and in the north-eastern India. Tripathi (1977) analysed the possible consequences of a complete eradication of the weed flora from agro-ecosystems. Alteiri (1983) on the basis of a detailed review emphasized upon weed management as opposed to weed control.

Obviously, one of the important roles of the weeds in the cropland is related to reduction in soil erosion, protection of the soil surface from solar radiation and improved soil micro-climate (Moody, 1975; Tripathi, 1977; Chacon and Gliessman, 1982). Ramakrishnan and his co-workers (Toky and Ramakrishnan, 1981; Mishra and Ramakrishnan, 1983a) studied the reduction of soil erosion by weeds in jhum lands and observed considerable loss of nutrients before the plant cover is established. The role of weeds in checking run-off and infiltration losses becomes obvious in a 5-year old weed dominated jhum fallow, as compared to the losses during the cropping phase.

Another important positive role of the weed lies in the recycling of the nutrients, through organic manure. Mishra and Ramakrishnan (1984) studied nitrogen budget of three jhum cycles of 15-, 10-, and 5-years at higher elevation of Meghalaya, where nitrogen recycled through weeds was estimated to range from 4.8 to 20.8 Kg ha^{-1} of which about 1/6th is ploughed back into the soil and the rest is routed eventually via the manure pit of the village ecosystem (Mishra and Ramakrishnan, 1982).

Crop residues and weeded out biomass is used as a mulch by the farmers of Tanzania (Acland, 1971). Stigter argued that mulch used as shade by the traditional farmer of Tanzania is for the management of micro-climate in order to increase land productivity and yield capacity. De Schlippe (1956) indicated that weeds are useful elements in maintaining soil fertility in agroecosystems.

A variety of weeds are also used as food. The plants like *Gnetum montanum* and *G. gnemon* are important foods of the Naga tribe (Ramakrishnan, 1984). Leaves of *Amaranthus sp.*, *Chenopodium album*, *Portuluca olevacea*, *Celosia argentia*, *Euphorbia caducifolia* are used as vegetables. Rhizomes of *Typha* when pulverized yield a sweet flour. *Eichchornia crassipes* has been recommended as a poultry feed. Weeds also have many other general uses. Dry bushes of *Capparis decidua*, *Crotalaria burhia* and *Imperata* *cylindrica* are used as thatching material. *Thysanolaena maxima* is used for brooms. *Hedychium* is used as a medicine for insect bite.

Natural weed management in slash and burn agriculture (jhum) is dependent upon the length of the fallow phase after the land is cropped. The weeds being the predominant component of the early successional communities upto 5 years of fallow regrowth (Toky and Ramakrishnan, 1983a), continuous imposition of short cycles of 5 years or less tends to exaggerate the weed potential in the cropping system.

Present study:

Slash and burn agriculture popularly called 'jhum' in India and variously termed locally in the country (Takenglu 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, 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 available for cropping. 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 decades research experience by his group in this field of specialization. In an another review (1984) he also focussed upon the science behind shifting agriculture and its value for an integrated development of the tribal areas of the north-east India.

As a result of perturbation to the forest ecosystem by man or by natural means such as fire will drastically affect the environment in the tropics and sub-tropics 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) an ecosystem approach (Franforth and Golley, 1974; Ramakrishnan *et al.*, 1983). However, our knowledge of the adaptive strategy of individual species under a varied environment after perturbation is more important for better understanding of the vegetation recovery process. The need for such studies has been emphasized by many workers (Gomez-Pompa and Vazquez-Yanes, 1974; Golley and Medina, 1975; Bazzaz, 1979; Toky and Ramakrishnan, 1982; Saxena and Ramakrishnan, 1984b).

Mikania genus with about 250 species of herbaceous or slightly woody vines belongs to the family compositae (Asteraceae). Most commonly known species are *M. cordata*, which is native to the old world *M. scandens*, which is confined to north-America and M. micrantha, which is a native of tropical America and Caribbean region. It is now reported to be in Asia and the south Pacific (Parker, 1972). Parker (1972) also reported this species from Assam and Kerala in India, Bangladesh, Sri Lanka, Malaysia and Indonesia and concluded that this may one of the most aggressive weed in the continent. Robinson (1934) stressed the need of more taxonomic work on *Mikania sp.* of the old world and Pacific islands.

Mikania propagates both through sexual and asexual means. It produces thousands of wind dispersed seeds. Thus hand weeding or cultivation without destruction or drying of stems may do little to control this weed (Holm *et al.*, 1978). Craig and Evans (1946) reproted an alarming rate of spread of *M. cordata,* due to the movement of stem materials by streams is an important means of dispersal. However, (Bamber, 1909; Burkill, 1935; King, 1966) its dispersal in the old world may be through its use as a ground cover, which is a recommended practice in Sri Lanka, Indonesia and Malaysia.

Mikania species occur in open and disturbed places. It is common in young secondary forests (Toky and Ramakrishnan, 1983a) in forest clearings and in plantation crops (Borthakur, 1977; Dutta, 1977) and Wastelands. *M. cordata* grows in partial shade but can not tolerate dense shade (Macalpine, 1959). Burkill (1935), and Craig and Evans (1946) stated that *M. cordata* takes up large quantities of potassium. According to Caum (1940) coconut and other tree crops in Malaysia were abandoned because of intrusion by *M. cordata*, Further, he described large bread fruit trees (*Artocarpus altilis*) being killed by this weed.

Due to its aggressive growth habit, this species competes with seedlings and mature crops (Dutta, 1965), but is also makes plucking difficult when it grows over the top of tea bushes (Kasasian, 1971). There is evidence from Malaysia and Indonesia that the effects of M. cordata on a crop cover may extend beyond the normal competition for nutrients, ligh and soil moisture (Mainstone and Wong, 1966; Wong, 1964; Wycherley and Chandapillai, 1969; Seth, 1971). Guha and Watson (1958) found lower rates of nitrification in soils mixed with leaves and stems of M. cordata. However, it did not affect ammonification. Wong (1964) found that M. cordata contains substances which inhibit the growth of rubber and tomato plants. Water ectracts (1 and 2%) of oven-dried stem and leaf materials significantly depressed dry weight and nitrogen and phosphorus content of tomato seedlings. However, M. cordata has been reported to be susceptible to parasitic attack by Cuscuta chinensis in Sri Lanka (King, 1966).

M. cordata is used as a cure for snake bite and scropion bites in South Africa (Watt and Breyerbrandwijk, 1962) as a remedy for itch in Malaysia and poultice for wounds in Java (Burkill, 1935).

Little is known about such an important species as M. micrantha on its growth, biology and ecology. The present study therefore, was undertaken to investigate the demographic, ecophysiological and adaptive strategies of Mikania micrantha, a perennial vine under varied environment after slash and burn agriculture. An attempt has also been made to study the ecological role of this weed in successional fallows after shifting agriculture, in north-east India. An analysis of different weed husbandary practices both from ecological and economic view points was analysed and the present study also considers nutrient budgeting and internal cycling in slash and burn agriculture system under 5- and 20-year jhum cycles under varied weeding regimes, at lower elevation of north-eastern part of India.

STUDY AREA AND CLIMATE

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

Fig. I. Location of study area.

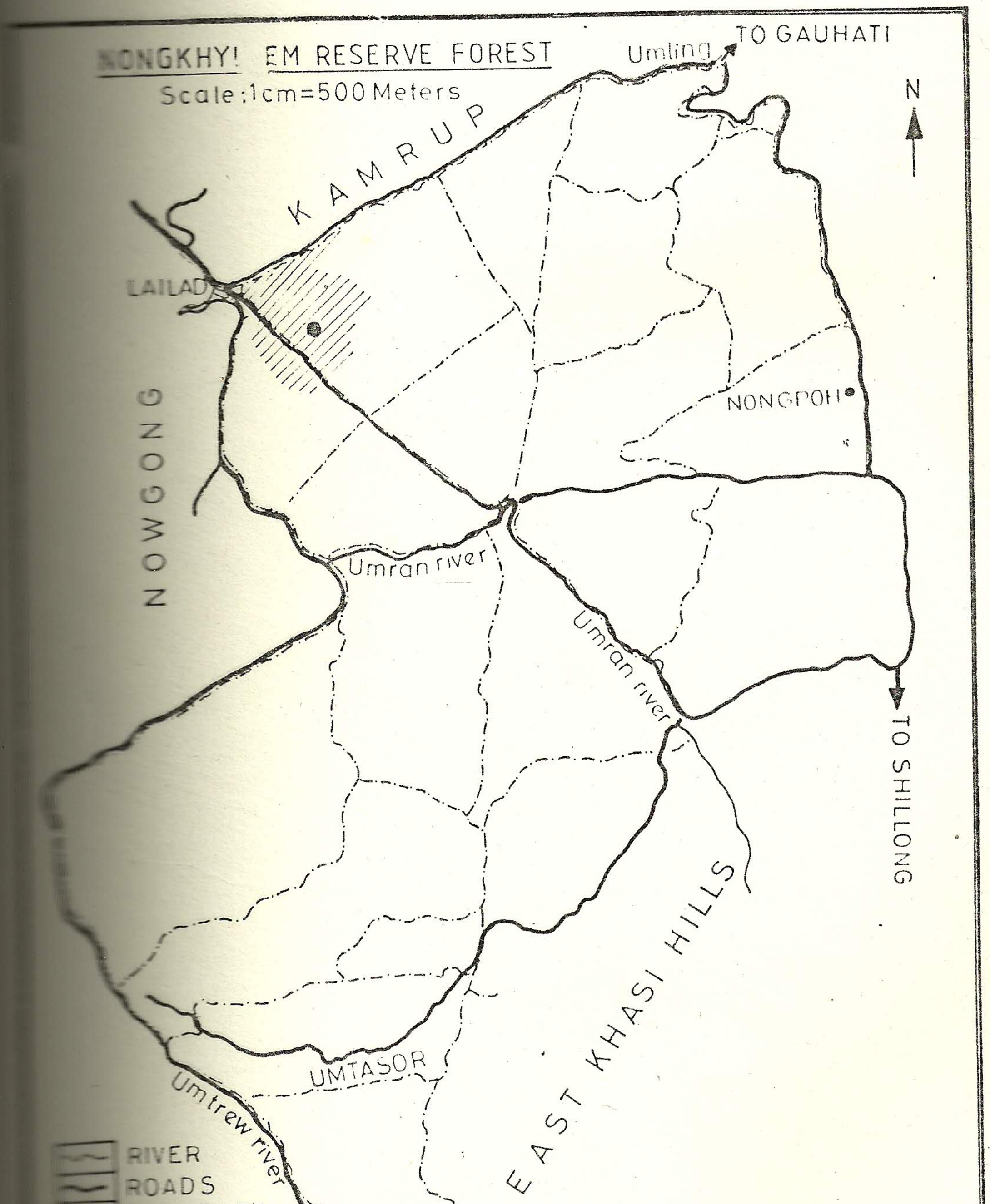
NONGKHYLLEM RESERVE FOREST
Scale:1cm=500 Meters
Umling
TO GAUHATI
N
KAMRUP
LAILAD
NOWGONG
NONGPOH
Umran river
Umran river
TO SHILLONG
EAST KHASI HILLS
UMTASOR
Umtrew river
RIVER
ROADS
BOUNDARY
STUDY AREA

Fig. I

Fig. II. Ombrothermic diagram for the study area. Mean monthly maximum (   ) and minimum (   ) temperatures; monthly rainfall(   )

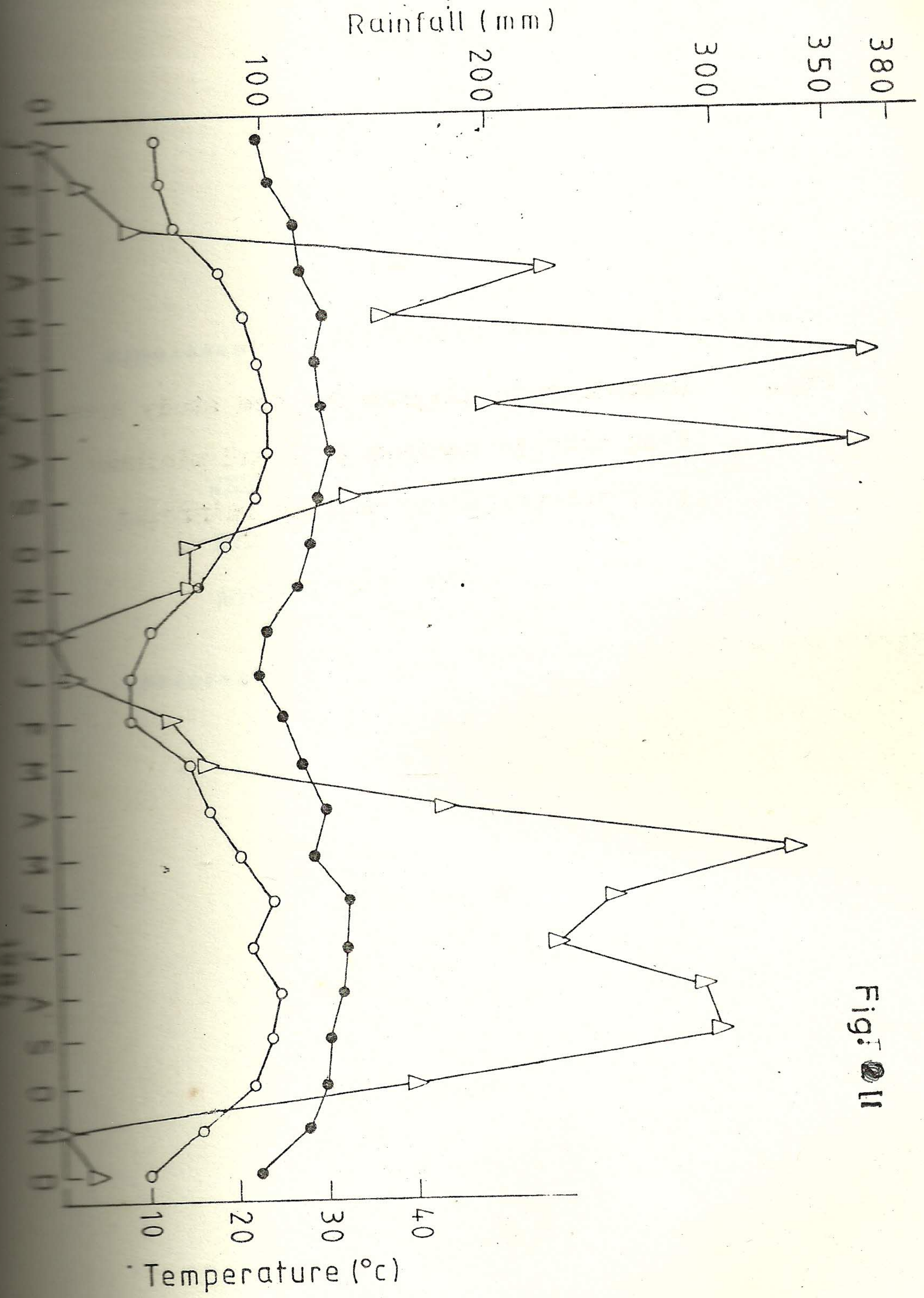
Rainfall (mm)
100
200
300
350
380
0
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
10
20
30
40
Temperature (°c)

Fig. 11