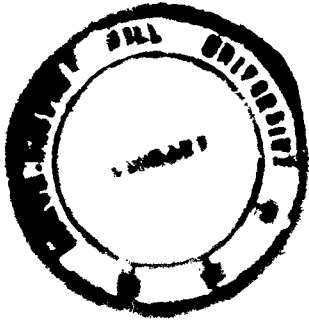


BIOLOGY OF *Imperata cylindrica* (L.) BEAUV.

ABSTRACT



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DEPARTMENT OF BOTANY
SCHOOL OF LIFE SCIENCES

SUBMITTED IN
FULFILMENT OF THE REQUIREMENT OF
THE DEGREE OF

DOCTOR OF PHILOSOPHY

TO

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ABSTRACT

The study deals with the ecology of an important weed of the north-eastern region, namely Imperata cylindrica (L.) Beauv. This species is found in highly disturbed sites. They form early successional species after slash and burn agriculture (locally called jhum), as part of the weed community during the first 5-6 years. Under short jhum cycle of 4-5 years (the length of the intervening fallow phase between two successional croppings), this weed along with others forms part of an arrested succession. Regeneration through extensive underground rhizomes contributes to the vigour and rapid spread of this species. Reproduction through seeds also occur under intense biotic disturbance. The present study deals with its altitudinal adaptation, demography and population dynamics of natural as well as introduced population, resource allocation strategies and possible control measures.

1. Studies on adaptational behaviour of two populations of Imperata cylindrica (L.) Beauv. along an altitudinal gradient.

In the present study reciprocal transplants of two populations of Imperata cylindrica from a low elevation at Burnihat and a high elevation at Shillong was done to study their growth behaviour. The lower elevation population showed vigorous growth when grown in its native site than when transplanted to an alien site at higher elevation. The higher elevation population showed a more vigorous growth at lower elevation site than in its native site. This greater vigour of the two populations at lower elevation is related to more favourable temperature conditions. Allocation pattern for biomass

in the two populations did not show any difference at the two altitudes.

Concentration of nutrients such as nitrogen, phosphorus and potassium was more in the two populations when raised at Shillong compared to that at the lower elevation at Burnihat. Allocation of phosphorus and potassium was more for the below-ground organs in the populations at both sites compared to the allocation of nitrogen. Though accumulation of nitrogen, phosphorus and potassium followed a similar trend with the biomass accumulation in the above-ground and below-ground parts, the phosphorus accumulation in the below-ground organs showed a sharp increase for the Shillong population raised at Shillong compared to that for the Burnihat population.

Nutrient uptake efficiency was more in the two populations raised at Burnihat whereas nutrient use efficiency was higher in the case of phosphorus only in the two populations grown at Shillong. Vegetative effort was similar in the two populations raised at the different altitudes. Poor growth behaviour in the two populations when raised at higher elevation Shillong may be attributed to the low soil nutrient status and environmental conditions such as temperature. The present studies suggest the existence of altitudinal ecotypes within the species, though the two populations show a high degree of phenotypic plasticity.

II. Population dynamics of *Imperata cylindrica* (L.) Beauv. var *major* related to slash and burn agriculture (jhum) in north-eastern India at two different altitudes.

Imperata cylindrica is a noxious weed coming up in early successional fallows after slash and burn agriculture (jhum) which is prevalent in the north-eastern hill regions of India. The

regeneration and establishment patterns through tillers is more vigorous in younger fallows and is drastically curtailed in older ones as evident from mortality/natality patterns and age structure of the tiller populations. The regeneration of the tiller was enhanced in burnt plots as compared to unburnt plots. Differences were observed with respect to recruitment pattern in different cohorts studied. This was related to environmental conditions as well as to increase intra- and/or inter-specific competition. The implication of the results in natural control of this weed under longer slash and burn cycles and arrested succession under shorter cycles has been discussed.

III. Fate of introduced Rhizomes and seeds of Imperata cylindrica (L.) Beauv. after slash and burn agriculture (Jhum) in north-eastern India at two different altitudes.

Establishment of the introduced populations of Imperata cylindrica through seeds and rhizomes was studied in 0, 3, 5 and 10-year old fallows with or without the associated herbaceous vegetation. The establishment of the population through both these decreased drastically with the age of the fallow. While the removal of associated herbaceous vegetation improved establishment only in a 0-year old fallow, absence of such a difference in older fallows is related to the presence of the larger shrubs and trees in the community. Mortality was a continuing risk the introduced populations had often to face rather than it being confined to the early phases of establishment alone. Further, density dependant mortality was evident with higher mortality rate at higher densities of the introduced population. The significance of these results

are discussed from the point of view of weed vigour in jhum fallows.

IV. Growth and resource allocation of *Imperata cylindrica* (L) Beauv. after slash and burn agriculture (jhum) in north-eastern India at two different altitudes.

Growth and resource allocation strategies of *Imperata cylindrica*, an important early successional rhizomatous perennial species, were studied in fallows after slash and burn agriculture at two elevations in Meghalaya. In this species, reproduction is through vegetative sprouts and seeds reproduction is seldom attempted except under stress. The growth of the above-ground parts from the perennating rhizome was rapid in the 0-year old fallow. In 3- and 5-year old fallows, the build up of the under-ground perennating organs was rapid. A greater allocation of biomass to stem component and relatively lesser allocation in older fallows to the leaf component, as compared to the younger fallows may be related with the need of the species to grow taller in older fallows for shade avoidance. The vegetative reproductive allocation increased markedly with the age of the fallow and this may help its success as a weed in the jhum plots during the subsequent slash and burn and cropping. Preferential allocation of nutrients like nitrogen, phosphorus and potassium to the leaf component would help in quicker growth and establishment in the initial phases of fallow regrowth while more allocation of nutrients to the rhizome in a 5-year old fallow would help in its survival through another slash and burn cycle. The decrease in nutrient uptake efficiency of *I. cylindrica* with the age of the fallow may be related to decline in

plant vigour, competition and reduced nutrient availability. The decreased nutrient use efficiency in older fallows may also be a function of reduced vigour of the plants. Since phosphorus is an element absorbed in larger quantities by the herbaceous vegetation, the high phosphorus use efficiency of I. cylindrica may be a conservative mechanism as far as this nutrient is concerned. The growth and allocation strategy of this perennial weed coming after slash and burn agriculture is indicative of its extreme ruderal behaviour.

V. Control of Imperata cylindrica (L.) Beauv.

The study deals with the various aspects of the control of Imperata cylindrica (L.) Beauv. In experiment conducted with pure stands of this weed, glyphosate (0.8 kg ai/ha) in two applications at 6-week interval gave lasting control in terms of top growth and damage to the under-ground parts. Although only a low degree of control was observed through sickling, the dry weight of shoot and soluble sugar and starch declined to a level which can be compared to the most effective herbicide treatment obtained through glyphosate. Application of dalapon (3.0 kg ai/ha) followed by paraquat (0.4 kg ai/ha) for six times at 2-week interval provided only short term control through damage to the aerial parts only without any effect on the under-ground rhizomes. Six rounds of application at interval of 15 days or three applications at 10 days interval followed four more at 20 and 30 days intervals gave better control. A 15 days interval and application at longer intervals than 10 days after three rounds can be more effective. Application of glyphosate in August and September was most effective for controlling this weed which coincides with adequate moisture content in the soil. Further, during the active period of growth this

weed was more susceptible to glyphosate.

The results presented here show that successful control of a rhizomatous perennial like I. cylindrica can be obtained with a herbicide such as glyphosate which is rapidly absorbed and translocated before the compound itself is damaged through metabolic activity, as suggested by Sprankle et al., (1975). Further, a herbicide with foliar application and phloem-translocated at a proper stage of growth of the weed and in the presence of adequate moisture in the soil is effective to get sufficient basipetal translocation to the under-ground organs. Another aspect that comes out of the study is that repeated application of contact herbicide such as paraquat can have only limited control of the aerial mass without killing the under-ground vegetative rhizome.

Biological elimination during secondary succession after 5-6 years of fallow regrowth through a jhum cycle of 10 years or more is perhaps the most effective control measure for this weed.

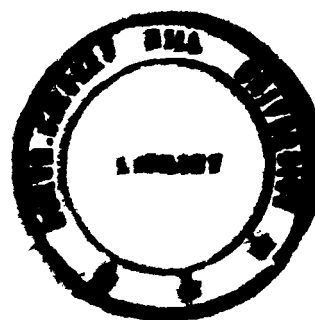
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**S. N. SARMA
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**SUBMITTED IN FULFILMENT OF THE REQUIREMENT OF
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DOCTOR OF PHILOSOPHY**

To



**NORTH-EASTERN HILL UNIVERSITY
SHILLONG, INDIA**

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"Biology of Imperata cylindrica (L.) Beauv."
submitted by Shri S.N. Sharma, M.Sc. for the
degree of Doctor of Philosophy of the North-
Eastern Hill University, Shillong embodies
the record of original investigation carried
out by him under my supervision. He has been
duly registered and the thesis presented is
worthy of being considered for the award of
the Ph.D. degree. This work has not been
submitted for any degree of any other
university.

Date 23 April 1985

Place: Shillong


(P.S. Ramakrishnan)
Supervisor

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S. N. Sharma

S N SHARMA

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PREFACE

The thesis deals with the ecology of an important weed of the north-eastern India, namely Imperata cylindrica (L.) Beauv. This species is found in highly disturbed sites, such as jhum sites which are subjected to repeated slash and burn operations. They also occur elsewhere as a difficult weed to eradicate in tea plantations in upper Assam. Under short jhum cycles, where the slash and burn operations are more frequent with about 4-5 years as is common now in the region, the weed assumes serious proportion with an arrested succession dominated by this species. The vigour of the weed is chiefly due to the extensive mat of under-ground rhizomes with rapid regeneration of aerial shoots.

The present study concerns itself with the altitudinal adaptation of I. cylindrica which grows upto an elevation of 1700 meters in Meghalaya which is the subject matter for discussion in Chapter 2 followed by a General Introduction in Chapter 1. This is followed by a detailed study of the demography and population dynamics of I. cylindrica at two altitudinal situations in fallows developing upto 5 years soon after cropping under the slash and burn agricultural system. These studies form the topic of discussion in Chapter 3. Chapter 4 deals with the fate of introduced populations of I. cylindrica in these fallows, through seeds and rhizomes. In Chapter 5 the resource allocation pattern changes in I. cylindrica during fallow

regrowth is considered as this would determine the regenerative ability of this species. In all these chapters from 3-5, the objective is to assess the biotic regeneration of this weed during the early phase of secondary succession following slash and burn agriculture. Chapter 6 deals with physical and chemical control procedures that could be adopted for checking this weed as this is particularly important under plantation crops where the growth and vigour of this species assumes serious proportions. The last chapter (Chapter 7) is a general discussion summarising the major findings of this work on I. cylindrica and discussing it in the light of existing literature on the species.

The chapters are organised as independant papers, each with its own Introduction, Methods of Study, Results and Discussion. Therefore, some repetition was unavoidable. A summary is given at the end of each chapter. References are placed along with each chapter.

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CHAPTER I
GENERAL INTRODUCTION



Weed biology

Weeds are considered to be troublesome and undesirable component in the world vegetation. According to Baker (1974), "A plant is a weed if in any specified geographical area its populations grow entirely or predominantly in situations markedly disturbed by man". A plant is assigned as a weed not only on the basis of its characteristics but its relative position with reference to other plants and man. The common definitions of a weed are: "a plant out of place" or "a plant with a negative value" or "a plant or a part of plant interfering with the objectives of man" (Muzik, 1970). Even a plant that is useful is a weed when it grows where it is not wanted. Thus all plant species may, at one time or another be classified as weeds.

The concept of a weed did not exist before agriculture. The frequency, intensity and duration of physical environmental disturbances usually necessary for agriculture have increased the importance of weeds to a great extent (Young and Evans, 1976). The intensive system of land management practices by man break-down the natural equilibrium of plant communities and new habitats are continually created which offer fresh opportunities for colonization of unwanted plants and these frequently become serious weeds. Since weeds have unique characteristics for adaptation, they thrive well in any environment, or try to shape themselves in the changed situations.

Weeds often form a serious negative factor in crop production and are responsible for marked losses in crop yield. The weediness of a plant is not an absolute character either possessed or not possessed by plants but exists more likely as a spectrum of characters which exists in varying degree in plants (Hart, 1976).

A large percentage of pernicious weeds are alien i.e. they are not native species, but rather introduced from other countries by man either knowingly or unknowingly. Pritchard (1960) reported on the basis of a comparative study between the native and introduced species of Eupherbia cyperissiens and Hypericum perforatum, that the growth of the introduced ones was more aggressive in American continent than in the native Europe. Eupaterium odoratum, E. adenophorum, Parthenium hysterophorus, Phalaris minor, Avena fatua, Lantana camara, Argemone mexicana, Striga angustifolia are some of the common Indian weeds that are introduced from other countries.

Depending upon their life cycle, weeds can be classified as annuals, biennials or perennials. Ecological studies on the weeds reveal many hidden features of plant life. To study the various stages in the life cycle of a plant from their appearance either through seeds or perennating root stock till death, regular phenological observations are essential (Barsal, 1978).

Some of the weeds are distributed far and wide which are said to have a large ecological amplitude, while there are others which

are restricted in distribution. For the sake of convenience, the weeds could be divided and classified in relation to their dominant association such as: (i) weeds of crop fields, (ii) weeds of fallow land, (iii) aquatic weeds and (iv) parasitic weed.

Non-weed concept

Recently weeds have been viewed as an useful component in agroecosystems and may play an important role in ecosystem management of the future. Studies by Chacon and Gliessman (1982), Saxena and Ramakrishnan (1984), Mishra and Ramakrishnan (1984) suggested that the non-weed concept is an essential ingredient of traditional rotational bush fallow agrosystems in different parts of the world and in north-east India where the practice is locally known as 'Jhum'.

Obviously, one of the important roles of the weeds in the crop land is related to reduction in soil erosion, protection of the soil surface from solar radiation and improved soil micro-climate (Chacon and Gliessman, 1982). Ramakrishnan and his co-workers (Toky and Ramakrishnan, 1981; Mishra and Ramakrishnan, 1983) studied the checking 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 become obvious in a 5-year old weed dominated fallow when compared with the agro-ecosystems types under different jhum cycles (the length of the intervening fallow period between two successive croppings in the same site is a jhum cycle).

Another important positive role of the weed lies in the recycling of the nutrients through organic manure. When the jhum farmer in north-east India does 3 to 4 partial weeding during the cropping season at lower elevation all the weeds removed from the plot are ploughed back into the soil (Swamy and Ramakrishnan, unpublished) which provides nutrients to the crop plants. In a study on the nitrogen budget of three jhum cycles of 15, 10 and 5 years at higher elevation of Meghalaya (Mishra and Ramakrishnan, 1984) the 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.

A variety of weeds are also used as a feed. The plants like Gnetum montanum and G. gnemon are important feeds of the Naga tribe. Leaves of Amaranthus spp., Chenopodium album, Portulaca oleracea, Celosia argentea, Euphorbia caducifolia are used as vegetables. Rhizomes of Typha when pulverized yield a sweet flour. Richhornia crassipes has been recommended as poultry feed.

Weeds have many other general uses. Dry bushes of Capparis decidua, Crotalaria burhia and Imperata eylindrica are used as thatching material. Another grass species Thysalonaema maxima is used for brooms. Hedychium is used for medical purpose.

Apart from these beneficial effects, weeds around crop areas (Van Emden, 1965; Price, 1976) or within the plantings (Attleri et al., 1977; Reet, 1973) can significantly alter the insect

population and the resultant damage on the control of soil pathogen. Gliessman and Garcia (1979) have considered the possibility of controlling one weed by another.

Autecological studies

Studies on ecological life history are important for an understanding of the biological and ecological equipment of the species in relation to environmental factors (Ramakrishnan, 1960a, 1960b). Importance of such life history studies has been stressed by Pelton (1951, 1953), Tansley (1946) and Whitehead (1957). Salisbury (1942) realised the importance of autecological studies for its own sake and also for a better understanding of plant communities and perhaps these ideas led him to put forth a scheme of the "Biological Flora of British Isles".

In India life history studies have been done by a number of workers (Mishra and Siva Rao, 1948; Bakshi, 1952; Pandeya, 1953; Mall, 1956). Ramakrishnan (1960a, 1960b, 1960c, 1961, 1963a, 1963b, 1963c, 1964) made a detailed ecological study of some annual and perennial weeds in and around Varanasi. In Euphorbia hirta, Ramakrishnan (1958) observed two distinct ecotypes: an 'erect type' growing in moist localities, and a 'prostrate type' growing in dry hard soils. The plant is found throughout the year flowering and fruiting freely. The seeds have no dormancy period and germinate under favourable conditions of moisture.

In Echinochloa colona (Ramakrishnan, 1960b) seeds germinate just after first few showers in the beginning of the rainy season,

flowering and fruiting start by middle of August and completes its life cycle by the middle of October. Two ecotypes were observed in this species: (i) the tall form, growing under moist to water-logged conditions and (ii) the short form growing in comparatively drier localities. The plant is typically a calcifuge growing best in calcium poor soils.

In Eclipta alba (Ramakrishnan, 1960c) the seeds can withstand a high degree of water-logged condition and germinate best under diffused light. The seed output was low in non-calcareous soils and increased with the increase in calcium in the soil.

In Euphorbia thymifolia (Ramakrishnan, 1961) two ecotypes were recognised: (i) the 'red form' and (ii) the 'green form'. The former was a facultative calcicole occurring in both calcareous and non-calcareous soils and the latter restricted only to non-calcareous soils.

In Setaria glauca Ramakrishnan (1958) distinguished three distinct ecotype populations: (i) 'the long paniced form', growing in moist to very moist soils, (ii) 'the short paniced form', growing on loose dry sandy lean soils and (iii) 'the intermediate form', growing on the top of old mud and brick walls.

Plasticity versus ecotypes

In recent years a great deal of interest centres around the adaptability of individuals to varying environmental influences. Two distinct viewpoints have emerged: (i) that the population may be a stable unit implying thereby the existence of distinct

populations evolved to suit distinct environmental situations, the ecotypes and (ii) that the individual genotype assumes different characteristics showing both morphological or physiological manifestations. These unstable forms which are due to the plasticity of the same genotype are variously termed as 'ecads' or 'ecophenes' (Ramakrishnan, 1972).

The significance of phenotypic plasticity in plant species has been extensively dealt by Bradshaw (1965). The growth behaviour of weeds over a wide geographical, latitudinal or altitudinal range is controlled by the climate of the area, microclimate and edaphic characters. Adaptation to varied climatic and edaphic factors of the environment is one of the most important factors lying behind the success of a weed species. The ecological importance of phenotypic plasticity is that it tends to make an individual adaptable to more than one habitat.

The genetical adaptability results in the evolution of distinct stable populations to suit distinct environmental situations. Turesson (1922) suggested that the main advantage of adaptation by permanent genetic changes appears to be that under such a system the individual may already be in the appropriate state before the critical environmental changes occur. Myers and Bernmann (1963) observed phenotypic variation in Abies balsamea in response to altitudinal and geographical gradients. Wu and Jain (1978) studied the genetic and plastic responses in Bromus rubens in natural population and stated that the phenotypic plasticity is an important property for the adaptability of this

species under a range of environmental conditions. He further showed that 12-27% of the total geographic variations was contributed by genetic variation whereas 73-85% was non-genetic. Figier et al. (1977) working with nine natural populations of Hedysarium coronarium found phenotypic variability and grouped these populations in five morphologically defined sets depending on different genetic pool and thus demonstrated the existence of both genetic and phenotypic plasticity. Bradshaw (1959,1960) studied the population differentiation in Agrostis tenuis and found that population originating from contrasting habitats differed considerably in their ability to tolerate different extreme conditions. He showed that the growth of lowland population in the upland plot was seriously affected by winter conditions and the growth of upland populations in the coastal plot was affected by salt storm spray, suggesting that environment is the dominant factor in determining population differentiation. Bradshaw (1959) further noted that the concept of variation within a species being limited to major differences of the nature of ecotypes cannot therefore be held in A. tenuis. The environment by its selective pressure imposes its own pattern on the differentiation of the species which often may be physiological in nature.

Climatic ecotypes

Turesson (1922,1925) was the first to demonstrate from his comparative studies on plant population, that the observable differences in the field tend to be maintained as such, thus showing the existence of climatic races or climatic ecotypes. He

further showed that the differences between ecotypes are genetically determined and they are the products of the selective action of the differential environmental factors. Later Clausen et al. (1940,1948) in America has shown the existence of chains of climatic races in a number of perennial species ranging from sea level to above timber line in California and has recognised atleast eleven climatic ecotype in Achillea along a 200 mile transect across California. They showed marked differences in the physiological features of these ecotypes like the pattern of dormancy of the buds, flowering and fruiting and resistance to cold. Gregor (1930,1946) working with sea plantain, Plantago maritima came to the conclusion that whilst certain ecotypes may be characterised by variational discontinuity, often variation tends to be continuous along a clear ecological gradient to denote which he coined 'ecoline'.

Cooper (1964) found climatic variations in forage grasses in mediterranean and temperate regions and showed that local varieties of forage grasses are closely adapted in their life cycles to local limiting climatic factors and that it is based on physiological features such as temperature and day length requirements for flowering and leaf and tiller development. Eagles (1971) and Ostgard and Eagles (1971) have recognised climatic races in Norwegian and Portugese populations of Dactylis glomerata depending upon their photoperiodic and temperature requirements. Cooper and McWilliam (1966) examined the effect of variation in climatic factors in Mediterranean populations of Phalaris tuberosa and

observed temperature induced differences between populations with regard to germination of seeds, floral induction, rate of leaf expansion etc. Similar work is also available for a number of north American prairie grass species (McMillan, 1964, 1965). Grant and Hunter (1962) working with Calluna vulgaris reported that variation in growth habit and growth forms change with the change in altitude. They also reported that the maturity type is related to the length of the growing season, populations originating from areas having shorter growing season are composed of individuals of early maturity type than from those areas where growing season is longer. Grant (1971) further reported that the floral development in a number of perennial grasses were delayed with increase in altitude due to the change in temperature conditions.

Bjorkman and Holmgren (1963) compared the response of photosynthetic apparatus to different light intensities during the growth of the populations of Solidago virguarea from exposed to shaded habitats. They found an inhibition of photosynthetic activity by strong light in case of populations from shaded habitats when grown in strong light, the plastids were poor in chlorophyll, irregular and partly fragmented. Differences in Hill activity in three different altitudinally diverse populations of Taraxacum officinale have been reported by May (1975, 1976). Slatyer and Ferrer (1977) reported variation in the temperature optima for photosynthesis in the altitudinal populations of Eucalyptus pauciflora.

Work on climatic races in Indian plant species is unfortunately very meager. Kaul (1965) recognised four seasonal populations in

Xanthium strumarium which differed in morphological feature like leaf, fruit shape and growth habit and in physiological features like light and temperature requirements. Kaul (1966) recognised the existence of two chromosomal races in Ageratum conyzoides. Seasonal ecotypes have also been recognised in Chenopodium album (Ramakrishnan and Kapoor, 1974) who suggested temperature and photoperiod interaction at various stages of growth of the summer and winter populations within this species.

Edaphic Ecotypes

Edaphic ecotypes are the genetically determined physiological types each adapted to a limited range of soil conditions. Kruckeberg (1954) was one of the first to have demonstrated the existence of edaphic races differentiated as a response to difference in calcium occurring on and off serpentine and non-serpentine soils. Ramakrishnan (1972) has reviewed the work on edaphic ecotypes under three headings: (i) physical characteristics of the soil, (ii) macro-nutrients in the soil and (iii) micro-nutrients in the soil.

Soil physical factors have often been recognised as a basis for ecotypic differentiation. Ramakrishnan (1958) recognised two ecotypes in Euphorbia hirta, an erect type and a prostrate type, the former growing in moderately moist localities and the latter on dry hard soil exposed to trampling. Similarly in Echinochloa colona Ramakrishnan (1960a) observed two ecotypes (i) a tall form growing in very moist to waterlogged soils and (ii) short form

growing in drier localities. In Setaria glauca (Ramakrishnan, 1963) three ecotypes were observed in response to soil moisture and texture. McKell et al. (1960) recognised two distinct races of Dactylis glomerata based on their adaptability to soil moisture stress. McCown et al. (1977) showed that the pattern of perennial grass distribution was primarily determined by variation in soil permeability. Heins and Walkers (1979) demonstrated the effect of soil temperature and photoperiod resulting in the variation in growth of Alistroemeria regina.

Calcium in the soil has been recognised to be an important chemical factor affecting the restriction of various species to their respective soil types. Thus calcicoles are generally defined as those plants which naturally occur in calcareous substrata and do not grow in acidic soils, while calcifuges are those which inhabit exclusively non-calcareous and acidic soils (De Silva, 1934). Ramakrishnan (1961) recognised two ecotypes in Euphorbia thymifolia, the red form and the green form as a direct response to soil calcium status. The former had a wide range of tolerance for calcium while the latter was an obligate calcifuge. Similar studies have been extended to Cynodon dactylon (Ramakrishnan and Singh, 1966), Tridax procumbens (Ramakrishnan and Jain, 1965) and Adhatoda vasica (Ramakrishnan and Bisht, 1966). Existence of ecotypes in relation to soil calcium has been observed by other workers in species like Festuca ovina (Snyden and Bradshaw, 1961), Trifolium repens (Snyden and Bradshaw, 1962) Agrostis tenuis (Bradshaw, 1959; Jowett, 1964).



Ramakrishnan (1968a) while working on calcareous and acidic populations of Melilotus alba has shown a significant interaction between pH and calcium influencing the behaviour of contrasting populations. One of the first reports of ecotypic difference in relation to soil phosphorus was that by Snyder and Bradshaw (1962) in the natural populations of Trifolium repens. The results not only showed a differential response to phosphorus by these ecotypes but also differences in the content of other elements like iron, sodium, potassium and calcium. Milton (1940) from his manurial experiments on Agrostis and Festuca grasslands showed significant increase in the relative abundance of Agrostis tenuis in relation to Festuca ovina with addition of phosphate.

Very little is known about the response to nitrogen and potassium within a given species. Ramakrishnan and Gupta (1972) observed in case of Cynodon dactylon that calcareous ecotype within the species gave better yield at low nitrogen level and reverse was shown for the non-calcareous one. Differences between natural populations in response to potassium has been reported by Snyder and Bradshaw (1962) within the populations of Trifolium repens. Such a differential response to potassium was also reported by Ramakrishnan and Gupta (1972).

Not much is known about adaptation at the sub-specific level over a short time period in an area. The work on Chenopodium album (Kapeer and Ramakrishnan, 1973; Ramakrishnan and Kapeer, 1974) is one of the few such studies regarding populations from the same area which are adapted to different seasonal differences in light

and temperature. A number of adaptive differences were observed between the two populations which ensure their distribution in time.

With the realisation of the fact that the selection pressure could result in population differentiation, it is reasonable to assume that continued biotic pressure would lead to differentially adapted genotypes. The concept of biotic races was recognised by Stapledon (1928) when he distinguished a number of ecotypes in Dactylis glomerata. Ramakrishnan (1958) in Euphorbia hirta, Gadgil and Solbrig (1972) in dandelions and Abrahamson and Gadgil (1973) in the case of golden rods showed differences in populations from disturbed sites and from more mesic undisturbed sites.

Demography and population dynamics

The population of a species colonizing a habitat passes through different growth phases with the passage of time. Initially, the population grows exponentially till the resources become limiting. Later on, if the birth and death rates become equal, the population size gets stabilized showing fluctuations around a mean value. The growth of the species populations, however brings about certain changes in the environment as well. The modified environment may prove to be unsuitable for the early colonizers where the population may disappear due to increased mortality. How long the species will continue to grow on a given habitat, of course depends on its capacity to adjust itself with the changing environmental conditions. The changes in the environment may, however, be reflected in the

fluctuations in population size. The study of these fluctuations in population size is referred to as population dynamics, a term for the first time proposed by Elton (1933). According to him, population dynamics concerns with the rate of increase, decrease and the influence of the environmental factors on the size of the populations.

While extensive studies have been done on the population dynamics of animal population little attention has been given to the study of plant populations (Harper, 1961). The main causes which have hindered the study of plant populations are the plasticity and vegetative reproduction (Harper, 1961,1967). However, in the last two decades, the population dynamics of plants has received impetus, inspite of the difficulties in handling plants.

The behaviour of a population is dominated by birth, death and migration of populations. The rate of population growth is generally expressed as the increase in the number of individuals per unit time. Lotka (1931) and Volterra (1931) proposed separately different theoretical equations for calculating the population growth rate which were experimentally confirmed by Gause (1934). Gause put forward the famous 'Gause hypothesis' which suggests that two species having identical ecological niches cannot survive together for long time. This was supported by Frank (1957) Tantaway and Soliman (1967). However, Koch (1974) for the first time suggested that two species can co-exist on one biotic resource which was also confirmed and supported by McGhee and Armstrong (1977) and Armstrong and McGhee (1980).

Verhulst (1938) proposed the first logistic mathematical expression of continuous population growth which was later elaborated by Pearl and Reed (1920) in the following equation:

$$\frac{dN}{dt} = rN \left(\frac{K-N}{K} \right)$$

where N is the number of individuals, t the time, r intrinsic rate of population growth, K carrying capacity and $\frac{dN}{dt}$ represents the rate of change in population size. Harper and White (1974) put forward an equation for the study of population dynamics in plants as: $N_{t+1} = N_t + \text{Birth} - \text{Death} + \text{Immigrant} - \text{Emigrant}$ where N_t = number of individuals of population at time 't' and N_{t+1} = number of individuals at time 't + 1'.

The plant populations consist of two levels of population organization as suggested by Harper and White (1974). One, the number of individuals per unit area (colonies) and the other, the number of shoots or leaves or axillary buds per plant. The early seedling phase of a plant's life is generally considered the most risky and this risk is exaggerated due to increasing density of the same or another species. 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: (a) a reduction in seed output or lowered rate of vegetative reproduction and (b) a reduction in the chance

of individual survival (Harper and Gajic, 1961; Ramakrishnan and Kumar, 1971a,b). Just as in a population of single species density stress intensifies the expression of small differences (genetic and environmental) between individuals, so in mixed populations density stress may exaggerate and exploit inter-specific differences. The experimental model of de Wit (1960) are superbly designed to study the behaviour of two species in mixture. In this model the two species are grown together at varied proportions while the 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 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 Clatworthy, 1963).

The population 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 (Marshall 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.

Study on population dynamics of perennial plants has received little attention. Sarukhan and Harper (1973) made a detailed study of demography of three species of Ranunculus in a grassland situation which was analysed mathematically by Sarukhan and Gadgill (1974). Mack (1976) studied the survivorship of Cerastrium atrovirens Howthorn and Cavers (1976) studied the demography of perennial herb Plantago major and P. rugelli.

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-year 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 fallow, where the plant cover was sparse, had maximum recruitment. Working on population dynamics of Eupatorium odoratum Kushwaha et al. (1981) observed that mortality patterns of individuals in 1,3,5,10 and 20-year old fallows increased with the age of the fallow and reported no recruitment 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 elevation 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 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 died in winter as a result of drought and frost.

Population dynamics of rhizomatous plants is difficult because the connection between parts of a single genet is usually hidden below ground. For most clonal plants in which there are no genetic markers, population dynamics can be followed only for shoot modules (Harper, 1978). A growing plant gains new modules (birth) and loses old ones (death) and the size of the plants is determined by a balance between the births and deaths of its parts (Harper and White, 1974; Kays and Harper, 1974; Harper, 1977). A population of plants that maintains a constant density of shoots, may do this by a very rapid turn-over or no turn-over at all.

Such a flux can be measured by mapping or marking modules, preferably at birth and repeatedly recording the fates of the marked modules. The dynamics of shoots has been studied in populations of Carex arenaria by Noble (1976). The life histories of tiller modules have been studied on spaced populations of several agricultural important grasses such as Bromus inermis (Lamp, 1952), Phelum pratense (Langer, 1956), Festuca pratensis (Langer et al., 1964) and F. arundinaceae (Robson, 1968).

Callaghan (1976) suggested that the growth, reproduction and death of individuals in a plant population are affected by environmental factors within the frame-work of their genetic programme. The environmental factors may be biotic, such as grazing, predation and competition for the limited resources and abiotic such as cold,

heavy precipitation, frost, storm etc. which destroy the populations catastrophically (Warner Wilson, 1967).

✓ A considerable amount of literature has been accumulated on the mortality rates of plant populations over the last 15 years. Deevey (1947) on the basis of work with different populations concluded that in general the individuals follow three types of death and decay patterns. Heavy 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. The seedling mortality due to drought has been reported by Tazaki (1960), Peterson (1966), Cavers and Harper (1967), Friedman and Orsham (1975), Marquis (1976) and many other workers. This type of mortality represents Deevey type I survivorship curve. In contrast to the seedling population, the established plant populations show constant risk of death throughout their life span following Deevey type II survivorship curve (Tamm, 1956; Rabotnov, 1958; Sagar, 1959; Foster, 1964; Antonovics, 1972). The individual with long life span generally show a third category of survivorship Deevey type III with higher mortality in the last part of their life.

✓ 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 mortality is a continuing risk that the population has to put up with throughout its life cycle. However in Danthonia 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 Trichache californica, Bouteloua hirsuta and B. chondrosioides.

Harper and White (1974) reviewed the literature on longevity of various plant species. The determination of the exact age of the perennial species is difficult as no possible technique for estimating the age has been found out. Various techniques used to determine the age are based on anatomical and morphological features. Pigott (1955) found that the age of Cirsium acaulon can be accurately estimated by counting the number of leaf scars on the rhizome.

The most reliable method for estimating the age of perennial species is to follow the fate of the labelled seedlings or tillers of known age in permanent quadrats. This method has been successfully used by Tamm (1956, 1972a, 1972b). In Anthoxanthum odoratum, Antenovics (1972) observed that the 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 categorisation of individuals into various groups representing different age classes in a population. Age structure of a species may largely determine

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its survivorship. Williams (1970) and Antonovics (1972) observed differential decay rate 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).

Harper and White (1974) while studying the age structure of the population of a perennial species suggested that the seedling population may or may not be considered depending upon the observation period of the year as the seedlings tend to show 100% mortality in perennial grasses (Putwain et al., 1968). Richards (1952), Emlon (1972) and Schaal (1978) suggested that the unstable age structure of plant species observed may be due to large environmental fluctuations that may occur during critical periods in plants life. According to Rabotnov (1945, 1950a, 1950b, 1969) coeno population is characterised by various age groups of individuals based on the four main periods: (i) the period of primary dormancy, (ii) the virginal period, (iii) the generative period and (iv) the senile period.

Fire, which occurs frequently in some plant communities plays an important role in the regulation of the 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 Main, 1979). Toky and Ramakrishnan (1983), Saxena and Ramakrishnan (1984) also observed stimulatory effect of fire in the early phase of some secondary successional communities after slash and burn agriculture (jhum) in north-eastern India.

Fate of introduced populations has been studied by a number of workers (Chippindale, 1948; Tamm, 1950; Cavers and Harper, 1967; Putwain and Harper, 1970). These workers further showed that introduced rhizome survive better than the introduced seed. Various workers (Ellenburg, 1953, 1956; Odum and Odum, 1959; Harper, 1949a; Cavers and Harper, 1967; Putwain and Harper, 1970; Ramakrishnan and Jeet, 1972; Ramakrishnan, 1973) have shown that the distribution and abundance of a species is profoundly influenced by the associated vegetation in the community. Poor seedling establishment has been reported in established communities by Tamm (1956) and Cavers and Harper (1967). Putwain and Harper (1970) and Dwivedi and Tripathi (1980) found that amongst the associated species, grasses exercise the greater regulatory influence compared to dicots. Sagar (1970) noticed increased vegetative and reproductive growth of Plantago lanceolata when the associated vegetation was removed. Similar results was obtained by Kapoor and Ramakrishnan (1974) in the case of Echinochloa colonum. Established plant populations also affect the survival and growth of the newly recruited individual (Friedman, 1971; Andel and Rozema, 1974; Gupta and Tripathi, 1979; Yadav and Tripathi, 1981).

In some studies of plant population dynamics, different plant parts were considered as members of the population. Thus, Saeki (1960) in Phaseolus virissimus and Nicotiana tabacum and Gill and Tomilson (1971) in Rhizophora mangle studied the dynamics of leaf production. Bazzaz and Harper (1977) also studied the effect of light intensity and density of branching pattern and leaf dynamics in Linum usitatissimum. Gill (1971) observed the dynamics of bud production in Frazinus americana. Recently, detailed demography and population dynamics analysis of leaves on a tree has been done extensively by Ramakrishnan and his co-workers (Bhoj and Ramakrishnan, 1982; Ramakrishnan and Shukla, 1984) considering the leaves on the tree as a meta-population. These studies have been done considering the niche differences and occupation of early versus late successional trees. The studies show that the birth or death rates and the consequent turn-over of leaves is faster on the early successional trees compared to the late successional ones. The early successional trees, therefore, show a larger leaf population of the younger age groups compared to the late successional species. On the basis of this study the faster growth rate and the higher photosynthetic efficiency of the early successional tree species has been assessed.

Allocation pattern and reproductive strategy ✓

Recently much interest has centred on the ways in which organisms allocate their limited supply of energy and materials

to diverse life functions (Hickman, 1975). The concept that organisms have certain limited energy available to expend for different life purposes was put forward by Cody (1966). Considering clutch size in birds, he argued that the way in which an organism allocates its energy to such ends as reproduction, competition and predator avoidance is a characteristic of ecological and evolutionary importance. He used the term "Principle of allocation" to express this concept.

McArthur and Wilson (1967) pointed out that organisms in an open environment are selected for greater reproductive potential (r-selection) whereas organisms in a closed environment are selected for greater competitive ability (k-selection). Gadgil and Solbrig (1972) expanded the concept of r- and k- selection in plants and tried to formulate them more rigorously. They emphasized the r-strategy by invoking patterns of mortality rather than the "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; Wilbar et al., 1974).

Abrahamson and Gadgil (1973) suggested that the reproductive effort should decrease under shaded condition as more emphasis is given for vegetative growth for survival of the plants here. Similar pattern of resource allocation has been shown by a number of workers (Abrahamson and Gadgil, 1973; Gaines et al., 1974; Rose and Quinn, 1977).

Harper and Ogden (1970) described for the first time partitioning of dry matter and energy throughout the life cycle of different plant species. They made an experimental application of the theory "principle of allocation" to the life cycle of Senecio vulgaris grown under different stress conditions and pointed out that the proportion of allocation of biomass may reflect the pattern of energy allocation provided there is a strong correlation between total biomass and total calories. This was later supported by a number of workers (Abrahamson and Gadgil, 1973; Snell and Burch, 1975; Hickman and Pitelka, 1977). Harper and Ogden (1970) also suggested certain major patterns of energy allocations in annual, biennial and perennial plants quantitatively. 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 by reducing reproductive budget (Harper and Ogden, 1970; Hickman, 1975; Peterson and Bazzaz, 1978; Bell et al., 1979). Clark and Burk (1980) showed the adaptive significance of such a strategy in the two annuals Camissonia beethi and Plantago insularis. The former had a longer life cycle and it tended to maintain higher levels of non-structural carbohydrates for vegetative growth whereas the latter started its reproductive growth early and allocated higher proportion to reproductive growth by reducing the allocation to vegetative organs.

Saxena and Ramakrishnan (1982) studied the reproductive efficiency in three categories of secondary successional herbaceous

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communities such as early successional non-sprouting, early successional sprouting and late successional populations in shifting agriculture (jhum) and found that early successional non-sprouting populations were reproductively (sexual) more efficient whereas early successional sprouting populations allocated more to vegetatively reproducing organs. On the other hand early successional sprouting populations showed an inverse relationship between vegetative and sexual reproductive effort. The strategy of late successional species seems to be to maximise vegetative growth in a closed habitat.

A difference in allocation strategy in perennials with different growth habit have been demonstrated by a number of workers (Turkinton and Cavers, 1978; Howthorn and Cavers, 1978; Pitelka, 1977). An important feature of the reproductive strategy of perennials depend upon the nature of sexual and vegetative reproduction. It has been shown that sexual reproductive allocation remains generally fixed towards different environmental stresses, whereas vegetative reproductive allocation shows plasticity towards different environmental conditions (Ogden, 1974; Thomas, 1974; Abrahamson, 1975a,b). Ogden (1974) working with rhizomatous plant Tussilago farfara indicated that most of the energy required in flowering process came from the reserves stored in the rhizomes. Saxena and Ramakrishnan (1983) working with resource allocation in perennial rhizomatous species I. cylindrica found more biomass allocation to the underground rhizomes with the growth of the plant. Mooney and Billings (1960)

and Kimura (1970) found a strategy of early spring flowering powered by stored reserves in rhizomes in alpine and sub-alpine species.

The importance of stress and disturbed condition in the allocation of biomass was considered by Grime (1974). He defined 'stress' as any factor limiting plant growth like shortage of light, water and nutrients and 'disturbance' as any factor responsible for the loss of biomass like herbivory, pathogenicity and human activities. Thus Grime (1974, 1979) recognised stress tolerance as a strategy of plants under unproductive environment.

A critical review of the methods for estimating reproductive efforts in plants have been given by Kawano and Nagai (1975). The most widely adopted method is that of Harper and Ogden (1970) where the ratio of reproductive growth to total biomass is considered as reproductive effort. While such an approach has yielded valuable information, little effort has been made in order to relate reproductive growth strategy with leaf growth (Bazzaz and Harper, 1977; Primack, 1977). This approach should have received more attention particularly in view of the fact that leaf as an organ is the chief region of photosynthetic activity. McNaughton (1975) showed a negative correlation between vegetative reproductive growth and foliage growth in the population of Typha latifolia from different climatic regions.

Saxena and Ramakrishnan (1982) working with early successional and late successional plant species in slash and burn agricultural system found that late successional species had high leaf area

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ratio compared to early successional species as the adaptation in the former is to synthesise and maintain the maximum light intersection surface due to a low light regime habitat, whereas the latter occupying a productive and open environment divert their resource to other life purposes as growth and reproduction. They further showed a negative correlation of leaf area ratio with the reproductive effort in an early successional non-sprouting species and positive correlation of leaf area ratio with that of reproductive effort in early successional sprouting species which indicates that reproductive success depends upon the productive efficiency in the former and vigour of the over all plant in the latter. Keeley and Keeley (1977) showed that non-sprouting chaparral shrubs Arctostaphylos glauca have higher reproductive allocation compared to the sprouting species Arctostaphylos glandulosa. They could not show differences between the two regenerative strategies and suggested that reproductive cost here is small and may be averaged over a long period of time.

While considerable work has been done on the allocation of biomass/energy to the different life processes, 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 (Harper and Ogden, 1970). Van-Andel and Vera (1977) working with annual plant Senecio sylvaticus and perennial plant Chamaenerion angustifolium observed that in annual species reproductive allocation of biomass was independent of the nutrient level. He also found more allocation

of nutrients to the reproductive structures in annual species whereas in perennials allocation to the vegetative organs was more in the latter part of the plant's life.

Saxena and Ramakrishnan (1983) studied the growth, allocation pattern and nutritional status of some dominant annual weeds such as Borreria articularies, Cassia tora, Ageratum conyzoides and Erigeron linifolius in shifting agriculture (jhum) in north eastern India and observed differences in the allocations of biomass and nutrients. In all species, reproductive allocation of nitrogen and phosphorus was higher than that of biomass and potassium. They further showed that allocation of biomass and nutrients to leaves decreased during growth in all the species and this was more pronounced at the time of reproduction.

Saxena and Ramakrishnan (1983) also studied the growth and allocation patterns of dry matter and nutrients (nitrogen, phosphorus and potassium) in four important perennial weed species such as Eupatorium odoratum, Grewia elastica, Imperata cylindrica and Thysanolaena maxima. They found that among the four species E. odoratum exhibited a greater allocation of its biomass as well as nutrients to stem component as compared to the other three species which can 'sprout' after fire. The two rhizomatous species (I. cylindrica and T. maxima) diverted greater proportion of dry matter as well as nutrients to below ground tissue compared with the two non-rhizomatous species (E. odoratum and G. elastica). They further showed that the two C_4 plants I. cylindrica and T. maxima had higher nutrient uptake efficiency inspite of their low nutrient demand per unit dry matter production.

Weed control

The practice of weed control is as old as the origin of agriculture itself. Since they often compete with the crop for water and nutrients and sometimes even for light energy, keeping them in check is important. Weed control methods may be physical, biological or chemical (David and Sen, 1981).

Different physical methods of weed control include (a) soil cultivation, (b) mowing, (c) flooding, (d) burning and (e) mulching. Cultivation of the soil, combined with hand removal, was the only effective method of weed control in the earliest period of agriculture (King, 1974). Tillage is effective on most annual weeds which involves lifting of weeds from the soil, cut-out and burial of all growing points. Often the land has to be cultivated in preparations for seeding and this provides some measures of the weed control at the same time. For perennial weeds repeated cut-off or burial is needed until the underground parts are killed by carbohydrate starvation. In India Hosmani and Setty (1972) noted that emergence of both monocot and dicot weeds was significantly reduced by repeated harrowing. Dauley (1977) observed maximum number of species (8-9) under no tillage and practically no weed under deep ploughing treatment.

Mowing is a reasonably effective way of controlling different weeds. It is useful for certain annual weeds, enough to prevent flowering and seeding. This practice is relatively ineffective on perennial weeds. However, repeated mowing not only

prevents seed production of perennial weeds, but also may starve underground parts (Klingman, 1973). Some common weeds of lawns like Euphorbia thymifolia, Phyla nodiflora, Cyperus rotundus can be effectively kept low by mowing. The best time to start mowing is usually when the underground root reserves are at a low ebb and should be timed with the stage of maturity in order to remove the flowers before they mature into seeds (David and Sen, 1981).

Flooding by water is an age old technique for weed control (Arai and Miyahara, 1956). This method is used in weed control in paddy fields and in other crop lands as well. The flooding checks the weed growth and proves fatal by denying oxygen to the roots and leaves, thereby preventing the life processes. Hosmani and Setty (1972) observed that weeds are effectively controlled in paddy by submergence of field to a depth of 5 cm. Robbins et al. (1956) has reported the control of some obnoxious weeds such as Centaurea repens, Convolvulus arvensis and Solanum carolinense by this method.

The use of fire is another age-old method of removing undesirable vegetation (King, 1974). Humphrey (1949) reported the control of Prosopis velutina, Aplopappus tenuisecus and Opuntia fulgida using fire. The control of weeds by fire is due to coagulation of protoplasm in the cell. The plant cell can resist the temperature upto 45-55°C; weeds can tolerate beyond this in certain species. Sen and Chatterji (1965) reported that seeds of Calopterus procera could stand a dry heat of 90°C for three

hours without affecting its germination. Knake et al. (1965) noted that fire may be used for selective weed control in onion, cotton and corn, which are cultivated in rows. Sen (1978) reported a decreased growth and yield of crop plants due to burning at different weeds.

Mulching checks the weed growth by preventing photosynthesis, which results in the killing of weeds (David and Sen, 1981). The materials used for mulching includes dry straw, hay, manure, rice hulls, twigs etc. Agricultural plastic is a relatively recent innovation and appears to have many desirable characteristics. Swarbrick and Dominiak (1973) recommended that standard polythene film of normal thickness (0.20 mm) is sufficient to prevent the penetration of different grass roots.

In biological control of weeds, several insects, plant pathogens, fungi, parasites and animals are involved. Perkins and Swezey (1924) were the first to report biological control of Lantana camara by an introduced insect. The most outstanding example of the control of a weed pest through the agency of insect is the destruction of Australian prickly pear cacti, Opuntia inermis and O. stricta by a moth borer Cactoblastic cactorum. An outstanding success was also achieved in biological control of Opuntia vulgaris by the introduction of mealy bug, Dactylopius ceylonicus. In India, biological control of Lantana camara has been reported by using the insect Teleonemia scrupulosa in Hyderabad (Verma and Sadatulla, 1973), and Salvina by using a bug Paulmia accuminata (Anon, 1976). Control of Cyperus rotundus

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by stem boring weevil (Athesapeuta cyperi) has been reported by Frick et al. (1978). The importance of biological control lies in that it could be most effective without any environmental problems provided it is planned judiciously.

Carpenter (1944) reported the control of Opuntia spp. by Fungus Fusarium after the discovery of twelve fungal diseases in this species by Wolf (1912). Control of weed Rubus fruticosus through a rust Kuesneola albida to a great extent was noted by Wager (1947). Rudakov (1960) reported the control of Cuscuta by two fungi namely Alternaria and Cladosporium. There are a few characteristics of plant pathogens which make them desirable agents for biological control. Because of their large number and diversity, the probability of finding a plant pathogen with the prerequisites are greatly improved. They are often host specific and their use to control obnoxious species would not endanger desirable plant species. They are easily disseminated and once established are self maintaining.

Different animals have long been known as biological agents in the control of different weeds by grazing. The chief grazing animals include cattle, sheep, goats, camels etc which may have selective grazing on weeds. Stahler and Carlson (1947) reported that sheep grazing reduced the stand of Convolvulus arvensis in the fields. Judd (1889) reported that birds can also be considered as biological means of weed control by eating the weed fruits or seeds, thereby destroying the next generation.

Chemical control

Chemical methods of weed control began in the early part of nineteenth century when Bonner (1896) in France showed that a solution of copper sulphate would kill charlock plants which were growing with cereals. Rabate (1934) demonstrated that dilute sulphuric acid could also be used for this purpose. Bolly (1908) was also an early experimenter with different herbicides and described the action of this group of chemicals as caustic or burning and having no translocation. This group of chemicals are called contact herbicides that kill all growth regardless of the species of plants. These include such materials as petroleum oils, dinitrophenols and solutions of such salts as sodium arsenite, sodium chlorate, ammonium thiocyanate, ammonium sulfamate, dinitro compounds, diquat and paraquat.

With the introduction of the plant hormone era in plant physiology in the late 1920's and early 1930's and with the chemical identity of the first active substance of this nature in plants established as 3-indoleacetic acid by Kogl et al. (1934), the stage was set for spectacular advances in both the theoretical and applied fields. Zimmerman and Hitchcock (1942) published their work with the substituted phenoxy acid of which 2,4-D is one. They were first to demonstrate the physiological activities of this group of compounds.

Herbicides are classified on the basis of their mode of action into different types (Woodford, 1957; Kasasian, 1960; Brian, 1964).

Contact herbicides are those which result in burning of the tissue and is primarily effective at a high concentration. Oils, sulphuric acid, iron sulphate, copper sulphate and dinitro compounds, paraquat are examples. Templeman and Sexton (1946) demonstrated the herbicidal action of phenyl carbamates which interfere with the process of cell division at some stages. Trichloroacetic acid and chloral derivatives (Barrons, 1949) are also believed to be cell toxins. One of the newer herbicides within this group, dalapon (2,2-dichloropropionic acid) is a highly effective grass toxicant and freely transported in phloem and Xylem and can be applied to either soil or foliage. Woodford (1957) reported that trichloroacetic acid is known to react with the growth of root and shoot segments more possibly with the natural auxins of plants. Redemann and Meikle (1955) have suggested that dalapon might act as an anti-metabolite to pyruvic acid and enzyme systems involving pyruvate as a substrate are inhibited by dalapon.

Auxin type growth regulating chemicals encompasses all herbicides that increase cell elongation in shoot tissue and have physiological action resembling that of 3-indolacetic acid (Woodford, 1958). Substituted phenoxy-acetic acids namely 2,4-D (2,4-Dichlorophenoxyacetic acid) and 2,4,5-T(2,4,5-Trichloroacetic acid) as well as derivatives of MCPA (2-Methyl-4-Chlorophenoxy-acetic acid) are widely used organic herbicides of this group. Woodford (1957) described the mode of action of 2,4-D and its related compound as abnormal cell division, malformed leaves and stems, wide spread derangement of metabolic and physical processes

and death. This group of herbicides are systemic, causing death by downward translocation from leaf to root as well as selective, when applied to a mixed population of plants will injure or kill certain species with little or no injury to others. In recent times, glyphosate (N-phosphomethyl-glycine) has been found to be a most effective translocated herbicide against both broadleaved weeds and grasses (Crafts, 1975).

A number of compounds have been reported from time to time that suppress the development of chlorophyll in plants. They include sulphanilamide, some tetrone acid derivatives and carbamates (Hammer and Turkey, 1951). The only useful herbicide having this property is amino triazole. Monuron, diuron and fenuron are three herbicides which are inhibitors of chlorophyll formation. These compounds are highly toxic and persist in the soil and now-a-days are used as pre-emergent herbicides (Woodford, 1957). Simazine is another of the herbicides which affect the photosynthetic process. It was first announced by Gast et al. in 1956 as a promising pre-emergence herbicide. At higher concentrations it acts as a soil sterilant. Hilton et al. (1963) observed that water soluble triazines are effective only when absorbed by roots and movement occurs with the transpiration stream to the leaves.

Chemical Control of Imperata cylindrica

Successful control of I. cylindrica by using different herbicides have been reported by a number of workers. Coomans (1974) studied the control of I. cylindrica in established crops and

observed that three applications at 3 week intervals of dalapon at 5 kg/ha could control this weed to a considerable extent. Dickens and Buchanan (1972) reported an effective control of top growth of I. cylindrica on non-cropped sites by dalapon at 9.5 kg/ha. Ivens (1973) in a series of experiments on I. cylindrica found good control by dalapon for 11 months at rates of 15 and 20 kg/ha. Ho Thien et al. (1975) from Indonesia demonstrated that dalapon-sodium is an extremely effective herbicide against I. cylindrica. Under fully open conditions a single application of 16.8 kg/ha dowepon gives good control of sheet of I. cylindrica while at 20-25 kg/ha dowepon results virtually complete kill.

Dickens and Buchanan (1972) reported the role multiple application of paraquat at 1 kg/ha for the control of I. cylindrica. Post-emergence application of paraquat at 0.56 kg/ha followed by 0.28 kg/ha after 3-weeks gave effective control of I. cylindrica as reported by Harper (1972). Lee (1974) reported that I. cylindrica was effectively controlled with three applications of paraquat at 0.28 kg/ha or with dalapon at 7 kg/ha followed by two applications of paraquat at 0.28 kg/ha.

Much is known on the control of perennial grasses with glyphosate (N-phosphonomethylglycine) first introduced in 1971 (Moshier et al., 1976). This is a non-selective, post-emergence herbicide with excellent toxic activity on a diverse group of perennial grasses. Glyphosate also has been shown to be absorbed and translocated basipetally in numerous annual and perennial

herbaceous plants. Due to its rapid translocation, the rhizome growth of perennial grass like I. cylindrica can be effectively controlled by reducing rhizome reserves and carbohydrate content in the plant.

Ivens (1973) observed long term control of I. cylindrica at 4 kg/ha. Wong (1973) also reported prolonged control with 0.57-4.5 kg ai/ha in a rubber plantation. In a preliminary study, under field conditions, Rao et al. (1976,1977,1978) showed that glyphosate was superior to many other herbicides in controlling I. cylindrica. Mosavi (1979) studied the effect of soil moisture on the activity of glyphosate in green house conditions and observed that application of glyphosate under field capacity reduced the rhizome and shoot dry weight than under moisture stress conditions. Yeoh and Pushparajah (1976) observed a better control of this weed with glyphosate at 2.2 kg/ha in sandy soil than dalapon at 16.8 kg/ha. The present study considers the relative importance of physical control through sickling and other chemical controls using different dosages.

Present study

Imperata cylindrica (L.) Beauv. (Graminaceae) a native of the old world, is a perennial rhizomatous grass and is a major weed in parts of the high rainfall areas in the tropics although it is found in the warm temperate zone (Holms et al., 1975) as well. It is widely distributed in Australia, Africa, the southern half of Asia and the pacific islands. In the new world it is found in Argentina, Chile, Colombia, Florida and West Indies. Although confined to areas that are quite warm, it also is found in Japan and New Zeland.

Its habitat includes the dry sand dunes of sea shores as well as swamps and river margins. It grows in grasslands, among cultivated annual crops and in plantations. It quickly enters abandoned farm lands, may be seen along rail roads and highway embankments and on both deforested and forested areas. It can tolerate long dry spells on light soils and water logging in heavy soils. It makes adequate growth in both nutrient rich and poor soils. The plant grows upto an altitude of 2700 m (Holms et al., 1975).

Hubard et al. (1944) classified this species into five groups, each with a varietal status i.e. major, africana, europea, condensata and latifolia. The variety 'major' has wide distributions.

The species reproduces by seeds and by extension of a very vigorous rhizome system. Aerial flowering culms arise from terminal or auxillary buds of the rhizomes or from the basal portion of the

another aerial culm. Some individual plants flower very frequently and some never flower at all. Flower formation however occur only during hot period (Hubard et al.,1944). Burning and slashing stimulates flower formation especially in the dry season.

I. cylindrica is a serious weed in north-eastern India and forms an important component of the secondary successional environment in fallows developing after slash and burn agriculture (jhum) (Ramakrishnan et al.,1980). Shifting cultivation, involving slash and burn process followed by mixed cropping is a predominant practice of this region. I. cylindrica is an early colonizer, Shortening of the jhum cycle (the intervening fallow period between two successive croppings on the same site) to 4-5 years in this region due to human population pressure has resulted in luxuriant growth of this weed, often through an arrested succession (Ramakrishnan et al.,1981; Toky and Ramakrishnan, 1983; Mishra and Ramakrishnan,1983).

In view of the extreme weediness of this species in fallows at both low and high elevation of Meghalaya, a comparative study of the two populations were made with respect to demography and population dynamics of this species and the ecophysiological attributes in relation to biomass production and allocation and nutrient uptake and use efficiencies and allocation patterns were considered. The possible chemical control measures, atleast in restricted areas, has been considered.

Fig 1.1 Ombothermic diagram of the study area at
Burnihat. Mean monthly maximum (○),
minimum (●) temperature. (▲), rainfall.

fig. 11

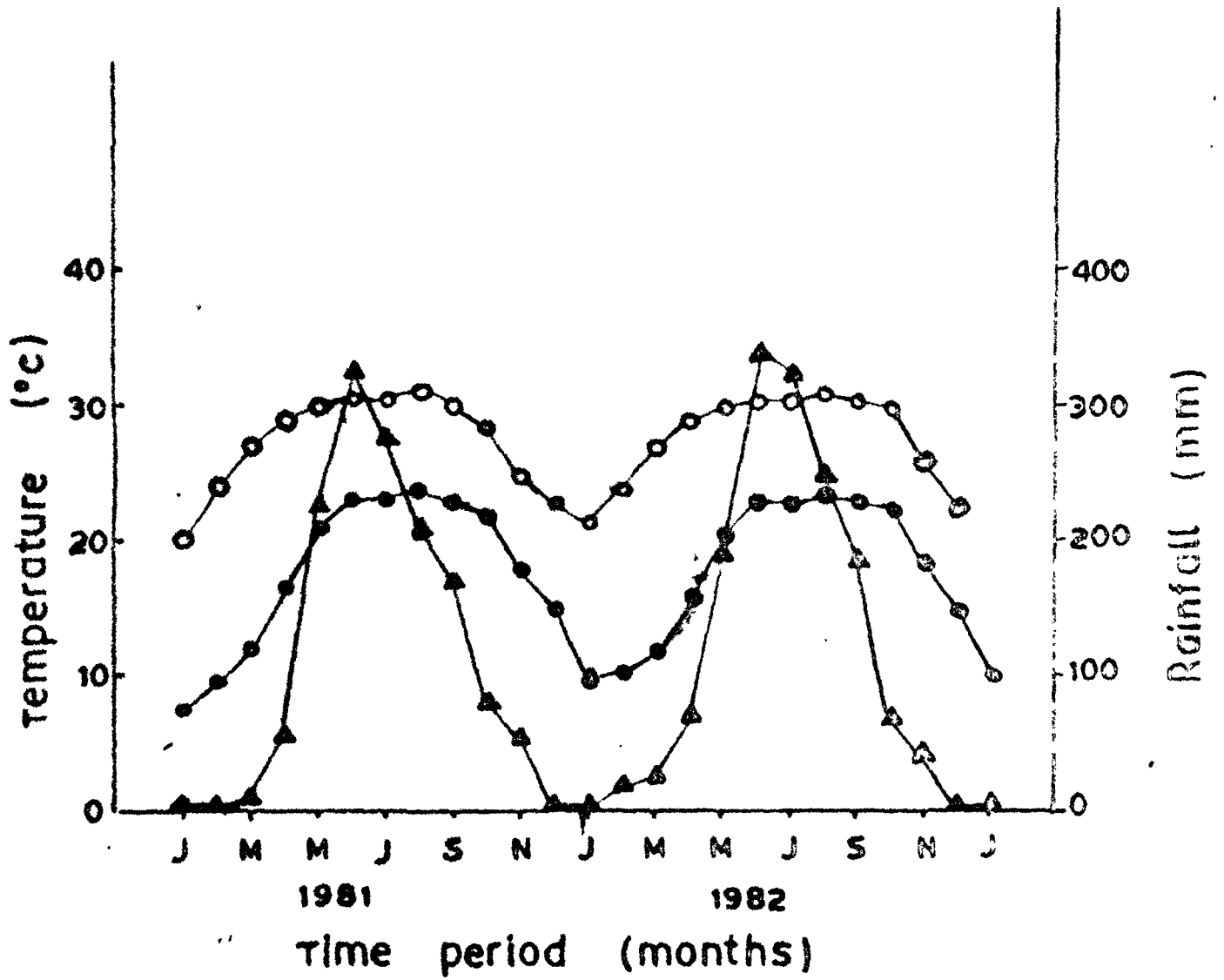


Fig 1.2 Ombothermic diagram of the study area at Shillong.
Mean monthly maximum (O), minimum (●), temperature.
(▲), rainfall.

fig. 1.2

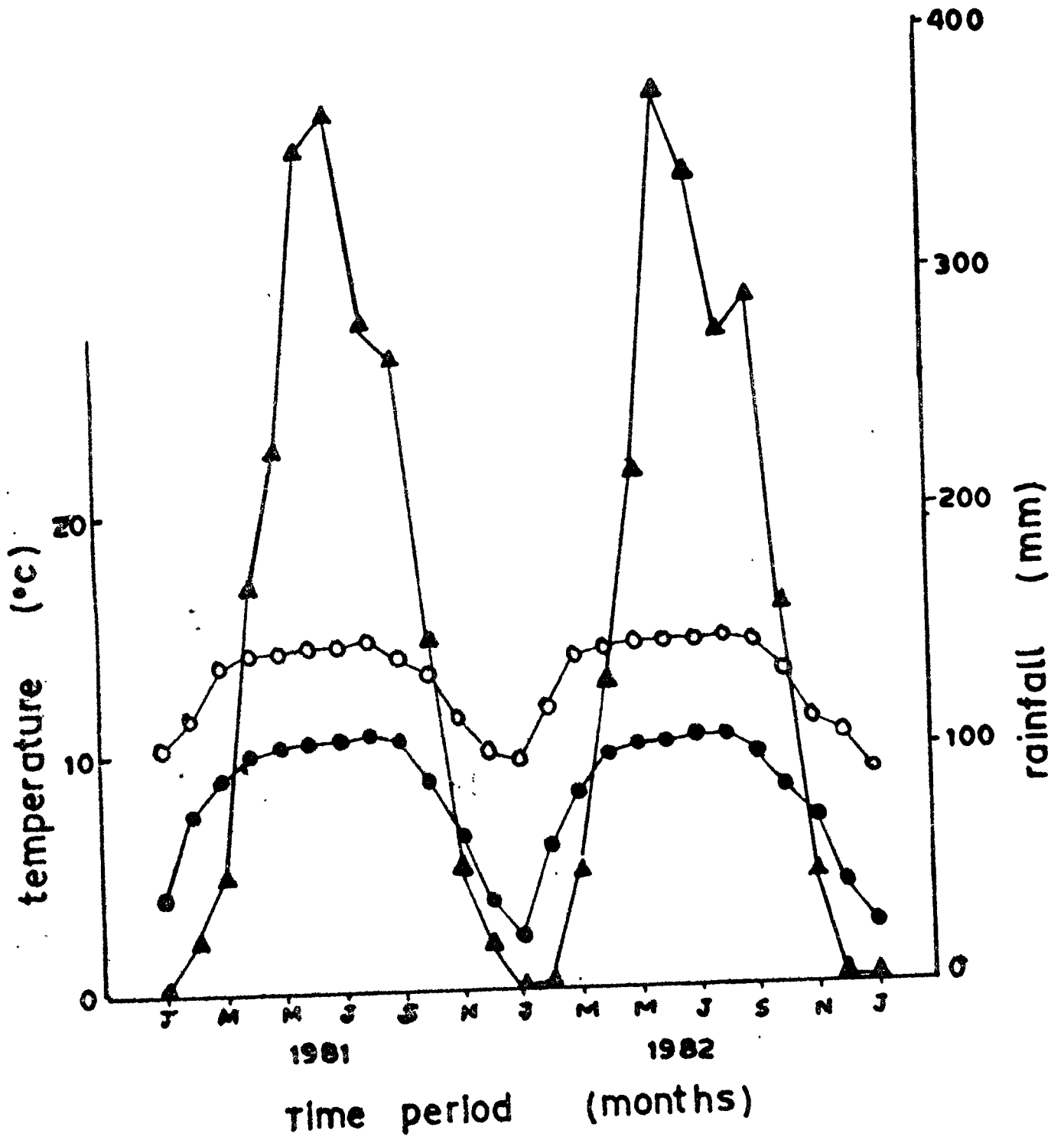
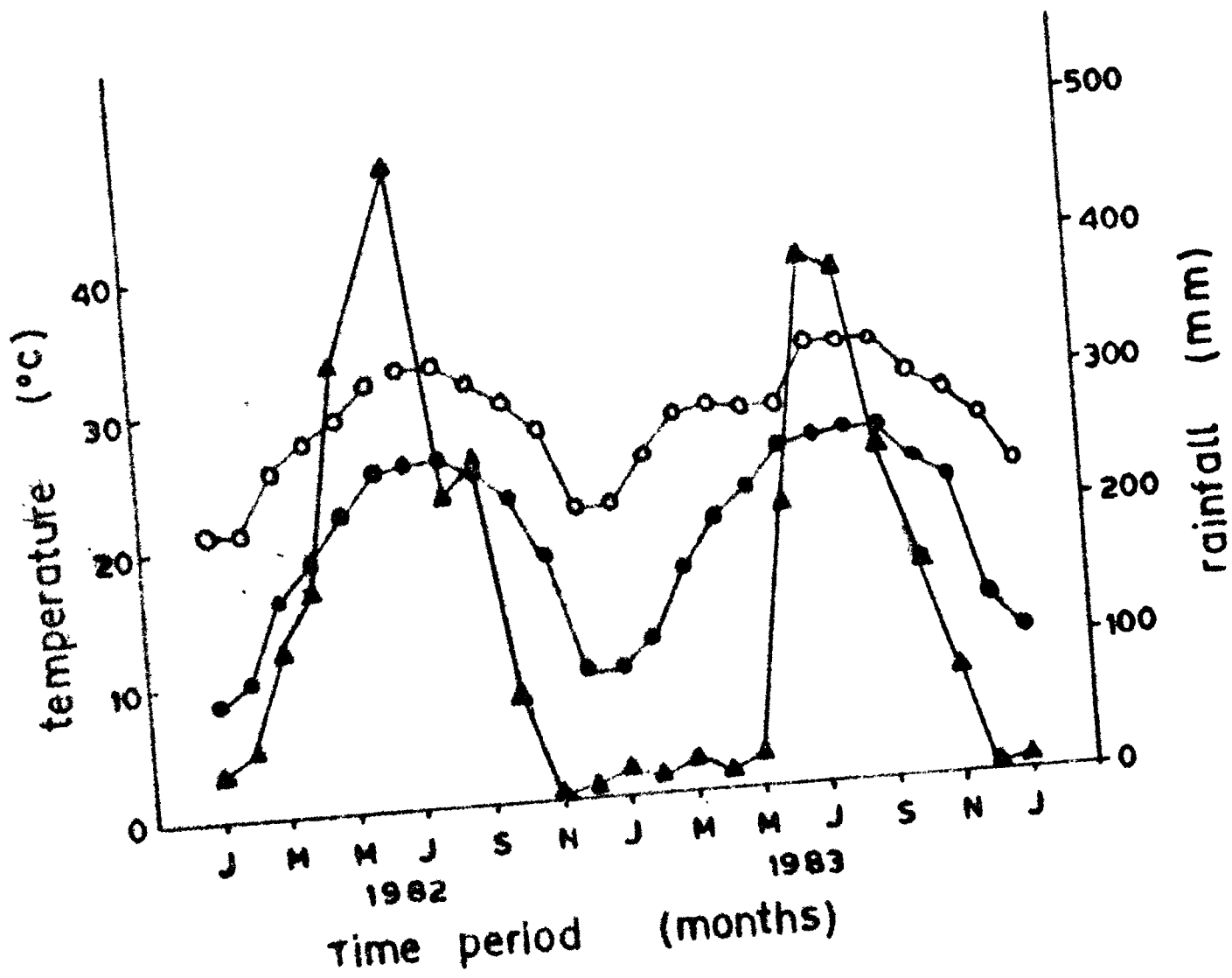


Fig 1.3 Onbothermic diagram of the study area at Jorhat. Mean monthly maximum (○), minimum (●) temperature. (▲), rainfall.

fig. 13



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CHAPTER II

**STUDIES ON ADAPTATIONAL BEHAVIOUR OF TWO
POPULATIONS OF IMPERATA CYLINDRICA(L.)
BEAUV. ALONG AN ALPITUDINAL GRADIENT**

INTRODUCTION

A species which has a wide ecological amplitude may be adapted to different environment either through a process of differentiation of ecological races (Turesson, 1922, 1925) or through phenotypic plasticity (Bradshaw, 1972). The documentation of ecotypic differentiation on an altitudinal basis is available through many studies (Barter, 1955; Clausen, 1940; Myers and Bormann, 1963; May, 1975, 1976), following the classical work on climatic races by Turesson (1922, 1925).

Imperata cylindrica (L.) Beauv. has a wide geographical distribution although it is more abundant in the warmer regions of the World (Eussen and Soerjani, 1975). The plants grow upto an altitude of 2700 m and have wide adaptability to varied climatic conditions and soil types (Holms et al., 1977). In Meghalaya, north-east India, it is found to grow over an altitudinal range upto 1700 m. Through reciprocal transplant studies of two populations of Imperata cylindrica (L.) Beauv. Var major, one collected from Burnihat (100 m elevation) and another from Shillong (1500 m elevation) in Meghalaya (80°30' and 92°30'E; 25°30'E and 26°0'N) the present study aims at an understanding of ecotypic differentiation in this species versus Phenotypic Plasticity.

STUDY AREA AND CLIMATE

The study area was at Burnihat (about 85 km north of Shillong) at an elevation of 100 meters ($26^{\circ}02'N$, $91^{\circ}52'E$) and at Shillong ($25^{\circ}34'N$, $91^{\circ}56'E$), at an elevation of 1500 meters. The climate is monsoonic with most of the rainfall coming during May - September. The average maximum temperature at this period at Burnihat and at Shillong was $32^{\circ}C$ and $23.5^{\circ}C$ respectively, while the average minimum temperature was $24^{\circ}C$ and $16^{\circ}C$ respectively. The annual rainfall range from 2200 mm to 2500 mm. The winter is mild at lower elevation with an average maximum temperature of $24^{\circ}C$ and an average minimum of $12^{\circ}C$, whereas at Shillong it is more severe with an average maximum temperature of $15^{\circ}C$ and minimum of $7.5^{\circ}C$. The brief dry summer is from February to April.

METHODS OF STUDY

Pot culture experiments were done at Burnihat (100 m altitude) and at Shillong (1500 m altitude). Rhizomes collected from each site were divided into one-node ramets (with a healthy bud) of uniform weight (1 g) and raised separately in moist sand. Pots (20.8 cm diameter) were filled up with soil from that site and was thoroughly mixed to remove soil heterogeneity. The transplants of the Burnihat and Shillong populations were grown in these pots at the rate of 120 ramets/m². Transplantation was done in April, 1981 when the ramets were uniformly 2-leaved and about 3 cm in height. Each treatment was replicated four times.

Harvesting was done at monthly intervals. Growth characters such as plant height, number of tillers and leaf area was measured at each harvest. The harvested plants were separated into above-ground (leaf and stem) and below-ground (rhizome and root) components. The different components were dried at 85° ± 5°C for 24 hours and weighed. Leaf area estimation was done by using a planimeter. Leaf dry weight per unit area was based on 20 leaves per replicate. Leaf area ratio was calculated as leaf area (cm²) per unit (mg) biomass. Growth functions such as relative growth rate (RGR), and net assimilation rate (NAR) (Hughes and Freeman, 1967; Radford, 1967) were calculated as

$$RGR \text{ (mg mg}^{-1} \text{d}^{-1}) = \frac{I_n W_2 - I_n W_1}{t_2 - t_1}$$

$$\text{NAR} = \frac{(W_2 - W_1) (I_n A_2 - I_n A_1)}{(A_2 - A_1) (t_2 - t_1)}$$

(mg cm⁻² d⁻¹)

where, W_1 and A_1 are biomass and leaf area values at time t_1 and W_2 and A_2 are at time t_2 .

Concentration of different nutrients in the component organs were determined following standard methods (Allen, 1974). Thus nitrogen was analysed by micro-Kjeldahl method, phosphorus by molybdenum-blue method and potassium by flame photometry after dry ashing.

Nutrient uptake efficiency was calculated as mg nutrient absorbed per g root biomass following Blair and Codero (1978) and nutrient use efficiency as mg biomass produced per mg nutrient uptake. Vegetative effort was calculated on the basis of allocation to rhizome, as a percentage of dry matter production or nutrient uptake.

RESULTS

The growth performance of the species at two altitudinal sites at the end of the study period showed that in general *I. cylindrica* grew more vigorously at Burnihat than at Shillong. The two populations from Burnihat and Shillong raised in a neutral substratum at Burnihat, showed a significantly higher value for Burnihat population with respect to the height of the plant, number of tillers, leaf area/tiller and above-ground biomass. The ratio between above-ground and below-ground parts did not show any significant

Table 2.1 Growth behaviour of the two altitudinal populations of I. cylindrica in a neutral substratum at Burnihat and Shillong

	Burnihat site			Shillong site		
	Burnihat Population	Shillong Population	t(P=0.05)	Burnihat Population	Shillong Population	t(P=0.05)
Plant height (cm)	80.2	61.5	S	46.5	44.2	NS
No of tillers	20.0	16.0	S	8.0	9.0	NS
Leaf area/tiller (cm ²)	133.0	95.0	S	126.0	97.0	S
Above-ground biomass (g)	12.5	10.2	S	6.8	6.5	NS
Below-ground biomass (g)	12.8	12.1	NS	8.1	8.3	NS
Below-ground/above-ground ratio	1.02	1.2	NS	1.2	1.3	NS

Fig. 2.1 Increment in the dry weight yield (g/m^2) of two altitudinal populations of I. cylindrica in a neutral substratum at Burnihat and Shillong. (a) Above-ground parts, (b) Below-ground parts. Open circle, Burnihat population at Burnihat; closed circle, Shillong population at Burnihat; open triangle, Burnihat population at Shillong; closed triangle, Shillong population at Shillong. Vertical bers represent L.S.D. at $P = 0.05$.

Fig. 2.1

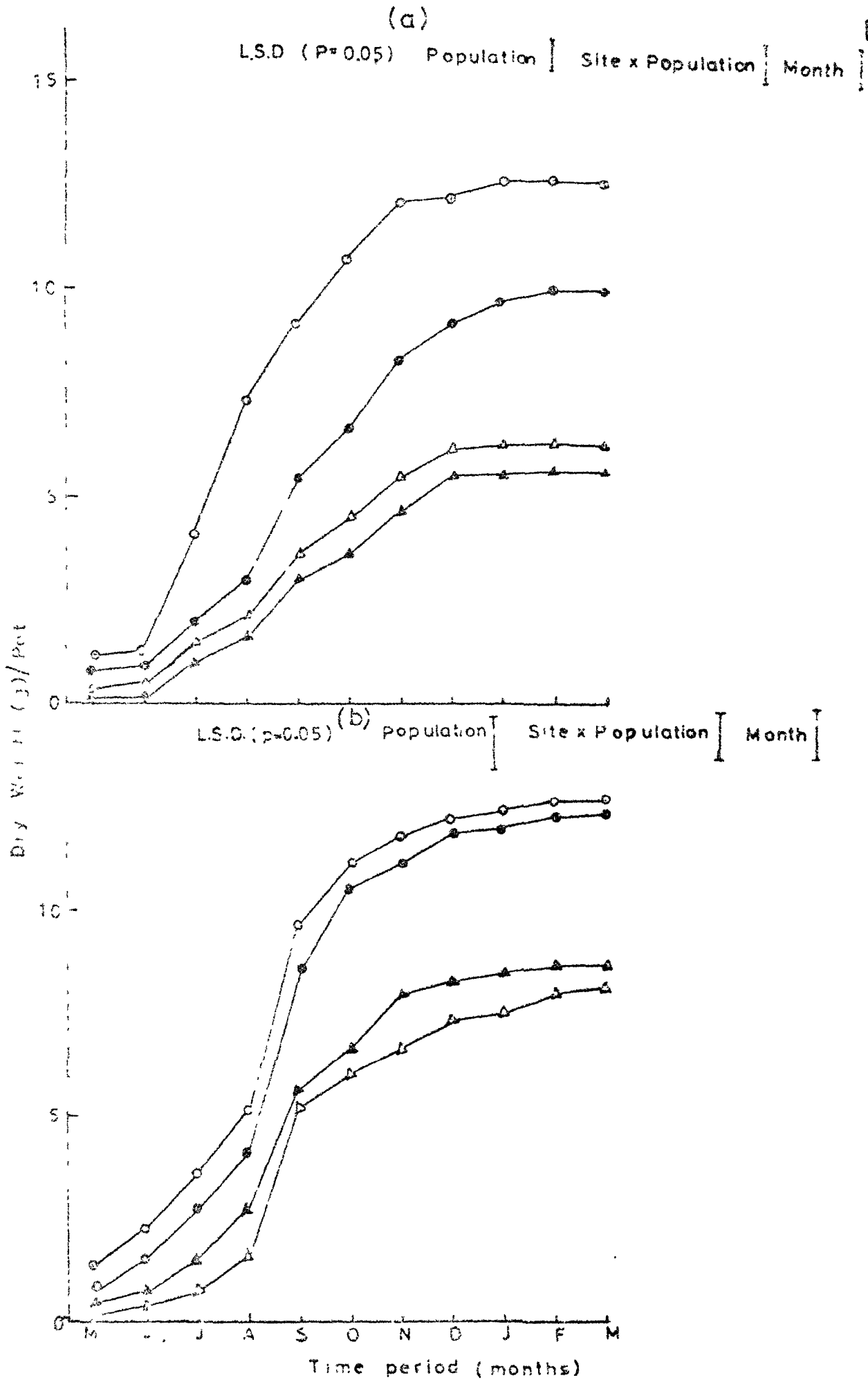


Table 2.2 Mean values (\pm S.E.M.) of growth functions of the ^{two} altitudinal populations of I. cylindrica during the growth period at Burnihat and Shillong.

Population	RGR $\text{mg mg}^{-1} \text{d}^{-1}$		NAR $\text{mg cm}^{-2} \text{d}^{-1}$		LAR $\text{cm}^2 \text{mg}^{-1}$	
	Burnihat	Shillong	Burnihat	Shillong	Burnihat	Shillong
Burnihat	0.0052 \pm 0.0014	0.0050 \pm 0.0024	0.0520 \pm 0.0120	0.0468 \pm 0.0220	0.2434 \pm 0.0920	0.1861 \pm 0.0825
Shillong	0.0041 \pm 0.0012	0.0042 \pm 0.0013	0.0312 \pm 0.0172	0.0342 \pm 0.0110	0.2270 \pm 0.0824	0.1971 \pm 0.0745

L.S.D. (P = 0.05)

Site & population 0.0024

0.026

0.16

Site x population 0.0032

0.032

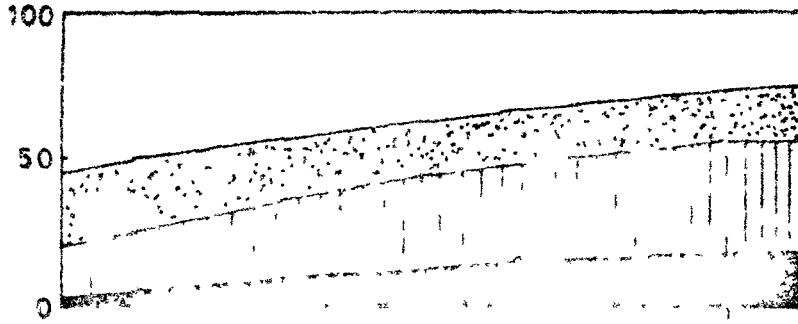
0.19

Fig. 2.2 Allocation pattern of biomass (percentage of the total) of two altitudinal populations of I. cylindrica in a neutral substratum at Burnihat and Shillong. (a) Burnihat population at Burnihat, (b) Shillong population at Burnihat, (c) Burnihat population at Shillong, (d) Shillong population at Shillong.

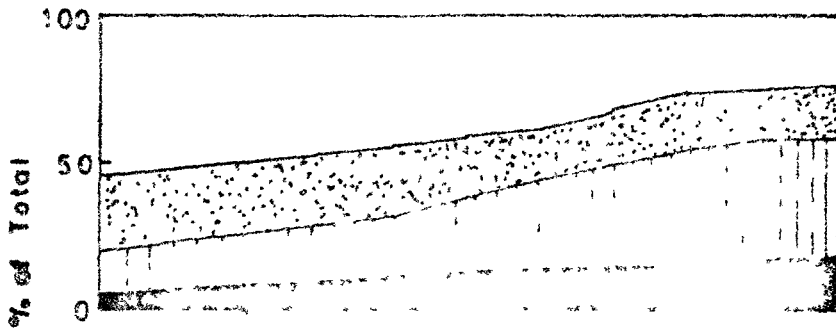
Fig. 2.2

Allocation of Biomass
(a)

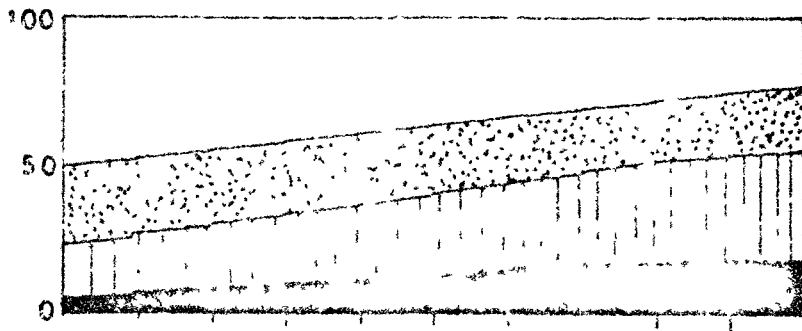
Leaf Stem Rhizome Root



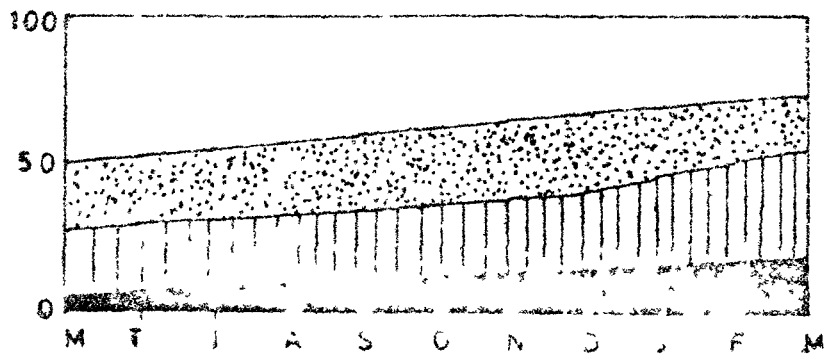
(b)



(c)



(d)



difference. However the two populations when grown at Shillong showed a decline in all growth characters but no significant difference was observed between the two populations except for leaf area per tiller (Table 2.1).

Dry weight yield per pot for above-ground parts of both the populations increased upto December and subsequently declined. The increase was more pronounced for the two populations raised at Burnihat than for those raised at Shillong where the yield was much lower. The final yield per pot was slightly higher for the Burnihat population compared to the Shillong population at Burnihat site only (Fig. 2.1a).

Though no significant difference was observed in the below-ground yield between the two populations raised at Burnihat and Shillong, the final values attained was markedly different at the two sites. Upto October the increment in below-ground biomass was sharper but declined subsequently (Fig. 2.1b).

No significant difference was observed between the two populations at a given site and for a given population at the two different sites, with respect to RGR, NAR and LAR (Table 2.2).

The allocation pattern of biomass (expressed as a percentage of the total capital) to the different component parts was similar for the two populations at both sites (Fig. 2.2a,b,c,d). A higher allocation to the leaf and the stem components was observed initially when the growth started but subsequently allocation to the rhizome component increased sharply, at the expense of the other component

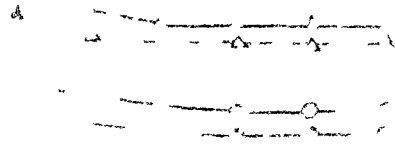
Fig. 2.3 Nutrient concentration (%) in the above-ground parts of two altitudinal populations of I. cylindrica raised at Burnihat and Shillong.

(a) Concentration of Nitrogen, (b) Concentration of phosphorus, (c) Concentration of potassium.

Open circle, Burnihat population at Burnihat;
closed circle, Shillong population at Burnihat;
open triangle, Burnihat population at Shillong;
closed triangle, Shillong population at Shillong.

Vertical bers represent L.S.D. at $P = 0.05$.

A. P. 7. 1. 4



2

Fig. 2.4 Nutrient concentration (%) in the below-ground parts of two altitudinal populations of I. cylindrica raised at Burnihat and Shillong.

(a) Concentration of nitrogen, (b) Concentration of phosphorus, (c) Concentration of potassium.

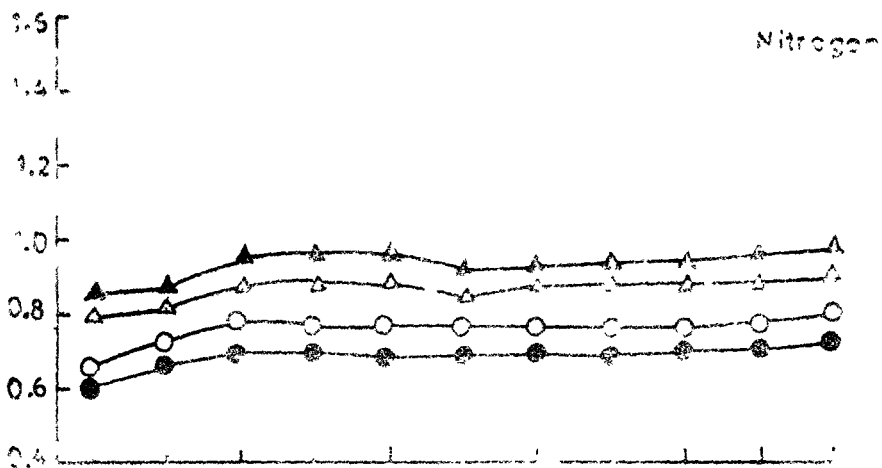
Open circle, Burnihat population at Burnihat; closed circle, Shillong population at Burnihat; open triangle, Burnihat population at Shillong. closed triangle, Shillong population at Shillong.

Vertical bers represent L.S.D. at $P = 0.05$.

(a)

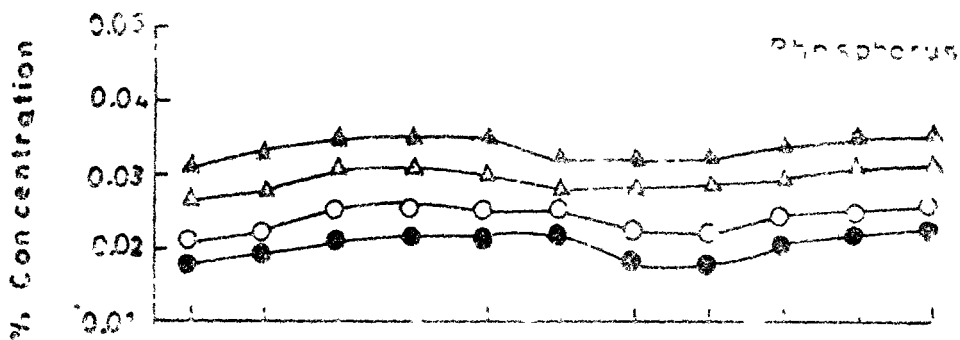
Fig. 2.4

U.S.D. ($P=0.05$) Population | Site | Population | Month |



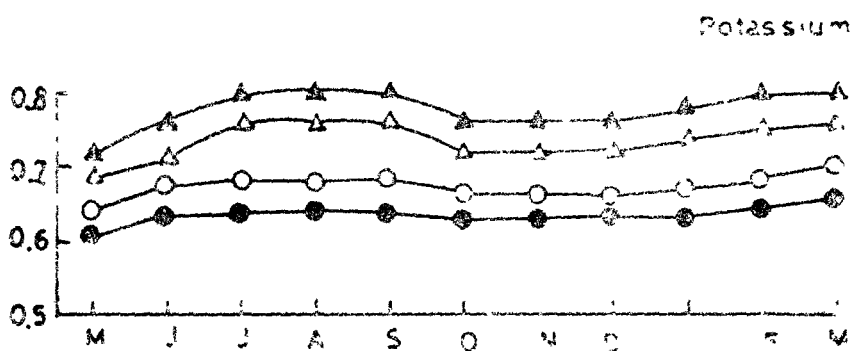
(b)

U.S.D. ($P=0.05$) Population | Site x Population | Month |



(c)

U.S.D. ($P=0.05$) Population | Site x Population | Month |



Time period (months)

Fig. 2.5 Allocation pattern of nitrogen (% of the total) of the two altitudinal populations of I. cylindrica raised a neutral substratum at Burnihat and Shillong. (a) Burnihat population at Burnihat, (b) Shillong population at Burnihat, (c) Burnihat population at Shillong, (d) Shillong population at Shillong.

Fig. 2.5

Allocatio of Nitrogen
(a)

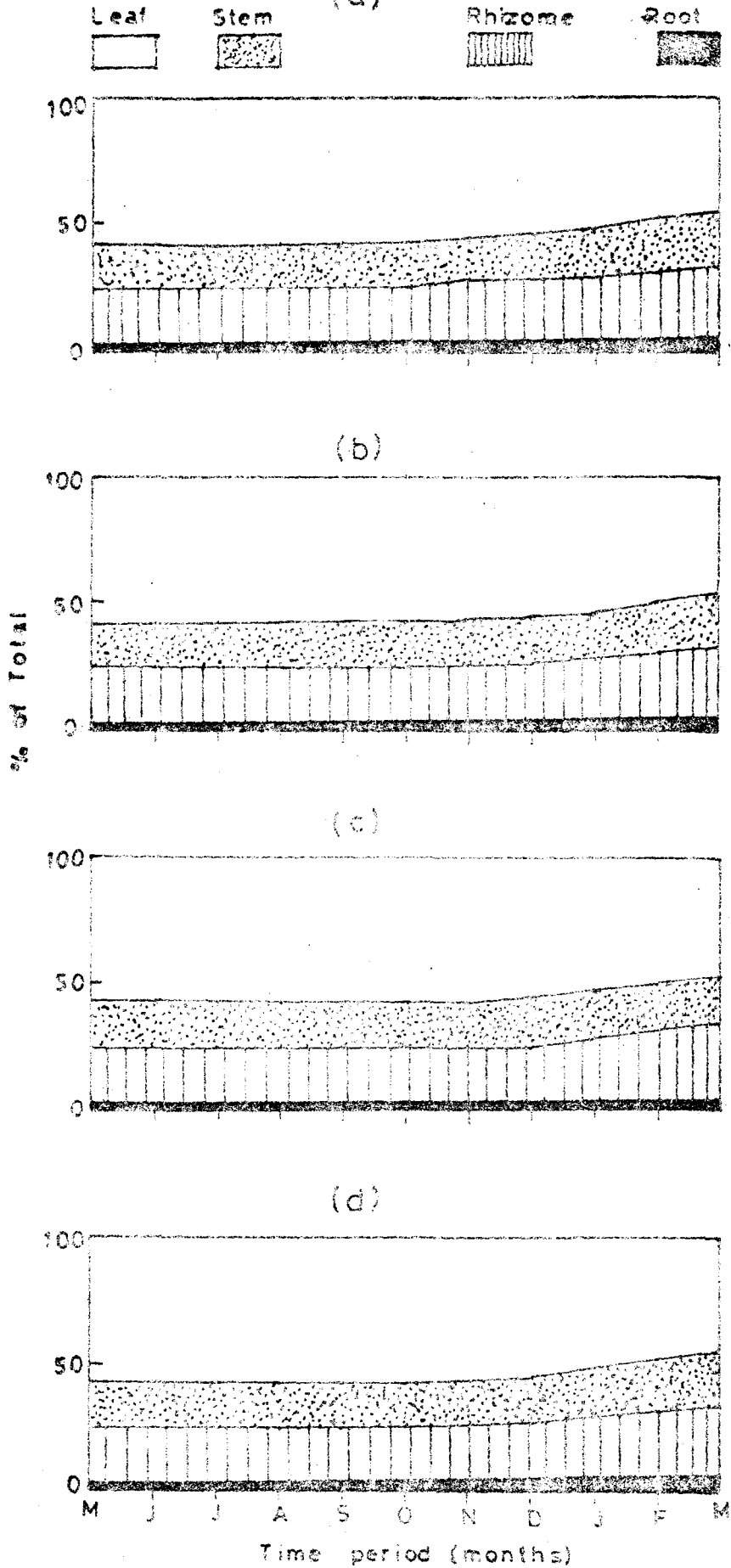


Fig. 2.6 Allocation pattern of phosphorus (% of the total) of the two altitudinal populations of I.cylindrica in a neutral substratum at Burnihat and Shillong. (a) Burnihat population at Burnihat, (b) Shillong population at Burnihat, (c) Burnihat population at Shillong, (d) Shillong population at Shillong.

Fig. 2.6

Allocation of Phosphorus

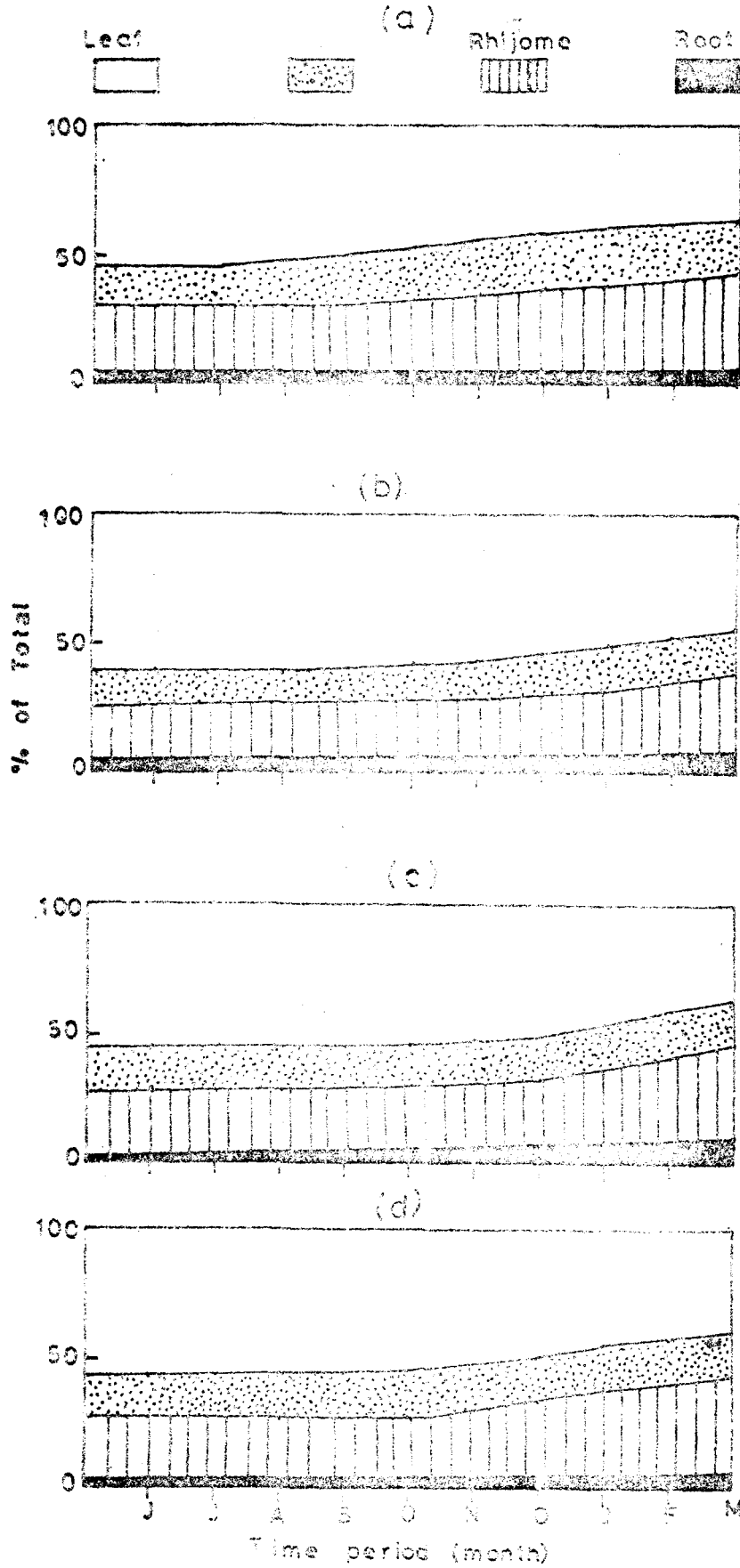
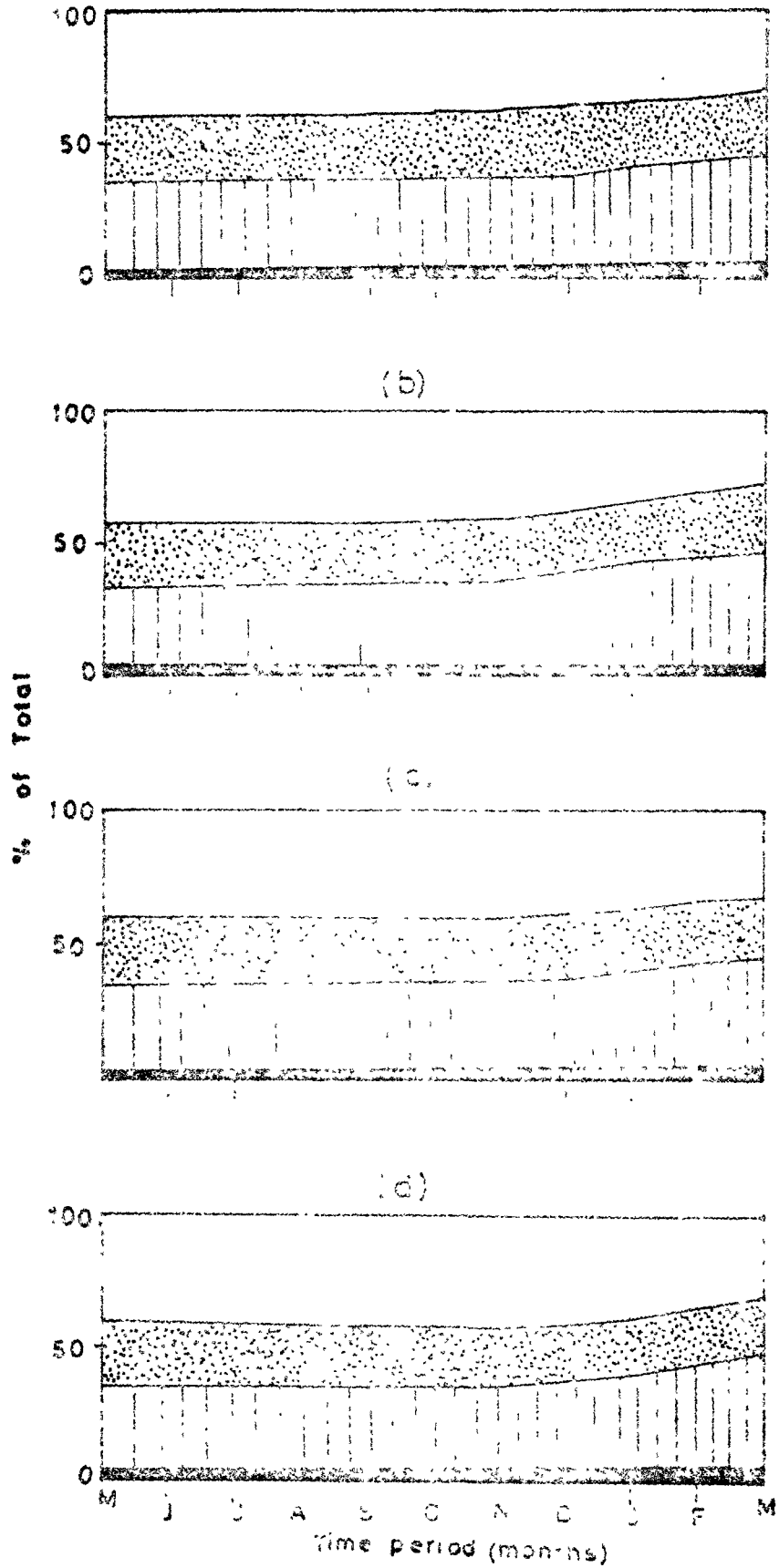


Fig. 2.7 Allocation pattern of potassium (% of the total) of the two altitudinal populations of I.cylindrica in a neutral substratum at Burnihat and Shillong. (a) Burnihat population at Burnihat, (b) Shillong population at Burnihat, (c) Burnihat population at Shillong, (d) Shillong population at Shillong.

Fig. 2.7

Allocation of Potassium

Leaf Stem Rhizome Root



Concentration of nutrients, such as nitrogen, phosphorus and potassium in the above-ground parts (Fig. 2.3a,b,c) was significantly higher in the two populations at Shillong compared to the populations grown at Burnihat. A general decline in the concentration of all nutrients was observed during the growth period.

Nutrient concentration in the below-ground parts (Fig. 2.4a,b,c) was significantly higher in the case of the two populations raised at Shillong compared to those raised at Burnihat. The concentration of all the three nutrients showed a seasonal fluctuation. High nutrient concentration was observed during the period of June to September with a subsequent decline in October to December followed by an increase again.

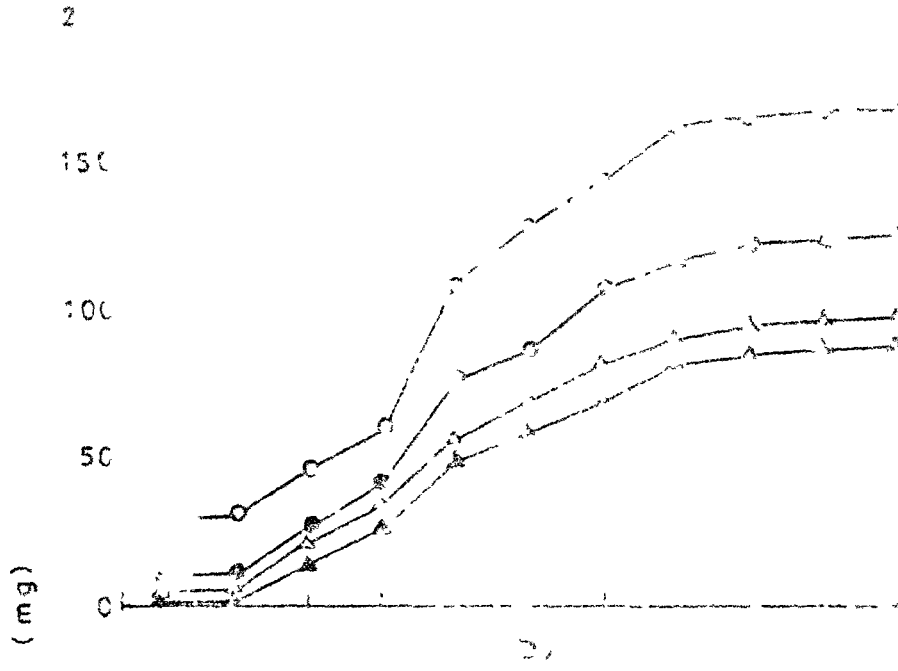
No significant differences were observed with respect to allocation of nutrients like nitrogen, phosphorus and potassium between the two populations at a given site and the same population at two different sites. However, the proportional allocation of phosphorus and potassium to the under-ground organs was more than that of nitrogen as seen from a comparison of Figures 2.5, 2.6 and 2.7.

Nutrient accumulation in the above-ground biomass increased sharply for the two populations at Burnihat site compared to that at Shillong so that the final level attained at the end of the one year growth period was more at the former site. Considering the two populations at a given site, Burnihat population had

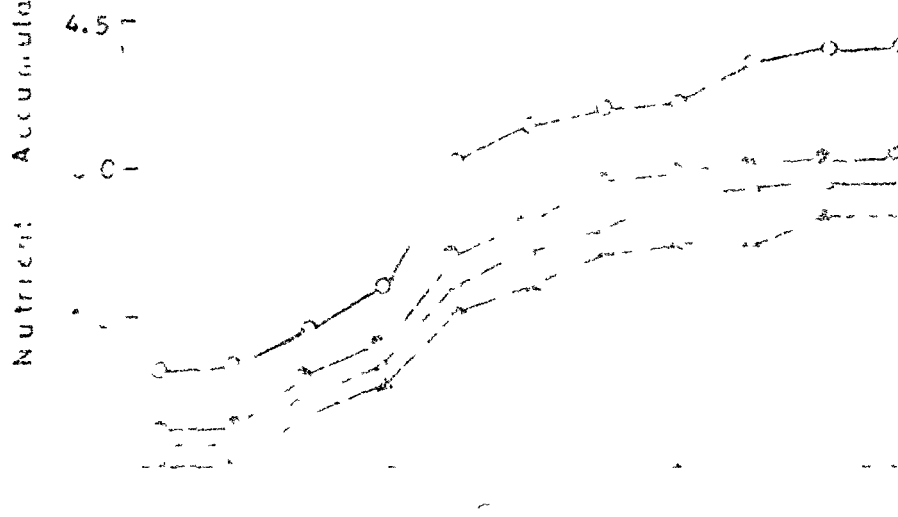
Fig. 2.8 Accumulation of nutrients (mg/m^2) in the above-ground parts of the two altitudinal populations in a neutral substratum at Burnihat and Shillong. (a) Accumulation of nitrogen, (b) Accumulation of phosphorus, (c) Accumulation of potassium. Open circle, Burnihat population at Burnihat; closed circle, Shillong population at Burnihat; open triangle, Burnihat population at Shillong; closed triangle, Shillong population at Shillong. Vertical bars represent L.S.D. at $P = 0.05$.

L.S.D. (P=0.05)

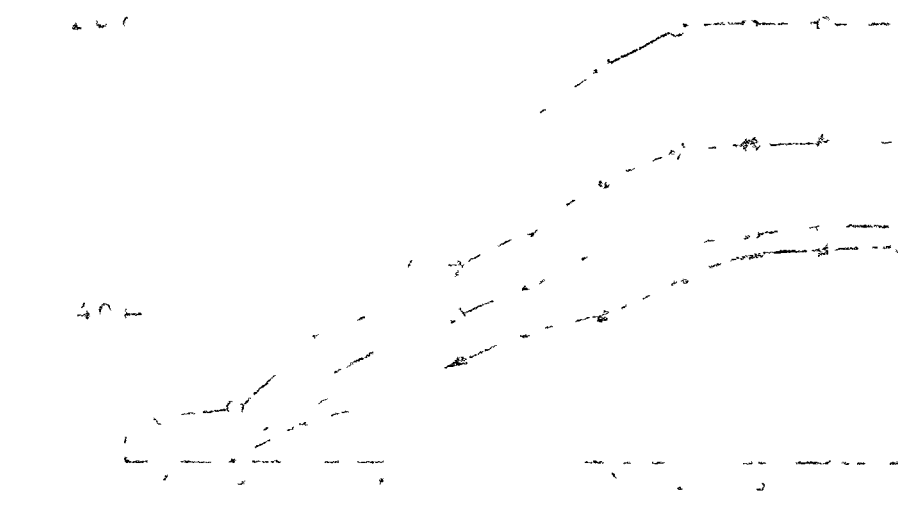
Time (days)



S.D. (P=0.05) Population of ...



S.D. (P=0.05) Population of ...



Time period (days)

Fig. 2.9 Accumulation of nutrients (mg/m^2) in below-ground parts of two altitudinal populations raised in a neutral substratum at Burnihat and Shillong. (a) Accumulation of nitrogen, (b) accumulation of phosphorus, (c) accumulation of potassium. Open circle, Burnihat population at Burnihat; closed circle, Shillong population at Burnihat; open triangle, Burnihat population at Shillong; closed triangle, Shillong population at Shillong. Vertical bars represent L.S.D. at $P = 0.05$.

Fig 2.9

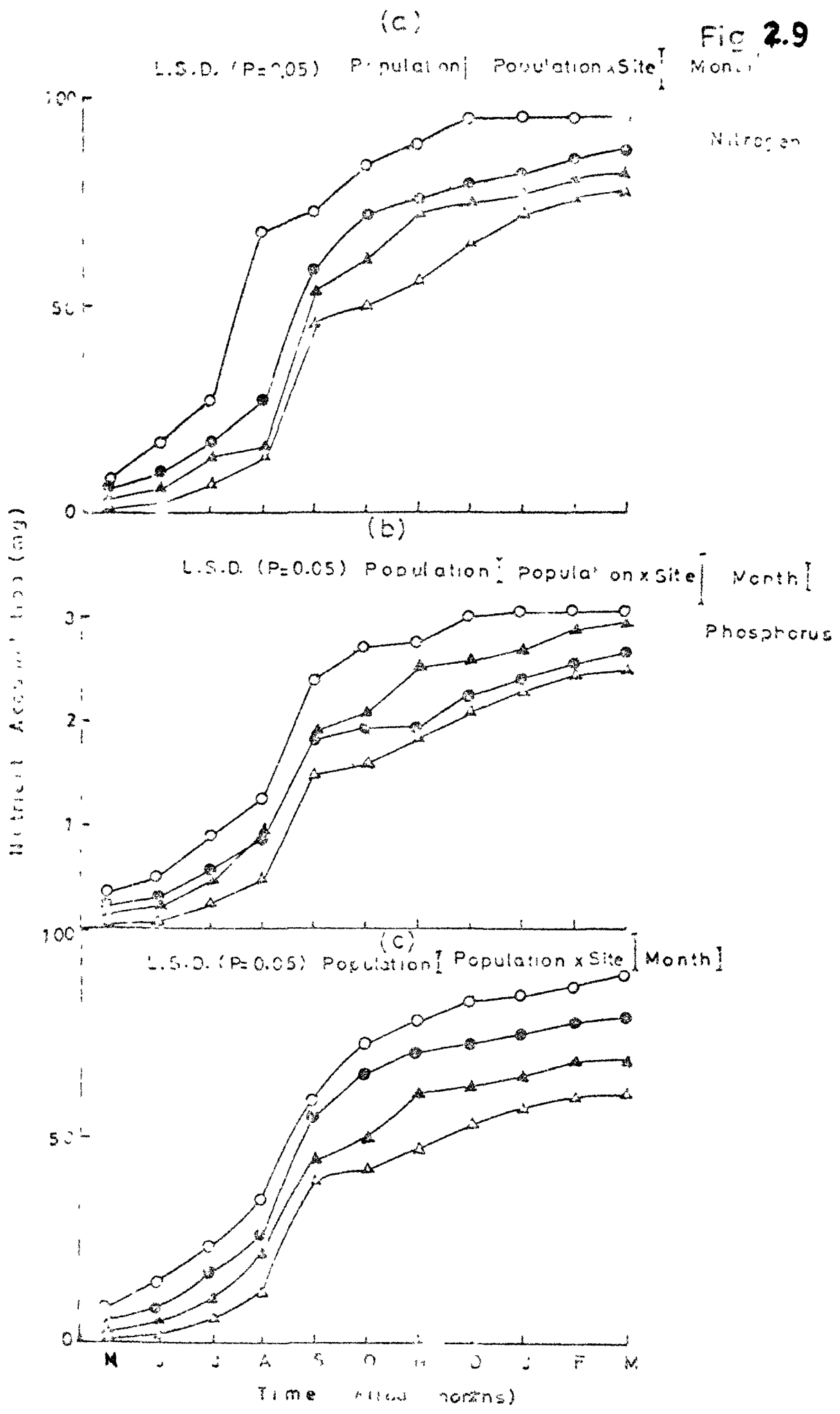


Table 2.3 Nutrient uptake efficiency (mg nutrient produced per g root biomass) of the two altitudinal populations of I. cylindrica in a neutral substratum at Burnihat and Shillong

Nutrient	Burnihat site			Shillong site		
	Burnihat population	Shillong population	t(P=0.05)	Burnihat population	Shillong population	t(P=0.05)
Nitrogen	108.0	96.0	S	69.0	72.0	NS
Phosphorus	5.2	5.0	NS	3.4	3.2	NS
Potassium	79.0	73.0	S	50.0	48.0	NS

a significantly higher rate of nutrient accumulation compared to the Shillong population at Burnihat site only (Fig. 2.8a,b,c).

Nutrient accumulation pattern in the below-ground organs at the two sites and between the two populations did not show any marked change on the rate pattern as was observed for the above-ground organs. However, a significant difference in nitrogen accumulation at the end of the growth period was observed between the Burnihat population raised at Burnihat and Shillong sites (Fig. 2.9a). As for phosphorus, the Burnihat population at Burnihat site and the Shillong population at Shillong site had significantly higher final accumulation values compared to the two populations at the alien site (Fig. 2.9b). For potassium the only significant difference noted was between the two sites, where the populations raised at Shillong had lower accumulation rate (Fig. 2.9c).

Nutrient uptake efficiency was significantly higher for the two populations raised at Burnihat compared to the two populations raised at Shillong. Population differences at the same site was observed only in the case of nitrogen and potassium at Burnihat site where the uptake by the Burnihat population was significantly higher compared to the Shillong population. Further, uptake efficiency was more for nitrogen followed by potassium and was least for phosphorus under all situations (Table 2.3).

Phosphorus use efficiency was significantly more for the two populations grown at Shillong compared to those raised at Burnihat.

Table 2.4 Nutrient use efficiency (mg biomass produced per mg nutrient absorbed) of the two altitudinal populations of *I. cylindrica* in a neutral substratum at Burnihat and Shillong

Nutrient	Burnihat site			Shillong site		
	Burnihat population	Shillong population	t(P=0.05)	Burnihat population	Shillong population	t(P=0.05)
Nitrogen	74.6	77.1	NS	76.3	75.9	NS
Phosphorus	1691.0	1665.2	S	1733.0	1750.0	S
Potassium	101.3	102.3	NS	107.2	106.8	NS

Table 2.5 Vegetative effort (allocation to rhizome as a percentage of dry matter or nutrient uptake) of the two altitudinal populations of *I. cylindrica* in a neutral substratum at Burnihat and Shillong

Biomass/Nutrient	Burnihat site			Shillong site		
	Burnihat population	Shillong population	t(P=0.05)	Burnihat population	Shillong population	t(P=0.05)
Biomass	32.0	30.2	NS	29.0	30.0	NS
Nitrogen	28.0	27.6	NS	25.0	23.0	NS
Phosphorus	21.3	21.2	NS	25.0	23.8	NS
Potassium	33.3	32.4	NS	32.0	32.5	NS

At Shillong site, the Shillong population had significantly higher phosphorus use efficiency compared to the Burnihat population, the reverse was the case at Burnihat site (Table 2.4).

Vegetative effort, when considered as a percentage of the biomass allocated to the rhizome showed no significant difference between the two populations nor between the two sites. When this was considered as a percentage of the total nutrients allocated to the rhizome, it showed a significant difference between the two sites in a manner that the same population raised at Shillong had lower allocation compared to those raised at Burnihat. A significant difference in the reproductive effort related to phosphorus allocation between the two sites was observed; the allocation was more at Shillong site than at Burnihat (Table 2.5).

DISCUSSION

Imperata cylindrica is an important weed with a wide altitudinal range reaching upto an elevation of 1700 m in Meghalaya. Such a wide altitudinal range has also been reported by Holm et al. (1977). This wide altitudinal range in a species is possible either through plasticity of a species or through adaptive differentiation into ecotypes as shown through many studies done by Ramakrishnan and his co-workers (Ramakrishnan and Jain, 1965a, 1965b; Ramakrishnan and Singh, 1966; Ramakrishnan and Gupta, 1972, 1973; Ramakrishnan and Nagpal, 1973).

Ecotypic differences observed are often quantitative than qualitative. Very often the differences are in terms of dry weight yield of the shoot or the root, the populations best adapted to a particular situation yielding best under more favourable situations (Ramakrishnan, 1960a, 1960b, 1968, 1969; Snyder and Bradshaw, 1962; Ramakrishnan and Singh, 1966; Ramakrishnan and Gupta, 1973; Ramakrishnan and Nagpal, 1973; Kapoor and Ramakrishnan, 1974). Accordingly, the low altitude Burnihat population of I. cylindrica was more vigorous in its growth in comparison to the Shillong population raised along with it at Burnihat. However such a difference between the two populations was not evident at the Shillong site. The generally poor growth of both the populations under the high altitude of Shillong situation may be partly related to lower temperature conditions and the more acidic and nutritionally poorer soil at Shillong. The impact of generally more favourable temperature conditions prevailing at the lower elevation at Burnihat is also reflected in the growth increment differences observed during the growing season at Burnihat and Shillong. Thus, there was a more pronounced increase in the growth of the two populations at Burnihat.

Though the allocation pattern of the biomass did not differ between the two populations at both altitudes, the two populations raised at higher elevation had generally lower yield for the below-ground organs suggesting that the vegetative reproductive efficiency of this species is also more at lower elevation than at higher elevation. It may be noted that Soerjani (1970) reported

a high optimum temperature for rhizome development in

I. cylindrica.

Tiller production is a mechanism by which population size increases in the case of vegetatively reproduced plant species. The Burnihat population generally showed higher ability for tiller production compared to the Shillong population. This is indicative of adaptation to rapid multiplication under more favourable environment at Burnihat. The generally lower number of tillers produced at Shillong situation may be a temperature effect. Chapin and Chapin (1981) studied the growth of Carex aquitilis at low and high temperature regions and observed that the small tiller size and low leaf production of arctic and alpine populations compared to hot spring population was correlated with low air and soil temperature, suggesting control of environmental factors over the growth of the species. The Burnihat population generally had much larger tillers with more leaf area both under low and high elevation situations; again suggestive of adaptation to more favourable temperature situations at Burnihat.

Allocation of biomass to the plant parts may be determined genetically or environmentally (Chapin and Chapin, 1981; Ramakrishnan and Kanta, 1976). Various workers (Cody, 1966; Harper, 1967) have stressed the ecological significance of allocation of energy to various activities during development of an organism. The process of growth, development and reproduction in a plant may be seen as a strategy of allocation of limited resources. Similarly in the allocation pattern of the biomass in the two populations at

the two sites indicate a strong phenotypic plasticity of the species population to adapt to the contrasting environmental conditions. Thus, vegetative effort which is expressed as a percentage allocation of biomass to rhizome component did not change in the two populations at either of the sites. A more initial allocation of biomass to the above-ground parts represents investment of energy in photosynthetic biomass (Clark and Burk, 1980) and subsequent increase in allocation to the under-ground rhizomes indicates the strategy of a vegetatively reproduced species (Abrahamson and Gadgil, 1973; Gaines et al., 1974; Roos and Quinn, 1977).

A higher concentration of nutrients in the two populations at Shillong parallels the findings of Chapin et al. (1975) who reported a smaller biomass with a higher nutrient content for the plants growing at low temperature region. A general decline in the nutrient concentration in the above-ground parts and simultaneous increase in the below-ground organs indicates a shift also, as reported by a number of workers in vegetatively reproducing species (Boyd, 1970; Boyd and Hess, 1970; Kvet, 1973; Chapin et al., 1975; Bernard and Selsky, 1977).

Accumulation of nutrients such as nitrogen, phosphorus and potassium is a function of the standing biomass in the green crop. An increase in the nutrient standing crop with the increase in the green standing crop was observed by Mason and Bryant (1975) in Typha angustifolia. Further, a nutrient rich standing crop was present through the winter and early spring in the two populations

at both sites. Boyd (1969,1970) and Boyd and Vickers (1971) pointed out that such a pattern is of considerable significance since plants with high winter value of standing crop and nutrient supply may be at competitive advantage during early spring growth.

Though no significant difference was observed in the allocation pattern of nutrients, nitrogen, phosphorus and potassium to the different organs, between the two populations and the two sites, the allocation of phosphorus and potassium to the underground organs is somewhat more than that of nitrogen in both the sites for both the populations. A large allocation of biomass and nutrients to the under-ground organs in I. cylindrica is to be expected in view of the rarity of sexual reproduction in the predominantly vegetatively reproducing species (Keeley and Keeley, 1977; Saxena and Ramakrishnan, 1983). These results also confirm the importance of nutrient allocation strategy in understanding growth strategy of species (Van Andel and Vera, 1977; Williams and Bell, 1981).

The Burnihat population had a higher nutrient uptake efficiency atleast with respect to nitrogen and potassium compared to the Shillong population in the Burnihat environment which is favourable to the former. However, the two populations did not show any difference at higher elevation. The generally low nutrient uptake efficiency of both the populations at Shillong situation may be due to the low soil temperature which hinders the nutrient uptake and release of nutrients from the soil organic matter (Chapin, 1981)

and also due to the relatively more acidic soil. Though low nutrient uptake efficiency is observed at low fertility level in soil this species tended to compensate it through increased proportional allocation of the biomass to the rhizome system (Saxena and Ramakrishnan, 1981) and more efficient use of phosphorus. A high nutrient use efficiency of phosphorus in the two populations raised at Shillong may be accounted as due to a high rate of absorption of this nutrient from a phosphorus deficient soil (Chapin, 1981).

The results presented here show a high degree of phenotypic plasticity as well as certain degree of genetic differentiation of populations over an altitudinal gradient. These adaptive features of I. cylindrica allow it to colonize a wide variety of environmental situations and yet make adequate growth and allocation for successful vegetative reproduction. An aspect that comes out of this study which is worth noting is that the allocation strategy to the vegetatively reproduced under-ground organs does not change in spite of observed differences in the growth of the two populations grown at different sites which would ensure adequate reproduction.

SUMMARY

In the present study reciprocal transplants of two populations of Imperata cylindrica from a low elevation at Burnihat and a high elevation at Shillong was done to study their growth behaviour.

The lower elevation population showed vigorous growth when grown in its native site than when transplanted to an alien site at higher elevation. The higher elevation population showed a more vigorous growth at lower elevation site than in its native site. This greater vigour of the two populations at lower elevation is related to more favourable temperature conditions. Allocation pattern for biomass in the two populations did not show any difference at the two altitudes.

Concentration of nutrients such as nitrogen, phosphorus and potassium was more in the two populations when raised at Shillong compared to that at the lower elevation at Burnihat. Allocation of phosphorus and potassium was more for the below-ground organs in the populations at both sites compared to the allocation of nitrogen. Though accumulation of nitrogen, phosphorus and potassium followed a similar trend with the biomass accumulation in the above-ground and below-ground parts, the phosphorus accumulation in the below-ground organs showed a sharp increase for the Shillong population raised at Shillong compared to that for the Burnihat population.

Nutrient uptake efficiency was more in the two populations raised at Burnihat whereas nutrient use efficiency was higher in the case of phosphorus only in the two populations grown at Shillong. Vegetative effort was similar in the two populations raised at the different altitudes. Poor growth behaviour in the two populations when raised at higher elevation Shillong may be attributed to the low soil nutrient status and environmental condi-

tions such as temperature. The present studies suggest the existence of altitudinal ecotypes within the species, though the two populations show a high degree of phenotypic plasticity.

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CHAPTER III

POPULATION DYNAMICS OF IMPERATA CYLINDRICA (L.) BEAUV.
VAR. MAJOR RELATED TO SLASH AND BURN AGRICULTURE (JHUM)
IN NORTH-EASTERN INDIA AT TWO DIFFERENT ALTITUDES

INTRODUCTION

Population dynamics of perennial rhizomatous plants is complicated because of their clonal growth resulting in discrete modular units, the 'rametes', the sum of these units representing the 'genet' (Harper, 1978). Since a single 'genet' forms fragmented phenotypes and new recruitment in the former is rare, the population dynamics of these species is determined more by birth and death of clonal modules (Noble et al., 1979). While the tiller dynamics of agriculturally important grasses have received attention in spaced populations (Lamp, 1952; Langer et al., 1964; Robson, 1968), such a study on perennial species under natural conditions has received little attention (Sarukhan and Harper, 1973; Harper, 1978; Doust, 1981).

Imperata cylindrica (L.) Beauv. var. major is a perennial grass coming up in plots under 'slash and burn' agriculture at lower elevations (Toky and Ramakrishnan, 1983) and at higher elevations (Mishra and Ramakrishnan, 1983) in north-eastern India and is an important weed more so when the slash and burn agriculture cycle (the intervening fallow period between two successive croppings on the same plot) is short (Saxena and Ramakrishnan, 1984). It is a tropical weed and has also been reported from other parts of the world under slash and burn agriculture system (Nye and Greenland, 1960). Beard (1953) suggested that this species is susceptible to shading while Schlippe (1956) reported stimulatory role of fire for its growth.

The present study deals with the tiller dynamics of natural populations of I. cylindrica at low and high elevations of north-eastern India upto a period of 5 years of fallow regrowth after slash and burn agriculture locally called as 'Jhum'. The study is also concerned with the effect of fire on tiller dynamics of the species. The objective is to assess the relative weediness of this species in early successional communities and to assess the biological control mechanisms operating in nature.

METHODS OF STUDY

1,3- and 5-year old jhum fallows were identified at Burnihat and at Shillong. The age of the fallow was calculated from the time the site was allowed naturally to regenerate after slash and burn agriculture (Ramakrishnan et al., 1981; Toky and Ramakrishnan, 1983; Mishra and Ramakrishnan, 1983) and was based on the information obtained through the village headman and the community structure of the fallow type. While selecting sites care was taken to ensure similar topography (40° angle), aspect (south facing), and site conditions.

In each fallow, two sets of three permanent quadrats of 1x1 m were laid out at random. While one set was burnt initially after slashing and drying the vegetational cover, the other set was left undisturbed. Slashing was done February, 1981 at both the sites and burnt after one month. In all the quadrats the initial population of I. cylindrica was identified using light metallic colour-coded tags. All the tillers present initially were assumed as

mature tillers since their age was not known. A tiller was considered recruited into the population if it had a minimum height of 3 cm. Observations on birth and death of tillers were recorded at monthly intervals for a period of two years.

The rate of death of mature tillers (Lotka, 1925) was calculated as follows:

$$\text{Rate of decay or death} = \frac{\log_{e}x_{n+1} - \log_{e}x_n + 1}{t_{n+1} - t_n}$$

where x_n = surviving plants at time t_n and

x_{n+1} = surviving plants at time interval $t_{n+1} - t_n$

RESULTS

Population flux

In the unburnt plots at Burnihat and Shillong, the size of the original population of I. cylindrica was significantly larger ($P > 0.01$) in a 1-year old fallow than in a 5-year old fallow, the 3-year old fallow having an intermediate population size. At the end of two-year study period, a similar difference was observed but with a reduced population size. The number of new individuals that arrived and established also declined in older fallows. The net loss due to mortality from the original population as well as from the new arrivals was higher in older fallows than in the younger ones. In 1- and 3-year fallows the expected turnover period was about two years (Table 3.1).

Table 3.1 Populations flux of I. cylindrica at two different altitudinal sites at Burnihat and Shillong (Figures in parentheses represent Shillong site)

	$F_1(b^-)$	$F_1(b^+)$	$F_3(b^-)$	$F_3(b^+)$	$F_5(b^-)$	$F_5(b^+)$
(a) No of tillers/m ² in October, 1980	163+10 (183+11)	0* (0)	77+10 (63+8)	0* (0)	22+3 (23+3)	0* (0)
(b) No of tillers/m ² in October, 1982	137+12 (86+6)	212+8 (130+6)	35+7 (25+5)	57+5 (50+6)	8+2 (6+2)	25+4 (14+4)
(c) Net change (b-a)	-26 (-97)	+212 (+130)	-42 (-38)	+57 (+50)	-14 (-17)	+25 (+14)
(d) Rate of increase (b/a)	0.84 (0.46)	- -	0.45 (0.39)	- -	0.36 (0.26)	- -
(e) No of tillers/m ² arrived between October, 1980 and October, 1982	312+7 (166+6)	413+8 (261+9)	97+5 (68+4)	120+8 (122+6)	48+4 (30+3)	63+5 (60+5)
(f) Total No of tillers lost between October, 1980 and October, 1982	338+6 (263+8)	201+4 (131+9)	139+3 (106+6)	63+5 (72+4)	62+4 (48+3)	38+4 (46+4)
(g) Tillers present in October, 1980 alive by October, 1982	17 (10)	0 (0)	4 (4)	0 (0)	0 (0)	0 (0)
(h) P.C. survival of tillers in(a) (g/a x 100)	9 (6)	- -	5 (6)	- -	- -	- -
(i) Expected time to complete turn over (years) (2/100-h x 100)	2.1 (2.1)	- -	2.1 (2.1)	- -	- -	- -
(j) Total tillers/m ² recorded during the study	475+8 (349+3)	413+6 (261+9)	174+6 (131+8)	120+4 (122+6)	70+5 (153+4)	63+6 (60+5)
(k) Annual mortality % of tillers (f/j x 100)	71 (75)	49 (50)	80 (80)	53 (59)	88 (90)	62 (77)
*Burnt site originally had		152+9 (161+8)		64+10 (60+8)		37+5 (26+5)
F_1 , F_3 and F_5 are 1, 3, and 5-year old fallow plots respectively.						

Fig. 3.1 Changes in the size of the tiller population in a 1-year old fallow at Burnihat. Circle, cumulative recruitment; square, cumulative mortality; triangle, net population size. Open symbol, unburnt plots; closed symbol, burnt plots.

Fig. 3.1

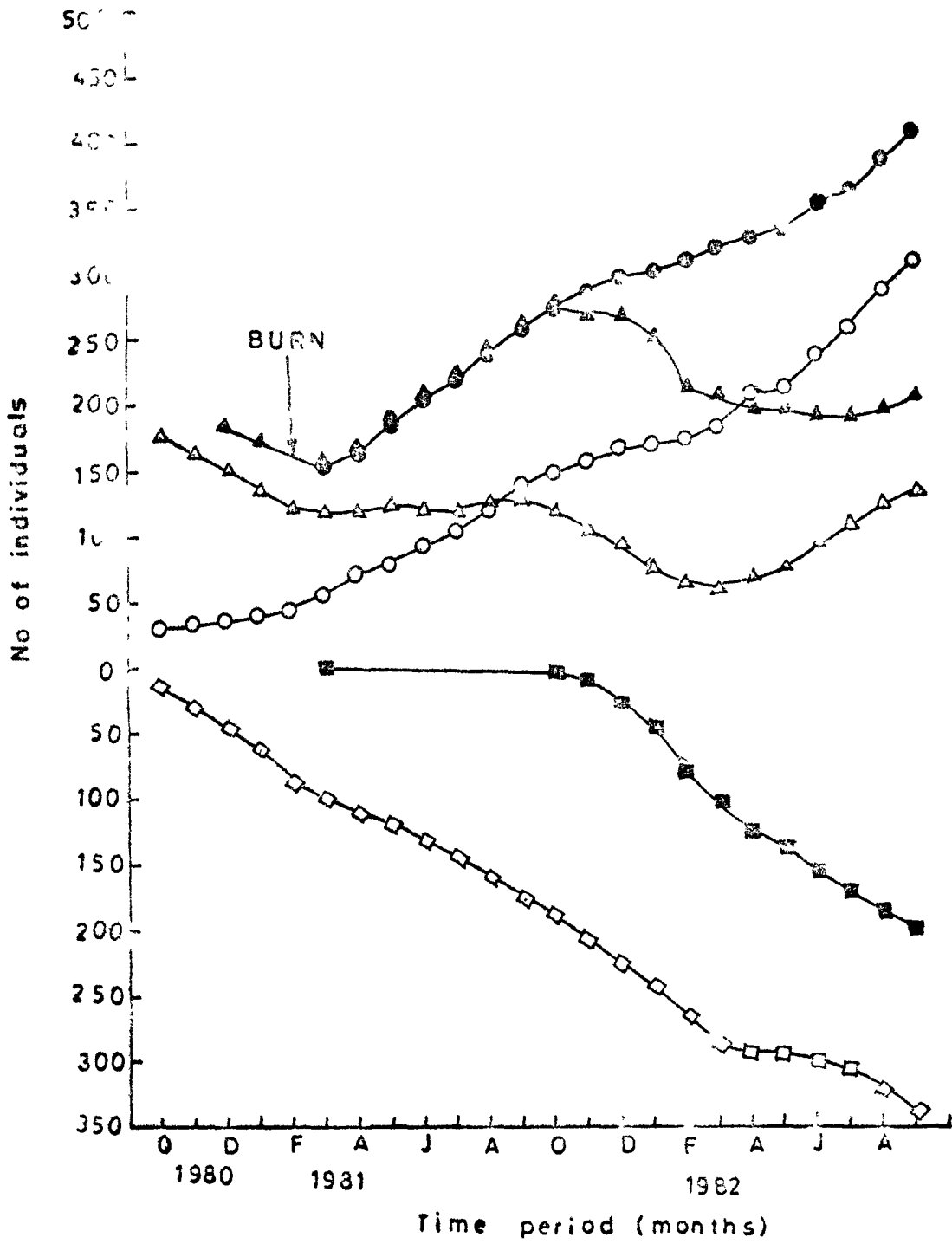
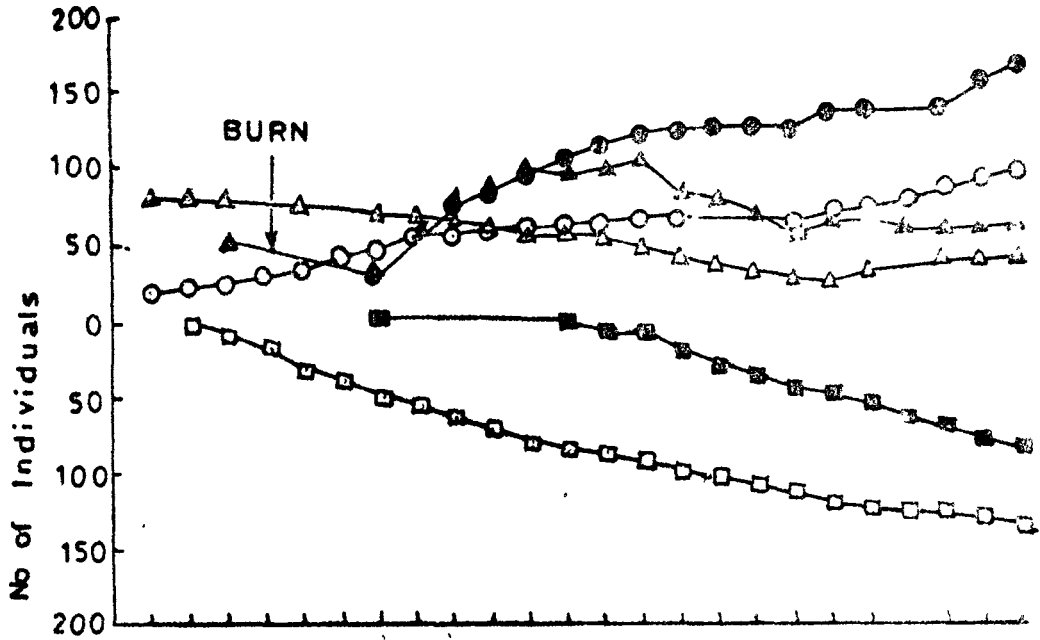


Fig. 3.2 Changes in the size of the tiller population at Burnihat. (a) 3-year old fallow, (b) 5-year old fallow. Circle, cumulative recruitment; squares, cumulative mortality; triangle, net population size. Open symbol, unburnt plots, closed symbol, burnt plots.

Fig.3.2

(a)



(b)

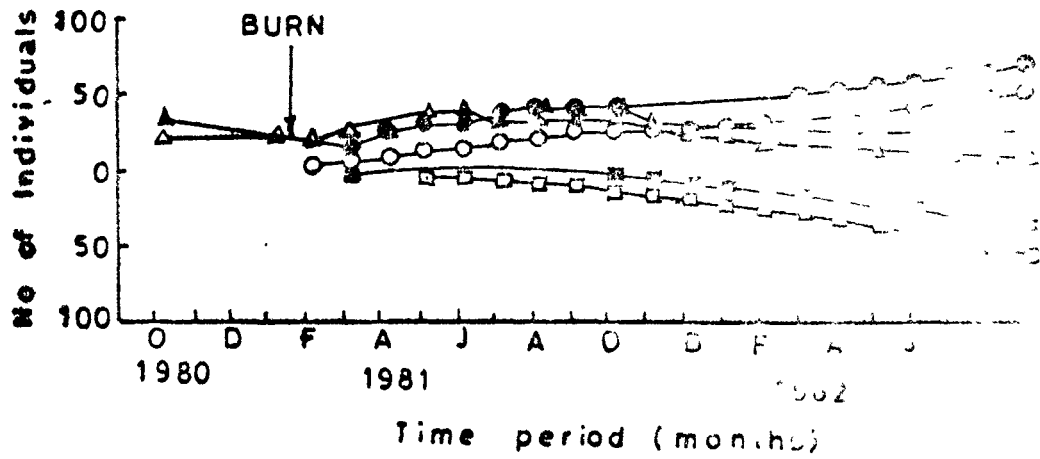
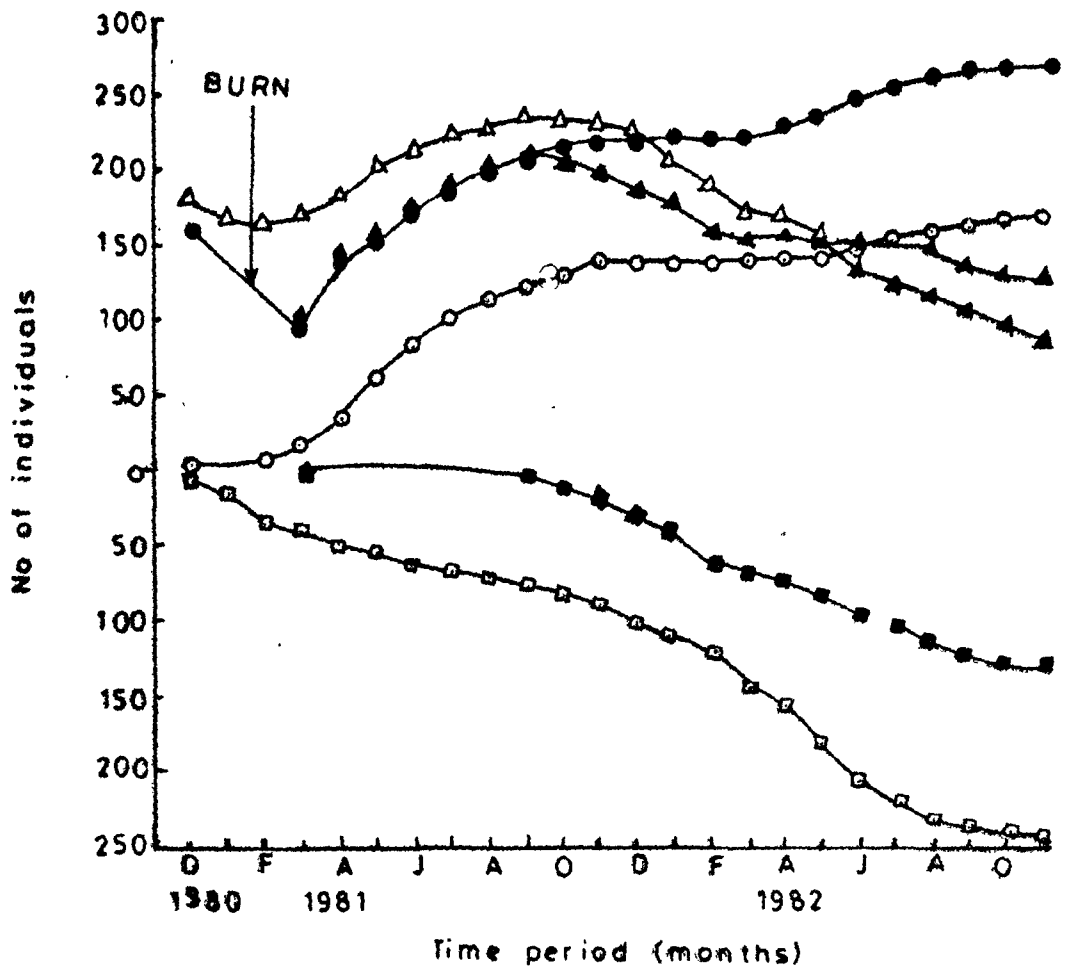


Fig. 3.3 Changes in the size of the tiller population in a 1-year old fallow at Shillong. Circle, cumulative recruitment; square, cumulative mortality; triangle, net population size. Open symbol, unburnt plots; closed symbol, burnt plots.

Fig. 2.3



66

The burnt plots had about the same number of tillers as the unburnt plots in the pre-burn stage, but lost all of them after the burn. However, a significantly higher ($P > 0.05$) number of tillers arrived after the burn compared to the number present at the pre-burn stage. The percentage mortality was lesser in the burnt plots compared to the unburnt plots so that a significantly larger number of tillers ($P > 0.05$) was present at the end of the study period. However, the population flux in the burnt plots related to the age of the fallow showed the same trend as for the unburnt plots, both at Burnihat and at Shillong (Table 3.1).

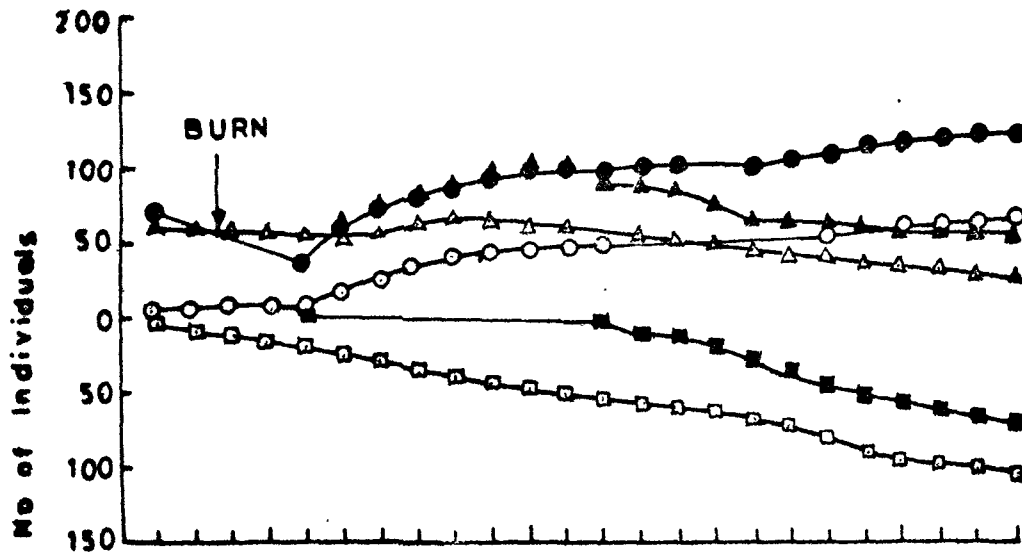
Cumulative mortality/natality pattern

An analysis of the cumulative birth/death pattern over a two-year period at Burnihat suggests (Figs. 3.1, 3.2a,b) that the population size changed more markedly in a 1-year old fallow than in a 5-year old fallow, the 3-year old fallow falling in between the other two. In a 1-year old fallow (Fig. 3.1), the recruitment to the population in both unburnt and burnt plots occurred steadily throughout the study period. However, a distinct difference in the natality pattern was observed between burnt and unburnt plots. In the former, the natality in population resulted in increased net population size upto November, 1981 without any mortality setting in and the net population size declined only subsequently. However, in the unburnt plots, the mortality was a continuing phenomenon right from the beginning of the study period. A similar pattern was observed for the 1-year old fallow at Shillong site too (Fig. 3.3).

Fig. 3.4 Changes in the size of the tiller population at Shillong. (a) 3-year old fallow, (b) 5-year old fallow. Circle, cumulative recruitment; square, cumulative mortality; triangle, net population size. Open symbol, unburnt plots; closed symbol, burnt plots.

Fig. 3.4

(a)



(b)

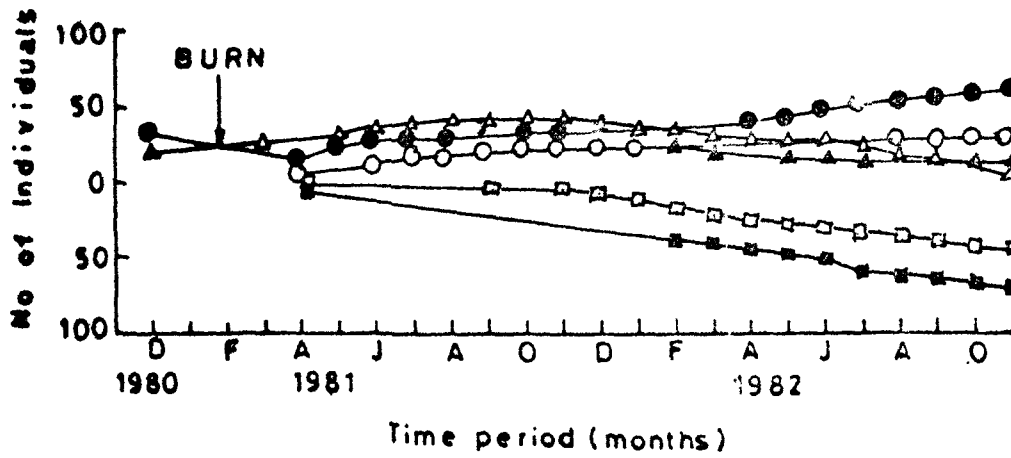


Fig. 3.5 Monthly rate of death of mature tillers at Burnihat. O, 1-year old fallow unburnt; ●, 3-year old fallow unburnt; △, 5-year fallow unburnt.

Fig. 3.5

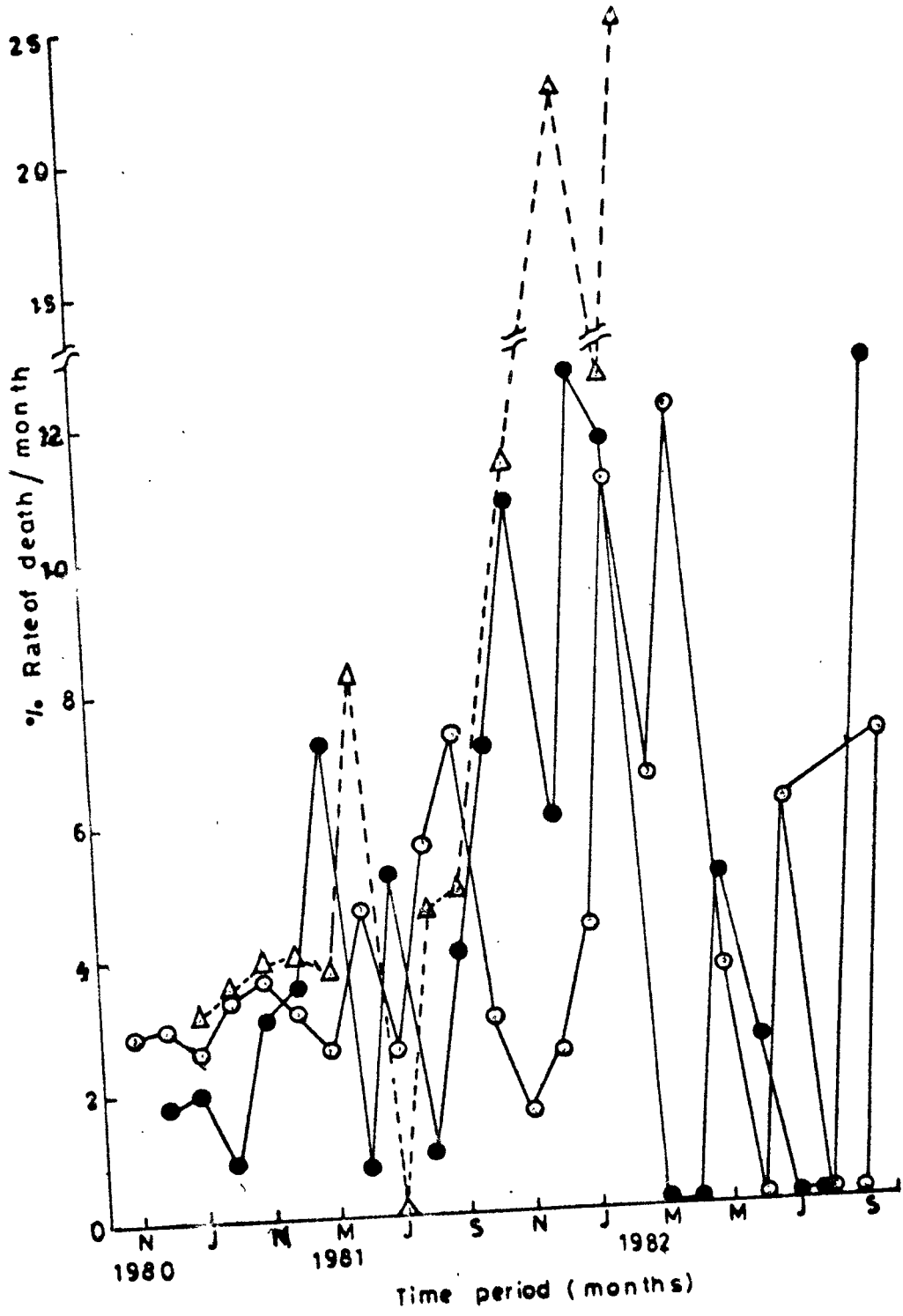
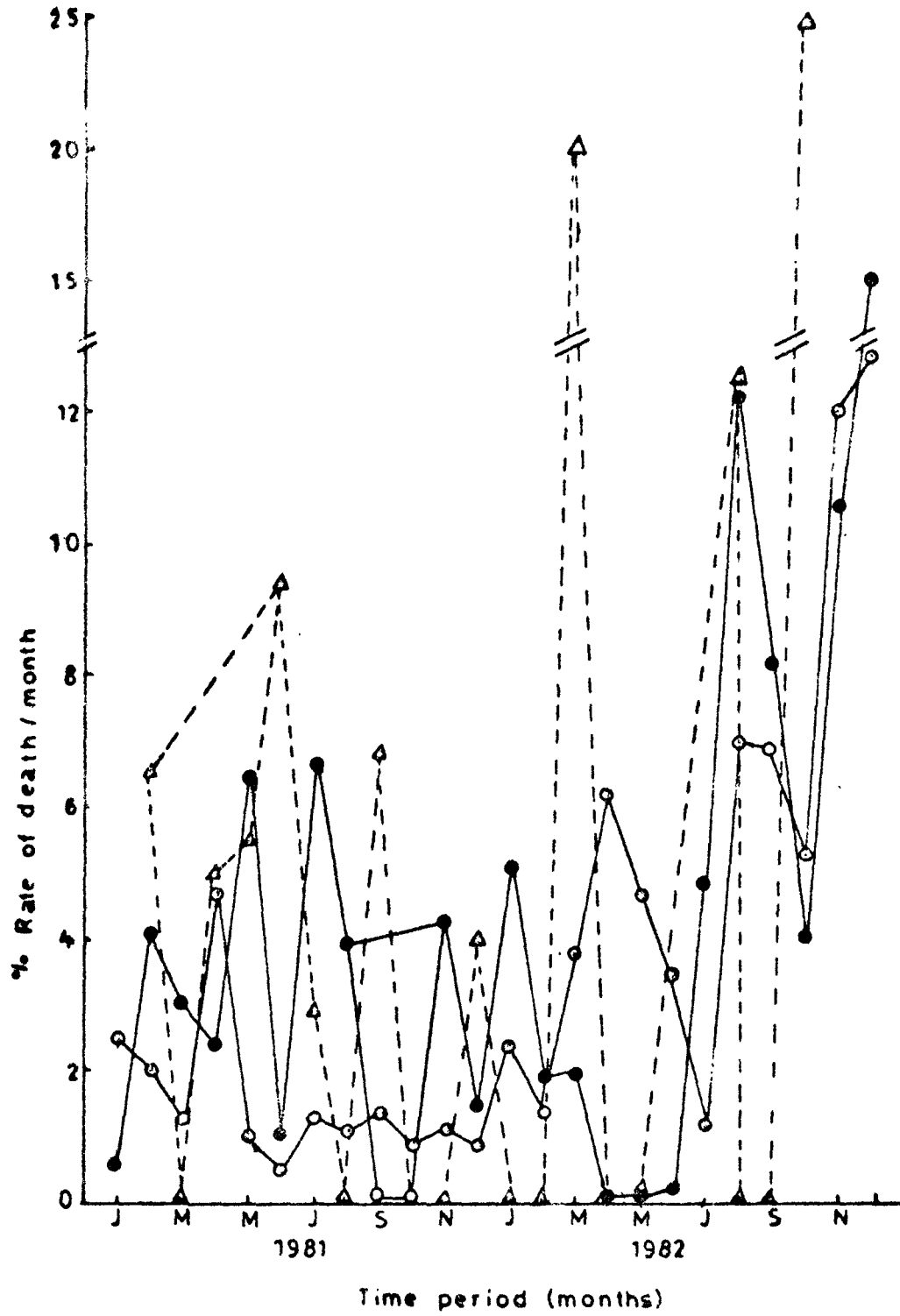


Fig. 3.6 Monthly death rate of mature tillers at Shillong.
(O), 1-year fallow unburnt; (●), 3-year old fallow
unburnt; (Δ), 5-year old fallow unburnt.

Fig.3.6



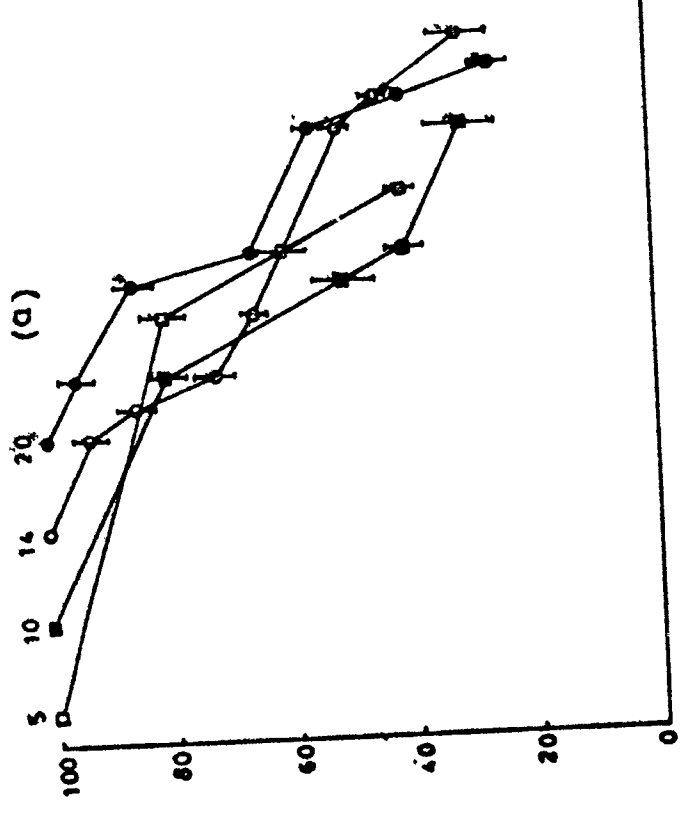
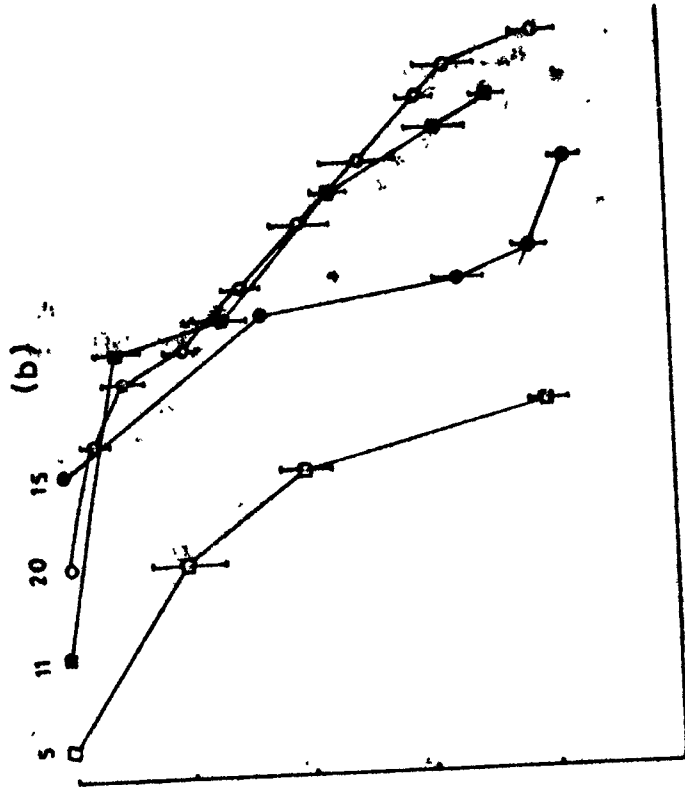
In a 5-year old fallow at both Burnihat and Shillong (Figs. 3.2b, 3.4b) these patterns were obliterated due to poor recruitment, high mortality and very small net population size during different months. In a 3-year old fallow at both the sites, the pattern was intermediate between 1- and 5-year old fallows (Figs. 3.2a, 3.4a).

The rate of decay of mature tillers during the two-years study period in the different fallows at both the sites is shown in Fig. 3.5 and Fig. 3.6. At Burnihat, tillers were marked in October, 1980 and at Shillong in December, 1980. Decay rate increased with the passage of time in all the fallows; peak periods of decay occurred at Burnihat at the end of the first growth season, after one-year period (December-March), whereas at Shillong peak period of decay occurred during the second year of the growing season (August-October). At both sites the decay rate was higher in older fallows than in younger ones. At both sites and in all the fallows, mortality rate tended to fluctuate between high and low values, often declining to 0. At Burnihat, all tillers in a 5-year old fallow decayed after one year period while at Shillong decay in a 5-year old fallow continued for almost the entire two year study period.

Survivorship

The survivorship patterns showed considerable differences between different sites and depending upon fallow age and alteration due to burning. The pattern also changed depending upon whether the cohort was of January, April, July or October (Figs. 3.7, 3.8, 3.9).

Fig. 3.7 Survivorship curve for four tiller cohorts of
January, (□); April, (■); July, (O); and
October, (●) in a 1-year old fallow.
(a) Unburnt plots at Burnihat, (b) Unburnt
plots at Shillong, (c) burnt plots at Burnihat,
(d) burnt plots at Shillong



(d)

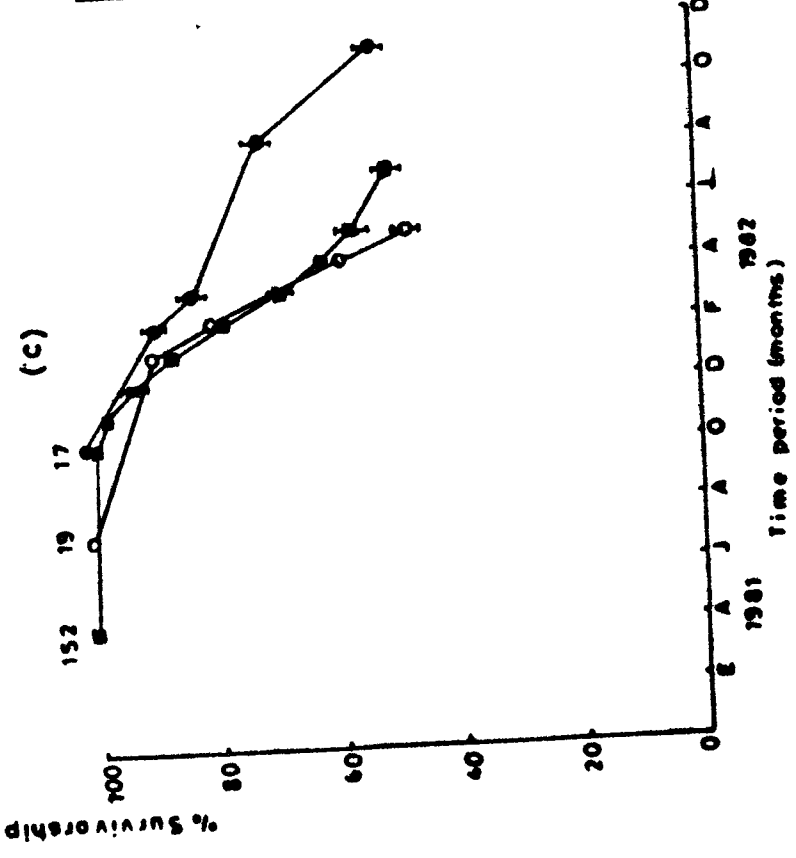
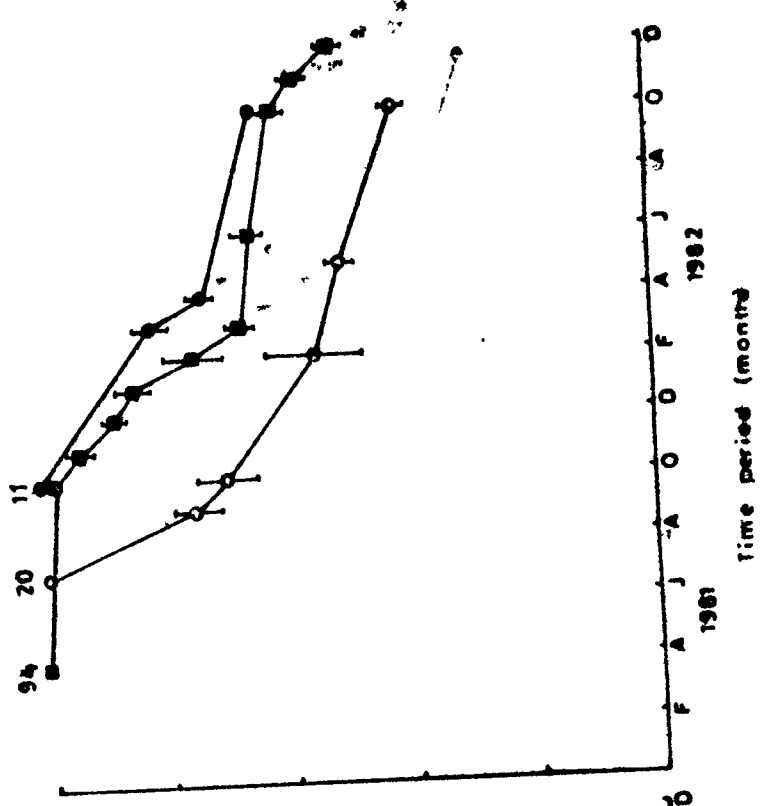
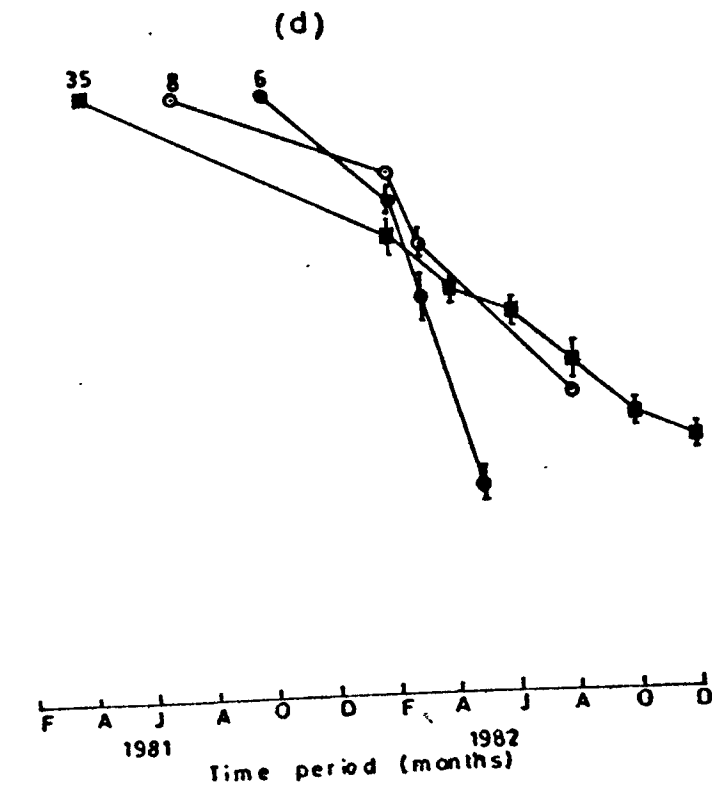
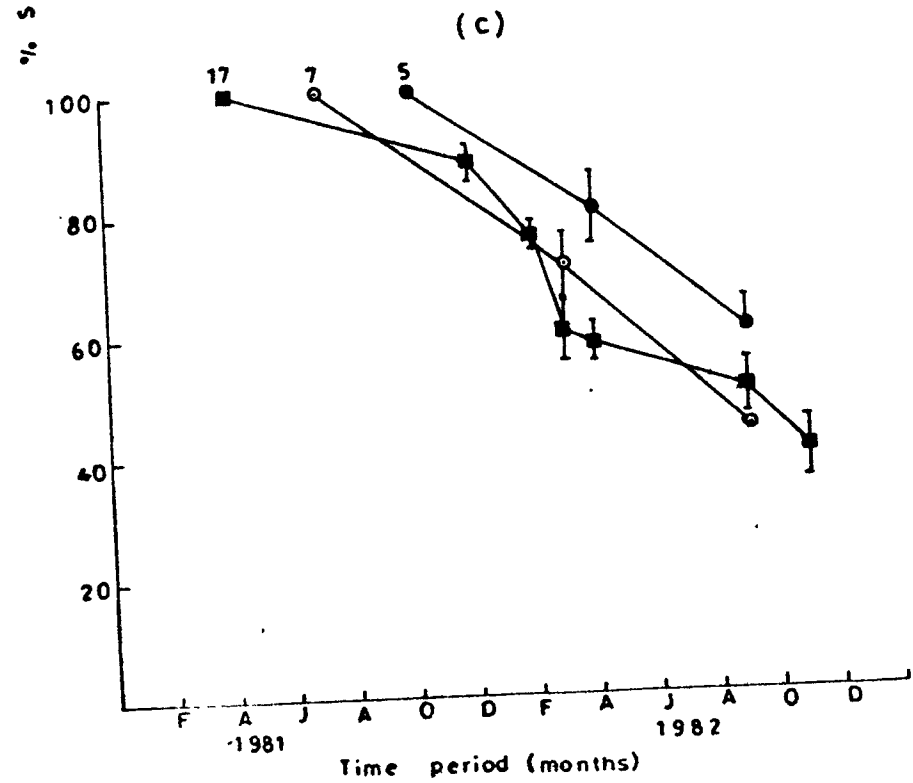
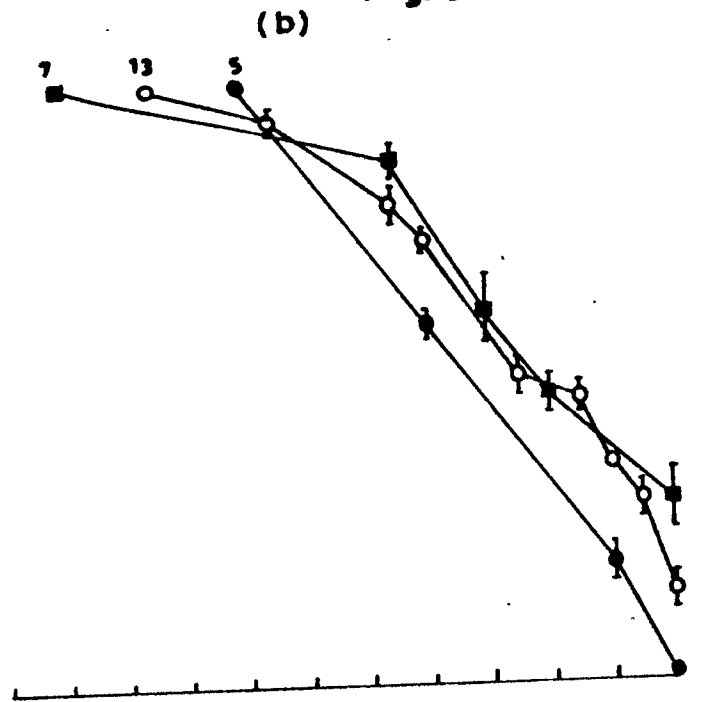
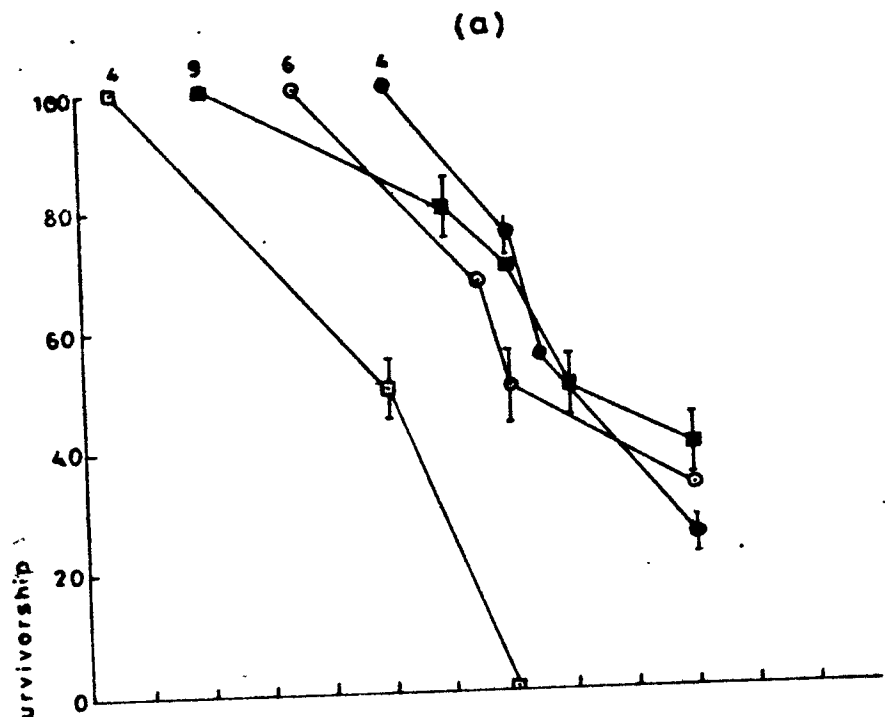


Fig. 3.8 Survivorship curve for four tiller cohorts of January, (□); April, (■); July, (○); and October, (●) in 3-year old fallow.

(a) Unburnt plots at Burnihat, (b) unburnt plots at Shillong, (c) burnt plots at Burnihat, (d) burnt plots at Shillong.

Fig. 28



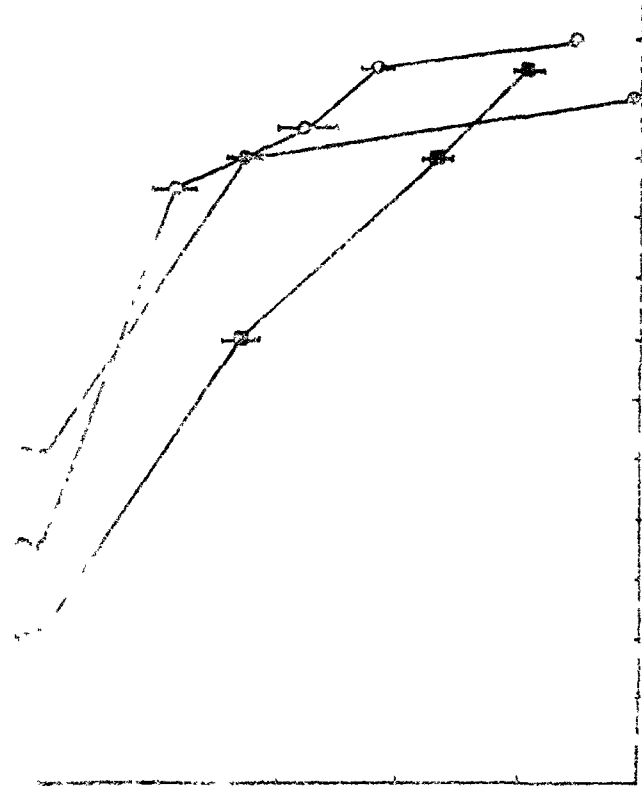
In a 1-year old unburnt fallow the initial cohort size increased from January to October at Burnihat (Fig. 3.7a), and at Shillong (Fig. 3.7b) it increased from January to July with a reduction in October. At Burnihat the cohort of July and October showed faster reduction in population size (1 year 1 month) compared to the other cohorts (about 1 year 6 months). At Shillong the cohorts coming late in the growing season (October and January) showed faster decline compared to the others. After the burn there was a sharp increase in population size compared to the pre-burn stage. In the burnt plots (at both the elevations), the size of the three cohorts decreased from April to October (Fig. 3.7c,d), unlike in the unburnt plots. Here again cohorts coming later in the season generally tended to decline faster.

In general, the 3-year old fallow started with a smaller population size and recruitment compared to a 1-year old fallow, though the burnt plots had larger population size than the unburnt plots (Fig. 3.8a,b,c,d). In the unburnt plots at Burnihat (Fig. 3.8a) the April cohort was the largest whereas at Shillong (Fig. 3.8b) it was the July cohort. While at Burnihat the January cohort showed sharper decline in population size compared to other cohorts, at Shillong it was the October cohort which declined sharply. In both the burnt sites (Fig. 3.8c,d) population decline was slower and the ultimate population size at the end of the two-year period tended to be larger.

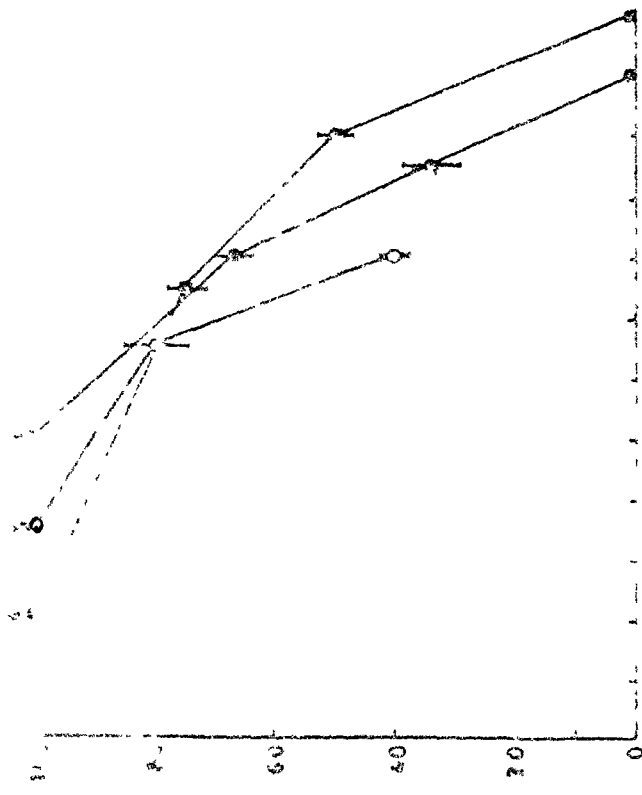
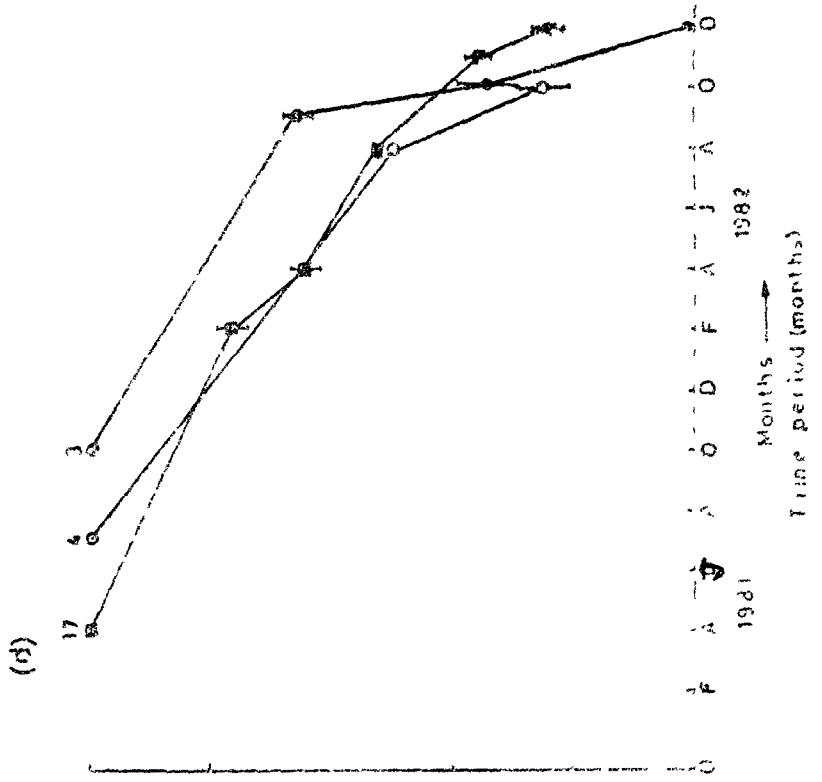
Fig. 3.9 Survivorship curve for four tiller cohorts of April, (■); July, (○); and October, (●); in a 5-year old fallow.

(a) Unburnt plots at Burnihat, (b) unburnt plots at Shillong, (c) burnt plots at Burnihat, (d) burnt plots at Shillong.

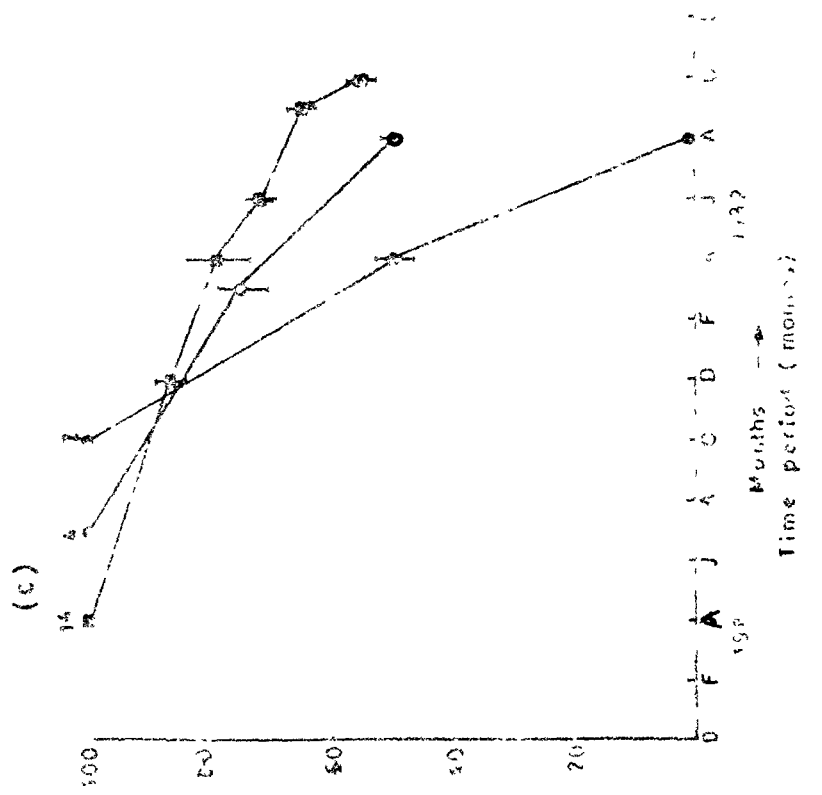
Fig. 3.9



(d)



(c)



Survival %

1982

1981

1982

1981

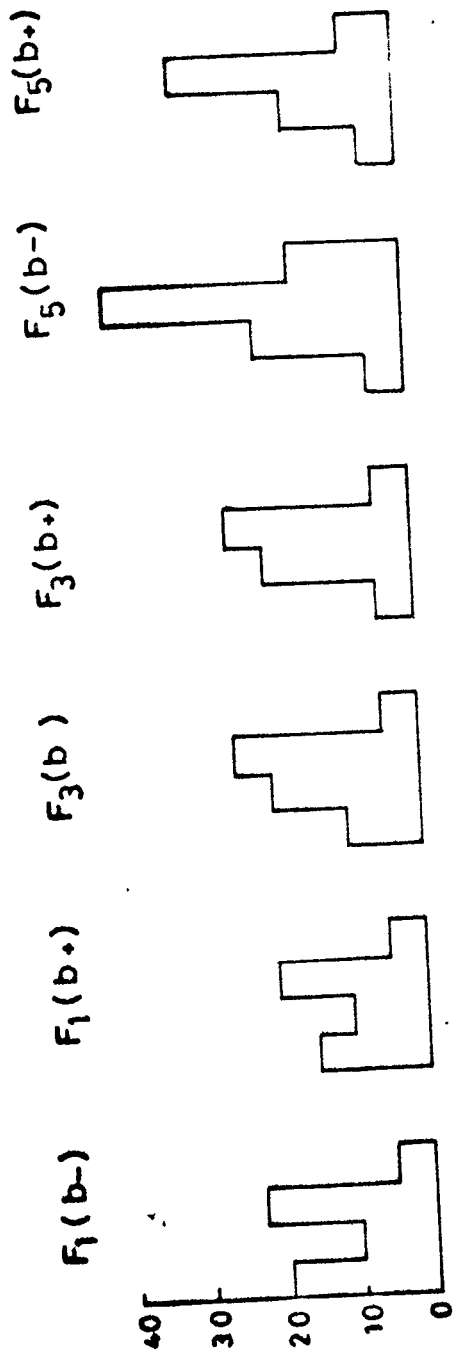
Months →
Time period (months)

Months →
Time period (months)

Fig. 3 .10 Age class distribution attained at death by the tillers born during the study at different sites. (a) Burnihat, (b) Shillong. Age classes (year) 1, 0-0.5; 2, 0.6-1.0; 3, 1.0-1.5; 4, 1.6-2.0.

Fig 3.10

(a)



% Frequency

(b)

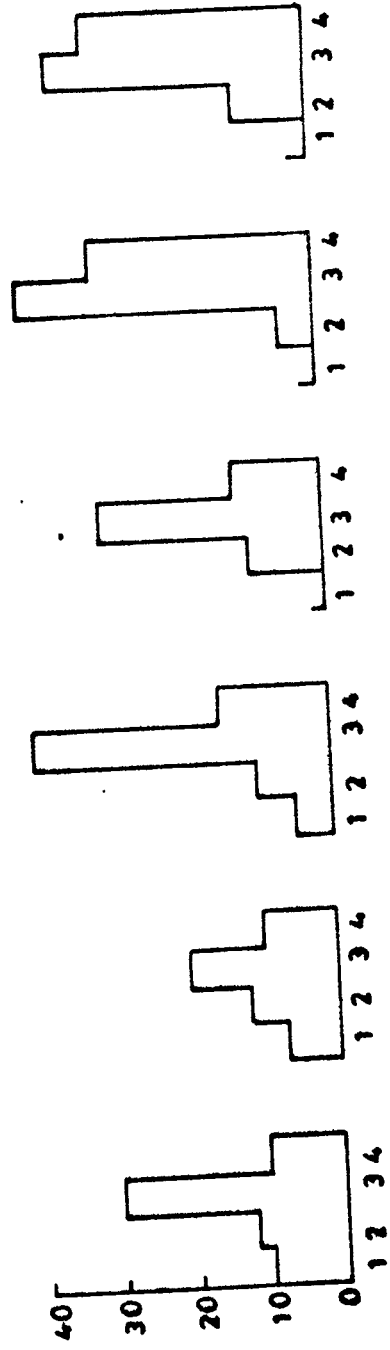
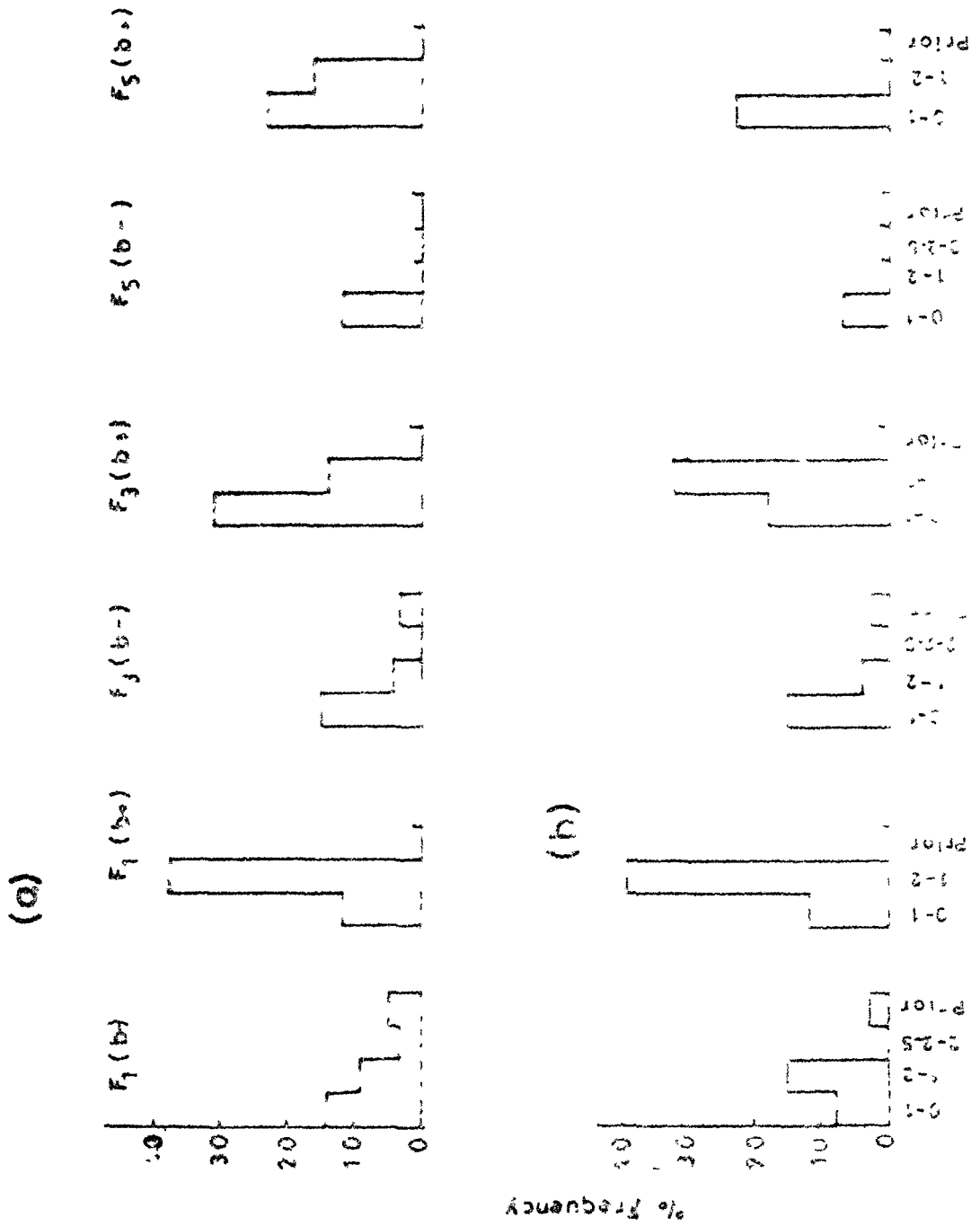


Fig. 3.11 Age structure of living tillers at the end of the study period after two years. (a) Burnihat, (b) Shillong.
0-1, 1982; 1-2, 1981; 2-2.5, 1980; prior, before 1980.

Fig. 3.11



The cohort size of the population in a 5-year old fallow was even smaller than the 3-year old fallow at both sites (Fig. 3.19a,b,c,d). Initial cohort size of the unburnt plots at both sites (Fig. 3.9a,b) was largest for the July cohort. In the unburnt fallow at Burnihat no individual of April and October cohorts survived and only 40% of the July cohort survived. In the unburnt plots at Shillong, on the other hand, the October cohort died completely. In both the burnt sites of a 5-year old fallow, initial cohort size declined from April to October (Fig. 3.9c,d). The October cohort at both sites died completely before the end of the study period.

Age structure of tiller population

At Burnihat and at Shillong the age structure of the tillers that came and died during the study period showed difference due to age of the fallow, but did not show much difference due to burn (Fig. 3.10). In general, in all the fallows, death was more in the age group of 1 to 1.5 year age class. However, this tended to be more pronounced in older fallows; in a 1-year old fallow considerable death also occurred in the age group of 0-6 months.

At both the sites, the age structure of the living population (Fig. 3.11) in the unburnt plots had a broader age distribution compared to the burnt plots where the younger age groups were more abundant. With the age of the fallow, in unburnt plots, older age groups declined markedly.

DISCUSSION

Population stability is a rare phenomenon in successional habitats, where a number of environmental factors change with community development. I. cylindrica found in early successional fallows of 5 to 6 years of age after slash and burn agriculture, is subjected to frequent cutting and burning, particularly when the slash and burn cycle is a short one of less than 5-6 years. Further, a number of micro-environmental changes occur during the early phase of secondary succession, such as fast changes in the moisture and nutrient status in the soil (Toky and Ramakrishnan, 1981; Ramakrishnan and Toky, 1981), improved light availability and rapid colonization of the site by a number of herbaceous weedy species (Saxena and Ramakrishnan, 1984) resulting in competition for nutrient resources in the soil that are in short supply and subsequent shading caused by larger shrubs and trees that come up after about 5-6 years of fallow regrowth (Toky and Ramakrishnan, 1983; Mishra and Ramakrishnan, 1983).

Population flux

The size of the original population of I. cylindrica and the survival over a period of two years at both low and high elevation sites at Burnihat and Shillong got markedly reduced with the age of the fallow so much so that in a 5-year old fallow the ultimate population size was extremely small compared to a 1-year old fallow. Recruitment of new tillers also declined sharply with the age of the fallow. These results are indicative of the unfavourable

condition created by increased intra- and inter-specific competition for the available resources (Harper and White, 1974; Howthorn and Cavers, 1976). Alteration in the micro-environment of the different fallows through burning seems to enhance the tiller population size that comes up immediately after the burn and during the subsequent two-year period compared to the unburnt plots. Burning seems to have a promotary effect on recruitment through tillers as also suggested by Schlippe (1956).

Mortality/natality patterns

Pronounced monthly/seasonal differences in the mortality/natality patterns of the tillers in a 1-year old fallow as compared to 3- and 5-year old fallows are related to larger population flux in the 1-year old fallow. In the unburnt plots mortality is a continuing risk throughout the entire period of two years. However, the absence of any mortality occurring upto a period of 6-7 months after tiller recruitment after fire in the burnt plots is suggestive of lesser competition for available resources from other species. Subsequently, mortality here is too a continuing risk throughout the life cycle, rather than being exaggerated in the younger stages only (Ramakrishnan and Kumar, 1971; Kapoor and Ramakrishnan, 1975), and adjustment in numbers took place all the time in relation to increase in size of the plants (Harper, 1967), and the increased intra- and inter-specific competition (Harper and White, 1974).

Survivorship of Cohorts

In a 1-year old fallow at Burnihat where inter-specific competition may not be very severe, intra-specific competition seems to determine the rate of decline in population size so that in the unburnt plots decay of tillers was more rapid in July and October cohorts where more initial recruitment occurred. In a 1-year old fallow at Shillong, however, decay rate seems to be more related to season so that faster rate was observed during the winter period (October and January cohorts). In the burnt plots, however, decay rate was slower than in unburnt plots, again suggesting promotary effect of fire; decay rate here seems to occur late in the growing season. In older unburnt fallows of 3- and 5-year at Burnihat and Shillong, decay rate of tillers was more for those cohorts coming late in the season and climate, perhaps, plays a more important role in the decay rate of the different cohorts. Decay rate was generally more in older fallows.

Age structure of the tillers

Age structure of dead and living populations of a species in a community suggests to a great extent the health of the population as a whole. The fact that there was an increase in the size of the dead population belonging to the age groups of 1 to 1.5 years with increase in the age of the fallow and that there was a more uniform age class distribution in younger fallow suggests that tillers are eliminated more frequently in the older fallows compared to the younger fallow. Conversely, the more frequent occurrence of younger tillers of the living population in



3- and 5-year old fallows suggests that though recruitment may occur here, the chance of it reaching maturity is lesser compared to a 1-year old fallow.

In conclusion it may be mentioned that I. cylindrica is naturally controlled in the jhum fallows if the jhum cycle is more than 5-6 years due to partly increased competition in older fallows and partly due to shading effect of larger shrubs and trees. Kushwaha and Ramakrishnan (1982) have shown that shading under experimental conditions has an adverse effect on the growth of I. cylindrica and that allocation of biomass to underground perennating organs got markedly reduced. Where the jhum cycle is a short one of less than 5-6 years, I. cylindrica tends to stabilize in the fallows as natural control mechanisms do not operate resulting in arrested succession of weedy species (Ramakrishnan et al., 1981; Toky and Ramakrishnan, 1983). Another significant observation that emerges out of this study is the fire related promotary effect on recruitment and establishment of tiller population of this important weed of the slash and burn agriculture system.

SUMMARY

Imperata cylindrica is a noxious weed coming up in early successional fallows after slash and burn agriculture (Jhum) which is prevalent in the north-eastern hill regions of India. The regeneration and establishment patterns through tillers is more vigorous in younger fallows and is drastically curtailed in older ones as

evident from mortality/natality pattern and age structure of the tiller populations. The regeneration of the tiller was enhanced in burnt plots as compared to unburnt plots. Differences were observed with respect to recruitment pattern in different cohorts studied. This was related to environmental conditions as well as to increase intra- and/or inter-specific competition. The implication of the results in natural control of this weed under longer slash and burn cycles and arrested succession under shorter cycles has been discussed.

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CHAPTER IV

FATE OF INTRODUCED RHIZOMES AND SEEDS OF IMPERATA
CYLINDRICA (L.) BEAUV. AFTER SLASH AND BURN AGRI-
CULTURE (JHUM) IN NORTH-EASTERN INDIA AT TWO
ALTITUDES

INTRODUCTION

The studies on population dynamics of vegetatively propagated perennial species has only started receiving attention in recent times (Marshal and Sagar, 1965; Kays and Harper, 1974). Many of these studies deal with the demography and dynamics of naturally established plant populations. Much less is known on the fate of introduced populations under different natural environments.

Earlier studies on the fate of introduced populations through rhizomes and seeds (Chippindale, 1948; Tamm, 1956; Cavers and Harper, 1967; Putwain and Harper, 1970) suggest that the former tend to survive better as compared with individuals of seed origin. The present study deals with introduced population in the form of tillers and seeds of Imperata cylindrica (L.) Beauv. in fallows of different ages upto 10-years after slash and burn agriculture. Since the presence and abundance of associated species may profoundly influence establishment pattern (Ellenberg, 1953; Odum and Odum, 1959; Harper, 1964), the present study also deals with this aspect.

I. cylindrica is a perennial weed coming during and after cropping under slash and burn agriculture at elevations upto about 1500 meters in Meghalaya. This species is an important component in jhum fallows upto about 5-6 years, after which it gets naturally eliminated during secondary succession (Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983a) due to shading. Under shorter jhum cycles of 5-year or less, this species forms an important component of the arrested weed community (Saxena and Ramakrishnan, 1984).

METHODS OF STUDY

0, 3, 5 and 10-year old jhum fallows were identified at low elevation at Burnihat and at high elevation at Shillong. The age of the fallow was calculated from the time the site was allowed to naturally regenerate after slash and burn agriculture.

In each fallow, rhizome pieces with one emergent vegetative bud at densities of 25, 50 and 100 per m² and seeds at the rate of 100, 200 and 500 per m² were introduced. The numbers present after one month was considered for calculation of percentage increase/decrease in the population size occurring subsequently. A rhizome was considered established on production of atleast one new leaf from the vegetative bud. A seedling was considered germinated on the appearance of the plumule above the soil surface. In each fallow, introduction was done in six 1x1 m plots. Half of the plots were undisturbed with the existing vegetation and the other half had the existing vegetation removed. All treatments were replicated three times.

RESULTS

Early successional communities

The secondary successional communities analysed upto 10 years of fallow development both at Burnihat (Table 4.1) and at Shillong (Table 4.2) show that they are dominated by weedy species upto 5 years of regrowth. In fresh fallow at Burnihat Borreria hispida and Imperata cylindrica are the important weeds, but in 3- and 5-year old fallows, Eupatorium odoratum forms an important

Table 4.1 Important value indices of major associated plant species at Burnihat

Species	F ₀	F ₃	F ₅	F ₁₀
<u>Ageratum conyzoides</u> L.	12.0	-	-	-
<u>Arundinella bengalensis</u> (Spreng) Druce	6.5	4.2	-	-
<u>Borreria hispida</u> (L.) K. Schurr.	20.2	-	-	-
<u>Bauhinia variegata</u> L.	3.0	7.0	9.0	15.2
<u>Callicarpa arborea</u> Roxb.	-	2.3	5.2	10.6
<u>Careya arborea</u> Roxb.	7.1	8.2	-	10.2
<u>Cedrela toona</u> Roxb.	5.2	6.7	5.2	5.8
<u>Cyperus pilosus</u> Allinoid	10.0	-	-	-
<u>Desmodium triquetrum</u> DC.	4.0	5.2	7.2	-
<u>Eupatorium odoratum</u> L.	-	78.5	67.2	7.2
<u>Eugenia tetragona</u> Wight.	4.0	5.0	7.0	9.4
<u>Ficus hispida</u> L.	-	4.5	7.2	14.4
<u>Imperata cylindrica</u> (L.) Beauv.	20.2	15.2	12.4	-
<u>Litsaea assamica</u> Hk. f.	-	-	-	7.2
<u>Maesa indica</u> Wall.	-	-	5.2	11.2
<u>Osbeckia crinita</u> Benth.	6.0	8.0	-	-
<u>Setaria glauca</u> (L.) Beauv.	7.0	7.5	-	-
<u>Schinus wallichii</u> (DC.) Korth.	-	2.4	5.8	20.2
<u>Vitex peduncularis</u> Wall.	-	-	11.2	40.2
<u>V. glabrata</u> Br.	-	-	10.2	11.4

Table 4.2 Important value indices of major associated plant species at Shillong

Species	F ₀	F ₃	F ₅	F ₁₀
<u>Ageratum conyzoides</u> L.	8.3	4.0	-	-
<u>Anaphelis contorta</u> L.	12.5	8.2	-	-
<u>Artemisia parviflora</u> L.	8.4	5.2	2.0	-
<u>Artemisia valaris</u> L.	-	-	-	5.2
<u>Bidens bitunalis</u> L.	9.5	-	-	-
<u>Dichranopteris linearis</u> Burm. f.	-	11.4	12.0	14.2
<u>Drymaria cordata</u> L.	13.0	-	-	-
<u>Eleagnus latifolia</u> L.	-	-	-	7.2
<u>Eupatorium adenophorum</u> Spreng.	5.4	21.8	45.2	7.3
<u>Galium mollugo</u> L.	8.0	2.0	-	-
<u>Hypochaeris radiata</u> L.	18.5	29.2	5.0	-
<u>Imperata cylindrica</u> (L.) Beauv.	30.5	25.4	7.0	-
<u>Lantana camara</u> L.	-	11.2	12.5	5.9
<u>Myrica esculenta</u> Buch. Ham.	-	-	-	6.2
<u>Osbeckia crinita</u> Benth.	-	10.1	21.2	10.2
<u>Panicum khasianum</u> Munro.	1.5	3.2	-	-
<u>Pinus kesiya</u> Royle (Seedling)	-	7.0	5.0	9.2
<u>Pinus kesiya</u> Royle (Tree)	-	-	-	34.5
<u>Plantago major</u> L.	28.0	8.2	-	-
<u>Pteridium aquilinum</u> (L.) Kuhn ex Dicken	-	-	20.2	9.8
<u>Rubus micropetalus</u> Gard.	6.2	8.5	5.3	15.2
<u>Rubus ellipticus</u> Sm.	-	2.8	4.2	7.2
<u>Sida cordifolia</u> L.	-	-	5.2	6.8
<u>Smilax aspera</u> L.	-	-	4.6	5.4

Fig. 4.1 Number of individuals expressed as a percentage of the initial tiller number introduced into a 0-year old fallow at the end of one year study period at densities of 25, (○); 50, (●); and 100, (△); at Burnihat. (a) Without associates, (b) With associates.

Fig. 4.1

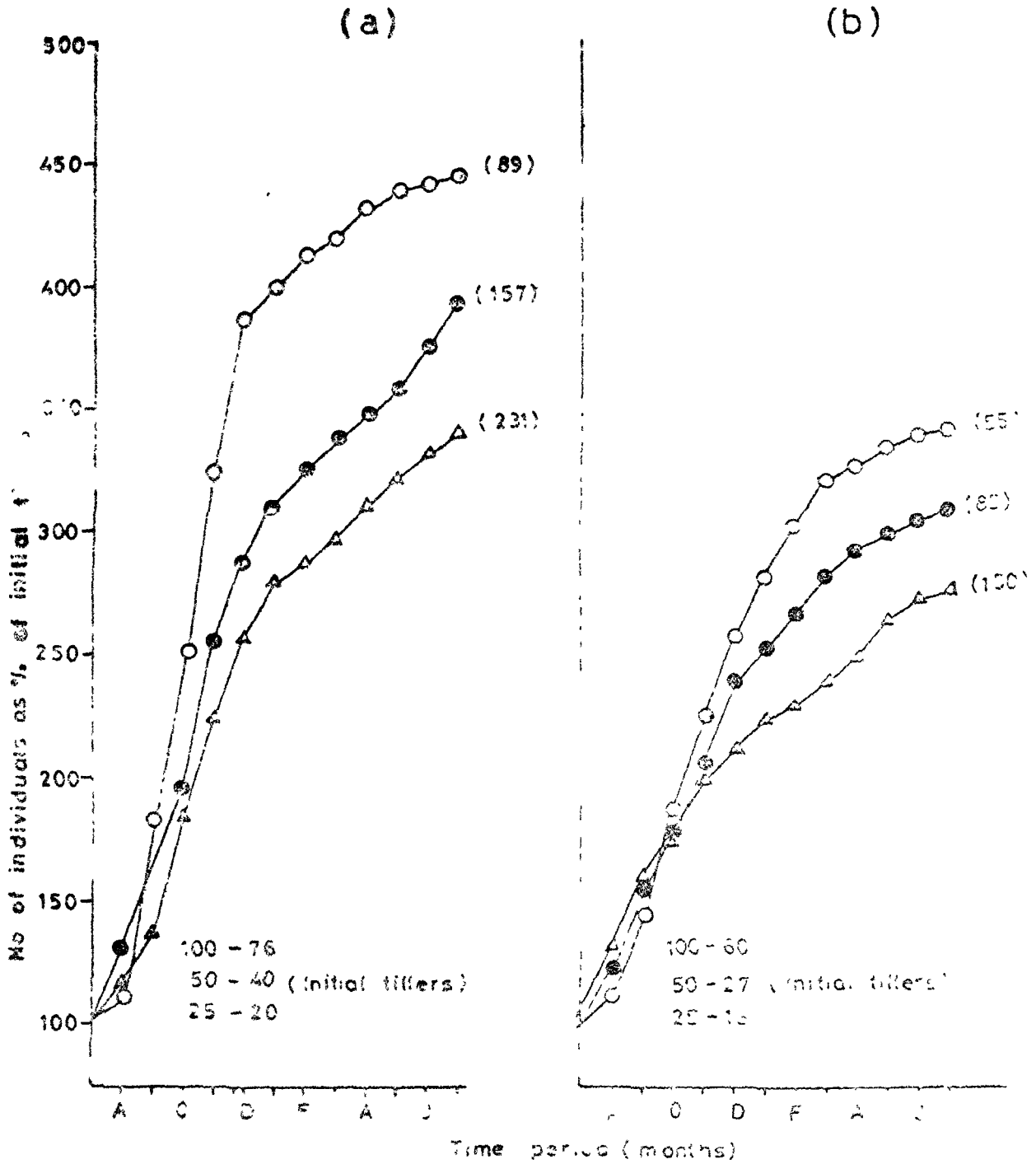
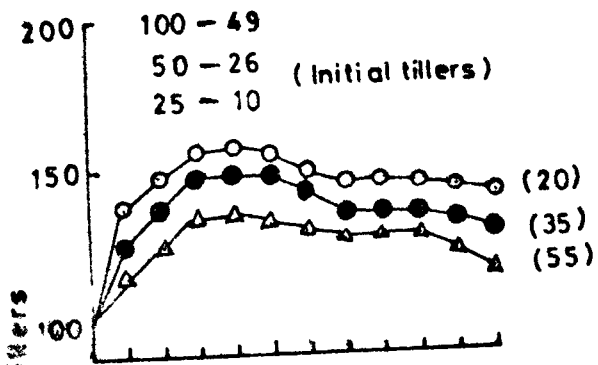


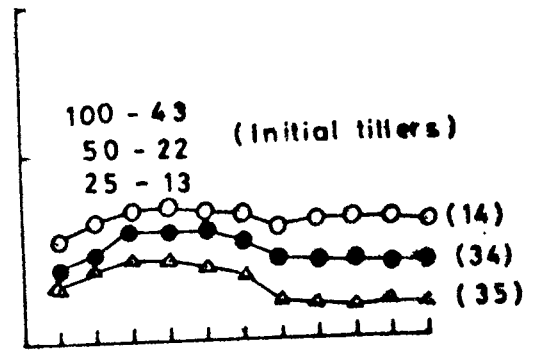
Fig. 4.2 Numbers of individuals expressed as a percentage of the initial tiller number at the end of one year study period at densities of 25 (O), 50 (●), and 100 (Δ) introduced at Burnihat. (a) 3-year old fallow without associates, (b) 3-year old fallow with associates, (c) 5-year fallow without associates, (d) 5-year old fallow with associates, (e) 10-year old fallow without associates, (f) 10-year old fallow with associates.

Fig. 4.2

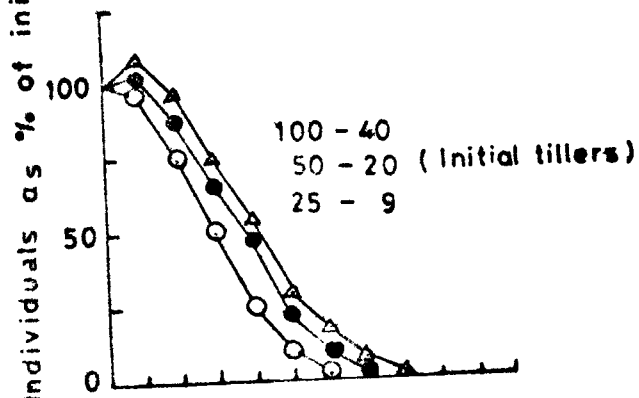
(a)



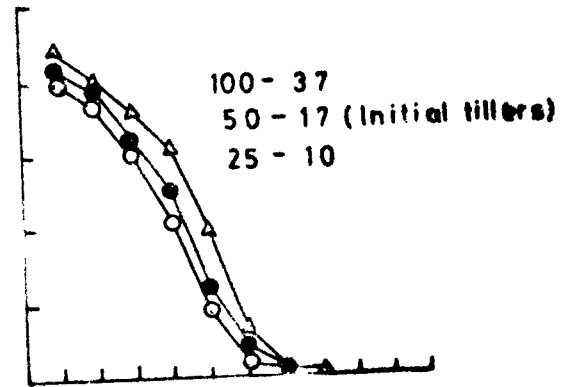
(b)



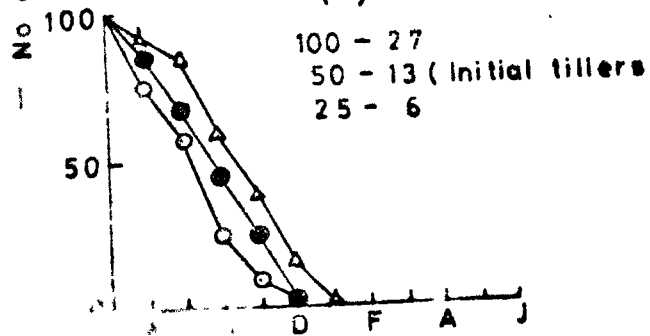
(c)



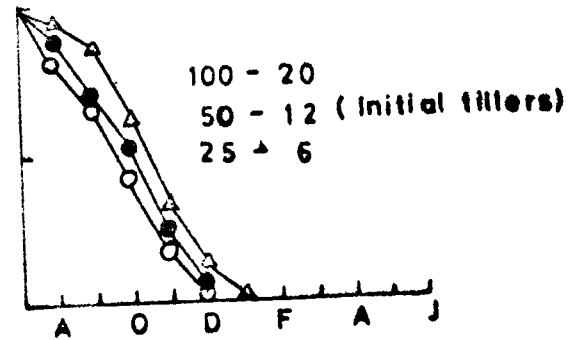
(d)



(e)



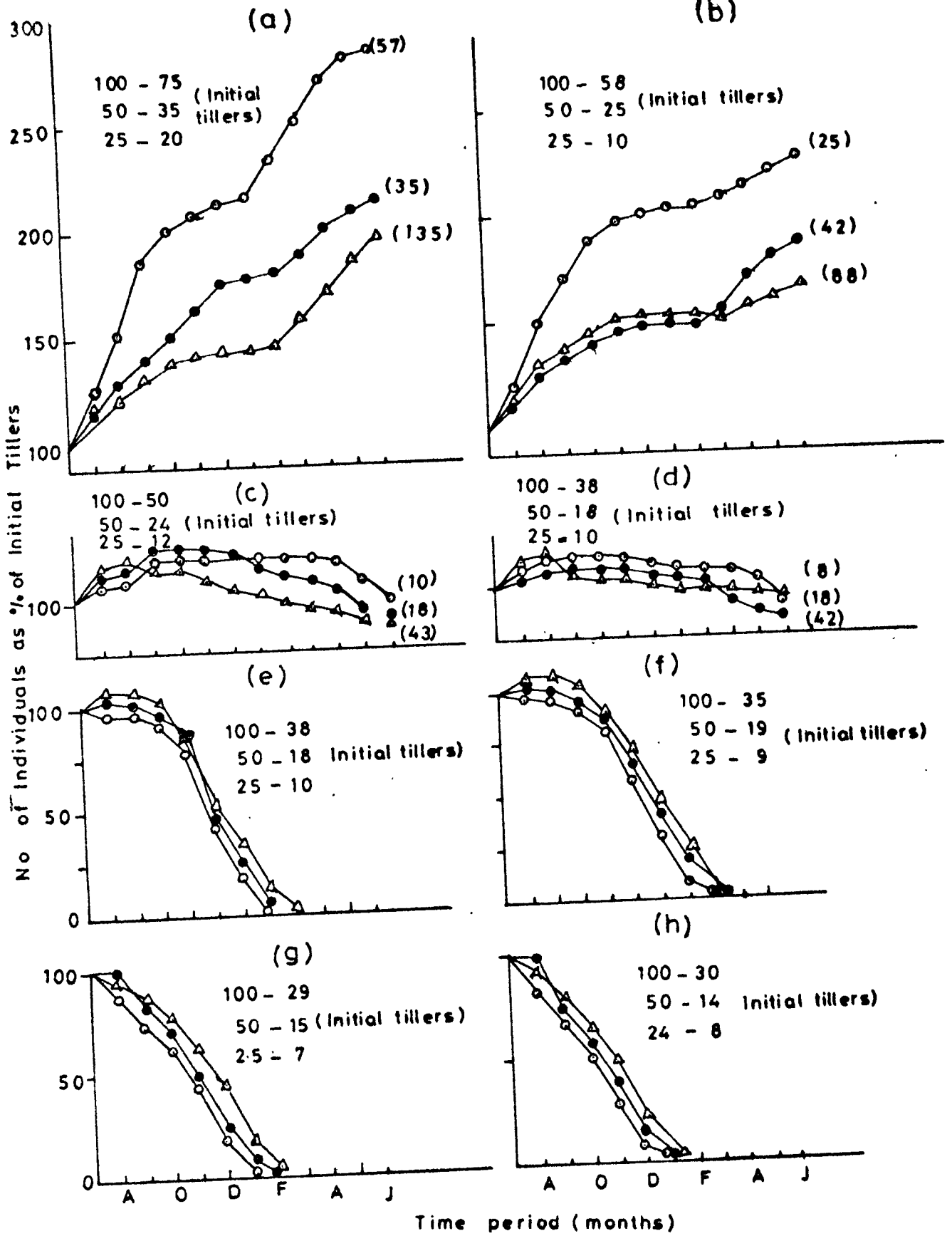
(f)



Time period (months)

Fig. 4.3 Number of individuals expressed as a percentage of the initial tiller number at the end of one year study period at densities of 25 (○), 50 (●), and 100 (Δ) introduced at Shillong. (a) 0-year old fallow without associates, (b) 0-year old fallow with associates, (c) 3-year old fallow without associates, (d) 3-year old fallow with associates, (e) 5-year old fallow without associates, (f) 5-year old fallow with associates, (g) 10-year old fallow without associates, (h) 10-year old fallow with associates.

Fig. 4.3



component in the community. In a 10-year old fallow there is a drastic decline in weedy species. A number of shrubs and trees come up such as Bauhinia variegata, CalliCARPA arborea, Ficus hispida, Schima wallichii and Vitex peduncularis. At Shillong, Plantago major, Anaphelis contorta, Hypochaeris radiata, Drymaria cordata are important species in a 0-year old fallow. In 3- and 5-year old fallows Eupatorium adenophorum, Dichranopteris linearis and Pteridium aquilinum also occur. In a 10-year old fallow, shrubs such as Osbeckia crinita, Rubus micropetalus and trees such as Pinus kesiya come up with the decline of weed species.

Fate of introduced tiller population

In a 0-year old fallow the establishment of tillers after one month of introduction was generally higher in the cleared plots than in the plots with the associates. Though the actual number of tillers established was higher in all the plots where the initial number was higher, the percentage establishment in relation to the original number was higher in the plots with lower initial density. Cleared plots had higher percentage establishment compared to the uncleared plots. The site at Shillong in general showed lower size in ultimate tiller population as well as percentage establishment compared to the site at Burnihat (Figs. 4.1a,b; 4.3a,b).

At the end of one month after introduction the number of tillers established in a 3-year old fallow was lower in the cleared and uncleared plots compared to 0-year old fallow. Unlike in a

Fig. 4.4 Fate of introduced seeds: percentage survival of seedlings at densities of 100 (○), 200 (●), and 500 (Δ) at the end of one year study period at Burnihat. (a) 0-year old fallow; (b) 3-year old fallow; (c) 5-year old fallow; (d), 10-year old fallow.

Fig. 4.4

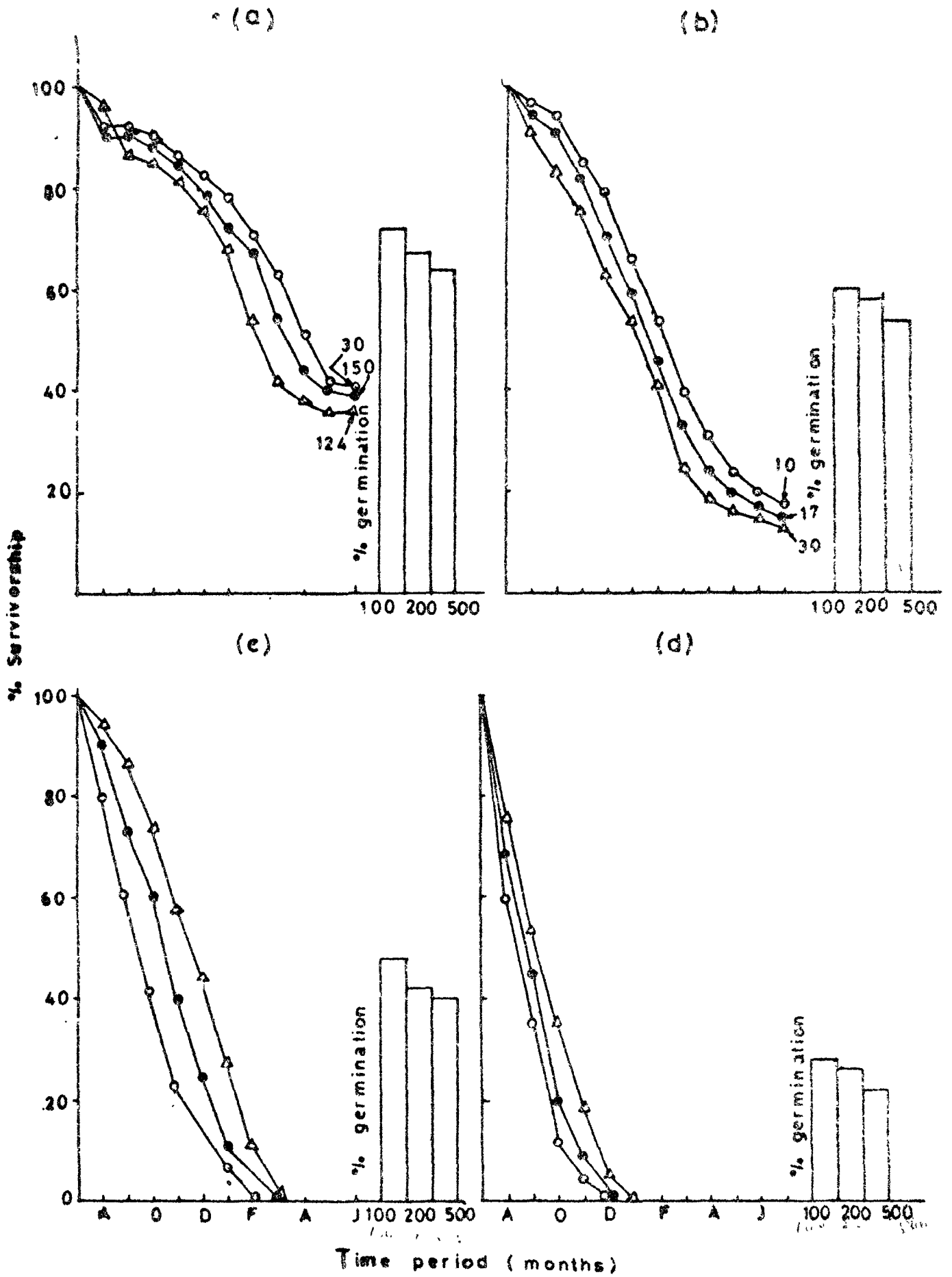
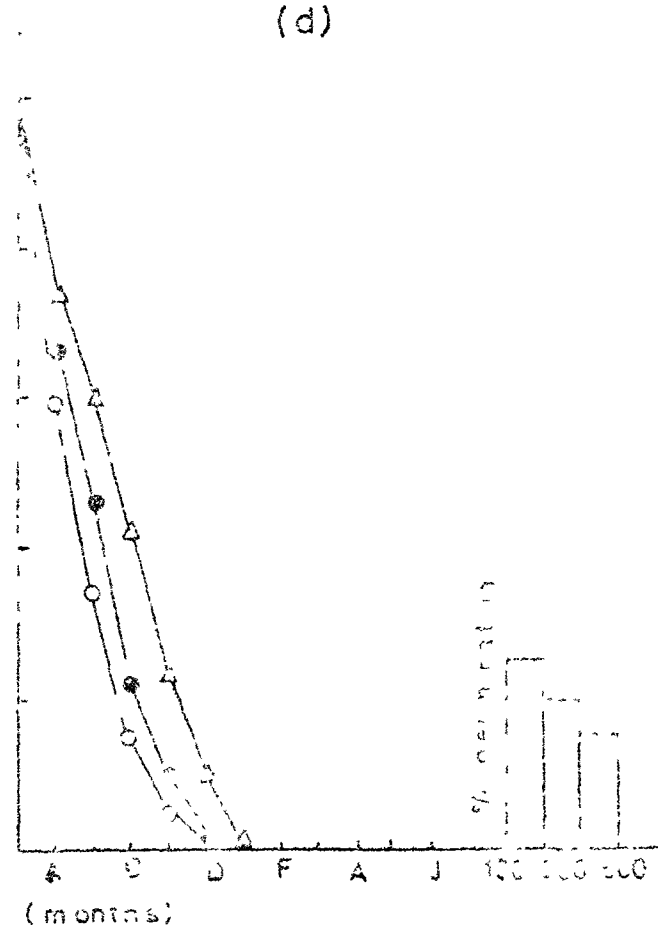
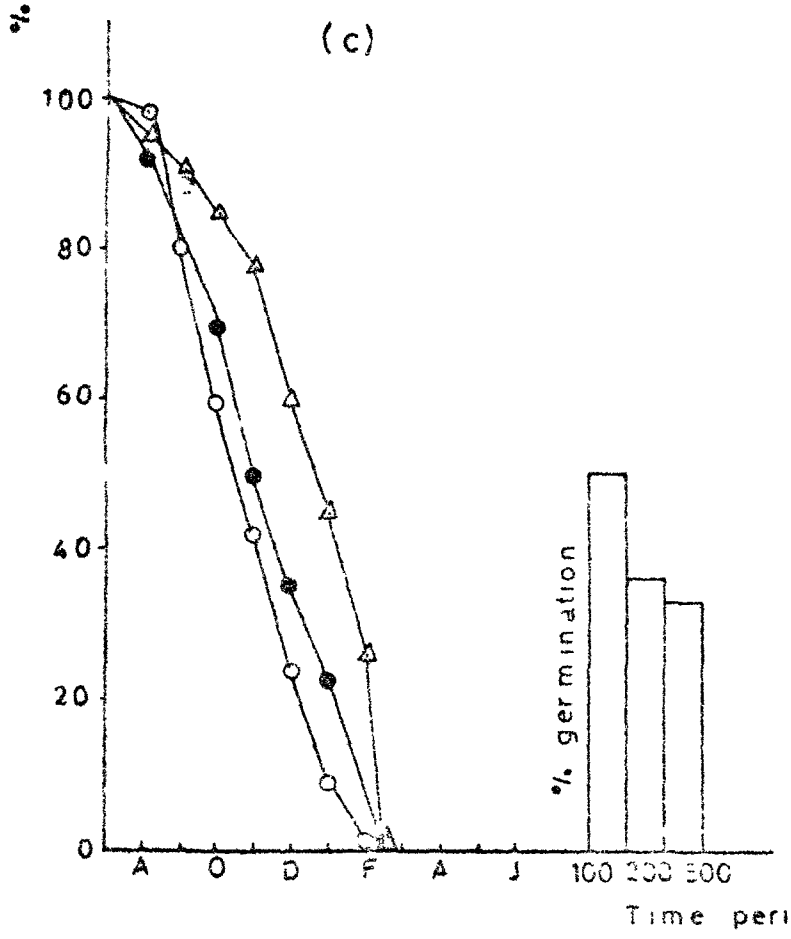
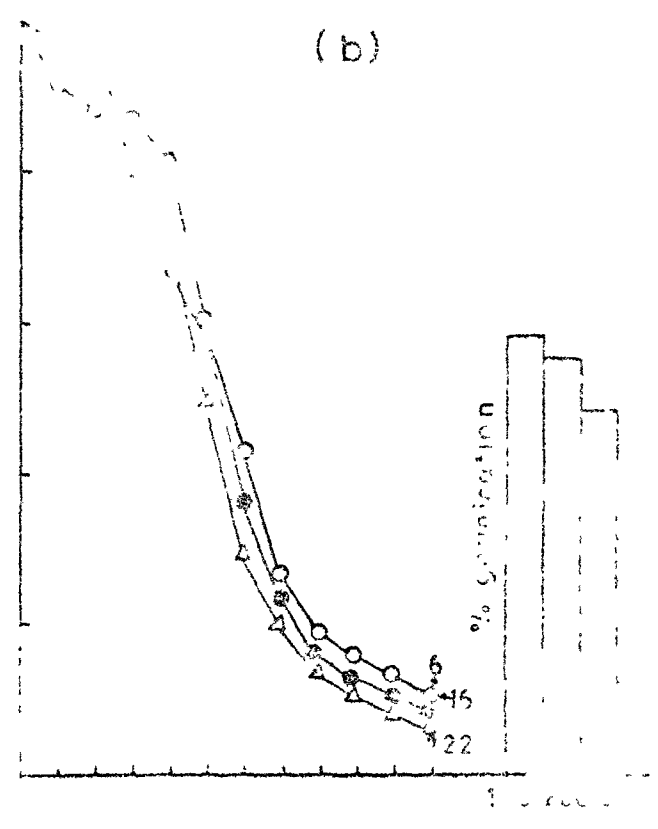
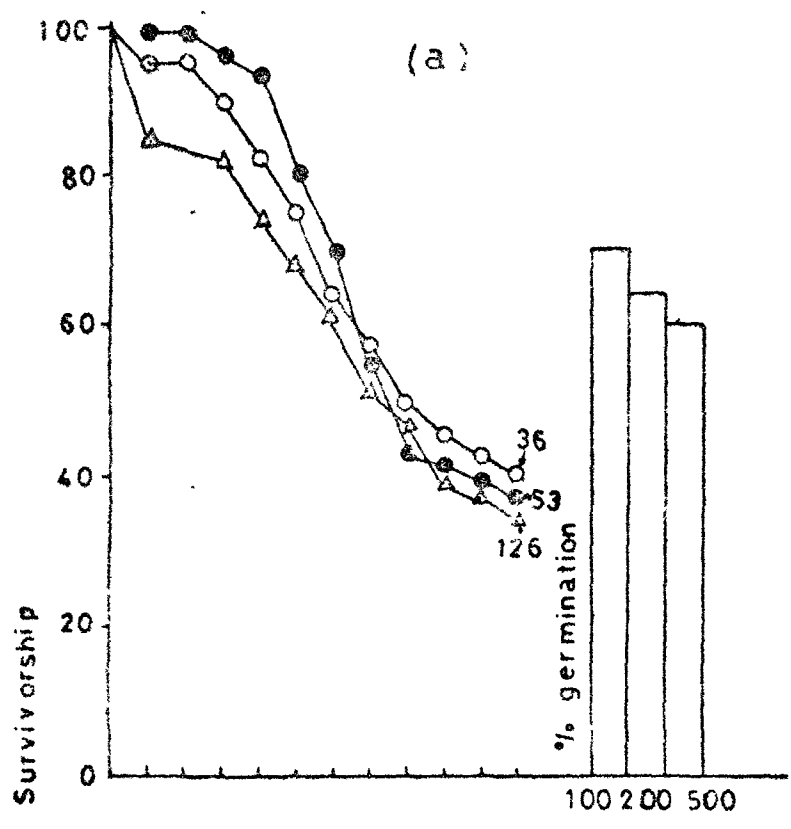


Fig. 4 .5 Fate of introduced seeds:percentage survival of seedlings at densities of 100 (○), 200 (●), and 500 (Δ) at the end of one year study period at Shillong. (a) 0-year old fallow, (b) 3-year old fallow, (c) 5-year old fallow, (d) 10-year old fallow.

Fig. 4.5



0-year old fallow, the population size did not change much during the one year period. Establishment at Burnihat was higher ($P > 0.05$) compared to Shillong (Figs. 4.2a,b; 4.3c,d).

In a 5-year old fallow the establishment of tillers was lower than in a 3-year old fallow. Though there was higher establishment of tillers in cleared plots compared to uncleared plots and at Burnihat compared to Shillong, all the tillers died in all the plots by February, after six months of introduction (Figs. 4.2c,d; 4.3e,f).

In a 10-year old fallow establishment of tillers was lowest as compared to other fallows. Further, in all the plots all the tillers died by December after five months of introduction, (Figs. 4.2e,f; 4.3g,h).

Fate of introduced seeds

At Burnihat, germination and establishment of seedlings declined in all the fallows with increased in density (Fig. 4.4a, b,c,d). Further, germination and establishment of seedlings also drastically declined with the age of the fallow. Seedlings survived declined markedly after August, this decline being more pronounced in older fallows. While in 0- and 3-year old fallows the population tended to stabilize by September in the following year, in 5- and 10-year old fallows individuals died by January-February. A similar pattern was also observed for the introduced population at Shillong (Fig. 4.5a,b,c,d).

Table 4.3 Leaf area/leaf (cm²) (Mean values) of Imperata cylindrica grown from rhizomes in 0-year and 3-year old fallows at Burnihat and Shillong. (A) with associates, (WA) without associates.

Site Fallow	Burnihat	Shillong	t(P=0.05)
0-Year (A)	25.0	20.3	S
0-Year (WA)	28.0	22.2	S
3-Year (A)	14.2	10.5	S
3-Year (WA)	16.5	11.8	S
LSD (P = 0.05)	3.54	2.82	

Table 4.4 Biomass/tiller(g) (Mean values) of Imperata cylindrica grown from rhizomes in 0-year and 3-year old fallows at Burnihat and Shillong. (A) with associates, (WA) without associates.

Site Fallow	Burnihat	Shillong	t(P=0.05)
0-Year (A)	0.2714	0.2013	S
0-Year (WA)	0.3180	0.2415	S
3-Year (A)	0.1390	0.1030	NS
3-Year (WA)	0.1870	0.1301	NS
LSD (P = 0.05)	0.042	0.026	

Leaf area/leaf and biomass/tiller

Individual leaf area of introduced tillers declined drastically in a 3-year old fallow compared to a 0-year old fallow at Burnihat and at Shillong sites (Table 4.3). Further, leaf area was higher in plots without associates compared to those plots with associates. Burnihat site had more leaf area than Shillong site. A similar pattern was observed for dry weight yield per tiller when a 0-year old fallow was compared with a 3-year old fallow and plots with or without associates in each case (Table 4.4).

DISCUSSION

After slash and burn agriculture at both lower and higher elevations in Meghalaya, a number of changes occur in the micro-environmental conditions. The temporarily nutrient enriched soil (Ramakrishnan and Toky, 1981; Mishra and Ramakrishnan, 1983b) is soon depleted of its nutrients due to run-off and infiltration losses (Toky and Ramakrishnan, 1981; Mishra and Ramakrishnan, 1983c). This depletion of nutrients is also aggravated during the first few years of rapid transfer of nutrients from the soil to vegetation component which develops rapidly (Toky and Ramakrishnan, 1983b; Mishra and Ramakrishnan, 1983d). During the first few years of fallow regrowth, changes also occur in light availability at the ground level along with alteration in evapo-transpiration. Imperata cylindrica at both low and high elevations have to adapt themselves to these drastically changing environmental conditions,

both physical and biological.

The germination and establishment of tillers of I. cylindrica was generally higher in fresh fallows and decreased drastically in a 3-year old fallow. In 5- and 10-year old fallows all the tillers died off within a few months. This may be related to decreased light availability and more competitive conditions in older fallows. This is supported by the differences observed in germination and establishment pattern which was reduced when the tillers were associated with other species as compared to the plots from where the associates were removed, in a 0-year old fallow. In older fallows this difference between plots with associates and without them was not obvious. In a fresh fallow the interference was mainly due to broad leaved herbaceous associates that restricted light penetrating to the ground level for the establishment of the transplants, but in the older fallows the canopy was due to larger shrubs and tree saplings and that is why the removal of herbaceous associates had little effect in the establishment of the transplants.

The effect of the associated species may partly be due to decreased light availability but also be related to competitive factors. The influence of competition from the associated species was shown by Harper and Chancellor, (1959) where the establishment and growth of Rumex species was determined by the associated grass Lolium perenne. Similar competitive relation have been shown by Kapoor and Ramakrishnan (1974) in the case of Echinochloa colona with or without the associated graminaceous or non-graminaceous species in the grasslands at Chandigarh.

The generally lower germination and establishment of the tillers of I. cylindrica at higher elevation at Shillong may be related to (a) lower temperature conditions related to altitude, (b) lower pH of the soil related to the decomposition of pine litter, and (c) the presence of undecomposed pine litter itself on the surface of the soil for a considerable period of time which physically hamper establishment. The increase in seedling mortality with increase in the age of the fallow could also be accounted as due to decreased light availability and increased competition from the associates with increase in fallow age.

Percentage seedling mortality was higher at higher sowing densities. Such a density-dependant mortality pattern has been observed in many other studies (Ramakrishnan and Kumar, 1971; Ramakrishnan and Jeet, 1972; Ramakrishnan and Khattar, 1973; Kapoor and Ramakrishnan, 1975). Seedling mortality was severe and a continuing phenomenon for more than a year from July when seeds germinated. This suggests that mortality is a continuing risk that an introduced population has to face and is not restricted to the early seedling phase alone, as also reported by Ramakrishnan and Kumar (1971) for pure populations. Here adjustment in numbers occur all the time with respect to increase in size of the plants of the same population and the other species in the site. In older fallows, mortality was total within 6-8 months after seed germination, as also for the establishment of the tiller populations. Earlier studies in demography of Eupatorium adenophorum (Ramakrishnan and Mishra, 1981) and on I. cylindrica (Kushwaha et al., 1983) suggest that the weed population gets

eliminated during secondary succession after 5 to 6 years of fallow regrowth which is confirmed by our own studies presented in Chapter 1 and the present studies on the fate of introduced populations. This biotic control of a weed like I. cylindrica if the fallow period is long, is disturbed under a shorter jhum cycle of 4-5 years resulting in arrested succession of weeds (Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983a).

SUMMARY

Establishment of the introduced populations of Imperata cylindrica through seeds and rhizomes was studied in 0, 3, 5 and 10-year old fallows with or without the associated herbaceous vegetation. The establishment of the population through both these decreased drastically with the age of the fallow. While the removal of associated herbaceous vegetation improved establishment only in a 0-year old fallow, absence of such a difference in older fallows is related to the presence of the larger shrubs and trees in the community. Mortality was a continuing risk the introduced populations had often to face rather than it being confined to the early phases of establishment alone. Further, density dependant mortality was evident with higher mortality rate at higher densities of the introduced population. The significance of these results are discussed from the point of view of weed vigour in jhum fallows.

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CHAPTER V

GROWTH AND RESOURCE ALLOCATION OF IMPERATA CYLINDRICA
(L.) BEAUV. AFTER SLASH AND BURN AGRICULTURE (JHUM)
IN NORTH-EASTERN INDIA AT TWO ALTITUDES

INTRODUCTION

Partitioning of the available resources for various life activities such as maintenance, growth and reproduction is important from the ecological as well as evolutionary histories of plants (MacArthur and Wilson, 1967; Harper and Ogden, 1970; Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973; Hickman, 1975; Pitelka, 1977; Bazzaz, 1979). The resource budget of plants may be limited by a number of limiting factors such as water, photosynthates and nutrients. Most of the studies on allocation pattern are concerned with biomass or energy. Little attention has been given to the allocation of nutrients which may be equally important in situations with a limited supply (Van Andel and Vera, 1977; Williams and Bell, 1981).

Natural population of a perennial rhizomatous species such as Imperata cylindrica (L.) Beauv. that comes up in fallows after slash and burn agriculture (Jhum) differ markedly in demographic features depending upon the age of the fallow. This reflects adaptation to different seral stages of disturbed and successional environments. In addition to difference in demographic data, it would be useful to identify distinct strategies by describing resource allocation. The abundance of each species in successional habitats can be determined by these strategies (Howthorn and Cavers, 1978).

Saxena and Ramakrishnan (1983) studied the growth and allocation patterns of perennials with different regenerative strategies establishing subsequent to slash and burn. They (Saxena

and Ramakrishnan, 1984) also studied the change in strategy of Eupatorium odoratum in successional environments. The present study concerns the resource allocation pattern of I. cylindrica coming up in fallows of different age after slash and burn agriculture.

METHODS OF STUDY

0,3 and 5-year old fallows (three replicates) were identified at Burnihat (26°02'N, 91°52'E) and at Shillong (25°34'N, 91°56'E). The resource allocation pattern of natural populations of I. cylindrica in each of these fallow plots was studied in three randomly marked 50 x 50 cm quadrats that were harvested every month, throughout the growing season.

The harvested plants were separated into above-ground (Stem and leaf) and below-ground (root and rhizome) components. Different components were dried at 80°C ± 5°C for 48 hours and weighed. Leaf area estimation was done by using a planimeter and leaf dry weight per unit area was based on three replicates and 20 leaves per replicate. Leaf area ratio was calculated as leaf area (cm²) per unit (mg) biomass. Growth functions such as relative growth rate (RGR) and net assimilation rate (NAR) (Hughes and Freeman, 1967; Radford, 1967) were calculated as:

$$\text{RGR} = \frac{I_n W_2 - I_n W_1}{t_2 - t_1}$$

(mg mg⁻¹d⁻¹)

$$\text{NAR} = \frac{(W_2 - W_1) (I_n A_2 - I_n A_1)}{(A_2 - A_1)(t_2 - t_1)}$$

(mg cm²-1 d⁻¹)

where W_1 and A_1 are biomass and leaf area values at time t_1 and similarly W_2 and A_2 at time t_2 .

Concentration of different nutrients in the component organs was determined following standard methods (Allen, 1974). Thus nitrogen was analysed by micro-Kjeldahl method, phosphorus by molybdenum-blue method and potassium by flame photometry, after dry ashing.

Nutrient uptake efficiency was calculated as mg nutrient absorbed per g root biomass following Blair and Cordero (1978) and nutrient use efficiency as mg biomass produced per mg nutrient uptake. Vegetative effort was calculated on the basis of allocation to rhizome as percentage of current dry matter or nutrient uptake.

RESULTS

Natural population studies

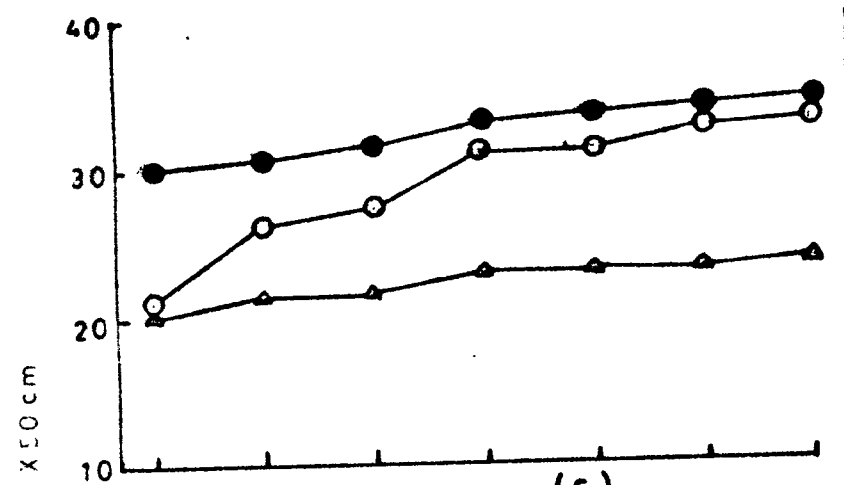
The increment in above-ground biomass in different fallows during the observation period at Burnihat from June to December is shown in Fig. 5.1a. The increment was pronounced in a 0-year old fallow but was not so in older fallows. In the initial stages a marked difference was observed in above-ground biomass between 0- and 5-year old fallow on the one hand and 3-year old fallow on the other. At the end of the growth period 0- and 3-year

Fig. 5.1 Biomass increment during the growth season of I. cylindrica in different fallows. (a) above-ground biomass at Burnihat, (b) above-ground biomass at Shillong, (c) below-ground biomass at Burnihat, (d) below-ground biomass at Shillong. Open circle, 0-year old fallow; closed circle, 3-year old fallow; open triangle, 5-year old fallow. Vertical bars represent LSD at P=0.05.

Fig. 5-1

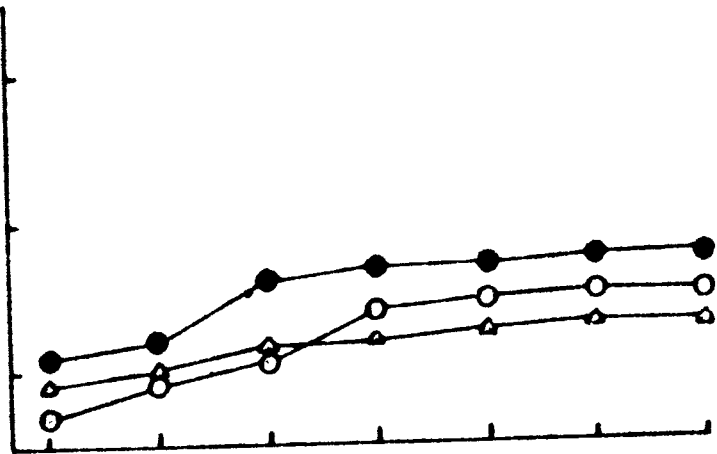
(a)

L.S.D. (P=0.05)
Treatment | Month |



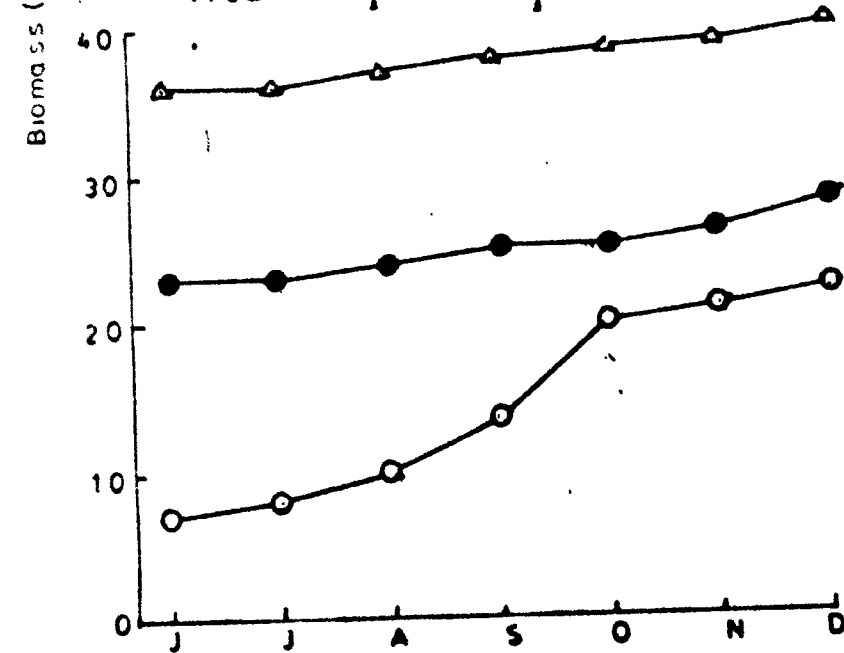
(b)

L.S.D. (P=0.05)
Treatment | Month |



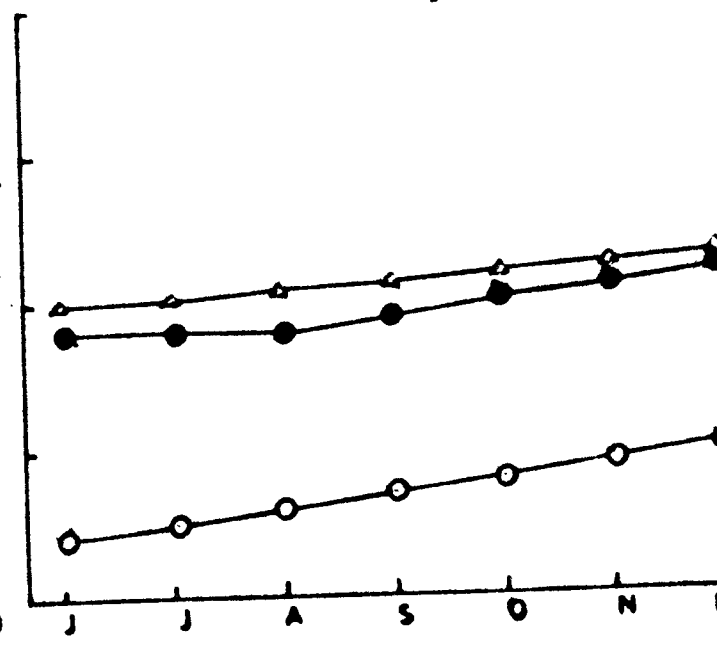
(c)

L.S.D. (P=0.05)
Treatment | Month |



(d)

L.S.D. (P=0.05)
Treatment | Month |



Time period (month)

Biomass (g)/50 X 50 cm

Fig. 5.2 Leaf area/tiller (cm^2) increment during the growth season of I. cylindrica in different fallows. (a) Burnihat, (b) Shillong. Open circle, 0-year old fallow; closed circle, 3-year old fallow; open triangle, 5-year old fallow. Vertical bars represent LSD at $P=0.05$.

Fig. 5.2

(a)

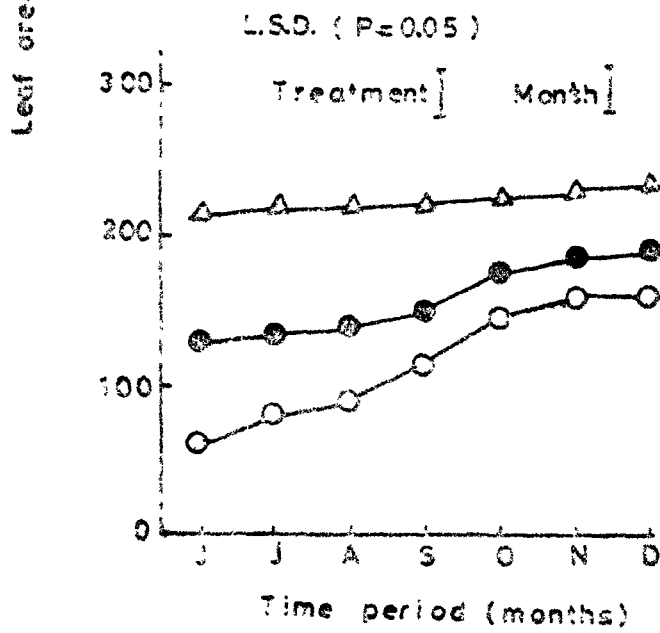
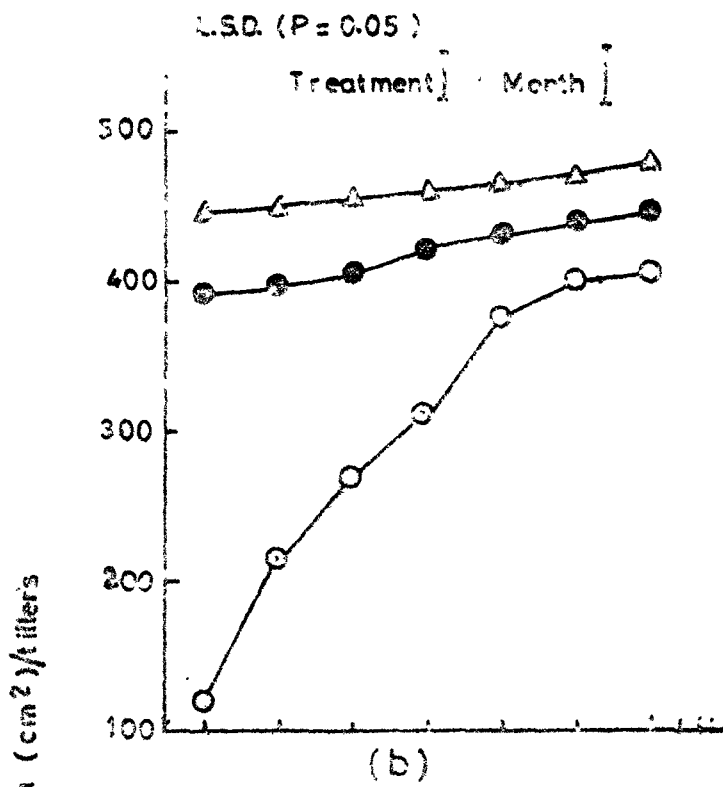


Table 5.1 Mean values (\pm S.E.M.) of growth functions of Imperata cylindrica in different fallows at Burnihat and Shillong

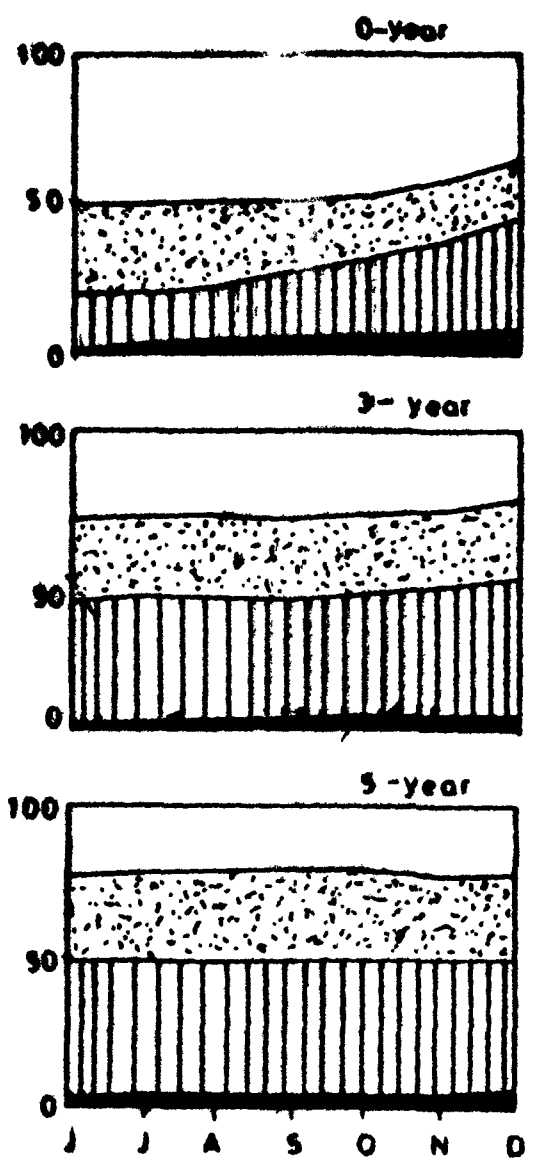
Fallow	Site	RGR mg $\text{mg}^{-1} \text{d}^{-1}$	NAR mg $\text{cm}^2^{-1} \text{d}^{-1}$	LAR $\text{cm}^2 \text{g}^{-1}$
0-Year	Burnihat	0.0154 \pm 0.0093	0.0950 \pm 0.0533	0.0830 \pm 0.0543
	Shillong	0.0102 \pm 0.0020	0.0801 \pm 0.0062	0.0720 \pm 0.0580
3-Year	Burnihat	0.0008 \pm 0.0002	0.0150 \pm 0.0052	0.0225 \pm 0.0050
	Shillong	0.0006 \pm 0.0001	0.0062 \pm 0.0024	0.0170 \pm 0.0085
5-Year	Burnihat	0.0003 \pm 0.0011	0.0052 \pm 0.0008	0.0110 \pm 0.0084
	Shillong	0.0002 \pm 0.0001	0.0022 \pm 0.0008	0.0120 \pm 0.0072

Fig. 5.3 Allocation of biomass to different components
(expressed as a percentage of the total capital)
during the growth period of I. cylindrica in
different fallows. (a) Burnihat, (b) Shillong.

Fig. 5.3

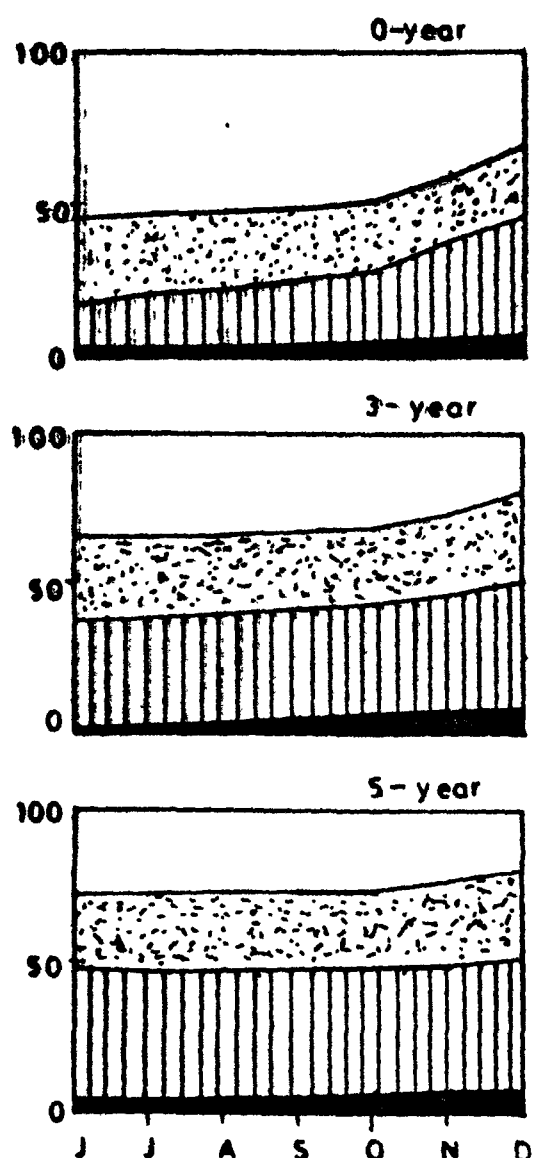
(a) Location of biomass

Leaf Stem



(b) Allocation of biomass

Rhizome Root



Time period (months)

old fallows had higher biomass compared to 5-year old fallow. A similar difference as at Burnihat, between the biomass in different fallows at the beginning and end of the growth period was observed at Shillong too, but this was less pronounced here (Fig. 5.1b).

Though below-ground biomass increment was more pronounced in a 0-year old fallow both at Burnihat (Fig. 5.1c) and at Shillong (Fig. 5.1d), the initial and the final biomass attained in the 0-year old fallow was the lowest while that in the 5-year old fallow was the highest.

Increase in the leaf area per tiller at Burnihat (Fig. 5.2a) and at Shillong (Fig. 5.2b) was very sharp in 0-year old fallow compared to 3- and 5-year old fallows. However, in older fallows a higher initial and final leaf area was noted. The difference between the three fallows was less pronounced at the end of the growth period than at the beginning when 0-year old fallow started with a much smaller leaf area.

The three growth functions, namely RGR, NAR and LAR are given in Table 5.1 for Burnihat and Shillong. Fresh fallows had higher values for all growth functions and these decline markedly with the age of the fallow.

Allocation pattern of biomass expressed as a percentage of the total capital for both Burnihat (Fig. 5.3a) and Shillong (Fig. 5.3b) showed similar differences with the age of the fallow. The allocation of biomass to the rhizome and stem portions increased sharply with fallow age. On the other hand, the allocation to the leaf decreased with fallow age. While in

Fig. 5.4 Nutrient concentration in I. cylindrica during the growth period in different fallows at Burnihat. (a), (b), (c), above-ground parts; (d),(e),(f), below-ground parts. Open circle, 0-year old fallow; closed circle, 3-year old fallow; open triangle, 5-year old fallow. Vertical bars represent LSD at P=0.05.

(d) Fig. 5-4

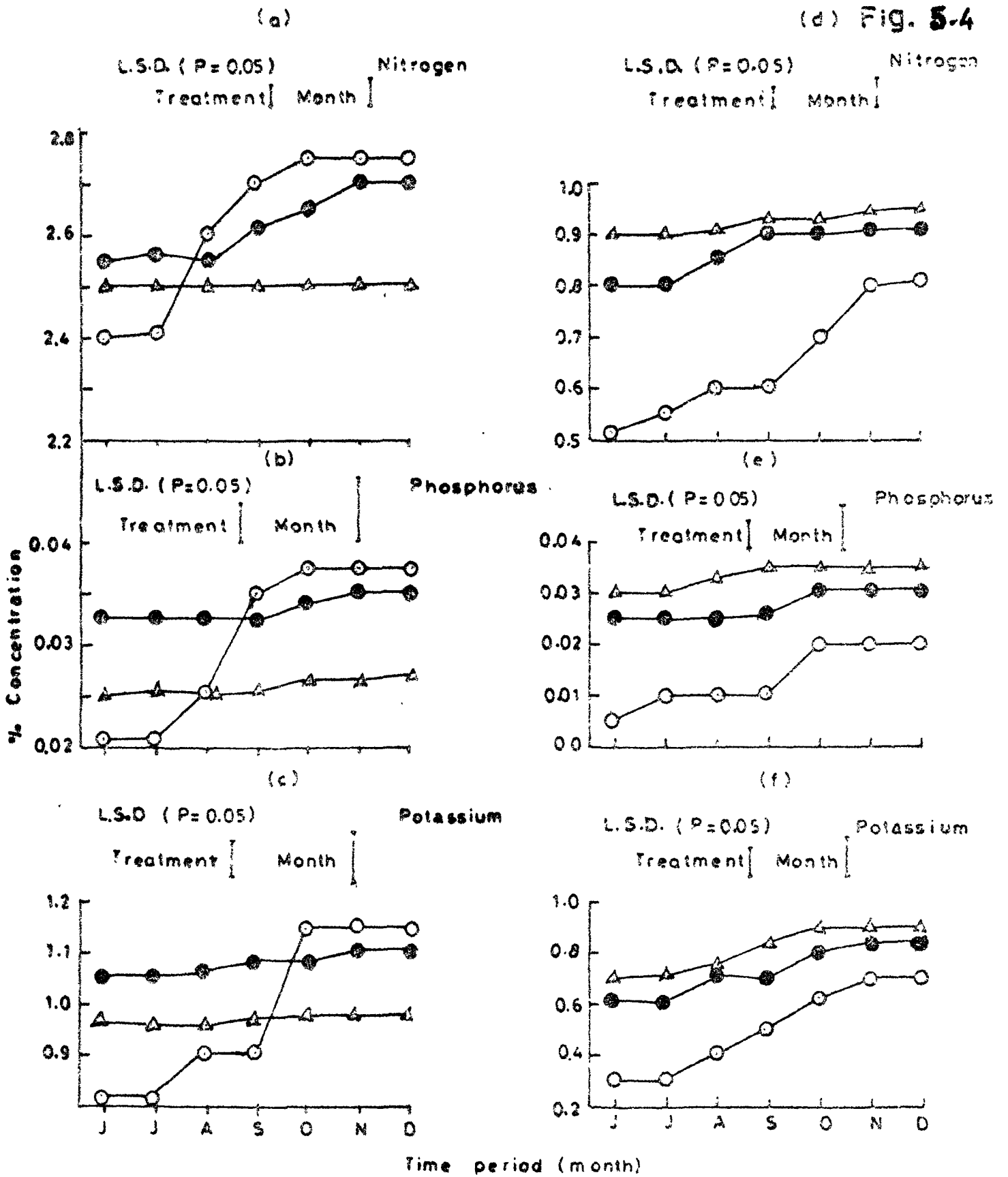
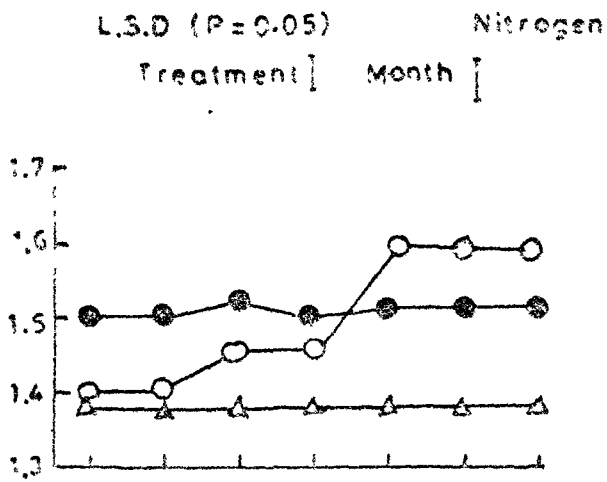


Fig. 5.5 Nutrient concentration in I. cylindrica during the growth period in different fallows at Shillong. (a),(b),(c), above-ground parts; (d),(e),(f), below-ground parts. Open circle, 0-year old fallow; closed circle, 3-year old fallow; open triangle, 5-year old fallow. Vertical bars represent LSD at $P=0.05$.

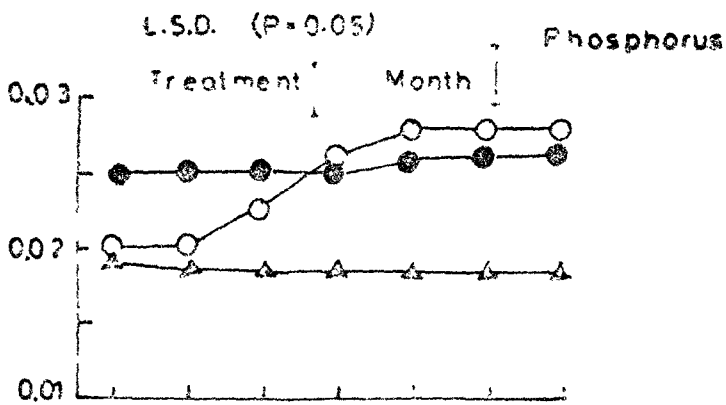
Fig. 5-5

(3)

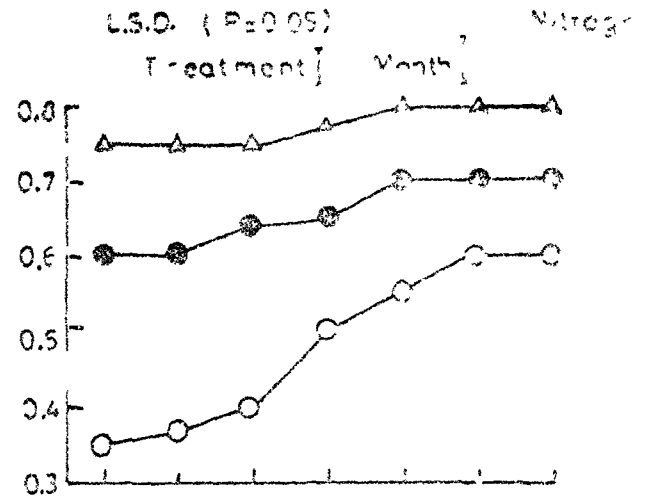
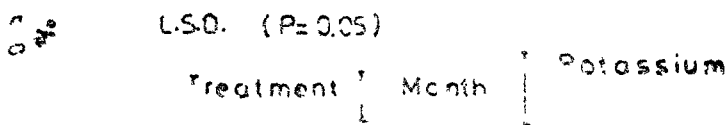
(a)



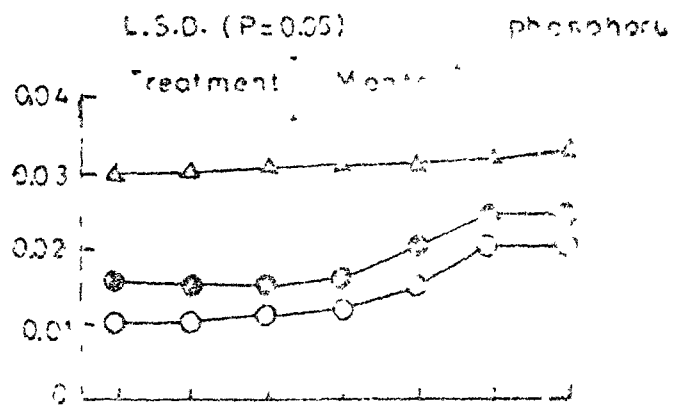
(b)



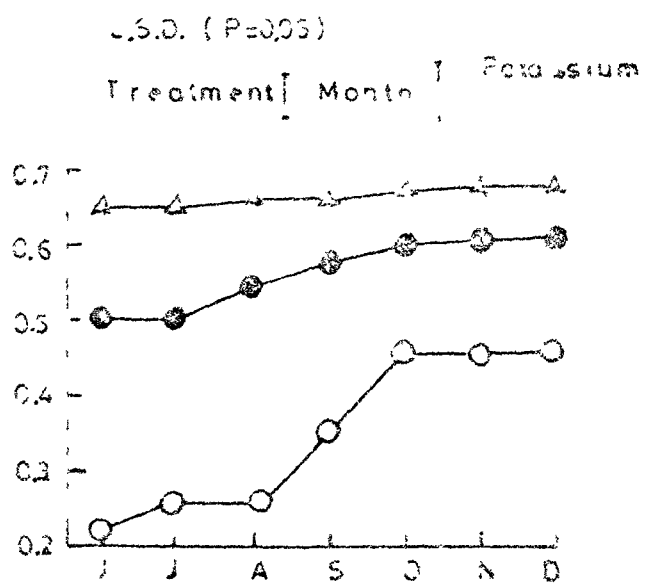
(c)



(e)



(f)



Time period (Months)

Table 5.2 Mean concentration (\pm S.E.M.) of nutrients in leaf tissue of I. cylindrica in different fallows at Burnihat and Shillong

Fallow	Site	Nitrogen	Phosphorus	Potassium
0-Year	Burnihat	2.0 \pm 0.15	0.08 \pm 0.03	1.3 \pm 0.09
	Shillong	2.0 \pm 0.12	0.08 \pm 0.03	1.0 \pm 0.07
3-Year	Burnihat	1.8 \pm 0.10	0.05 \pm 0.01	1.0 \pm 0.08
	Shillong	1.8 \pm 0.12	0.05 \pm 0.02	0.9 \pm 0.06
5-Year	Burnihat	1.8 \pm 0.10	0.05 \pm 0.009	0.9 \pm 0.07
	Shillong	1.8 \pm 0.10	0.05 \pm 0.009	0.9 \pm 0.08

Fig. 5.6 Allocation of nitrogen to different components (expressed as a percentage of the total capital) of I. cylindrica during the growth period in different fallows of 0, 3 and 5-years at Burnihat (a) and Shillong (b).

Fig. 5.6

(a)

(b)

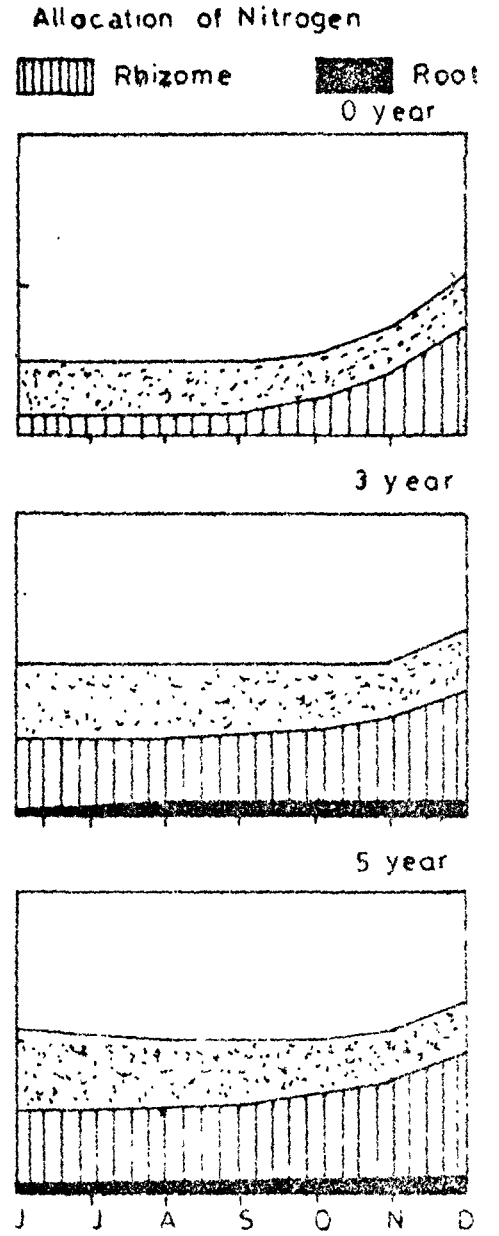
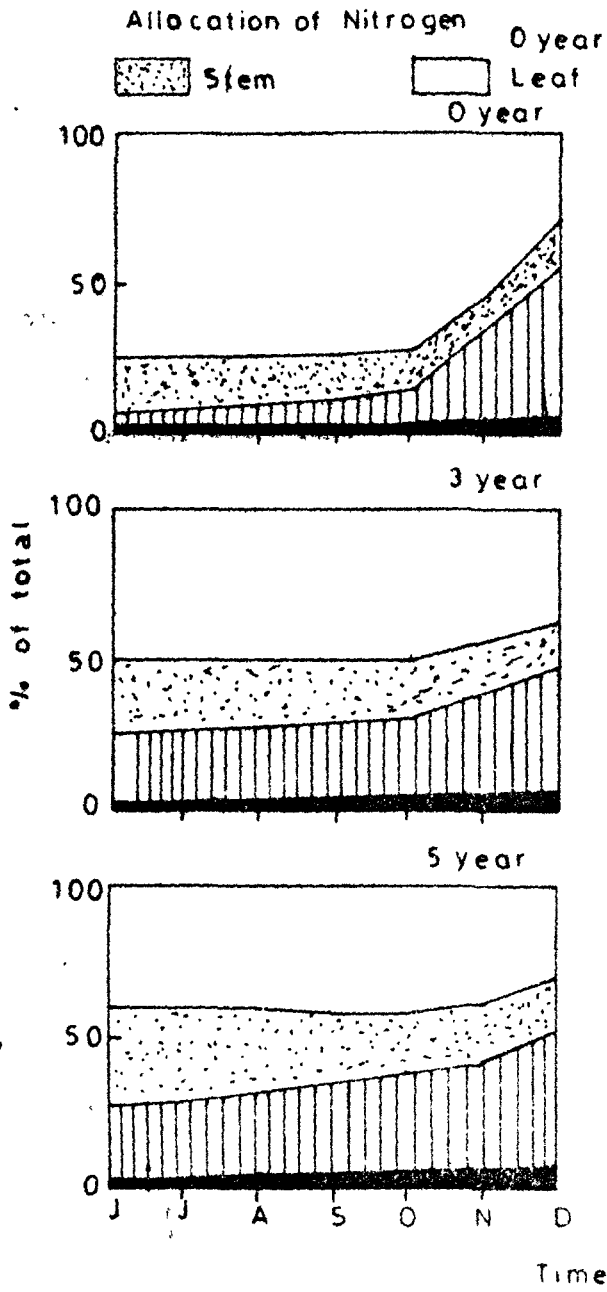


Fig. 5.7 Allocation of phosphorus to different components (expressed as a percentage of the total capital) of I. cylindrica during the growth period in different fallows of 0, 3 and 5-years at Burnihat (a) and Shillong (b).

Fig. 5.7

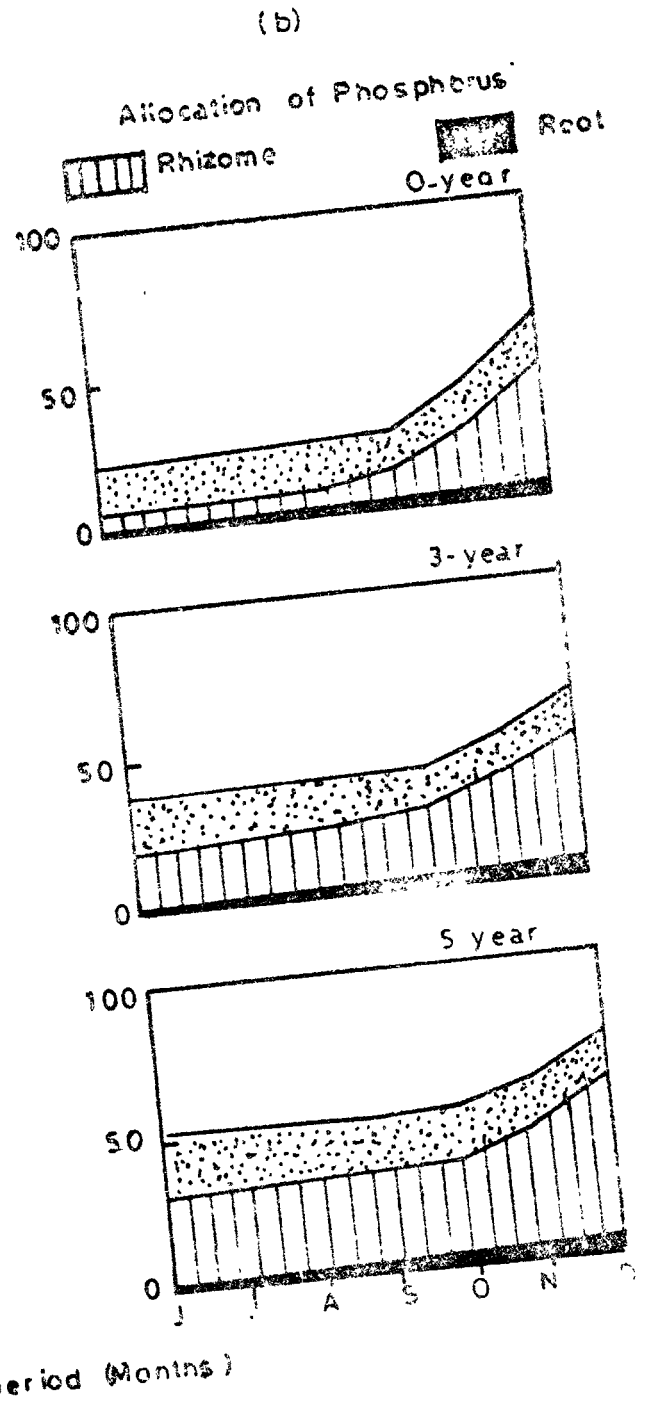
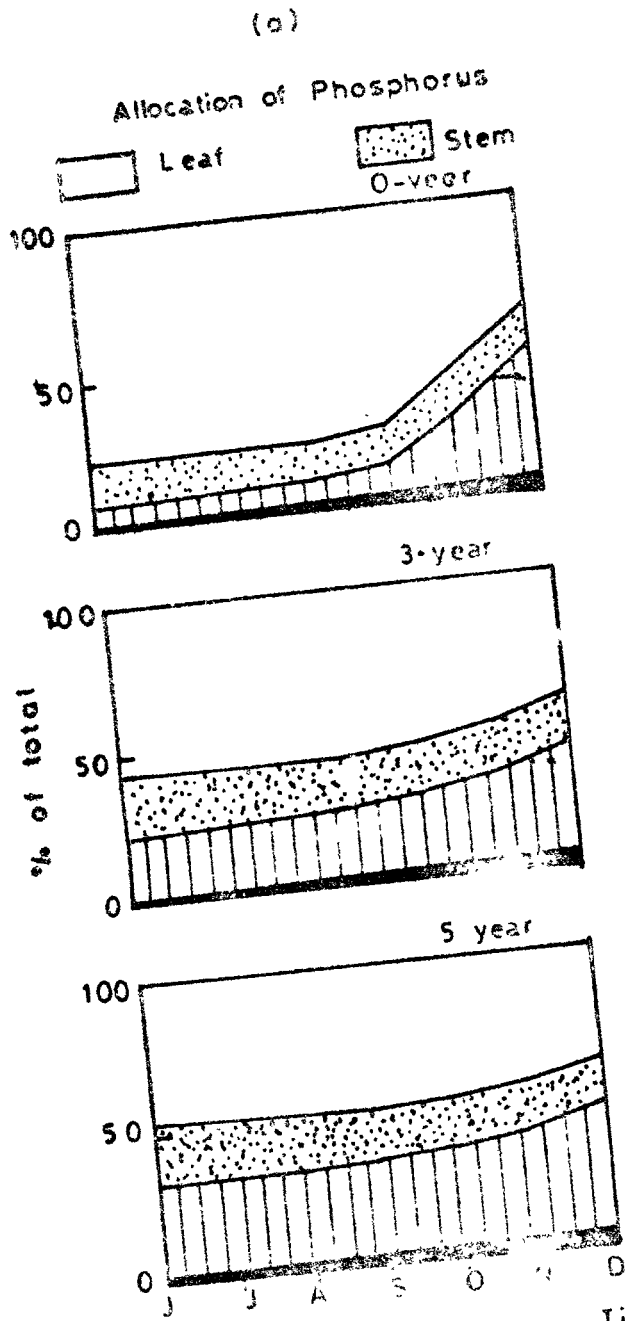
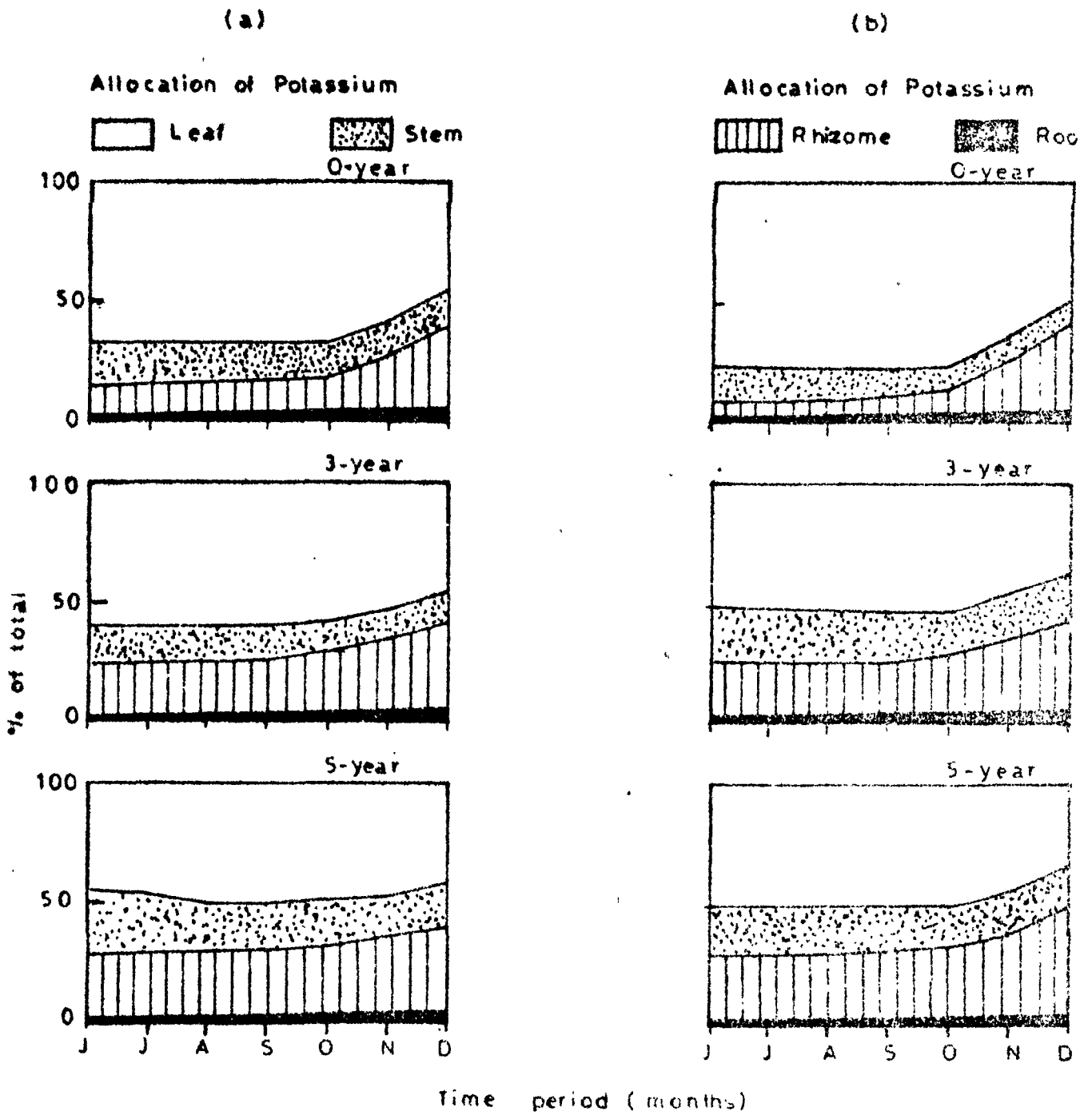


Fig. 5.8 Allocation of Potassium to different components (expressed as a percentage of the total capital) of I. cylindrica during the growth period in different fallows of 0, 3 and 5-years at Burnihat (a) and Shillong (b).

Fig. 5.8



older fallows biomass allocation to different components tended to remain more or less steady during the growth period, in a 0-year old fallow, it increased from June to December.

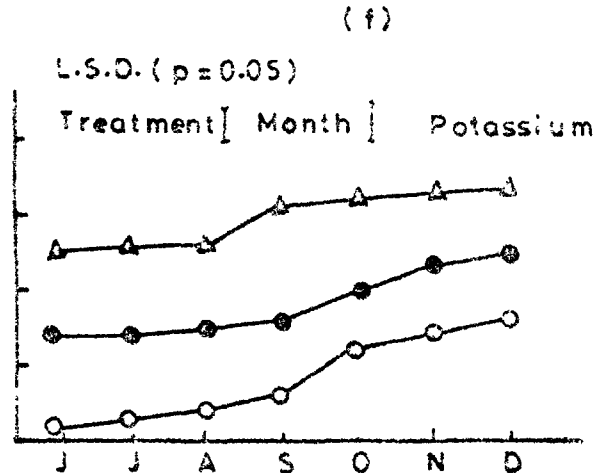
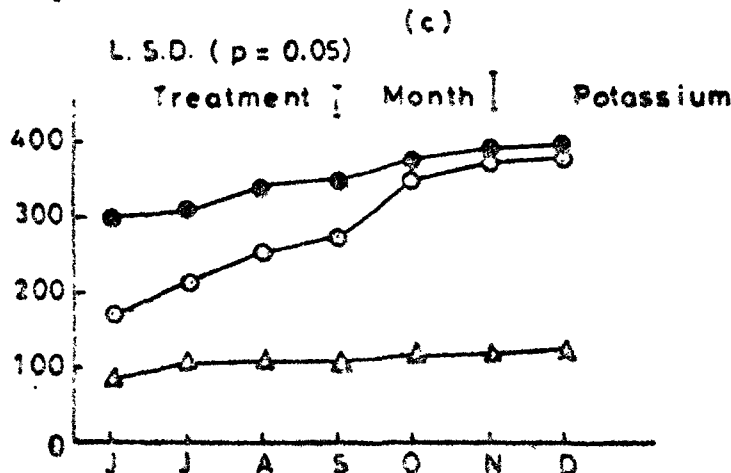
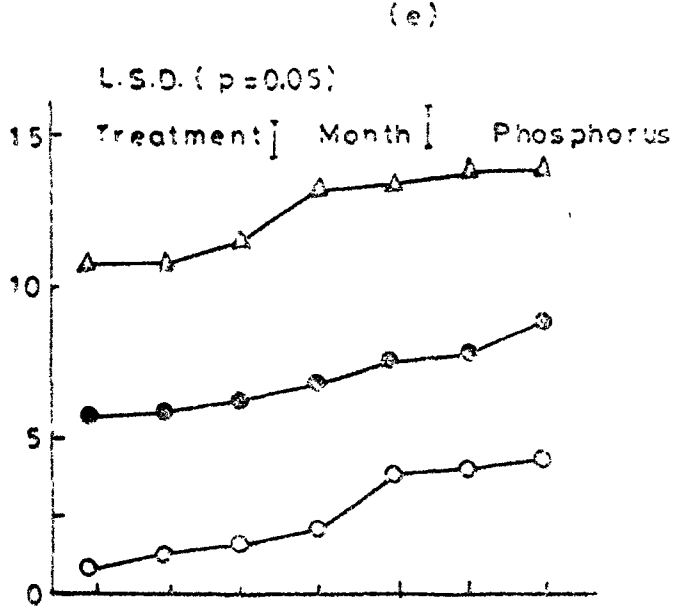
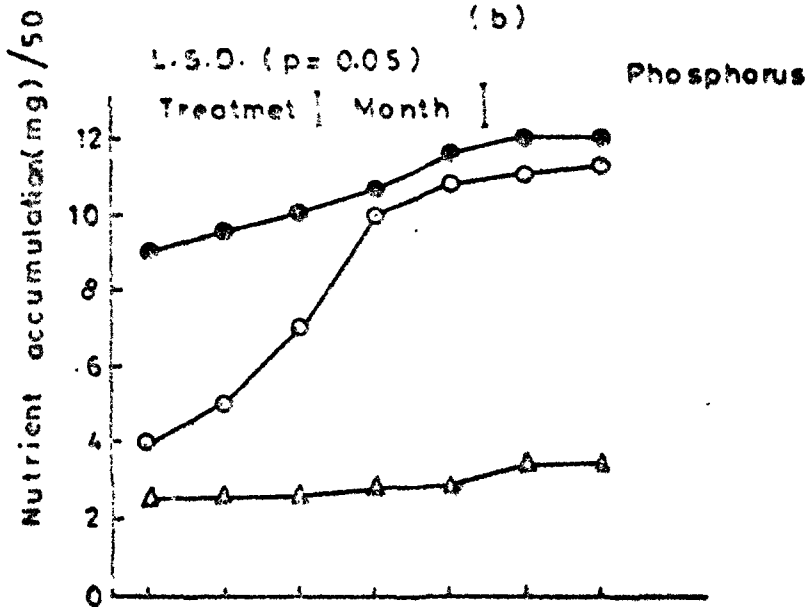
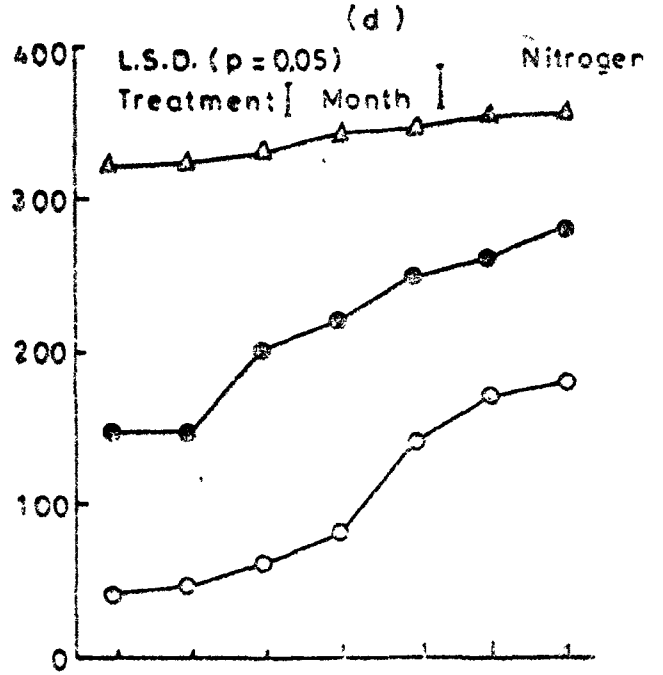
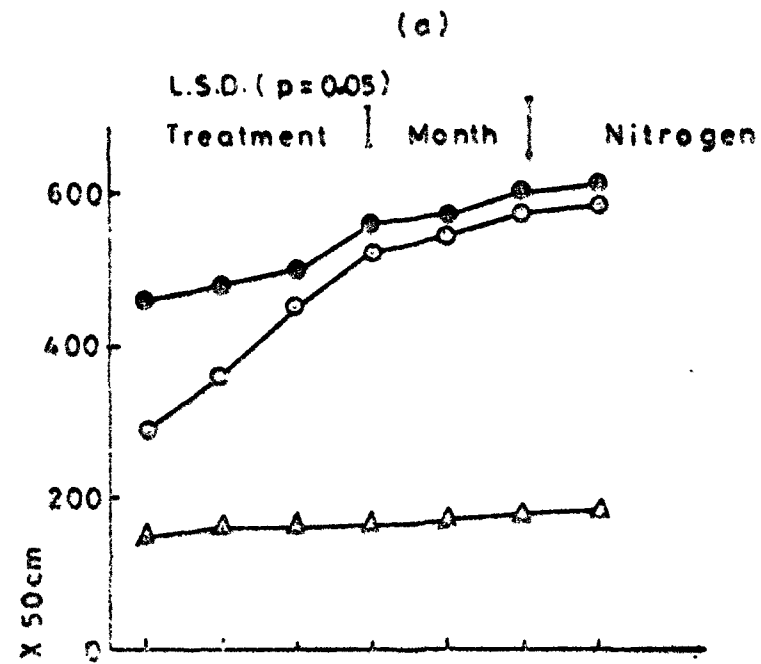
Nutrient concentration in the above-ground and below-ground parts of I. cylindrica at Burnihat (Fig. 5.4a,b,c,d,e,f) and at Shillong (Fig. 5.5a,b,c,d,e,f) showed similar patterns for nitrogen, phosphorus and potassium in the different fallows. On both locations, nutrient concentration in the above-ground parts increased sharply in the 0-year old fallow during the growth period. Starting in June with a relatively lower concentration in a 0-year old fallow as compared to the other fallows, the concentration became higher than that of the other two fallows towards the end of the growth period in December. At the end of the growth period, the 5-year old fallow had the lowest concentration of the three nutrients, followed by the 3-year old fallow.

Concentration of nutrients in the leaf tissue was maximum in the 0-year old fallow compared to 3- and 5-year old fallows (Table 5.2).

The allocation pattern of nitrogen (Fig. 5.6a), phosphorus (Fig. 5.7a) and potassium (Fig. 5.8a) at Burnihat and these nutrients at Shillong (Figs. 5.6b, 5.7b, 5.8b) showed a similar pattern. The allocation to the leaf component decreased with the age of the fallow. However, the allocation to the stem component increased slightly but that to the rhizome increased sharply with fallow age. While the allocation to the rhizome increased

Fig. 5.9 Nutrient accumulation in I. cylindrica during growth period in different fallows at Burnihat. (a),(b),(c), above-ground parts; (d),(e),(f), below-ground parts. Open circle, 0-year old fallow; closed circle, 3-year old fallow; open triangle, 5-year old fallow. Vertical bars represent LSD at $P=0.05$.

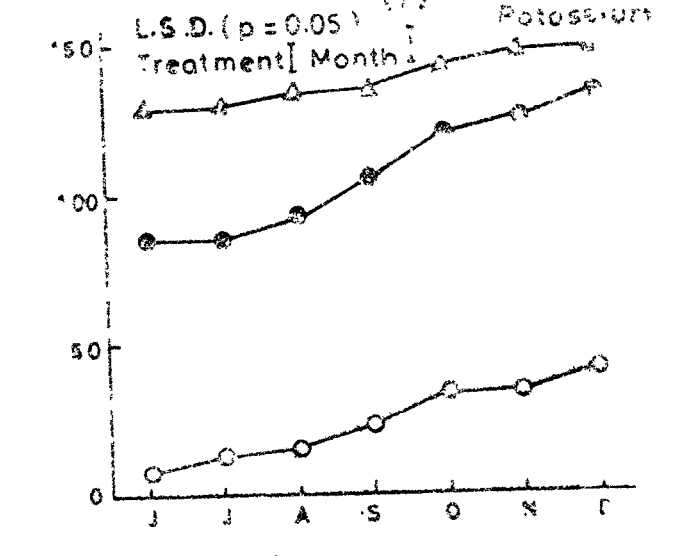
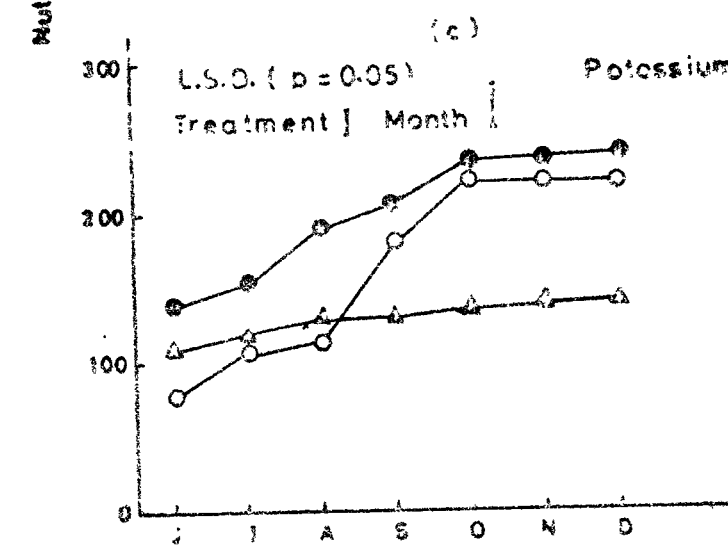
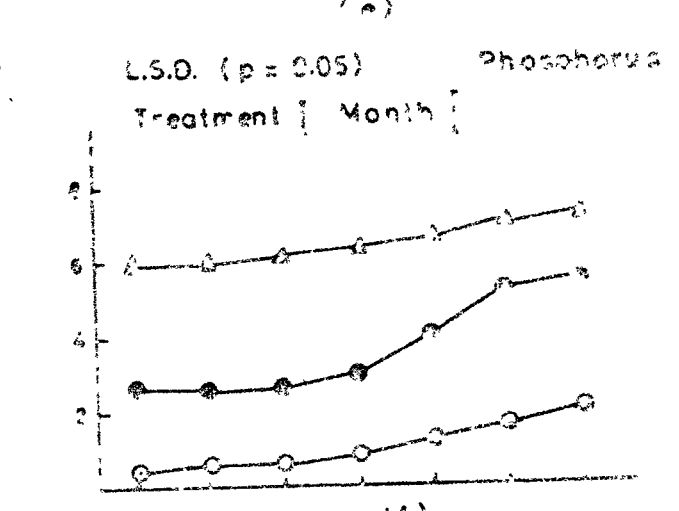
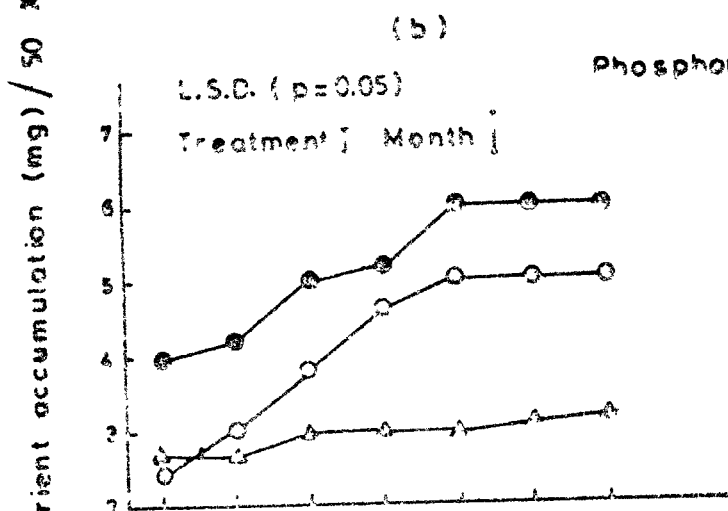
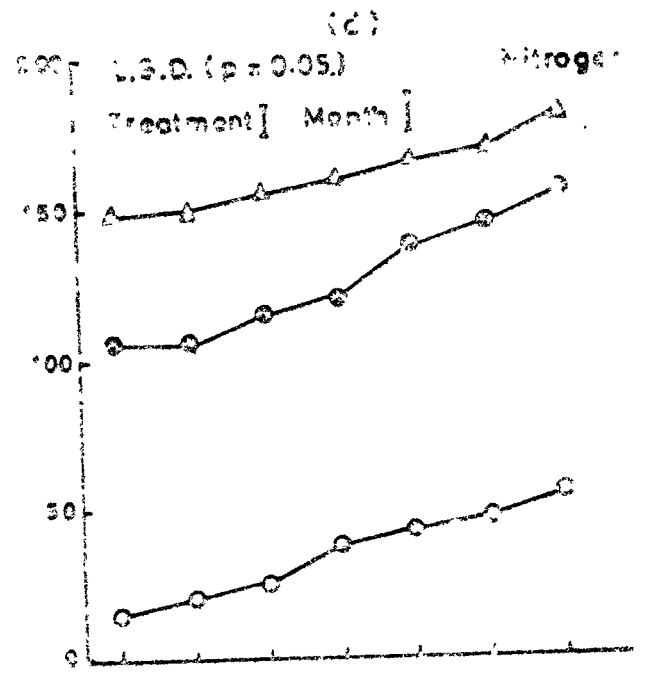
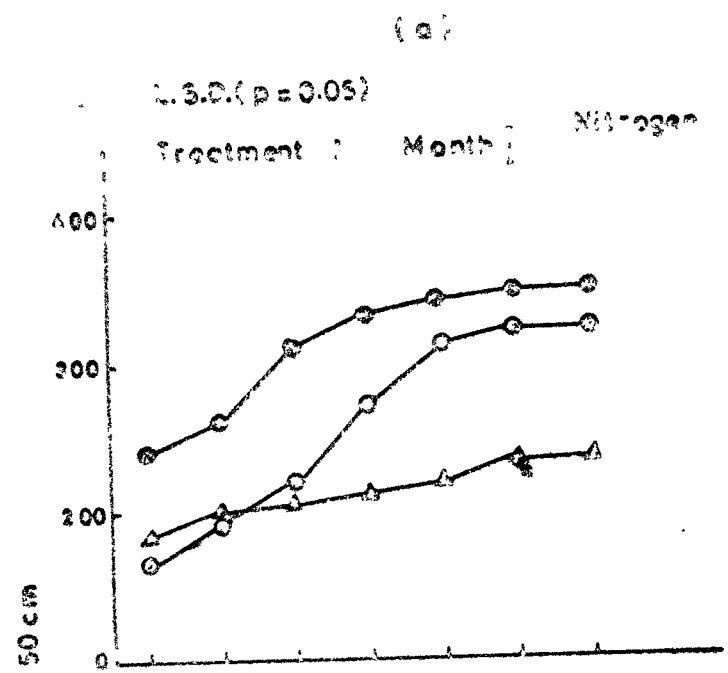
Fig. 5.9



Time period (Months)

Fig. 5.10 Nutrient accumulation in I. cylindrica during growth period in different fallows at Shillong. (a),(b),(c), above-ground parts; (d),(e),(f), below-ground parts. Open circle, 0-year old fallow; closed circle, 3-year old fallow; open triangle, 5-year old fallow. Vertical bars represent LSD at $P=0.05$.

Fig. 5.10



Time period (months)

Table 5.3 Nutrient uptake efficiency (mg nutrient absorbed per g root biomass) of *I. cylindrica* in different fallows at Burnihat and Shillong

↓ Fallow	Nitrogen			Phosphorus			Potassium		
	Burnihat	Shillong	t(P=0.05)	Burnihat	Shillong	t(P=0.05)	Burnihat	Shillong	t(P=0.05)
0-Year	192.0	158.0	S	5.6	4.2	S	118.0	115.2	S
3-Year	71.0	65.0	S	3.0	2.6	S	68.2	67.0	NS
5-Year	54.2	52.3	S	2.1	1.8	S	52.3	49.3	NS
L.S.D. (P=0.05)	4.40	3.52		0.77	0.62		3.82	3.25	

markedly towards the end of the growth period in each of the fallows, that to the stem and the leaf component decreased.

The nutrient accumulation in the above-ground biomass at Burnihat for nitrogen, phosphorus and potassium shown in Fig. 5.9a,b,c showed that the 5-year old fallow had the lowest level of accumulation compared to 0- and 3-year old fallows. 3-Year old fallow showed highest accumulation at a given time though in a 0-year old fallow accumulation increased sharply from June to December, almost equalling the 3-year old fallow by December. A similar pattern was also observed at Shillong (Fig. 5.10a,b,c).

Nutrient accumulation in the below-ground biomass at Burnihat (Fig. 5.9d,e,f) and Shillong (Fig. 5.10d,e,f) was lowest for a 0-year old fallow and more for the 3-year old fallow, the 3-year old fallow being intermediate between the other two. In 0- and 3-year old fallows, accumulation was faster during the growth period compared to the 5-year old fallow.

Nutrient uptake efficiency in general was very high in a 0-year old fallow but declined sharply in older fallows (Table 5.3). Uptake efficiency was more for nitrogen followed by potassium and least for phosphorus. While significantly higher uptake efficiency was noted with respect to nitrogen and phosphorus for the Burnihat site compared to Shillong, no such difference between the sites was noted for potassium.

Table 5.4 Nutrient use efficiency (mg biomass produced per mg nutrient absorbed) of I. cylindrica in different fallows at Burnihat and Shillong

Fallow	Nitrogen			Phosphorus			Potassium		
	Burnihat	Shillong	t(P=0.05)	Burnihat	Shillong	t(P=0.05)	Burnihat	Shillong	t(P=0.05)
0-Year	43.0	37.0	S	902.3	898.2	NS	52.0	49.2	NS
3-Year	20.0	17.4	NS	602.4	589.0	NS	26.3	23.8	NS
5-Year	12.0	10.3	NS	280.2	275.3	NS	12.2	13.4	NS
L.S.D. (P=0.05)	4.32	3.80		5.42	4.85		3.20	2.95	

Table 5.5 Vegetative effort (allocation to rhizome as % of current dry matter production or nutrient uptake) of *I. cylindrica* in different fallows at Burnihat and Shillong

↓ Fallow	Biomass		Nitrogen		Phosphorus		Potassium					
	Bur-nihat	Shi-liong t(P=0.05)	Bur-nihat	Shi-liong t(P=0.05)	Bur-nihat	Shi-liong t(P=0.05)	Bur-nihat	Shi-liong t(P=0.05)				
0-Year	58.1	58.3	NS	36.3	25.0	S	50.0	40.0	S	53.0	40.0	S
3-Year	71.4	72.0	NS	46.2	34.2	S	61.2	65.2	S	40.2	45.3	S
5-Year	75.0	74.2	NS	52.0	41.1	S	83.0	70.4	S	46.2	50.0	S
LSD(P=0.05)	3.60	3.25		2.82	3.02		2.92	4.05		2.90	3.45	

Nutrient use efficiency also decreased with the age of the fallow, for all the three nutrients (Table 5.4). Use efficiency was maximum for phosphorus followed by potassium and nitrogen. Site difference was observed only for nitrogen in the 0-year old fallow.

Vegetative effort expressed as a percentage of the current biomass production to rhizome component showed that this significantly increased with the age of the fallow, at both sites (Table 5.5). A similar pattern was also noted when vegetative effort is considered in terms of nutrients such as nitrogen, phosphorus and potassium. Though differences in this regard was not observed between the two sites with respect to biomass, the nutrient allocation was slightly higher at Burnihat than at Shillong.

DISCUSSION

The adaptation of a rhizomatous weed like Imperata cylindrica which come up after slash and burn agriculture should be to capitalize upon the nutrients which are already depleted after the cropping period (Ramakrishnan and Toky, 1981; Toky and Ramakrishnan, 1981; Mishra and Ramakrishnan, 1983a,b). The growth of the above-ground parts from the perennating rhizome is very rapid in a 0-year old fallow due to the stored food resources in the rhizome and due to the open environment where light is not a limiting factor and that the competition from other species in the community is minimal. The decline in growth

of the above-ground and below-ground organs with the age of the fallow could be partly related to competition from other species such as Eupatorium odoratum (Kushwaha et al., 1983). Further, reduced light availability in older fallows would be another important factor as shown by Kushwaha and Ramakrishnan (1982) and also shown by others (Bennet and Rao, 1968; Crutwell, 1968; Bussen and Wirjohardja, 1973). However, the build-up of the under-ground organs with age of the fallow is very high.

I. cylindrica is a species that multiplies mostly through vegetative sprouts; sexual reproduction is seldom attempted except under conditions of severe stress. It has been shown that frequent clipping or burning, particularly during the dry season is essential for successful flowering of this species (Kushwaha et al., 1983). Gill (1975) also reported a similar behaviour for a number of post-fire shrubs. These observations support the prediction of Wilson (1971) that reproduction will seldom be attempted when on the average it fails.

The initial decline in the below-ground biomass allocation in June when growth starts in a 0-year old fallow and the simultaneous increase in the above-ground biomass allocation explains rapid transfer of resources from below to above-ground organs. However, in the latter part of the growth season, there is a build up in the allocation to the below-ground organs. It may be noted here that earlier studies (Saxena and Ramakrishnan, 1983) suggests that the slower growth rate of I. cylindrica compared to E. odoratum, another perennial is to some extent compensated

due to high initial reserves stored in the underground organs and transported for shoot growth (Schier and Zasda, 1973).

Quantification of reproductive effort in perennials is complicated as production of the previous years is added on to that of the next year (Ogden, 1974; Hickman, 1975; Kawano and Nagai, 1975). While in these studies sexual reproductive effort is often considered as a proportion of the existing biomass or 'new growth' (in the cases where current growth is easily distinguished from the old growth e.g. over-wintering of shoot every year) the importance of the under-ground vegetative propagules are often ignored (Mooney and Billings, 1960; Bradbury, 1973). Studies on perennials with or without vegetative reproduction in jhum fallows (Saxena and Ramakrishnan, 1983; Saxena and Ramakrishnan, 1984) is one of the few attempts to understand the growth strategies of perennials during secondary succession.

A greater allocation of biomass to stem component in older fallows as compared to the younger fallows may be related with need of the species to grow taller in older fallows for shade avoidance. Greater allocation to leaf component in younger fallows would help in maximizing photosynthesis under the high light regime in these. While reproduction here is through extensive rhizomes, the allocation to this component increased markedly in older fallows. Thus the vegetative reproductive effort in this species showed a high degree of plasticity to change in environmental conditions in the initial phase of succession as shown for the other vegetatively propagated perennial colonizers (Ogden, 1974; Thomas, 1974; Abrahamson,

1975a,b). The strategy to conserve more resources through preferential transfer of photosynthate to the rhizome in older fallows may help in the success of this species as a weed in the jhum plots during the subsequent slash and burn and cropping.

The allocation strategies often done on the basis of biomass alone (Harper, 1977) do not give a complete picture. Recent studies of Thompson and Stewart (1981) and that done by Saxena and Ramakrishnan (1983) suggest that nutrient allocation strategy is equally important particularly for reproductive growth since reproductive structures can make no contribution in this regard.

The allocation strategy of nitrogen, phosphorus and potassium are distinctly different for I. cylindrica in the different successional fallows. Greater allocation of nutrients to leaf component in a 0-year old fallow compared to older fallows and conversely more allocation to the under-ground rhizomatous propagules in older fallows again suggests of a high degree of plasticity to occupy changing environment of seral community. Preferential allocation to leaf in a 0-year old fallow, perhaps, would help in quicker establishment and rapid growth in the initial phases while the strategy for more allocation to rhizome in a 5-year old fallow would help in its survival through another slash and burn cycle to which the plots under an older fallow may be subjected. Such a conservation of biomass and nutrients in the under-ground rhizome (Harper and Ogden, 1970) in older fallows would be a strategy

to overcome subsequent stress conditions. This is also indicative of the extreme ruderal behaviour of this species where such species under stress divert resources to reproductive organs (Hodgson and Blackman, 1956; Hickman, 1975; Raynal and Bazzaz, 1977; Van Andel and Vera, 1977; Foulds, 1978).

Seasonal changes in the concentration of nutrients is often related to the peak period of growth. Mason and Bryant (1975) working on other rhizomatous plants in a wet land found that concentration of nutrients in above-ground parts increased with the emergence of new shoots and reached a maximum at the peak period of growth. The above-ground and below-ground parts of I. cylindrica showed much variation in nutrient concentration in the different fallows, during the growth period from June to December. Thus nutrient concentration increased upto October coinciding with peak growth period for this species in a 0-year old fallow. However, in a 5-year old fallow where growth is extremely slow, the nutrient concentration did not show much variation in different months.

Total nutrient quantity and its increase during the growth period in different fallows is a function of the already existing biomass as well as the growth rate of the organ concerned. A high nutrient capital in under-ground organs compared to above-ground parts in older jhum fallows is expected because of accumulated under-ground biomass as the fallows age. However, the rate of accumulation of nutrients during a given growth season is more in a younger fallow of 0-year than in older ones and could be related to the vigour of growth of the individual as a whole.

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The lower uptake efficiency of I. cylindrica observed in older fallows may be partly related to reduced fertility levels due to losses from the system (Toky and Ramakrishnan, 1981; Mishra and Ramakrishnan, 1983a) and partly because of rapid uptake by the other members of the developing community (Ramakrishnan and Toky, 1981; Toky and Ramakrishnan, 1983; Mishra and Ramakrishnan, 1983b, 1983c). The phosphorus uptake efficiency is generally low compared to that of nitrogen and potassium. This efficiency further declined in older fallows, perhaps due to reduced vigour of plants. However, the proportion of phosphorus allocated to the under-ground organs was comparable to that of nitrogen and potassium (of Table 4.5). It may be noted here that the phosphorus accumulation in the developing herbaceous community during the first 5-years of fallow regrowth was very high (Toky and Ramakrishnan, 1983; Mishra and Ramakrishnan, 1983c). Perhaps, the rapid transfer and storage of phosphorus in the under-ground rhizome would help I. cylindrica to conserve this nutrient in the rhizome as it would be in short supply in the soil pool at this stage of secondary succession since all herbaceous species compete for it. This would also explain the extremely high nutrient use efficiency for phosphorus obtained in this study. The general decline in the nutrient use efficiency observed for nitrogen, phosphorus and potassium as the fallow ages could be related with the decline in vigour of this species with fallow age.

I. cylindrica coming through rhizomes after slash and burn agriculture has an immediate competitive advantage over other

annual and perennial herbaceous weeds due to the extensive under-ground rhizome that are built up during the preceeding fallow regrowth as shown in this study. Rhizomatous species also have a nutritive advantage over those coming through seeds (Saxens and Ramakrishnan, 1983; Keeley and Keeley, 1977). This species shows a high degree of plasticity through different successional stages of fallow develepment. In the younger fallows, the strategy is to make quick growth of the aerial parts to maximize photosynthesis. In the older fallows, the strategy is to build the resources within the perennating organs (Under-ground rhizome) in order to ensure its survival through another slash and burn cycle.

SUMMARY

Growth and resource allocation strategies of Imperata cylindrica, an important early successional rhizomatous perennial species, were studied in fallows after slash and burn agriculture at two elevations in Meghalaya. In this species, reproduction is through vegetative sprouts and seed reproduction is seldom attempted except under stress. The growth of the above-ground parts from the perennating rhizome was rapid in the 0-year old fallow. In 3- and 5-year old fallows, the build up of the under-ground perennating organs was rapid. A greater allocation of biomass to stem component and relatively lesser allocation in older fallows to the leaf component, as compared to the younger fallows may be related with the need of the species to grow taller in

older fallows for shade avoidance. The vegetative reproductive allocation increased markedly with the age of the fallow and this may help its success as a weed in the jhum plots during the subsequent slash and burn and cropping. Preferential allocation of nutrients like nitrogen, phosphorus and potassium to the leaf component would help in quicker growth and establishment in the initial phases of fallow regrowth while more allocation of nutrients to the rhizome in a 5-year old fallow would help in its survival through another slash and burn cycle. The decrease in nutrient uptake efficiency of I. cylindrica with the age of the fallow may be related to decline in plant vigour, competition and reduced nutrient availability. The decreased nutrient use efficiency in older fallows may also be a function of reduced vigour of the plants. Since phosphorus is an element absorbed in larger quantities by the herbaceous vegetation, the high phosphorus use efficiency of I. cylindrica may be a conservative mechanism as far as this nutrient is concerned. The growth and allocation strategy of this perennial weed coming after slash and burn agriculture is indicative of its extreme ruderal behaviour.

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CHAPTER VI

CONTROL OF IMPERATA CYLINDRICA (L.) BEAUV.



INTRODUCTION

Imperata cylindrica (L.) Beauv. is a rhizomatous perennial grass with high regenerative power and is a serious weed in several countries in south-east Asia (Eussen and Werjuhardja, 1973), Africa (Ivens, 1973) and some parts of the United States (Tabor, 1952). The weed has a wide ecological amplitude and generally invades cultivated lands that are abandoned or cleared areas for cropping (Eussen et al., 1976). It is also a serious weed in tea plantations in north-east India (Rao et al., 1976).

Mechanical control of this weed is achieved in Malaya (Mitchell, 1959), Java (Haigh, 1951), and Sri-Lanka (Sandanam and Jayasinghe, 1977) by forking out the rhizome to a depth of 45 cm. This method although effective, is uneconomic in terms of time and labour. Effect of slashing in the control of the above-ground and under-ground parts has been reported by Sandanam and Jayasinghe (1977) from Sri-Lanka. Other mechanical methods such as repeated ploughing, discing (Hartley, 1949; Knox and Cole, 1973) are possible only in a terrain which is suitable for the use of tractors and are economically justifiable only if the weed population is dense and covers a large area (Coomans, 1976).

Chemical control of I. cylindrica has been attempted with varying degrees of success in various parts of the world (Seth, 1970; Dickens and Buchanan, 1972, 1975; Ivens, 1973; Soedarsan et al., 1975; Yeh and Pushparajah, 1976; Wong, 1976, Rao et al., 1981). At present three herbicides, namely paraquat, dalapon

and glyphosate are commonly used for control of this rhizomatous weed. Of these, paraquat is a post-emergent contact herbicide with very less degree of translocation whereas dalapon and glyphosate are post-emergent and translocated herbicides. Being a contact herbicide, paraquat does not prevent regeneration of rhizomatous species with one application. As a result, it needs to be applied more than once to obtain satisfactory control (Rao and Kotoky, 1982). Although dalapon and glyphosate both have translocated properties, the latter has a wide area of application and has been found to be superior to the former at much lower doses (Wong, 1975, 1976; Yeoh and Pushparajah, 1976; Rao et al., 1981) on a diverse group of perennial grasses (Moshier et al., 1976). On the other hand, application of dalapon followed by paraquat at lower dose has been found to be more effective than when applied alone (Ollunuga, 1975; Soerjani, 1970; Seth, 1970; Dickens and Buchanan, 1975; Yeoh and Pushparajah, 1976; Sandanam and Jayasinghe, 1977).

The control achieved with various means has in most cases been evaluated only by visual assessment of top growth which does not necessarily reflect the degree of real control achieved since the effect on the under-ground system may be the decisive factor in the control of rhizomatous grass (Sandanam and Jayasinghe, 1977). The present study deals with the effect of sickling the grass and chemical treatments on top growth control as well as underground parts. The long-term effect of repeated application of paraquat at different time intervals is also studied. The effect of glyphosate at various growth stage of the weed is also observed.

STUDY AREA AND CLIMATE

The study was carried out at Tocklai Experimental Station, Jorhat (94°12' E and 26°47' N) in Assam at an elevation of 92 meters.

The climate of the area can be divided in three distinct seasons: Summer which extends from April to May with occasional pre-monsoon rain. Rainy season extends from June to September. The mean annual rainfall is between 2000 mm to 3000 mm, a major fraction of which comes during the monsoon. The winter is mild and extends from December to February. The average maximum summer temperature is 30°C and the minimum winter temperature is 18.5°C.

METHODS OF STUDY

In the weed nursery of the experimental garden, beds with almost pure and thickly populated Imperata cylindrica were selected and three separate experiments were conducted.

Experiment 1

Plots of 4 m x 1.5 m were marked out in the nursery beds with almost pure and heavy stand of I. cylindrica. The experiment was of randomised block design with three replications conducted during the period from May, 1983 to October, 1983. The treatments were as follows:

- 1/5/71
1. Control (untreated)
 2. Sickling to ground level, in weeks -
0, 2, 4, 6, 8 and 10
 3. Sickling to ground level, in weeks -
0, 4, 8, 12, 16 and 20
 4. Glyphosate 0.8 kg ai/ha, 0 week -
Blanket spray, spot application
after 6 to 8 weeks
 5. Paraquat 0.4 kg ai/ha, in weeks -
0, 2, 4, 6, 8 and 10
 6. Dalapon 3.0 kg ai/ha, + Paraquat 0.4 kg ai/ha; (Sequential)
in 0 week - dalapon, paraquat in weeks -
1, 3, 5, 7, 9 and 11

Herbicides were sprayed using Backpack-Knapsack sprayer fitted with WFN 040 floodjet fan type nozzle. The fluid used was at the rate of 500 lit/ha. Sprayings were done on sunny days.

Percentage control of the weed relative to the untreated control plots was assessed by visual scoring (0 - no effect to 10 - complete kill) at weekly intervals. Regeneration was considered as decline from the control. From each plot, before each follow up application, rhizomes were removed from an area measuring 30 cm x 30 cm and regeneration was studied by planting 50 rhizomes randomly in pots. At the end of the experimental period, three plant samples from three 50 cm x 50 cm quadrats in each plot in a treatment were removed from a depth of 45 cm and an average was obtained for the plot. In each of the above quadrats an average numbers of tillers was also determined. The plants were further separated into shoot and rhizome and dry weights were determined after oven drying at $65^{\circ} \pm 5^{\circ}\text{C}$ for 48 hours.

Soluble sugars and starch content in the fresh rhizome were determined after 3- and 6-months after the spray by following standard methods. Soluble sugar was determined by the modified method of Dev Choudhury and Bazaaj (1976) and starch was determined by the methods of McCreedy et al. (1950).

Experiment 2

Plots of 2 m x 1.5 m were marked out in an almost pure and heavy stand of Imperata cylindrica. Paraquat (0.4 kg ai/ha) was applied in the form of commercial dichloride salt formulations (trade name, Gramoxone, 24%). The spraying was done on the foliage of I. cylindrica by using Backpack Knapsack sprayer fitted with WFN 040 floodjet fan type nozzle at different time intervals.

The treatments were as follows:

- 1. Paraquat 0.4 kg ai/ha - 0,10,20,30,40,50 days interval
- 2. " " - 0,10,20,40,60,80 " "
- 3. " " - 0,10,20,50,80,110 " "
- 4. " " - 0,15,30,45,60,75 " "
- 5. " " - 0,15,30,55,80,105 " "
- 6. " " - 0,15,30,60,90,120 " "

A randomised block experiment with three replicates was conducted during the period from May to December, 1983. Visual assessment of treatmental effect was observed in the scale of 0-100 (0 - full cover, 100 - no cover) on the basis of the extent of ground cover by the target weed at different periods during the course of the experiment.

Experiment 3

Glyphosate at two different concentrations was sprayed to a well established stand of I. cylindrica at different times of the year in a randomised block trial with three replications. The plot size was 2 m x 1.5 m. Applications of glyphosate were made in March, April, July, August, September and October, 1983. Observations were made after one month and after nine months of each spray.

A separate experiment was initiated to determine the phytotoxicity of glyphosate when applied to I. cylindrica at different growth stages. Growth stages were established after initial sickling of the grass to the ground level before the application of glyphosate. The growth stages were as follows:

- I foliage 5 to 8 cm tall - no heads on I. cylindrica
- II foliage 15 to 18 cm tall - fully headed I. cylindrica
- III foliage 20 to 25 cm tall - fully headed I. cylindrica
- IV foliage 25 to 30 cm tall - fully headed I. cylindrica
- V foliage 35 to 40 cm tall - ^{fully}headed I. cylindrica
- VI foliage 45 to 50 cm tall - mature headed I. cylindrica

Glyphosate was applied at two different rates, 0.8 kg ai/ha and 1.2 kg ai/ha. The quantity of fluid used was at the rate of 500 litres/ha. Visual scores on the effect of the treatments were observed on the basis of the scale 0-100 where 0 - no control and 100 - full control.

RESULTS

Experiment 1

Visual estimates of top growth control by different treatments (Fig. 6.1) showed that glyphosate (C.8 kg ai/ha) was effective. After the first spray on 5 May, a steady increase in the top growth control was observed upto week five (80%). Thereafter, the rate of control tended to decline. After the second spray which was a spot application at week 7, a complete kill was observed at week 14 (100%).

Six applications of paraquat (0.4 kg ai/ha) at 2-week interval upto week 10 and application of dalapon initially (3.0 kg ai/ha) followed by six applications of paraquat at 2-week interval could control upto 80-85% only during the treatment period; at the end of the experimental period the control was to an extent of 20-30%.

Sickling the grass to the ground level six times at 2-week interval led to a progressively increased degree of control from 30% after first sickling to 70% after the sixth sickling. Regrowth occurred when sickling was discontinued and subsequently the degree of control was only about 25% at week 24. Sickling six times at 4-week interval was not effective in control. After the first sickling the regrowth was so fast that before the second treatment full growth was noticed. However, in the subsequent sickling the percentage control increased so that after the fourth sickling the control was 60% with further decline upto 30% at the end of the experimental period.

Fig. 6.1 Effect of manual and chemical methods of control of top growth of Imperata cylindrica as assessed by visual scoring. Open triangle, sickling at 2-week interval; closed rectangle, sickling at 4-week interval; open rectangle, glyphosate (0.8 kg ai/ha); closed circle, paraquat (0.4 kg ai/ha); open circle, dalapen-paraquat (3.0 kg ai/ha, 0.4 kg ai/ha).

Fig. 6'1

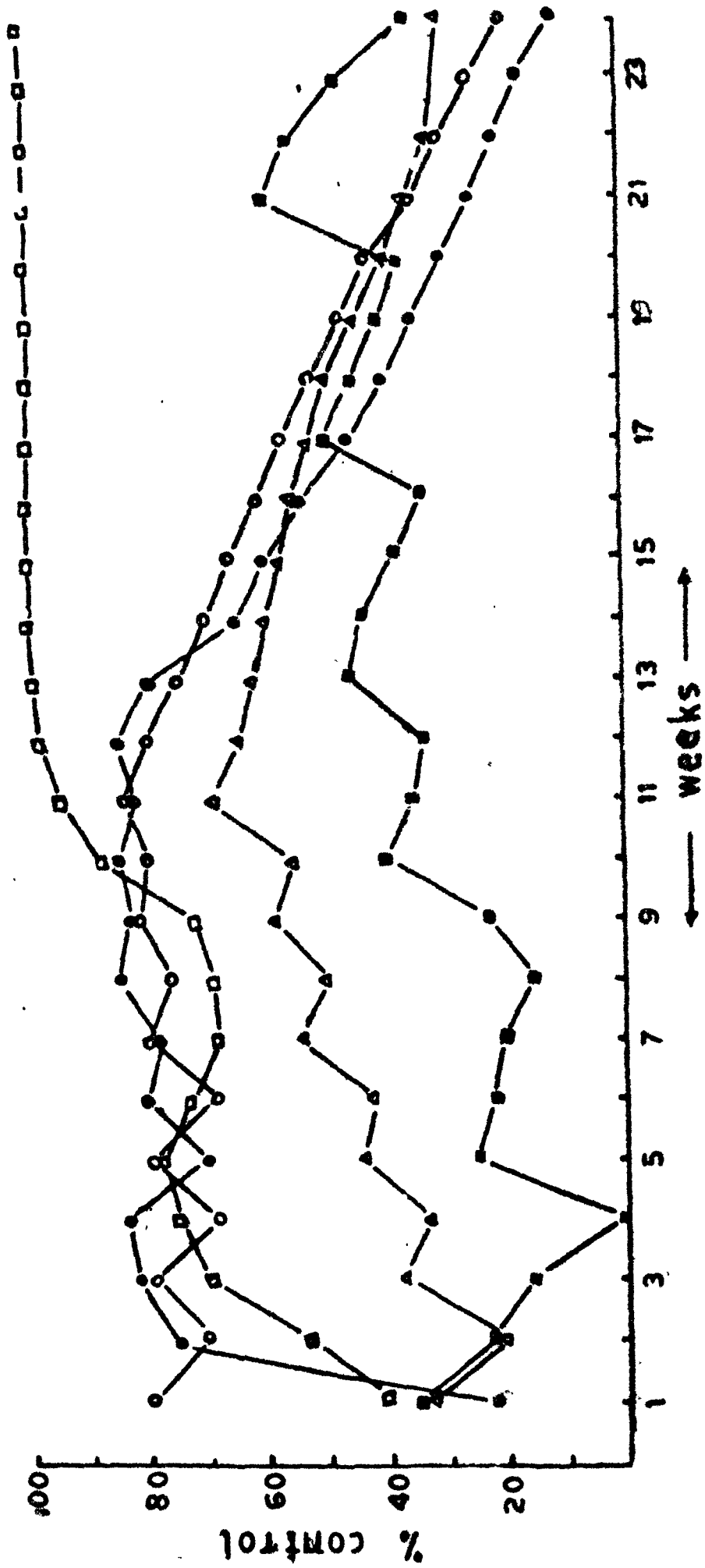


Table 6.1 Effect of manual and chemical control measures on I. cylindrica. Dry weight of plant parts and number of tillers per quadrat (values are transformed to \sqrt{X} , where X is the actual number, given in parenthesis

Sl. No.	Treatments	Dry weight(g)		Number of tillers/quadrat
		Shoot	Rhizome	
1.	Control	4.4230 (19.56)	5.4000 (29.16)	7.5090 (58)
2.	Sickling 2-week interval	2.2932 (5.33)	4.0410 (16.33)	6.7911 (47)
3.	Sickling 4-week interval	2.3429 (5.50)	4.2027 (17.66)	6.2486 (46)
4.	Glyphosate 0.8 kg ai/ha	2.0082 (4.03)	3.7635 (7.66)	4.2723 (18.1)
5.	Paraquat 0.4 kg ai/ha	2.7168 (7.53)	4.3492 (19.0)	4.3244 (20.6)
6.	Dalapon-paraquat (sequential) 3.0 kg ai/ha, 0.4 kg ai/ha	3.2745 (10.93)	4.5434 (20.8)	4.9011 (24)
L.S.D. (P = 0.05)		0.660	0.430	0.603

Dry weight yield of shoot

The dry weight yield of shoot at the end of the experimental period declined significantly in all the treatments compared to the control plots (Table 6.1). Application of glyphosate was significantly superior to dalapon-paraquat sequential treatment. Sickling the grass to the ground level was significantly superior than the dalapon-paraquat sequential treatment. However, no significant difference was observed between the two sickling treatments even between sickling, glyphosate and paraquat treatments.

Dry weight yield of rhizome

Application of herbicides and sickling the grass to the ground level reduced the dry weight yield of rhizome significantly compared to the control plots (Table 6.1). Glyphosate (0.8 kg ai/ha) was more effective resulting in significantly lower dry weight yield compared to other herbicide treatments. However, there were no significant difference between the other treatments.

Tiller density

All forms of chemical control resulted in significantly lower number of tillers compared to the untreated as well as the sickled plots. However, no significant difference was observed between the differentially chemically treated plots. Sickling the grass to the ground level significantly reduced the number of tillers compared to the untreated plots but not as effectively as the chemical treatments; the two regimes of sickling did not show any significant difference (Table 6.1).

Table 6.2 Effect of manual and chemical control measures on I. cylindrica. Amount (%) of soluble sugar and starch in the rhizome after 3-months and 6-months after treatment

Sl. No.	Treatments	Soluble sugar(%)		Starch(%)	
		August	November	August	November
1.	Control	17.30	20.0	7.1	6.09
2.	Sickling 2-week interval	13.40	9.1	5.5	3.70
3.	Sickling 4-week interval	15.20	11.9	5.9	4.22
4.	Glyphosate 0.8 kg ai/ha	9.45	3.0	5.0	3.00
5.	Paraquat 0.4 kg ai/ha	3.90	9.4	3.2	5.30
6.	Dalapon-paraquat (sequential) 3.0 kg ai/ha, 0.4 kg ai/ha	3.30	7.2	4.2	6.09
L.S.D. (P = 0.05)		0.457	0.525	0.647	0.664

Sugar and starch content

Sugar and starch in the rhizome showed differences due to different treatments and also at different time intervals of 3-months and 6-months (Table 6.2).

Soluble sugar was lowest under dalapon-paraquat treated plots and highest in sickled plots after 3-months of spray. The order being dalapon-paraquat > paraquat > glyphosate > sickling 2-week interval > sickling 4-week interval in preference to their effectiveness in reducing the sugar content. At the end of the study period after 6-months, the sugar content in the rhizome was found in the order of glyphosate > sickling 2-week interval > sickling 4-week interval > dalapon-paraquat > paraquat.

Starch content in the rhizome was lowest in the paraquat treatment and highest under sickling treatments after 3-months of spray. The order being paraquat > dalapon-paraquat > glyphosate > sickling 2-week interval > sickling 4-week interval in preference to their effectiveness in reducing the starch content. At the end of the study period the order was glyphosate > sickling 2-week interval > sickling 4-week interval > paraquat > dalapon-paraquat.

Regeneration of rhizome

Rhizome regeneration under different treatments at a time before each follow up application showed that applications of glyphosate, dalapon-paraquat and paraquat had resulted in reduced regeneration compared to sickled and control plots. No significant difference was observed between sickled and control plots. During

Fig. 6.2 Regeneration of *Imperata cylindrica* rhizome before each application of herbicides and manual control. Open circle, control plots; closed circle, sickling at 2-week interval; open triangle, sickling at 4-week interval; closed triangle, glyphosate (0.8 kg ai/ha); open rectangle, paraquat (0.4 kg ai/ha); closed rectangle, dalapon-paraquat (3.0 kg ai/ha, 0.4 kg ai/ha). Vertical bars represent LSD at $P = 0.05$.

Fig. 6.2

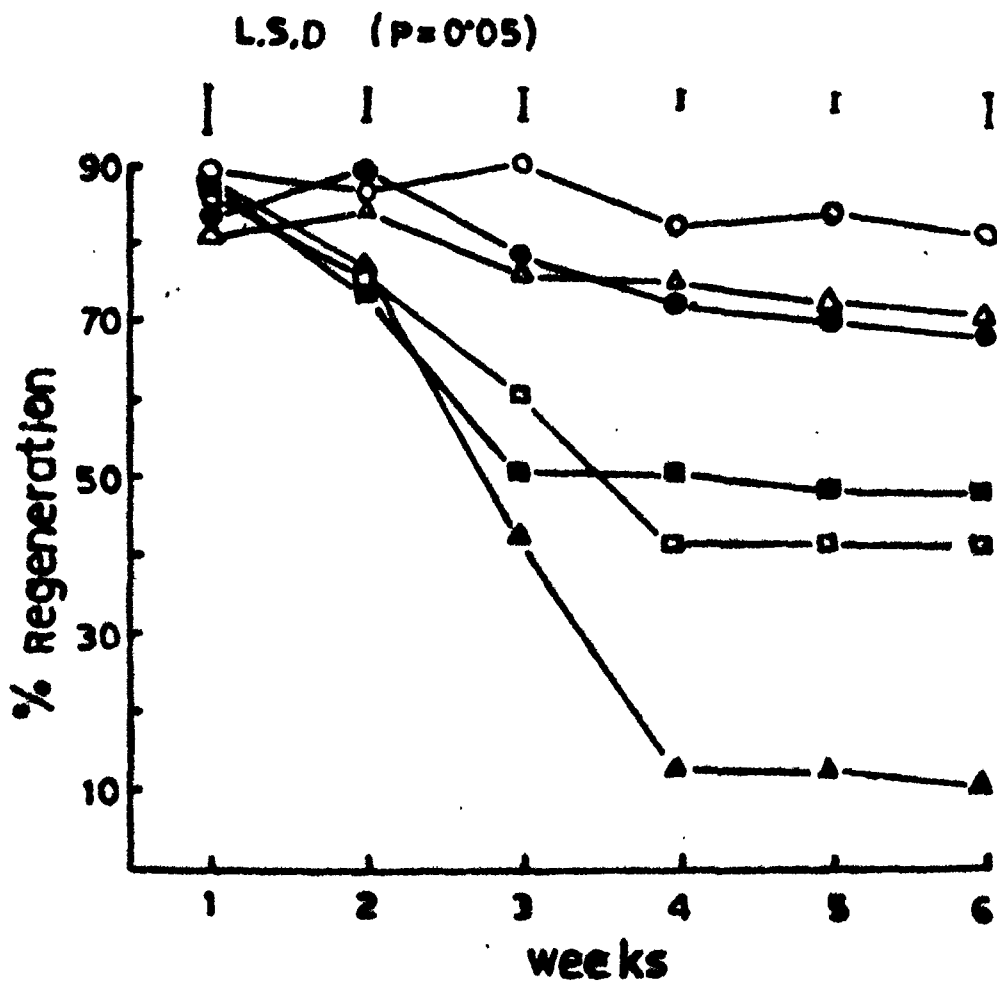


Table 6.3 Effect of variation⁴ interval period in different rounds of paraquat application on the control of Imperata cylindrica. Figures are log values of actual numbers (actual values given in parenthesis)

Treatment	Application Time ()						% Ground cover by <u>I. cylindrica</u> 140 days and 210 days of spray from 1st round	
	1st	2nd	3rd	4th	5th	6th		
				days				
1. Paraquat (0.4 kg ai/ha)	0	10	20	30	40	50	0.69897 (5)	1.66332 (46.6)
2. -do-	0	10	20	40	60	80	0.90325 (8.3)	1.62341 (41.6)
3. -do-	0	10	20	50	80	110	1.00000 (10)	1.36229 (23.3)
4. -do-	0	15	30	45	60	75	1.17609 (15)	1.54407 (35)
5. -do-	0	15	30	55	80	105	1.18000 (10)	1.60206 (40)
6. -do-	0	15	30	60	90	120	1.36229 (23.3)	1.61278 (41)

L.S.D. (P=0.05) 0.384 0.07389

Table 6.4 Application of glyphosate at different times of the year for the control of I. cylindrica

Rate kg ai/ha	Date of application	% Control on	
		<u>16 April, 1983</u>	<u>3 December, 1983</u>
0.8	10 March, 1983	50	40
1.2	10 March, 1983	60	70
		<u>25 May, 1983</u>	<u>20 January, 1984</u>
0.8	20 April, 1983	60	50
1.2	20 April, 1983	70	80
		<u>16 August, 1983</u>	<u>15 April, 1984</u>
0.8	14 July, 1983	70	80
1.2	14 July, 1983	80	90
		<u>8 September, 1983</u>	<u>10 May, 1984</u>
0.8	10 August, 1983	90	100
1.2	10 August, 1983	100	100
		<u>6 October, 1983</u>	<u>6 June, 1984</u>
0.8	20 September, 1983	70	90
1.2	20 September, 1983	90	100
		<u>12 November, 1983</u>	<u>8 July, 1984</u>
0.8	15 October, 1983	60	70
1.2	15 October, 1983	80	85

Table 6.5 Effect of various developmental stages on susceptibility of *I. cylindrica* to glyphosate, evaluated 15 weeks after treatment

Rate kg ai/ha	Stages of growth					
	I	II	III	IV	V	VI
	% Control					
0.8	10	95	95	90	60	50
1.2	20	100	100	100	90	90

Stage I, 5 - 8 cm tall

Stage II, 15 - 18 cm tall

Stage III, 20 - 25 cm tall

Stage IV, 25 - 30 cm tall

Stage V, 30 - 40 cm tall

Stage VI, 45 - 50 cm tall

the last phase of the experiment, glyphosate treated plots had the least regeneration and sickling resulted in highest regeneration in all the treated plots. The order being glyphosate > dalapon-paraquat > paraquat > sickling 4-week > sickling 2-week interval > in preference to their effectiveness (Fig.6.2).

Experiment 2

Visual assessment of ground cover by I. cylindrica at 140 days after the first application of paraquat showed that there was no significant difference between treatments 1,2 and 3. No significant difference was observable between treatments 4,5 and 6. Spraying at intervals of 10 days showed significantly less ground coverage as compared to other treatments. After 210 days from the first application, treatment 3 showed least cover compared to other treatments (Table 6.3).

Experiment 3

Early application of glyphosate at two concentrations gave lesser control compared to application in the month of August-September. In all the applications except the August application, the control was better with the higher dose. In August, however, both dosages had the same effect resulting in total control (100%). September application gave total control only with the higher dosage. Subsequently, the control was lesser (Table 6.4).

Effect of various growth stages on susceptibility of I. cylindrica to glyphosate is shown in Table 6.5. A visual estimate on weed control after 15 weeks after treatment showed

that stage I (5 to 8 cm tall) was least susceptible to glyphosate. Stages II, III and IV were highly susceptible and showed 90% to 100% control at lower and higher rates respectively. At subsequent stages the level of control was lower.

DISCUSSION

Imperata cylindrica being a vigorous rhizomatous species with short internodes and frequent lateral branches which develop into a mass of interoven rhizomes of great regenerative power (Seth, 1970; Soerjani, 1970), any control measure must check the growth of the under-ground organs. The results indicated that of all the treatments glyphosate (N-phosphonomethyl-glycine) could be the most effective herbicide for controlling this species. One spray with glyphosate at 0.8 kg ai/ha gave 80% top growth control after five weeks after application. A follow up spray at the same rate provided complete top kill at the end of the season. Wong (1976) also observed 94-95% control at 1.0 kg/ha given in a single application; a follow up spray improved the control upto 98-99% and continued to suppress the regeneration upto a period of 180 days. The effectiveness of glyphosate on I. cylindrica has also been reported by other workers (Andrew et al., 1974; Connel and Parting, 1973; Dickens and Buchanan, 1975; Ivens, 1973).

Sequential application of dalapon-paraquat or repeated application of paraquat alone could provide only a short term

control of top growth. Ollunuga (1975) reported a high level of control for a period of twelve weeks after application of dalapon at 5 kg/ha followed by paraquat after a week at 5 kg/ha.

Sickling the grass to the ground level generally increased control immediately after the treatment but regrowth started soon after. Repeated sickling at intervals of 2-4 week could suppress the growth substantially. Sandanam and Jayasinghe (1977) while making similar observations at Sri-Lanka suggested that the strategy for this control measure should be such that the sickling intensity and frequency should be increased at a stage of growth before the foliage change from 'sink to source'. This transition occurs at 50% control stage and sickling should be repeated when the growth declines to this level (Seth, 1970).

Though sickling was not as effective as dalapon-paraquat or paraquat treatment with respect to tiller density, it was nevertheless as effective as the latter treatments with regard to rhizome dry weight. This may be accounted as due to the fact that paraquat being a contact herbicide is more effective in killing the top portion of the plant. On the other hand sickling is effective in exhausting the rhizome reserve by allowing frequent regeneration of shoots. This confirms the findings of Sandanam and Jayasinghe (1977) on the effect of slashing I. cylindrica. Though sickling is environmentally a better form of control, the cost of labour is prohibitive.

A high degree of reduction in the rhizome dry weight in glyphosate treated plots was due to its persistent toxicity

resulting in the decomposition of rhizome mass. Glyphosate readily shows phototoxicity (Baird et al., 1971; Baird and Upcharch, 1972; Caseley, 1972) with a major part of the herbicide being moved into the rhizome within 24 hours after application to the foliage (Brockman et al., 1973; Lange et al., 1973). Initial activity is fairly slow following application; obvious herbicidal response may not be visible upto a week or so. The visible effect is manifested as a gradual wilting and yellowing of the treated plant tissue, and ultimate decomposition of the under-ground root or rhizome system (Spurrier, 1973).

Soluble sugar and starch content in the rhizome decreased on application of glyphosate and after two sickling treatment regimes with the passage of time only. In the case of paraquat and dalapon-paraquat (sequential) treatments, the decline in sugar and starch content was immediate but did not have a long term effect. This may be because of the fact that in the case of paraquat and dalapon-paraquat (sequential) treatments the effect is of a shorter duration related to being a contact herbicide (Fernandez and Bayer, 1977). On the other hand the effect of glyphosate is realized only after a long phase. Mosavi and Dore (1979) also reported a drastic loss of total carbohydrate by the application of glyphosate. Sickling deplets the rhizome reserves by allowing frequent regeneration and growth of the above-ground shoots (Sandanam and Jayasinghe, 1977).

Time interval at which chemical applications were done had an impact on the control. A short interval in the initial phase followed subsequently by longer intervals were found to be more effective. Rao and Kotoky (1979) also observed a delay in regeneration by extending the spray interval in subsequent rounds.

Lesser control through glyphosate during March-April may be due to the moisture stress in the soil as compared to July-August when the monsoon is at its peak activity. Due to moisture stress there is often temporary wilting of the leaves which perhaps interferes with the absorption and translocation of the herbicide, an observation also made by Whitewell and Santlemann (1978) in the case of Cynodon dactylon.

The differential phytotoxicity observed when glyphosate was sprayed on I. cylindrica at various developmental stages may be due to differences in the rate of absorption and translocation at different stages. More efficient control in the early stages of vegetative growth compared to that just prior to or soon after flowering may be because, the absorption and translocation of the chemical is optimal in the active phase of growth of the plant (Whitewell and Santlemann, 1978; Gottrup et al., 1976; Sprankle et al., 1975).

The results presented here showed that successful control of a rhizomatous perennial like I. cylindrica can be obtained with a herbicide such as glyphosate which is rapidly absorbed and translocated before the compound itself is damaged through

metabolic activity as suggested by Sprankle et al., (1975). Further, a herbicide such as glyphosate which has foliar application and is phloem-translocated when used at a proper stage of growth of the weed and at a time when soil moisture is adequate would give maximum control. Another aspect that comes out of the study is that repeated application of contact herbicide such as paraquat can have only limited control of the aerial shoot without killing the under-ground vegetative rhizome.

SUMMARY

This study deals with the various aspects of the control of Imperata cylindrica (L.) Beauv. In experiments conducted with pure stands of this weed, glyphosate (0.8 kg ai/ha) in two applications at 6-week intervals gave lasting control in terms of top growth and damage to the under-ground parts. Although only a low degree of control was observed through sickling, the dry weight of shoot and soluble sugar and starch declined to a level ^{which can be} compared to the most effective herbicide treatment obtained through glyphosate. Application of dalapon (3.0 kg ai/ha) followed by paraquat (sequential) for six times at 2-week interval provided only short-term control through damage to the aerial parts only without any effect on the under-ground rhizomes. Six rounds of application at interval of 15 days or three applications at 10 days interval followed four more at

20 and 30 days intervals gave better control. A 15 days interval and application at longer intervals than 10 days after three rounds can be more effective. Application of glyphosate in August and September was most effective for controlling this weed which coincides with adequate moisture content in the soil. Further, during the active period of growth this weed was more susceptible to glyphosate.

The results presented here show that successful control of a rhizomatous perennial like I. cylindrica can be obtained with a herbicide such as glyphosate which is rapidly absorbed and translocated before the compound itself is damaged through metabolic activity, as suggested by Sprankle et al., (1975). Further, a herbicide with foliar application and phloem-translocated at a proper stage of growth of the weed and in the presence of adequate moisture in the soil is effective to get sufficient basipetal translocation to the under-ground organs. Another aspect that comes out of the study is that repeated application of contact herbicide such as paraquat can have only limited control of the aerial mass without killing the under-ground vegetative rhizome.

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CHAPTER VII
GENERAL DISCUSSION



Under slash and burn agriculture of the north-eastern India, Imperata cylindrica (L.) Beauv. is an important component of the agricultural system and of the early successional secondary fallows (Toky and Ramakrishnan, 1983a; Kushwaha et al., 1983; Mishra and Ramakrishnan, 1983). This species is very vigorous due to the extensive under-ground rhizomes which are fire-resistant. In fact, frequent disturbance either due to slashing or burning, particularly during the dry season, is suggested to be a requirement for sexual reproduction to occur (Kushwaha et al., 1983; Schlippe, 1956).

The weed occurs under a variety of habitat conditions. Altitudinally, it is found right from sea level upto an altitude of 1700 m in Meghalaya. The wide ecological amplitude of this species could partly be accounted as due to extensive plastic adaptation in the species as shown through the present studies and partly be related to a certain degree of ecotypic differentiation of altitudinal populations which was more obvious during transplant experiments done in a neutral substratum at low elevations. The generally poorer growth of the populations of this species at high altitude may partly be due to temperature and partly to acidity in the soil under lower temperature. Similar temperature and acidity-dependant poorer growth of Carex aquitilis populations was also observed in arctic and alpine populations of this species by Chapin (1981).

The allocation pattern of biomass in the two populations at the two altitudinal sites indicate a strong phenotypic plasticity

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of the species population adapted to the contrasting environmental conditions. The vegetative effort was not different in the two populations at either of the two sites. A large allocation of biomass and nutrients to the under-ground organs in I. cylindrica is to be expected in view of the rarity of sexual reproduction in this predominantly vegetatively reproducing species. Since there are larger allocations of available resources to under-ground parts of regeneration, the sprouting species are expected to have less allocation to sexual reproduction as compared to non-sprouters (Keeley and Keeley, 1977; Saxena and Ramakrishnan, 1983).

A number of micro-environmental changes occur during the early phase of secondary succession, such as fast changes in the moisture and nutrient status in the soil (Toky and Ramakrishnan, 1981; Ramakrishnan and Toky, 1981). Subsequent shading caused by larger shrubs and trees that come up after about 5-6 years of fallow regrowth also create unfavourable condition (Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983). Rapid colonization of the site by a number of herbaceous weedy species would result in increased competition for nutrient resources in the soil (Saxena and Ramakrishnan, 1984).

Under such a transient environment of the early successional phase, the demography of I. cylindrica population is bound to change drastically with the age of the jhum fallow. The study done over a two year period showed that at both low and high elevation sites, the size of the original population was markedly reduced

with the age of the fallow so much so that in a 5-year old fallow the ultimate population size was extremely small compared to a 1-year old fallow. Similarly the germination and establishment of individuals through seed and tiller populations declined drastically in older fallows, so much so that in 5- and 10-year old fallows all the introduced individuals died.

The strategy of a weedy species coming soon after slash and burn agriculture should be to have either an efficient method of reproduction through seeds as in Eupatorium odoratum (Saxena and Ramakrishnan, 1982) or it should have an efficient vegetative reproduction as in I. cylindrica with extensive under-ground rhizomes. The growth of the above-ground parts from the perennating rhizome is very rapid in a 0-year old fallow due to the stored food resources in the rhizome and due to the open environment where light is not a limiting factor and that the competition from other species in the community is minimal. The decline in growth with the age of the fallow could be partly related to competition from other species such as Eupatorium odoratum (Kushwaha et al., 1983), and partly due to reduced light availability in older fallows as shown by Kushwaha and Ramakrishnan (1982).

The initial decline in the below-ground biomass in a 0-year old fallow and the simultaneous increase in the above-ground biomass explains rapid transfer of resources from below to above-ground organs. This is a strategy of under-ground perennating plant species to conserve the resources within the plant itself and transfer it to the growing organs at the time of need (Schier and Zasda, 1973).

A similar strategy was also observed by Saxena and Ramakrishnan (1983) in many sprouting species. The biomass allocation to under-ground organ component increased markedly in the older fallow, an effective strategy for survival during the subsequent slash and burn phase.

In a successional environmental during the early phases, on a steep slope abandoned after slash and burn agriculture, there is bound to be considerable heterogeneity in soil chemical characteristics. Such an environment is occupied by both C_3 and C_4 plant species. Our earlier comparative studies have shown (Saxena and Ramakrishnan, 1983) that C_3 and C_4 species are different with respect to nutrient uptake and use efficiency. C_4 species was shown to have a higher efficiency in this regard. The C_3 species with a large uptake and utilisation of nutrients for a given dry matter yield are suited to occupy nutrient rich microsites, while C_4 species with a lower uptake and higher efficiency of utilisation of nutrients can successfully colonise nutrient poor microsites. The C_4 species with a higher efficiency of nutrient use (Brown, 1978) were accompanied by a greater efficiency in nutrient uptake. This may be a case of parallel evolution with the C_4 strategy developed under the generally nutrient-poor status of tropical environment (Black, 1971; Brown, 1978) where efficient uptake of nutrients could be important for survival. This niche differentiation of the C_3 and C_4 species may ensure their co-existence in the post-burn environment I. cylindrica with a C_4 photosynthetic strategy is thus adapted to occupy nutrient poor micro-environmental site. The decline in the uptake efficiency of I. cylindrica

with the age of the fallow may be related to reduced availability of nutrient in older fallows where associated species in the fast developing community (Toky and Ramakrishnan, 1983b) compete for the available soil nutrients. The reduced nutrient use efficiency, on the other hand, may be related to the reduction in the vigour of this species in older fallows.

The natural control of I. cylindrica in normal course of slash and burn cycle would occur if the fallow period is longer than about 10-years (Toky and Ramakrishnan, 1983a; Mishra and Ramakrishnan, 1983) as it would naturally get eliminated from the successional community after about 5-6 years of fallow development as shown through the present studies. However, other methods of control assume importance under a short jhum cycle and under plantation conditions such as tea and rubber introduced into the region. It must be however noted that the chemical measures are expensive and therefore can have only limited application under plantation conditions where the cost can be effectively met with. Glyphosate was shown through this study to be an effective herbicide, as also suggested by others (Ivens, 1973; Dickens and Buchanan, 1972,1975). Effective control of both aerial and underground parts was achieved over a short term interval after application. Further, application during July-September when adequate moisture is available in the soil was found to be the most effective, as moisture stress could interfere with the absorption and translocation of this chemical (Whitewell and Santlemann, 1975). Under the shifting agricultural system, the more practical control

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measure would be to keep the jhum cycle long with a minimum fallow phase of 10 years so that this species could be biologically controlled during secondary succession.

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PLATE I Flowering in Imperata cylindrica in the field.



PLATE II Tiller formation in Imperata cylindrica
from rhizome.