

**CONTRIBUTIONS TO THE COMPARATIVE BIOLOGY
OF Eupatorium SPECIES**

Dev

PAPIYA DEV

**DEPARTMENT OF BOTANY
SCHOOL OF LIFE SCIENCES**



SUBMITTED IN FULFILMENT OF THE REQUIREMENT OF
THE DEGREE OF

DOCTOR OF PHILOSOPHY

TO



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

AUGUST-1981

North - Eastern



Hill University

P. S. Ramakrishnan
M.Sc., Ph.D., F.N.A., F.A.Sc., F.N.A.Sc.
Professor of Botany & Dean of the School

DEPARTMENT OF BOTANY
SCHOOL OF LIFE SCIENCES
SHILLONG - 793003

ep

I certified that the thesis entitled
"Contributions to the comparative biology of Eupatorium
species" submitted by Papiya Dev for the Degree of
Doctor of Philosophy of the North-Eastern Hill
University, Shillong embodies the record of original
investigation carried out by her under my supervision.
She 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
Degrees of any other University.

Date : 7 Aug. 81

Place: Shillong

P. S. Ramakrishnan
Signature of the Supervisor

ACKNOWLEDGEMENT

I feel exceedingly obliged in expressing my deepest gratitude to my esteemed teacher, Dr. P.S. Ramakrishnan, Professor in the Department of Botany, North-Eastern Hill University, for his astute guidance throughout the tenure of this investigation. Without his valuable guidance, candid criticism and useful discussions throughout the course of the work this investigation could not have been possible.

I am highly thankful to Prof. J.L. Harper, University College of North Wales, Bangore, U.K., and to Dr. B.A. Auld, Agriculture Research Centre, Australia, who always evinced a keen interest in this work. The valuable suggestions and fruitful discussion with them on the various aspects, are gratefully acknowledged.

I also benefitted immensely from Dr. R.S. Tripathi, Reader in Botany, for his active participation in individual and group discussions.

My very grateful thanks are due to Professor R.R. Mishra, Head of the Botany Department for providing me necessary laboratory facilities.

I wish to express my thanks to all the staff members of the Department for their kind cooperation and encouragement.

It is my utmost pleasure in thanking Mr. P.S. Ingty, Director, Soil Conservation, Dr. D.D. Joseph, Deputy Director, B.S.I. and Mr B. Barua, Scientist in charge and Dr. K.R. Dhiman (Scientist) from C.P.R.I. for rendering their kind help in various ways during my field work.

I am grateful to my parents whose love and inspiration stood by me throughout the course of this investigation.

My hearty thanks to all my friends for sharing my difficulties and for constant help in the field and in the laboratory.

I am thankful to Mrs. G. Barbhuiya, for helping me in statistical analysis, to Mr Salil Choudhuri and Mr. B.P. Panda for drawing and to Mr. Vijoy Das for photography.

I would fail in my duty if I do not express my thanks to Mr. S.N. Ramanujan and Mr. S. Ravindran for their help and cooperation.

I owe my thanks to Mr. R.R. Khongji and Mr. Gautam Bhattacharjee for typing out the thesis with sincere effort.

Lastly, I thank C.S.I.R., New Delhi, for financing the project.

Papiya Dew
2/8/81
PAPIYA DEV

C O N T E N T S

	<u>Page</u>
PREFACE
GENERAL INTRODUCTION	1 - 27
CHAPTER I: STUDIES ON <u>EUPATORIUM</u> UNDER FIELD CONDITIONS AND ITS ADAPTATIONAL BEHAVIOUR ALONG AN ALTITUDINAL GRADIENT	28 - 61
CHAPTER II: GERMINATION AND SEEDLING ESTABLISHMENT OF <u>EUPATORIUM</u> SPECIES	63 - 85
CHAPTER III: COMPETITIVE RELATIONSHIPS BETWEEN TWO CLOSELY RELATED SPECIES OF <u>EUPATORIUM</u> IN PURE AND MIXED STANDS	86 - 113
CHAPTER IV: COMPETITIVE RELATIONSHIP BETWEEN <u>E. ODORATUM</u> AND <u>E. ADENOPHORUM</u> LIVING IN THE SAME AREA	114 - 130
CHAPTER V: COMPETITIVE BEHAVIOUR OF <u>E. ADENOPHORUM</u> AND <u>E. RIPARIUM</u> AT DIFFERENT ALTITUDES	131 - 151
REFERENCES	152 - 184

PREFACE

The thesis deals with the comparative biology of three important weeds of north eastern hill areas of India, ^{These weeds} which come up usually after slash and burn agriculture (locally called Jhum) and form an important component of the first 5-6 years of secondary succession. When the Jhum cycle (the intervening fallow period between two successive cropping of the same site) gets reduced to 4-5 years as in the present case, this weed along with a few others form part of an arrested succession where the community is maintained more or less permanently at this weed stage. Hence this study is considered important and it is hoped to contribute to the basic understanding of the ecology of this weed.

The thesis starts with a general introduction followed by chapters on different aspects of the weed, ranging from field distribution, growth and adaptation and seedling establishment and competitive behaviour of different natural species populations in marginal habitats when they may occur naturally. Each of the chapters have been written in the form of papers for publication and hence some overlapping in writing could not be avoided. The thesis ends with a section on "Literature Cited".

GENERAL INTRODUCTION

Weed biology:

Weeds comprise the more aggressive, troublesome and undesirable elements of the world's vegetation (King, 1974). 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, (without of course, being deliberately cultivated plants)". The frequency, intensity and duration of physical ^{and} environmental disturbances usually necessary for agriculture have increased the importance of such weeds to a great extent (Young & Evans, 1976). The intensive systems of land management practised by man breakdown the comparatively stable equilibrium of natural plant communities and new habitats are continually created which offer fresh opportunities for plant colonization and these frequently become serious weeds.

? 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 exist in varying degrees^s in plants (Hart, 1976). The plant species which are difficult to exterminate are usually ^{classified} classed as noxious ^{known?} weeds, and represent the ultimate evolutionary strategy. According to Baker (1962) "the evolutionary success of an organism can be measured in terms of the number of individuals in existence, the extent of reproductive output,

the area of the world's surface that they can enter and their potentiality for putting their descendents in a position to continue the genetic line through time".

Salisbury (1942^a) has opined that "only by an intimate knowledge of diverse life histories of weeds one can hope to discover more vulnerable aspects of each that will enable us to combat them successfully". In India, considerable work on ecological life histories of weeds have been done by Mishra and co-workers (Mishra & Siva Rao, 1948; Mall, 1957; Ramakrishnan, 1960a, 1961a, 1963a; Tripathi, 1968, 1969).

An analysis of the weed flora in most of the countries shows that a large percentage of the weeds are ^{weed species?} alien i.e. introduced from other countries by man either deliberately or unwillingly. Muenscher (1955) estimated that of 500 species he studied which are weeds in the northern states of U.S.A., 39% are only native to north America, while 34% are indigenous to Eurasia. A comparative study between the native and introduced species of Euphorbia cyperisssians and Hypericum perforatum have shown that the growth of these species are more aggressive in introduced American continent than in the native Europe (Pritchard, 1960).

Any work in India, Europe, Asia?

Plasticity verses ecotypes:

The factors controlling spatial distribution and

growth behaviour of weeds over geographical, latitudinal or altitudinal range include the climate of an 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 weedy *weed* species. It has been found that such adaptive variability results either from phenotypic plasticity or from genetic divergence which in turn is a result of natural selection. The ecological importance of phenotypic plasticity lies in the fact that it tends to make an individual adaptable to more than one habitat. Due to this ~~fact~~ the plants differ in appearance by distinct morphological features in vegetative parts and reproductive vigour, yet they belong to the same homogenous genetic stock and are referred to as ecads (Doubenmire, 1959) whereas genetical adaptability results in the evolution of distinct stable populations to suit distinct environmental situations and are referred as ecotypes. 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 (Turesson, 1922). Wu and Jain (1978) while showing the genetic and plastic *studying* responses in geographic differentiation in Bromus rubens populations ^{found} showed that 12 ~~to~~ 27 % of the total geographic variation among natural population was contributed by genetic variation whereas 73 ~~to~~ 88 % was non-genetic variation in response to different local environments,

Split the sentence

4

suggesting that phenotypic plasticity is important for the wide adaptability of this species. The significance of this phenotypic plasticity in plants species has been extensively dealt by Bradshaw (1965). Mayers and Bormann (1963) while working with Abies balsema observed phenotypic variations in cones and leaves along altitudinal and geographical gradients. Figier^{et al.} (1977) reported phenotypic variability in the morphological characters of 9 natural populations of Hedysarium coronarium in north Tunisia and grouped these populations in 5 morphologically defined sets depending on different genetic pools and thus demonstrated the existence of both genetic and phenotypic plasticity.

Turesson (1922, 1925) was the first to determine the existence of a large number of climatic races in a number of European species which resulted from the genotypic response of the species populations to different climatic factors in the habitat. Later, Clausen et al. (1940, 1948) reported the existance of large number of climatic races in various species ranging from sea level to above timberline in California ranging from an altitude of 1,400 to 3,000 m. They showed marked differences in the physiological features of these ecotypes like the pattern of dormancy of of the buds, flowering, fruiting and resistance to cold. Gregor (1930, 1946) working with Plantago maritima, came to the conclusion that while certain ecotypes may be

characterized by variational discontinuity, often the variation is continuous along an ecological gradient to denote which he coined the "ecocline". Cooper and McWilliam (1966) working with Mediterranean populations of Phalaris tuberosa observed temperature-induced differences with regard to floral induction, leaf expansion, seed germination etc. Similar ^{reports were made by McMillan (1964, 1965)} work is also available for a number of north American prairie grass species reported by ~~McMillan (1964, 1965)~~, and also ^{by MacColl and Cooper, (1967)} for Mediterranean and north European forage grasses, (~~MacColl & Cooper, 1967~~). Cohn and Kucera (1969) demonstrated variations in the flowering sequence due to differential photoperiodic requirements in the latitudinal populations of Eupatorium rugosum. Hodgkinson and Quinn (1976, 1978) while working with Danthoria caespitose concluded that along the latitudinal and climatic gradients the higher growth rate and early anthesis and floral induction of the northern populations compared to that of southern populations was a result of genetic adaptation. Grant and Hunter (1962), working with altitudinal populations of Calluna vulgaris reported that variation in growth habit and growth forms change with change in altitude. They also reported that the maturity type is related to the length of the growing season at the site of origin of the population. Populations originating from areas having shorter growing seasons are composed of individuals of early maturity type than from those areas where growing season is longer. Hunter and

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 the climatic components of the altitudes. Corn and Hiesey (1973) while working with Hawaiian matrosideres demonstrated the existence of a number of climatic races along a transect from sea level upto an altitude of 8,500 ft. They observed the differences in plant height, leaf area etc. with a strong overlapping variation from site to site.

Bjorkman and Holmgren (1963) reported differential behaviour of the photosynthetic apparatus of Solidago virguarea from exposed and shaded habitats. Differences in the Hill activity and succinate dehydrogenase activity in the three different altitudinally diverse populations of Taraxacum officinale have been reported by May, (1975, 1976). Slayyer and Feror (1977) reported variation in the temperature optima for photosynthesis in the altitudinal populations of Eucalyptus pauciflora. In this case, as the site elevation increased, ^{and} site temperature ~~decreased~~, the peak rates of photosynthesis also decreased.

Work on climatic races in Indian plant species is, ^{however,} unfortunately very meagre. Kaul (1965) recognized four seasonal populations in Xanthium strumarium, each population suited to different seasons of the year. He also reported variations in morphological as well as physiological features in these seasonal populations. Similarly in a

study of seasonal populations of Chenopodium album, differences in temperature requirement to seed germination and temperature-photoperiod interactions were related ^{to} with seasonal distribution of the populations (Ramakrishnan & Kapoor, 1974).

Though the ecotypic studies were initially concerned with differentiation of population on a climatic and geographic basis, the demonstration of edaphic ecotypes specially from very narrow range of soil conditions was of great significance in the development of genecologic thoughts (Ramakrishnan, 1973). Considerable work has been done on edaphic ecotypes both in India and abroad. Ramakrishnan (1972a) ~~has~~ reviewed the work on edaphic ecotypes in relation to physical characteristics of the soil, ^{and} macro and micro nutrients.

Kruckeberg (1951) was one of the first to recognise the existence of two edaphic ecotypes in the case of Achillea borealis in relation to serpentine and non-serpentine soils. Ramakrishnan (1961b) noted ecotypic differences in Euphorbia thymifolia over a very short distance. In this species, the facultative calcicole and obligate calcifuge populations are distributed in a mosaic of soil situations where the non-calcareous alluvial soil had smaller or longer patches of calcareous nodules which determined their restrictive distribution pattern. The studies of Anthoxanthum odoratum population (Snaydon &

Davies, 1972) at the boundary between plots at the Park Grass experiment Rothamsted, where environmental conditions change very sharply indicate that physiological and morphologically diverse populations may maintain their identity over very short distances provided environmental conditions change very sharply.

Soil physical factors are often implicated in ecotypic differentiation. Heins and Walkins (1979) demonstrated the effect of soil temperature and photoperiod resulting in the variation in growth of Alistroemeria regina. McCown et al. (1977) showed that the pattern of perennial grass distribution was primarily determined by variation in sub soil permeability i.e. water storage capacity. Ramakrishnan (1958) recognised two ecotypes in Euphorbia hirta erect and prostrate types, the former growing in moderately moist habitat and the latter on dry hard soil exposed to trampling. Similarly, Echinochloa colonum had two ecotypes, a tall and a short form depending on the moisture stress (Ramakrishnan, 1960b). McKell et al. (1960) recognised two distinct races of Dactylis glomerata depending on their adaptability to soil moisture stress.

As discussed earlier soil nutrients have often been a basis for recognitions of ecological races. Ramakrishnan and his co-workers differentiated ecotype in Tridax procumbens (Ramakrishnan & Jain, 1965a),

Cynodon dactylon (Ramakrishnan & Singh, 1966), Adathoda vasica (Ramakrishnan & Bisht, 1968) in relation to exchangeable calcium in the soil. Such differences in relation to soil factors have been observed by other workers in species like Festuca ovina (Snaydon & Bradshaw, 1961), Trifolium repens (Snaydon & Bradshaw, 1962), Agrostis tenuis (Bradshaw, 1959; Jowett, 1964). At least two edaphic ecotypes have been recognised in Cynodon dactylon adapted to alkalinity in the soil (Ramakrishnan & Nagpal, 1973).

With the realization of the fact that the selection pressure could result in population differentiation, it is reasonable to assume that continued biotic pressure would lead to more 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 undisturbed mesic sites.

Germination and seedling establishment:

The production of a very large number of seeds, long lived seeds, efficient dispersal mechanism and self compatibility are all features which are often thought to contribute to the development of most successful weeds.

(Salisbury, 1942b; Baker, 1965; Hieser, 1965). The size, shape, structure and composition of seeds often determine the germination behaviour in different environments (Harper et al, 1970). Germination behaviour of the seeds in turn is determined partly by the dormancy mechanisms of the seeds and availability of suitable microsites for successful germination and establishment (Harper et al, 1970; Pemadasa & Lovell, 1974). The viable seeds of a species actually form the potential size of a population in an area. The length of time for which seeds can remain viable is extremely variable and depends both on the storage condition and on the type of the seed. In general, viability is retained best under conditions in which the metabolic activity of seeds is greatly reduced i.e. low temperature and high carbon dioxide. A variety of factors to which parent plant is exposed during seed formation and ripening can also profoundly affect subsequent viability of the seeds after dispersion. Such factors include water supply, temperature, mineral nutrition and light. However, the environmental factors are of secondary importance, compared to the genetic control of seed viability (Mayers ^{and} Poljakoff-Mayber, 1963). In addition, however, other factors are of great importance, particularly those which determine seed dormancy.

Dormancy is an important ecological factor that governs the survival and distribution of populations in

any habitat (Ramakrishnan, 1963b). Literature suggests that both innate and enforced dormancy are involved in controlling timing of germination. Under unfavourable conditions it confers a selective advantage on the species and the absence of dormancy may be helpful only under favourable conditions (Harper, 1957). The percentage of seeds which germinate in any given population slowly decreases with time.

In order that a seed can germinate, availability of suitable environmental factors are very important. Among the environmental factors which are more important in determining the germination behaviour of seeds are adequate supply of water, a suitable temperature and light conditions.

The initial step in germination is the reactivation of the system conserved during the seed maturation period and this activation starts with the imbibition of seeds under favourable conditions. Harper and Benten (1966) and Harper and Sagar (1963) have shown that the failure of seeds of some plant species to germinate was the result of delayed or insufficient hydration of the seeds, a condition brought about by the level of water table in the soil. Comes and Elberse (1976) showed a differential ability to germinate in different conditions of water availability in grassland herbs.

Among the different environmental factors, temperature plays an important role in the germination of the seeds. The temperature at which different seeds germinate and the range within which they germinate is determined by the source of the seeds, genetic differences within a given species, as well as age of the seeds (Mayers & Poljakoff-Mayber, 1963). Characteristics of the temperature response may be closely correlated with the geographical distribution of different species (Koller et al, 1962; Ramakrishnan, 1972b; Thompson, 1970a, 1973, 1978, 1980; Bhooj & Ramakrishnan, 1981). Thompson (1970b) has presented evidence to show that germination responses of seeds which are stored at room temperature in the laboratory may be correlated with the areas of origin and geographical ranges of the species from which the seeds were collected. Thus, species of Caryophyllaceae which occur in areas with a Mediterranean climate germinate rapidly at medium temperature (10 - 20°C) have low minima ($< 5^{\circ}\text{C}$) and rather low maxima for germination. Shamsi and Whitehead (1977) related geographical and ecological distributions of the two species of Epilobium with the temperature requirement for germination of the species and Sonia and Heslehurst (1978) related temperature requirements for germination of three species of Banksia to geographical distribution. It is usually accepted that the germination responses of populations within a species collected from

different localities vary (Vegis, 1963, 1965; Harper, 1965). Support to this view may be found in studies with diverse taxa as Tsuga canadensis (Sterns & Olson, 1958); Avena (Thurston, 1957, 1962); Euphorbia thymifolia and Tridax procumbens (Ramakrishnan, 1965a & b); Tynha sp. (McNaughton, 1966); Amaranthus retroflexus (McWilliam et al 1968); Festuca pratensis (Bruce et al, 1978).

Higher germination under alternating temperature regimes is an adaptive feature for many secondary successional weedy species. Pickett and Baskin (1973) showed higher germination of rag weed, Ambrosia artemisia, under alternating temperature rather than constant temperature. Mayeux and Scifres (1978) showed about 20% higher germination under alternating temperature in golden weed seeds. Favourable effect of fluctuating temperatures was found by Wakhloo (1964) for germination of Solanum xanthocarpum and Solanum nigrum seeds and by Dhar and Bhat (1978) for belladonna seeds.

Light is an important ecological factor and plays a crucial role during seed germination of many species (Rooden et al, 1970). While seed germination was totally inhibited in Erigeron limfolius under complete darkness (Ramakrishnan, 1963b) that of Euphorbia thymifolia was markedly inhibited under continuous light (Ramakrishnan, 1965a). Rooden et al. (1970) and Popay (1974) while investigating the nature of seed germination in some

tropical weed species, noted that in some seeds light is necessary for germination, some seeds germinate in total darkness, and for a few, germination in light is enhanced by the previous period of darkness.

Germination in soil is usually determined by the availability of a suitable microsite. Heterogeneity of the soil environment determines the success of a seed in producing an established seedling (Harper, 1965). The nature of the soil, its chemical composition, its physico-chemical structure and the depth in the soil or water content also determine germination in a given site (Mayer & Poljakoff-Mayber, 1963). Depth influences aeration as well as penetration of light. In nature, a large proportion of the seed population in the soil is probably located at depths to which no light penetrates naturally. For light sensitive seeds, in the soil population which are located at such depths, the absence of light means that the limits of the environmental complexes in which their germination will be possible will be considerably narrowed around the optimum. Thus species with light sensitive seeds will germinate either before they reach soil depths to which light does not penetrate, or after they are brought to the surface by some means. Wesson and Wareing (1967, 1969) demonstrated the critical role of light in controlling germination of buried seeds of several weedy species. Wide temperature fluctuations which extends only a few

cm below the soil surface may also act to increase germination rates of seed populations located there. The availability of water at a given period of time is another important factor. Uptake of water by seeds has been shown to be related to soil moisture stress of the habitat as well as to a combination of physical factors in Atriplex canescens (Springfield, 1965) and in Iva annua (Ungan & Hogan, 1970).

The size, shape, structure and composition of seeds can also determine the germination and seedling establishment. Thus, Cavers and Harper (1966, 1967, 1973) in Rumex and Palmblad (1969) in a number of weedy species showed the adaptive value of polymorphism and related it to the microclimatic conditions prevailing in the soil and to differences in the survival of heavy as compared to lighter seeds. Such polymorphic differential behaviour of seeds have also been noted in Chenopodium album (Harper & Williams, 1965) and also in tree species like Lagerstroemia parviflora (Shukla & Ramakrishnan, 1981).

Competition in pure and mixed stands:

An aspect which has received considerable attention of the weed biologists in recent years is the process of "competition". The competition is generally expressed by depression of growth of one group of plants by another.



102785

Two plants are in competition with each other when the growth of either one or both of them is reduced or their forms modified as compared to their growth or forms in isolation (Bleasdale, 1960).

The capacity to compete depends upon the requirements, ecological amplitude and efficiency in resource use of the various biotypes in an area. Moreover, the ability to compete for a given resource might be expected to change according to its availability. Competition generally occurs in its severest form among physiologically related organisms with overlapping niches (Odum, 1959). It is keenest when the individuals are most similar. In the words of Darwin (1859) "the struggle will almost invariably be most severe between individuals of the same species, for they frequent the same districts, require the same food and are exposed to same dangers". Over-population, therefore, result in a serious interference of one individual with another.

Usually the early seedling phases of a plant's life are considered to be the most risky and seedling phases of a plant suffer most from germinating in ground thickly stocked with other plants.

One of the earliest attempt to study self regulation of a number of populations of plants was made by Sukatshev (1928) who sowed Matricaria inodora at two densities in fertilized and unfertilized soil. At the end of a season's

growth the percentage loss from population was greater at the higher density and in the fertilized soil. Yoda et al. (1963) extended this type of observation on natural and artificial populations of plant species, and showed that there was a formal mathematical relationship between the mean size of the surviving plants and residual density at various stages in the development of a population. The number of surviving individuals is related to their mean weight as $W = CP^{-3/2}$, where W is the mean dry weight per plant, P , the density of plants remaining in the community and C is a constant which varies with the species. Such a relationship has been shown in many other species (White & Harper, 1970; Bazzaz & Harper, 1976; White, 1979). A very important aspect of the work of Yoda et al. is that it examines the responses of numbers as well as the individual plant size (i.e. both mortality and plasticity) to changing density. Similar work on mortal and plastic responses were reported by Harper and Gajic (1961) in Agrostemma githago; Harper and McNaughton (1962) in Papaver species; Palmblad (1968) in Capsella bursa pastoris and Plantago major; Marshall and Jain (1969) in Avena fatua and Avena barbata; Ramakrishnan and Khattar (1973) in Cassia species; Gupta and Tripathi (1980) in Dichanthium annulatum, which showed predominantly mortal and plastic responses to density. From these experiments and as well

those of Koyama and Kira (1956) on Fibre flax and Stern (1965) on clover, it seems that under conditions of density stress there is a forced sharing of limited resources, with a compensating plastic reduction in individual development, and that a hierarchy may develop in natural habitats and also in model experiments. While working with mortal and plastic responses of a number of weedy species and crops, Ramakrishnan and his co-workers (1971a & b, 1975a & b, 1977) have concluded that the way a species would respond would depend upon the growth rate of the species concerned.

According to Harper (1961) there are two main ways in which the response of plants to increasing density may regulate population size.

- a) A response in the reproductive capacity of individuals such that an increase in plant density leads to a reduced seed output or a lowered rate of vegetative reproduction. This type of response has been demonstrated many times for crop plants.
- b) The plastic reaction of individual plants to increasing density may exactly compensate for an increasing number of plants per unit area to give a "constant final yield curve"; this response has been emphasized by Kira et al. (1956). Alternatively there may be an over-compensating response on the part of individuals, giving a parabolic final yield curve of the type found by Clements et al.

(1929) for Helianthus annuus and by Hodgson and Blackman (1957) for Vicia faba. Both the parabolic and the constant final yield curves represent reactions to increasing density which confer on the population the properties of self regulating systems by permitting a rapid increase in number from low densities but placing self-curbing restrictions on further expansion as the density becomes greater.

Competition between individuals in a population (whether of same species or different species) may involve both the root system and shoot system. Competition involving root system can either be both for water and nutrients or for either of them. Russell et al. (1942) studied competition between sugarbeet and associated weeds and attributed it to the root system involving soil nutrients. Ramakrishnan (1961b) has demonstrated that root competition in the two ecotypes, the red and green forms of Euphorbia thymifolia competing with each other does not permit the obligate calcifuge (green form) to establish seedlings in the calcareous soil. Bandeen and Buchhaltz (1967) studied the effect of field fertilizers upon the growth of quack grass and maize and found that the competition between two species involved soil and root system. Harris (1967) has reported that competition between Bromus tectorum and Agropyron spicatum involved root system.

Competition involving shoot system is for light energy entrapped by leaves. Interference with supplies of light may be the most potent way in which one species may succeed at the expense of another (Harper, 1964). Black (1957, 1958) studied competition between two populations of Trifolium repens, one derived from large seeds and the other from small seeds. In mixture, the seedlings from the large seeded variety had larger cotyledons and therefore, maintained an increasing superiority and almost suppressed the other one after a few weeks. Almost similar results have been reported by Black (1960) while working on pure and mixed stands of the varieties of Trifolium subterraneum. Ennik (1960) from his competition studies on pure and mixed stands of Lolium perenne and Trifolium repens under low and high light intensities found the replacement of grass by clover under high light intensities, but under low light intensities the two species tended to stabilize, those with excess of clover tended to increase the grass content and vice versa. The ecological differentiation between the species which permit this stabilization is due to differential requirements of the two for nitrogen.

Just as in population of a single species, the stress of density intensified the expression of small differences between individuals, so in mixed populations, density stress, may exaggerate and exploit interspecific differences as shown by experimental model of de Wit (1960).

Van dan Bergh and de Wit (1960) grew Phleum pratense and Anthoxanthum odoratum at a range of proportions and compared the ratio of tillers of the two species after the first winter and ratio after the second winter. They found that in plots in which Anthoxanthum odoratum has been in excess, the proportion of Phleum pratense increased, where Phleum pratense was in excess, Anthoxanthum odoratum increased. Thus the mixture possessed self-stabilizing properties. A stabilizing situation is also found in mixtures of Lolium perenne and Trifolium repens (de Wit, 1960).

Competitive relationship existing between two closely related species have been studied by many workers, like (Harper, 1965; Harper & Chancellor, 1959; Harper & McNaughton, 1962; Cavers & Harper, 1967; Marshall & Jain, 1969; Ramakrishnan & Gupta, 1972; Ramakrishnan & Jeet, 1972) and poses an important ecological problem of as to how continued cohabitation of two species is possible without one succeeding at the expense of the other. This imply some type of differences in the biological equipments of the species which permits them to evade a decisive struggle for existence. Two species may cohabit in a mixture only if the population of each reacts specifically to the controlling influences of its own density (Harper, 1961). To understand the cohabitation of species it becomes necessary, therefore, to study the reaction of each species

to its own density and to compare this with its reaction to the density of the associated species. Grubb (1977) distinguished two main groups of suppositions while trying to explain how species can coexist in nature: (i) Suppositions associated with a heterogenous environment and (ii) those based on homogenous environment. Further, heterogenous environment may have many micro-habitat and thus the species cohabit (Harper, 1961; Grubb, 1977) whereas in a homogenous environment the co-existence of the two species results from functional niche differentiation (Van den Bergh & Braakhekke, 1978). Niche differentiation may be due to differential nutrient requirements or due to differential light requirements. Role of differential nutrient requirement in the co-existence of two species have been reported by Harper (1961) in legume and grasses, in Argemone maxicana and Argemone ochroleuca by Ramakrishnan and Gupta (1972) and in Chrysanthemum leucanthimum and Plantago lanceolata by Van den Bergh and Braakhakke (1978). Differential light requirement responsible for the co-existence of species have been demonstrated by Black (1957, 1958) in two populations of Trifolium repens, by Black (1960) in two varieties of Trifolium subterranean and Ennik (1960) in Lolium perenne and Trifolium repens.

The competitive relationship may also bring about a reversal in habitat preference as shown for ecotypic

populations of Melilotus alba, which may account for the restriction of these populations to their natural habitats (Ramakrishnan, 1970). Reversal of habitat preference has also been shown by Harper and Chancellor (1959) who grew Rumex species on clayey soil with or without Lolium perenne and found that in the absence of grass the establishment of Rumex crispus and Rumex obtusifolius was more successful under maintained water table. In the presence of the grass the most successful establishment of Rumex obtusifolius occurred under freely drained condition.

Present study:

Eupatorium, a noxious weed of the north-eastern region is an important component of the secondary succession initiated due to 'Jhum' or shifting agriculture (Ramakrishnan, et al, 1980). Shifting agriculture, involving 'slash and burn' process followed by mixed cropping is a predominant practice of this region. The shortening of the Jhum cycle (the time gap when secondary succession occurs during ^{the} fallow ^{period} development between two successive croppings) to 4 - 5 years in these regions due to human population pressure has resulted in the luxuriant growth of this weedy genus Eupatorium and vast areas are now virtually pure stands of this weed. Three species of this genus namely E. odoratum Linn. E. adenophorum Spreng and E. riparium Regel. have become very notorious and troublesome weeds of

this region and is almost impossible at present to control and eradicate.

The genus Eupatorium has about 1200 species (Malhotra & Jain, 1978) and is one of the largest genera in the family Asteraceae. The genus is nearly cosmopolitan in distribution but the vast majority of the species are American with the centre of distribution in the American tropic (Holm et al, 1977). In India 7 species were reported by Santapau and Henry (1973).

E. odoratum, in a few recent works is treated under the genus Chromolaena^{King} / & Robinson, 1970). It is reported to be a serious weed in 23 countries of the world including India, Malaysia, Ceylon, Thailand (Holm et al, 1977). In India it grows abundantly in the north-eastern region, in Kerala^a and in Madras (Moni, 1959; Rao, 1977). It is a serious menace to the teak samplings depriving them of the much needed sunlight^e for their growth (Moni & George, 1959), in the rubber plantations of south Kanara, E. odoratum is noticed to compete with the leguminous cover crops (Rai, 1976).

The rapidity with which the species had^{ve} spread has caused concern and stimulated investigation into possible eradication by chemical^s or biological control ^{methods} in different areas (Moni, 1959; Mohanlal, 1960; Crutwell, 1968, 1969, 1971; Sheldrick, 1968; Rai, 1976).

For this an understanding of the biology of this weed is required. The ecological aspects such as germination behaviour of the seeds, presence of ecological races of E. odoratum have been studied in Nigeria (Edward, 1974 & 1975). The development of embryo and female gametophyte has been described by Ghosh (1969). Mehra and Ramanandan (1975) reported high abnormal meiosis leading to high pollen sterility and Sullivan (1976) discussed the existence of allopolyploidy in Eupatorium. Khonglam and Singh (1980) reported that E. odoratum is a hexaploid with chromosome number 60 and is apomictic. Persistent feeding activity on the flower heads of this species by several important mosquito species had been reported by Brealand et al (1961). It is used as green manure in Cambodia in rice fields and for black pepper cultivation (Gerry, 1963; Litzemberger & Ho Tong Lip, 1968). However, the manure of this weed was found to be poisonous to fishes and increased the crop production indirectly by preventing the attack of nematodes and pathogens on the crop.

The neotropical weed Eupatorium adenophorum Spreng. (Syn. E. glandulosum H.B.K.) has explosively established ^{invasion?} in north-eastern region after its first noticeable invasion about 20 years ago. It is ubiquitous especially in open forest areas and cultivated fields throughout the state between 1066m to 2130 m (Dutta, 1978). It is a native of Mexico and was first recorded as naturalized plant in

California in 1896 (Fuller, 1961). It is thought to have been introduced to Hawaii around 1900 (Hosaka & Thistle, 1954). In Australia it was first found near Sydney in 1920 (Auld, 1970). In India, it is now common also in Darjeeling hills, in the Eastern Himalayas and Nilgiri and Pulney hills in south India (Mehra & Ramananda, 1976) and has encroached upon teak, rubber, tea and other commercial plantation (Dutta, 1978).

An analysis of the occurrence of E. adenophorum with respect to a number of environmental factors (Auld, 1969) revealed that rainfall, tree cover, steepness of land each appeared to influence the distribution and success of the plant. It was shown that it favours frost-free hillside localities, such as abandoned banana plantations and the plant is susceptible to frost (Auld, 1969) and usually absent from flat land. Germination experiments of these species showed low percentage viability. The viable seeds have a germination requirement for light. Seedlings display degree of tolerance to shading to 10 % day light (Auld & Martin, 1974). The species is a triploid with chromosome number 51 (Grant, 1953; Mehra & Ramanandan, 1975; Khonglam & Singh, 1980). Holmgren (1919) has shown the species to be apomictic, on embryological investigations.

In Australia, where E. adenophorum had become a problem in the New South Wales, parasites such as the

native crown boring cerambyoid Dihammus argentatus and the fungus Cercospora eupatorii had tended only to reduce the viability and spread of the weed in some localities (Auld, 1970a). Chemical control of this weed has also been tried in Australia (Auld, 1972). In India, mexican gall fly (Procecidochares utilis) was imported from New Zealand and released in both south and north-India hills to control the weed, but gall fly is susceptible to the native parasites Dimeromicrus keisenwelteri and Syntomopus (Gupta, 1977) which reduces its efficiency.

Literature on E. riparium is very meagre. It is an important weed in Australia and Hawaii (Auld, 1970a). Ecology of this species has been studied by Auld (1970a). The species is a triploid with chromosome number of 51 (Grnat, 1953; Khonglam & Singh, 1980).

In view of the extreme weediness of these three species of Eupatorium in the north-eastern region of India, an understanding of their comparative biology was considered important. Hence the present study deals with germination, growth and competitive adaptations of the three species occurring over an altitudinal range of near sea level to a height of 1900 m in Khasi Hills of Meghalaya (25°47' N and 92°47' E).