A STUDY ON COMPETITIVE INTERACTION BETWEEN *PASPALUM DILATATUM* POIR AND *TRIFOLIUM REPENS* L.

BY

PRABHAT PRADHAN

THESIS SUBMITTED IN FULFILMENT OF THE DEGREE OF
DOCTOR OF PHILOSOPHY IN BOTANY

NORTH-EASTERN HILL UNIVERSITY
SHILLONG, INDIA

SEPTEMBER, 1981

phone :
Grams : NEHU

North-Eastern Hill University

Lower Lachaumiere, Shillong - 793001 (Meghalaya)

Dr. R.S. TRIPATHI
Reader

DEPARTMENT OF BOTANY
SCHOOL OF LIFE SCIENCES

I certify that the thesis entitled "A study on competitive interaction between Paspalum dilatatum Poir and Trifolium repens L." submitted by Mr. Prabhat Pradhan, 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 : September 25, 1981
Place: Shillong

R.S. Tripathi
Signature of the Supervisor

Forwarded
R.R. Mishra
25.9.81

Head,
Department of Botany
School of Life Sciences
North-Eastern Hill University
Shillong, Meghalaya

C O N T E N T S

A C K N O W L E D G E M E N T S

It is my privilege to express my deep sense of gratitude to my revered teacher, Dr. R.S. Tripathi, Reader in Ecology, Department of Botany, North-Eastern Hill University, Shillong, for his able guidance, keen interest and constant inspiration throughout the course of this study.

I am grateful to Professor R.R. Mishra, Head of the Department of Botany and Dean of the School of Life Sciences, for encouragement, constant help and for providing laboratory facilities, and to Professor P.S. Ramakrishnan, former Head of the Department of Botany, for providing necessary facilities and help during his tenure.

I express my sincere thanks to my colleague, Mr. Sudhir Trivedi, who has been closely associated with me and helped me through many of my difficulties and to my other research colleagues - Dr. A.S. Yadav and Mr. J.P.N. Rai for their kind co-operation and help. I am also thankful to Mr. N.P. Goel of the Department of Geography and Mrs. G. Barbhuiya of the Department of Botany for statistical analysis of the data and to Mr. M.H. Barbhuiya and Mr. B.K. Das for drawing and photography works.

I wish to express my sincere thanks to Mr. Godfrey Pathaw for taking keen interest in cutting the stencils and to Mr. Anthony Nonglyer for cyclostyling.

I owe my deep sense of gratitude to my beloved parents and sisters for their inspiring counsels, encouragement and patience during the course of this study.

Dated : 25th September, 1981

Department of Botany
North-Eastern Hill University
Shillong 793 014

Prabhat Pradhan

(PRABHAT PRADHAN)

CHAPTER 1

GENERAL INTRODUCTION

Competition is one of the major processes responsible for change in community structure and development. The individuals which are more aggressive and strong competitors establish and grow better in a community while the weaker ones get eliminated. Competition is also presumed to be a dominant force in biological evolution, but very few testable hypothesis have emerged and almost all of our conclusions about the importance of competition in natural systems are still based on speculations and inference (Miller, 1967).

Malthus (1798) wrote, "Population, when unchecked increases in a geometrical ratio; which implies a strong and constantly operating check on population from the difficulty of subsistence." According to Clements, Weaver and Hanson (1929), De Candolle (1820) was the first to characterize plant competition. Darwin (1859) assigned a major role to competition between closely related species, in the process of natural selection. He wrote, "As the species of the same genus usually have, though by no means invariably much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera." He cited examples of the increase of the missel-thrush at the expense of song-thrush in Scotland, invasions in which one species of rat has displaced another, the spread of the Asiatic cockroach at the expense of a cogener, and the extermination of the native stingless bee of Australia by the imported hive bee." He also said "We can dimply see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature, but probably in no one case could be precisely say why one species has been victorious over another in the great battle of life," which still exists today as one of the central problems of competition theory. Odum (1953) also states that, "competition generally occurs in its severest form among physiologically related organisms with over-lapping niches". Similar conclusions have been drawn by Bleasdale (1960), Tripathi (1968), and others.

The word competition originated from the Latin verb 'competere', meaning 'to ask for the same thing that another does, which is fully preserved in the modern meaning of the word 'competition' which means the action of the endeavouring to gain, what another endeavours to gain at the same time, the striving of two or more for the same object, rivalry (Milne, 1961). According to Clements _et al._ (1929), two plants, no matter how close, do not compete with each other so long as the water content, the nutrient material, the light and the heat are in excess of the needs of both. When the immediate supply of a single factor falls below the combined demands of the plants, competition begins.

Harper (1961) is of the view that the word 'competition' lacked an independent scientific meaning because of its varied shades of meaning in sports, games, and economics. He suggested the use of the word 'interference' to describe the short and long-term hardships, which result to organisms from the proximity of neighbours except that it does not include the effect of parasites and predators. Donald (1963) agrees in principle with Harper's definition and maintains that 'competition occurs when each of the two or more organisms seeks the measure it wants of any particular factor or thing and when the immediate supply of the factor or thing is below the combined demand of the organisms.' Emlen (1973), suggested a non-circular and theoretically workable definition of interspecific competition and according to him "competition (interspecific) occurs when the two or more species experience depressed fitness (r_o or K) attributable to their mutual presence in an area."

The factors for which plants compete are water, nutrients, light, oxygen, carbon-dioxide and space; and in the reproductive phase agents of pollination and dispersal. The competition taking place among the members of the same species is called 'intra-specific' while the competition among the individuals of different species is referred to as 'inter-specific' competition.

It is assumed that since the individuals of a particular species are genetically same, their requirements for different resources would also be same. Thus, it is expected that the intra-specific competition is more severe than the inter-specific one. In the field of population biology, Harper and McNaughton (1962) have introduced two useful terms-self thinning and allien-thinning to indicate the intra-and inter-specific competition.

Gause (1934) cultured two species of Paramecium, P. caudatum and P. aurelia in a medium with a controlled food input and observed that when grown in mixture, P. aurelia emerged to be a stronger competitor and eliminated P. caudatum. The 'competitive exclusion principle' that emerged as a result of this research has become known variously as the "Gause Hypothesis", "Gause's Law" and the "Volterra-Gause Principle". A continued competitive stress among the members of two species with similar requirements for a limited resource is believed by some zoologists to result in the extinction of one of the species (Gause and Witt, 1935). This was supported by Crombie (1947); Park (1954); Hardin (1960) etc.

However, the competitive ability of competing species is sometimes controlled by the environmental conditions for sharing the same resources. For example, Slobodkin (1964) observed that Hydra littoralis and Chlorohydra viridessima coexisted in the dark while in the light, the latter excluded the former in mixture. Similarly, Tantawy and Soliman (1967) working on two species of Drosophila, found that D. melanogaster eliminates D. simulans at 25°C while the latter eliminates the former at 15°C after 180 days. Similarly, Park (1954), working on Tribolium spp. found that T. castaneum eliminates T. confusum, in hot and wet conditions while in cool conditions the latter tends to win..

The species could co-exist in nature by avoiding severe competition among them which might be possible: 1) if their nutritional requirements are different, 2) if they respond differently to external environmental factors, 3) if their growth form and phenology are different, 4) if the degree of susceptibility to external factors are different, 5) if there is some symbiotic relationships and 6) if there is no allelopathic effect to each other. Lieth (1960) showed for Trifolium repens and Lolium perenne that the two species form a mobile mosaic in which low clover density areas are invaded by the grass and vice versa. Harper and Clatworthy (1963) made an interesting study of co-existence of the two species of Trifolium, T. repens and T. fragiferum. Both the species have been reported by the workers to compete strongly for light, but due to difference in morphological characteristics and phenology they could co-exist in nature. Similarly, Ayala (1969, 1970) also concluded that the competitive exclusion principle does not operate in case of the populations of two fruit flies (Drosophila pseudoobscura and D. serrata), when cultured together in bottles. In spite of their morphological similarity and exhibiting interspecific competition, the two flies could co-exist.

The intensity of competition and the extent to which the competing individuals are affected by such competition are largely controlled by population density studied by many workers. Plants have been reported to respond to density increase through mortality or plastic reduction in growth. Clements, Weaver and

Hanson (1929) made an early experiment with Helianthus annuus by growing the plants at 2, 4, 8, 16, 32 and 64 inches from each other and showed that the plants showed reduced growth with increasing density. Similar plastic reduction in plant growth has been observed in several species by different workers (Donald, 1951; Hozumi, Koyama and Kira, 1955; Harper and Chancellor, 1959; Aspinall and Milthorpe, 1959; Puckridge, 1962; Tripathi, 1968; Timmis and Tanaka, 1976). It has been found that a few of the characters in plants are more plastic than the others; working on the plastic nature of 16 different characters in maize (Zea mays), Bonaparte and Brown (1975) have shown that the most plastic characters were grain yield per plant and yield per unit area, and the least plastic characters were ear row number and ear height.

The mortal response of the plant populations to density increase has been shown by many workers (Harper, 1960; Harper and McNaughton, 1962; Yoda et al., 1963; White and Harper, 1970). Yoda et al. (1963) have reported both mortality and plasticity in pure populations due to density stress. They established a relationship between the mean dry weight per plant and the density of surviving individuals, and propounded the well known $-\frac{3}{2}$ thinning law, which was later on confirmed by White and Harper (1970) and Kays and Harper (1974).

Besides being affected by competition from the individuals of their kind, the plants also have to face the hardships caused by the members of other species that might grow in their immediate vicinity. A number of workers have shown the effect of interspecific competition on the growth of various plant species (Sagar, 1959; Sagar and Harper, 1961; Harper and McNaughton, 1962; Harper and Clatworthy, 1963; Cavers and Harper, 1967; Bergh, 1968; Palmblad, 1968; Marshall and Jain, 1969; Tripathi and Harper, 1973).

A useful technique to study plant competition has been suggested by De Wit (1960). In De Wit's method species are planted both in pure and mixed situation at the same overall density. The ratios of the two species in mixed populations may also be changed according to the requirement. If there is no change in growth of the species in mixture over their growth in corresponding monocultures during the experimental period it may be inferred that no species succeeds at the expense of the other. The suppressed growth of a species in mixture would indicate its poor competitive ability while growth stimulation in mixed situation may speak of its competitive superiority over the other species.

Besides, De Wit and his associates (De Wit and Van den Bergh, 1965) introduced the concept of relative yield total (RYT) which could be used in comparing the space occupied by different species while competing with each other. When RYT equals one which is generally the case with cultivated crops except for legumes (Trenbath, 1974) the species are supposed to compete for the same space.

Most of the studies on plant competition have been done based on De Wit's replacement series. Some species have been reported to be more susceptible to 'intra-specific' while certain others are more sensitive to 'inter-specific' competition. It may so happen in competition that one of the competing species might be higher yielding by virtue of its nature than the other competing species, but in presence of the latter the former one might be suppressed in mixture (e.g. Van den Bergh, 1968). This is so called 'Montgomery Effect' (Montgomery, 1912).

Since plants compete for both the above- and belowground resources sometimes it becomes necessary to ascertain whether the competition for belowground resources (root competition) or for aboveground resources (shoot competition) is more crucial. A technique was suggested by Donald (1958) to study the root and shoot competition separately. Some other works where shoot and root competition have been separately studied are those of Aspinall (1960), Welbank (1961), Snaydon (1971), Rennie (1974) etc.

The effect of light on the competitive behaviour of plants has been greatly emphasised in a number of studies (Donald, 1958; Stern and Donald, 1962a, b) while in certain other studies the competition for soil factors has been shown to produce larger effects (Aspinall, 1960; Rhodes, 1968; Snaydon, 1971; Eagles, 1972). Some studies have also shown the importance of rooting depth on competitive interaction (Berendse, 1979, 1981).

The competition has also been studied among the populations of the same species differing in tolerance of a particular nutrient or groups of nutrients (Snaydon, 1962; Snaydon and Bradshaw, 1962; Ramakrishnan, 1965; Hutchinson, 1967).

Grass-legume interaction has been a popular aspect of study with special reference to soil nitrogen (Jones, 1963; De Wit et al., 1966; Abu Shakra et al., 1969; Reid, 1970; Litav and Zeligman, 1977). In grass-legume mixtures the nitrogen uptake of the grass can be influenced by the legume either by increasing the supply of available nitrogen in the root medium or by competing with the grass for available nitrogen (Simpson, 1965). Usually in such experiments the grass benefits more from the increase in nitrogen supply than it suffers from competition by the legume, and there is a net transfer of nitrogen to the grass (Walker et al., 1954; Russell, 1961; Bryan, 1962). In other studies, however, the competitive effect has been shown to be the larger one, resulting into the reduced nitrogen uptake by the grass (Willoughby, 1954; Davies, 1964; Simpson, 1965; Whitney et al., 1967).

The effect of light on grass-legume interaction has received the attention of large number of workers (Black, 1958; Stern and Donald, 1962a, b; Wilson, 1962; Donald, 1963; Chestnut and Lowe, 1970). The general conclusion from all experiments involving competition for light is that the component with its leaf area higher in the canopy is at an advantage. It is also likely that, if the leaves are horizontal, the advantage is greater than if they are erect (Stern and Donald, 1962a). If the taller component has a greater leaf area, its advantage is again correspondingly greater (Iwaki, 1959). The study of Ennik (1960) on pure and mixed populations of Lolium perenne and Trifolium repens have revealed that under high light intensity the clover replaces the grass whilst the two species tended to stabilize when the light intensity was low.

A number of studies have also been done on the effect of biotic disturbances like grazing, cutting, trampling etc. on the grassland species (Wilson, 1962; Edmund, 1962; 1963; Harper et al., 1965; Williams, 1969; Dale and Weaver, 1974; Liddle, 1975a; Blom, 1978b). It has been shown that the species of prostrate nature are more tolerant than the species of erect nature against clipping and trampling (Warwick and Briggs, 1978a, b; 1980; Warwick, 1980).

In field conditions, the seasonality of growth and phenology of the competing species is also an important aspect worth considering in competition studies. The time of emergence as it evades or affects the outcome of competition has been studied by various workers (Sagar, 1959; Black and Wilkinson, 1963; Tripathi, 1969; Ross and Harper, 1972; Litav and Isti, 1974; Gupta and Tripathi, 1979). The difference in phenology and non-coincidence of peak growth period of the two species of Trifolium, T. repens and T. fragiferum, have been considered by Harper and Clatworthy (1963) as the factors responsible for their co-existence. Similar conclusions have been drawn by

Turkington and Harper (1979a) in respect of the co-existence of Trifolium repens and Lolium perenne. Besides, biotic disturbances such as grazing, cutting and defoliation etc. may also determine the co-existence of species in nature (Pradhan and Tripathi, 1980).

The two species with asynchronous but partly over-lapping growth period might provide an ideal pair to study the mechanism of co-existence. Grass-legume interaction has been chosen as the subject of study for the present investigation and the species selected are Paspalum dilatatum Poir (grass) and Trifolium repens L. (legume). These two species grow abundantly in the grasslands of Shillong and have high fodder value. They also differ in their growth form as indicated by their natural habitats. The legume is a prostrate, low growing species while the grass has an erect growth form. Both the species are light demanding. Thus it is expected that the two species when growing in mixture might undergo intense competition for light.

By virtue of being a legume, T. repens can fix the atmospheric nitrogen with the help of bacteria (Rhizobium trifolii) occurring in its root nodules. It is expected that a part of the nitrogen fixed in such a manner might be shared by the grass in mixed sward situation where the two species grow as neighbours.

The grasslands in Shillong are subjected to frequent grazing, cutting and trampling. These biotic factors might play a significant role not only in maintaining the structure of the grassland community but may also decide the competitive success of the component species.

Considering the above facts, the present study on the competitive interaction between T. repens and P. dilatatum has been made to cover the following aspects:

1) A field study relating to the effect of simulated grazing.
2) Competitive success of the two species as affected by the growing season.
3) Effect of soil nitrogen on competitive success of the two species through sand culture studies.
4) Effect of light intensity on competition between the two species.
5) Effect of simulated trampling on growth of the two species in pure and mixed situations.

Further, T. repens has two distinct populations in and around Shillong, one population is characterised by the presence of 'V'-shaped white markings on the leaflets and the other population is devoid of such leaf markings. It has been suggested that the white leaf mark in T. repens is due to the air spaces present within the palisade tissue. Two linked groups of genes control leaf marking in T. repens (Corkill, 1971), the white leaf marks are controlled by multiple alleles at a locus in one of these groups (Brewbaker, 1955; Carnahan, et al., 1955). These leaf marks together with other leaf characters have been used to identify clones of Trifolium repens in the field (Harberd, 1963). Conflicting views exist on the adaptive significance of the white leaf markings in *T. repens*. Charles (1968) is of the view that the white mark of *T. repens* might help the grazing animals like sheep to form an image, so as to select it from the grass mixture, because of its palatability, while Cahn and Harper (1976b) have demonstrated that the grazing sheep avoids *T. repens* having white leaf markings.

T. repens also shows population differentiation in terms of hydrogen cyanide content (Corkill, 1942; Foulds and Grime, 1972; Paim and Dean, 1976). The hydrogen cyanide content in the cyanogenic form of *T. repens* account for its competitive superiority over *T. semipilosum* (Yamashita *et al.*, 1979). This aspect, however, has not been investigated in the present work. But, besides the aspects mentioned earlier, an attempt has also been made to study the competitive interaction between the two leaf morph populations of *T. repens*.

The experimental data on various aspects as given above have been presented in Chapters 3 to 9. The 'General Introduction' (present Chapter) discusses the present status of the subject in the light of the published work and also sets out the objectives of the thesis. A brief description of the climate, soil and vegetation of the study area and biology and growth of the two species in field situations is provided in Chapter 2. The results of the individual chapters have been discussed separately in each chapter. However, an attempt has also been made to integrate under 'General Discussion' (Chapter 10), the results and discussions contained in various chapters.