

**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

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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

*Forwaded
R. S. Tripathi
28.9.81*

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

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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_0 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 viridissima 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; Tirmis and Tanaka, 1975). 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; Palmlblad, 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 (Brendse, 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.

CHAPTER 2

DESCRIPTION OF THE STUDY SITE: SOIL, CLIMATE AND VEGETATION;
DISTRIBUTION AND MORPHOLOGY OF TRIFOLIUM REPENS AND PASPALUM
DILATATUM AND SOME FIELD OBSERVATIONS

STUDY SITE

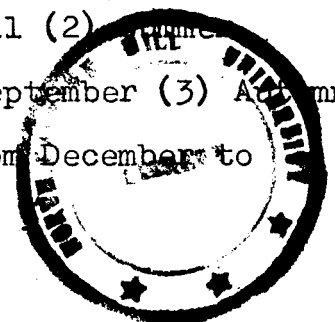
The field observations were taken in the grasslands of Shillong and adjoining areas and culture experiments were carried out on the campus of the School of Life Sciences, North Eastern Hill University, Shillong (Latitude 25.34°N and Longitude 91.56°E , altitude 975 to 1956 m).

Soil:

The Shillong plateau has mild undulating topography. The soil is lateritic with reddish brown colour and its texture is sandy-loam at the surface and silty-loam in deeper layers. It has originated from the hard rocks representing gneisses, schists and granite. It is believed that the hills of Shillong plateau and its surroundings were uplifted from the sea bed called 'Tethys sea' during the mesozoic and early tertiary times along with the origin of the great Himalayas (Zimba, 1977). The soil is **acidic** in nature (pH 5-6) and is rich in organic matter, nitrogen and phosphorus.

Climate:

The climate of Shillong is influenced by the south-west monsoons and north-easterly winter winds. Based on rainfall and temperature conditions the year can be divided into four main seasons - (1) Spring season from March to April (2) Summer season (including rainy season) from May to September (3) Autumn from October to November (4) Winter season from December to



February.

During the spring season, the temperature starts rising and the weather becomes relatively warmer as compared to the preceding winter months. During the period of April to June-July the temperature rises upto around 30°C. Sporadic rains are received at the end of April which is followed by wet period from May to September. The average annual rainfall ranges between 2,500-3,000 mm. Average rainfall and mean maximum and mean minimum temperature of different months from ~~May~~ January 1979 to December 1980 are given in Fig. 2.1.

The period of October - November represents a typical Autumn season with mild cold and usually without rains. The winter season is characterised by low temperature and dry spell of weather. The temperature drops down to a minimum of 1°C in the early part of January and also occasional frost can be seen in this period. The cold north-easterly winter wind blows which sometimes brings hailstorms. Sometimes there is occasional rain during the month of March which helps in germination and sprouting of the herbaceous annuals and perennials.

Vegetation:

The vegetation of Shillong can broadly be classified into:

- (1) Sub-tropical pine forest
- (2) The mixed evergreen forests

Fig. 2.1: The average monthly maximum and minimum temperature and rainfall of Shillong for the period from January 1979 to December 1980.

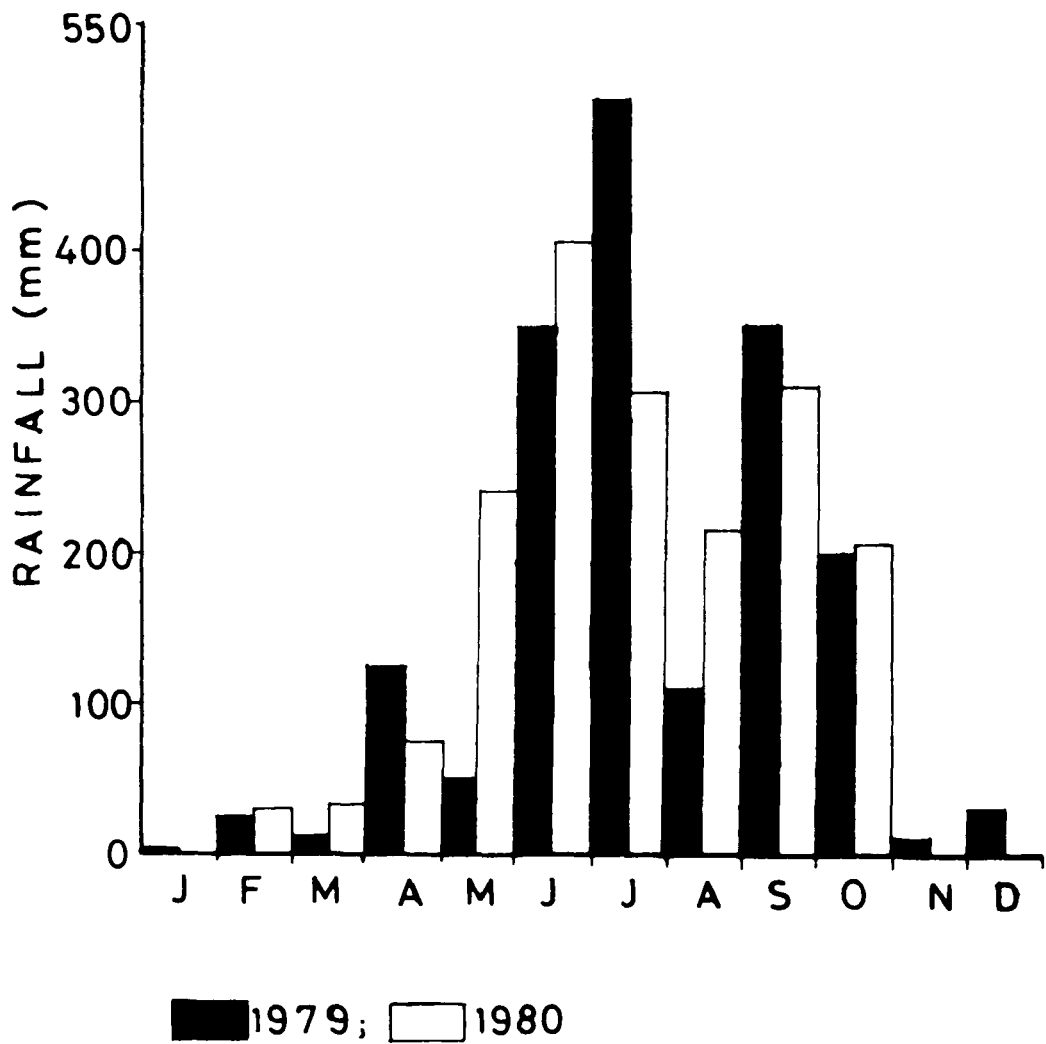
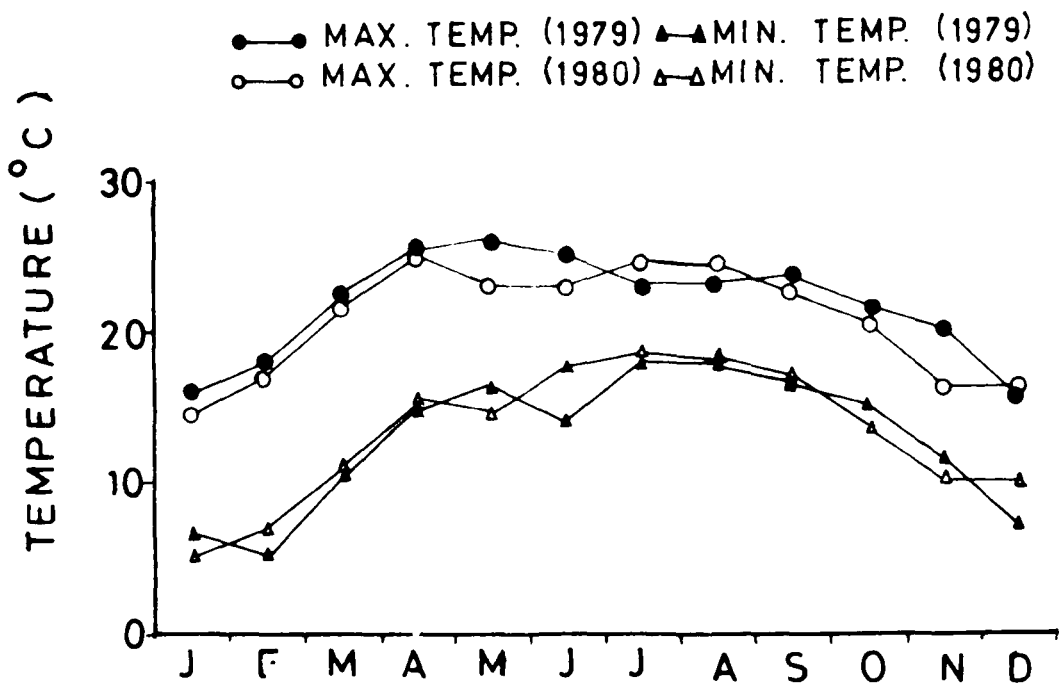


Fig. 2-1

Table 2.1: List of common plant species associated with T. repens and P. dilatatum in the grasslands of Shillong (data based on the observation in 6 quadrats in July 1980, average value \pm S.E.)

Plant species	Density/m ²
<u>Trifolium repens</u> L.	898 \pm 48.98
<u>Paspalum dilatatum</u> Poir	188 \pm 12.25
<u>Agrostis micrantha</u> Steud	360 \pm 47.35
<u>Eragrostis nigra</u> Nees ex Steud	161 \pm 14.69
<u>Cyanotis vaga</u> (Lour.) J.A. et J.H. Schult	10 \pm 1.25
<u>Axonopus compressus</u> (Sw.) P. Beauv.	90 \pm 12.25
<u>Pannisetum clandestinum</u> Hochst. ex Chlor.	12 \pm 4.08
<u>Centella asiatica</u> (L.) Urb.	5 \pm 0.82
<u>Hypochoeris radicata</u> L.	5 \pm 0.82
<u>Plantago major</u> L.	3 \pm 1.25
<u>Cyperus rotundus</u> L.	8 \pm 1.63
<u>Oxalis corniculata</u> L.	13 \pm 2.86
<u>Panicum brevifolium</u> L.	120 \pm 14.58
<u>Galinsoga parviflora</u> Cav.	12 \pm 2.04
<u>Galinsoga ciliata</u> (Rafin) Blake	6 \pm 1.22
<u>Imperata cylindrica</u> (L.) Beauv.	3 \pm 1.22

Density refers to the number of tillers in case of grass and sedge species, and each node bearing leaves and roots was considered an individual plant in case of T. repens and C. asiatica.

- (3) Temperate forest and
- (4) The rolling grasslands.

The sub-tropical pine forests which represent biotic climax are dominated by Pinus kesiya. It is found from an altitude of 1,000 m to 1,800 m. Other important tree species growing in these forests are Alnus nepalensis, Schima spp., Quercus spp., Cedrus deodara, Cryptomaria japonica etc. The understorey canopy of pine consists of many low growing trees, shrubs and herbaceous species like Symplocus spp., Rhododendron arboreum, Lantana camara, Eupatorium spp., Anaphilis spp., Desmodium spp. etc.

The sub-tropical mixed forests are confined to restricted areas and are much disturbed. These are dominated by Schima spp., Quercus spp., Alnus nepalensis, Erythrina arborescens and a number of Rosaceae members.

The temperate forests are confined to elevations from 1,800 m and above, chiefly in Upper Shillong and at Shillong Peak. The true temperate vegetation which represents the relic flora and gives an indication that probably the entire area was once covered by this type of dense vegetation and now has been degraded considerably due to human activities on these hills. The common trees in these forests are Quercus griffithi, Myrica esculenta, Betula alnoides, Rhododendron arboreum, Castanopsis spp., Photenia notoniam etc. A large number of shrubs like Daphne spp., Osbeckia spp. and beautiful orchids like Dendrobium

spp., Coelogyne spp., Pholidata spp., Pleione praecox and some lichens, mosses and ferns are found growing luxuriantly in these forests.

The rolling grasslands represent one of the most important vegetation types of this region. A vast area of Shillong and its adjoining regions are covered with grasslands which represent the seral condition in terms of succession. An important reason for the formation of grasslands in this region is the practice of primitive type of cultivation commonly called the 'Jhum cultivation' or 'Jhumming'. After the cultivation for 2 - 3 years, the area is abandoned because of nutrient depletion. These fallows are subsequently invaded by a large number of grasses, legumes and other dicots. Due to the biotic and human disturbances these areas are restricted to the grassland stage consisting of species like Paspalum dilatatum, Pennisetum clandestinum, Imperata cylindrica, Panicum brevifolium, Cyperus spp., Fimbristylis spp., Arundinella spp., Trifolium repens, Cassia spp., Desmodium spp., Crotalaria spp., Hypochaeris radicata, Plantago major, Erigeron spp., Galinsoga spp., Eupatorium spp. etc.

Paspalum dilatatum and Trifolium repens, which have been selected for the present study are quite important components of these grasslands. The important associates of P. dilatatum and T. repens as revealed by the field observations are listed in Table 2.1 (page 17).

Distribution and morphological characters of T. repens and P. dilatatum.

Trifolium repens:

It is commonly called as 'white clover' or 'Dutch clover'. The specific name 'repens' in Latin means creeping and refers to the growth habit of the plant.

It is found growing successfully in sub-tropical pasture along the moist coast from Northern New South Wales to Maryborough in South Queensland (Andrew and Bryan, 1955, cited by Hutton, 1970). It is also found in Europe, United States and N. Africa (Pearson, 1966). In India, it is found in Temperate and Alpine Himalayas upto 6,100 m and is considered to be an escape in Shillong plateau (Hooker, 1876).

The plant is a perennial, prostrate herb. Some populations are provided with white leaf-marking and some are devoid of it. It propagates with the help of stolons which root at the nodes, as well as by seeds. It has trifoliate glabrous leaves with long petiole arising from the nodes of stolons (Plate 1). Flowers white, ovary 6 mm long with 4 ovules, stigma capitate; fruits 2-4 seeded pods enveloped in the calyx tube; seeds ovoid, smooth, 2 mm across.

It is commonly found in pastures, waste places, lawns and along road sides. It forms a valuable pasture component because of its high digestibility and feeding value.

Paspalum dilatatum:

It is commonly called as 'Dollis grass' and is a native of South America (Hartley, 1964). It is found in northern temperate zone in Great Britain. In the southern temperate zone it is found in Argentina, Australia, New Zealand, South Africa and India (Holm et al., 1977).

The plant is a tufted perennial grass with a short underground rhizome. The culms are leafy at the base, erect or ascending upto 1.5 m tall (Plate 2). Leaves lanceolate, 10 to 25 x 0.3 to 1.2 cm in size mostly glabrous, lowest sheaths hairy basally, ligules membranous; inflorescence 3-5 spreading racemes, each 3-10 cm long; spikelets ovate, 3-4 mm long fringed with long, white silky hairs, purplish, 2 seriate, one sessile and other pedicellate, lower glume absent, the upper glume membranous, equalling the spikelets fringed with long white hairs on the margin; Lemma 2 dissimilar, the upper lemma faintly nerved, enclosing the bisexual floret, palea subequal, the lower lemma similar to the upper glume; lodicules 2; stamens 3; ovary glabrous; styles 2, free; grain biconvex lightly enclosed between the hardened lemma and palea. It has both vegetative and sexual modes of reproduction.

It occurs both on dry and wet soils in open pastures, lawns, wastelands and along the road sides. It forms valuable pasture because of its higher feeding value and digestibility. In some areas, it is grown with legume (T. repens) for higher

Plate 1: T. repens showing growth habit. Both unmarked and marked populations have similar growth habit.

Plate 2: P. dilatatum showing growth habit.

PLATE 1

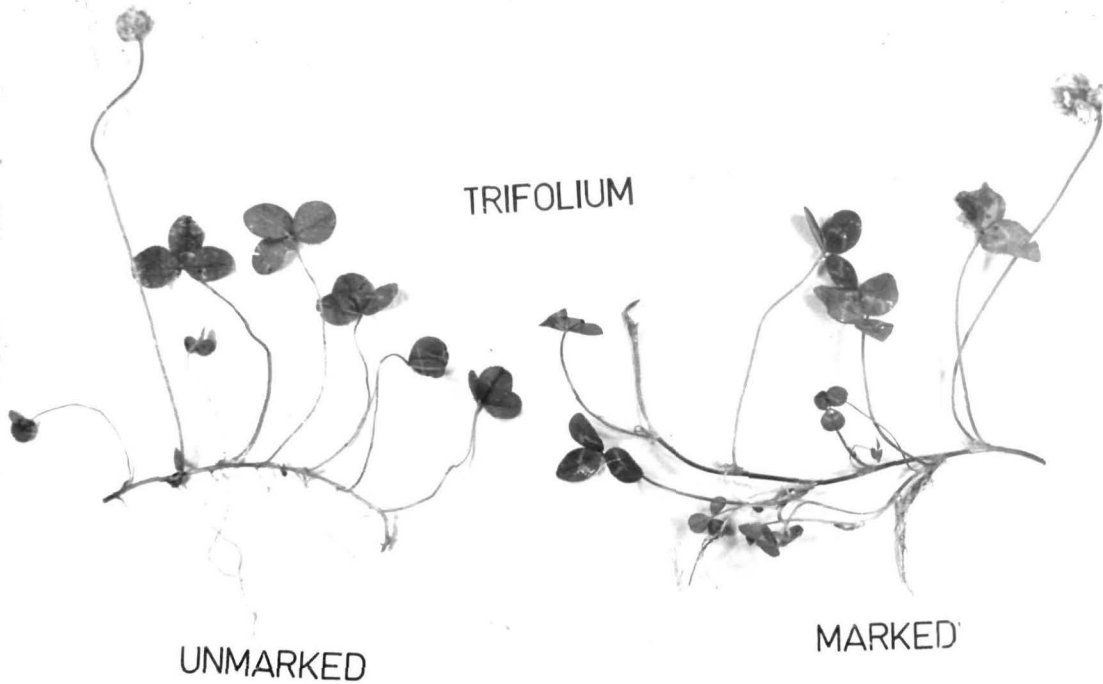


PLATE 2

production of the grassland swards (Holm et al., 1977).

FIELD OBSERVATIONS

Phenology of the two species:

T. repens and P. dilatatum occur abundantly in the grasslands of Shillong reproducing both by genets and rametes. T. repens bears stolons which creep just on the surface of soil rooting at the nodes, while P. dilatatum has strong underground rhizomes.

Both the species make negligible growth during winter months due to low temperature and moisture stress. With the rise in temperature during February, T. repens starts its growth. Sporadic rains received in March or April stimulates the growth, and a large number of leaves are produced. The flowering usually commences in the last part of April reaching its peak in May - June, when P. dilatatum and other grassland species are still in seedling stage.

The flowering along with seed setting in T. repens continues upto August, although sporadic flowering occurs throughout the year. Even during winter months one or two flowers are seen here and there. It produces a large number of seeds during the period from May to August but the seedlings have very little chance of survival in the established grasslands. Sometimes the seeds germinate, when the inflorescence is still attached to the plant which indicates that the seeds of

T. repens do not possess any dormancy.

After August it largely remains in vegetative stage producing rametes. A large number of plants die after August and maximum death is observed in January. New rametes are produced again from February.

P. dilatatum starts its activity from April with a large number of seedlings appearing in the grasslands. The old plants also show regeneration through the rhizomes during this month. Peak vegetative growth of the grass is attained during May and June followed by flowering in July-August. The peak flowering is, however, observed in August. Seed set starts in August-September and continues upto November, after which the plants bearing flowers and fruits die, due to low temperature and dry season during winter.

The seeds remain dormant for about 6 months after maturity. The seedlings have very little chance of survival and thus, the species mostly perennates through rhizomes. It overtakes T. repens in field situation after July while before this period the grasslands in Shillong are dominated by the legume. Plate 3 shows a patch of grassland in Shillong dominated by T. repens in May, 1978. The same patch is, however, dominated by P. dilatatum in August, 1978 (Plate 4), although they are sympatric in nature (Plate 5).

Growth of the two species in various field situations:

T. repens and P. dilatatum are sympatric species occur-

Plate 3: A patch of grassland in Shillong dominated by T. repens in May, 1978.

Plate 4: A patch of grassland dominated by P. dilatatum in August, 1978. This was earlier dominated by T. repens (see Plate 3).



PLATE 3



PLATE 4

Plate 5: T. repens and P. dilatatum are growing together
in grassland of Shillong showing their sympatric
nature.



PLATE 5

ring in the local grasslands exposed to varying degrees of grazing. They also occur in lawns, wastelands and along the roadsides. The growth measurements were recorded for plants growing on different habitats to get an idea as to how the two species behave in the field situations.

Effect of grazing: (Table 2.2)

In order to study the effect of grazing on abundance and growth of the grass and legume, two sites representing moderately and heavily grazed areas near the University campus were selected. Areas completely free from grazing and biotic disturbances were not available and so, the observations were recorded in moderately and heavily grazed areas only.

The field observations were taken in May and August, 1979, the periods which correspond to peak growth of T. repens and P. dilatatum respectively. Density, leaf area, aboveground biomass and seed output of both species were estimated. For density estimation, three quadrats of 50 cm² were laid in each of the two sites. These were further subdivided into 50 sub-quadrats of 10 sq. cm, for greater accuracy in counting the number of plants or tillers. After counting, the sample plots were utilized for estimating the aboveground biomass. Leaf area was estimated with the help of graph papers and the seed output was determined by counting of inflorescence per 50 cm², number of fruits per inflorescence and number of seeds per fruit.

Table 2.2: Growth of T. repens and P. dilatatum as affected by grazing pressure. The data were taken in May and August, 1979 (average/m² + S.E.).

Parameters	Species	Moderately grazed		Heavily grazed	
		May	August	May	August
Number of plants or tillers	<u>T. repens</u>	641±50	285±58	1,550±179	780±116
	<u>P. dilatatum</u>	359±44	356±14	95±17	230±17
Leaf area (sq. cm.)	<u>T. repens</u>	24,817±173	787±454	3,844±566	1,950±542
	<u>P. dilatatum</u>	5,068±289	18,815±647	593±64	2,618±323
Aboveground biomass (g)	<u>T. repens</u>	20.0±1.73	11.0±1.15	30.35±2.89	23.50±1.85
	<u>P. dilatatum</u>	71.80±8.66	142.40±2.89	19.00±3.46	92.00±1.45
Seed output	<u>T. repens</u>	5,148±670	-	16,615±1547	-
	<u>P. dilatatum</u>	-	5,541±786	-	1,122±323

The biomass was estimated by drying the plant material in an oven at 80°C for two days.

In May, T. repens showed higher density than P. dilatatum on both sites. In August too, density of the legume was more in heavily grazed situation while on moderately grazed site, the grass showed greater density than the legume. Tiller production by the grass was increased with relaxed grazing pressure.

Leaf area of T. repens decreased with increase in grazing pressure while that of the grass increased. There was reduction in leaf area of the legume from May to August while the grass showed an increased leaf area. The aboveground biomass of P. dilatatum was much greater than T. repens under moderately grazed situation but on the heavily grazed site the biomass of the legume was slightly more than that of the grass in May but it was reversed in August, although the differences were not wide.

The seed production by T. repens was much higher than the grass in both the situations. Further, the seed production by T. repens is enhanced by increased grazing pressure, while P. dilatatum produced more seeds in moderately grazed situation, as compared to heavily grazed site.

Effect of soil fertility: (Table 2.3)

In order to see the effect of soil fertility on growth performance of the two species, two sites representing high and

low fertility levels were selected. The areas beside compost manure represented high soil fertility site while the lawns with no supplemented manuring served as low soil fertility site.

In each of the sites three quadrats of 50 cm² were laid in July and the observations with regard to density, leaf area and aboveground biomass were recorded as described under grazing effect.

The density, leaf area and aboveground biomass of T. repens decreased with increased fertility level while P. dilatatum showed the reverse trend. The density and leaf area of T. repens were much greater than that of the grass under low fertility level but the aboveground biomass of the grass was higher.

Effect of trampling: (Table 2.4)

Alongwith the disturbances like cutting and grazing, the grassland species are subjected to severe trampling pressure by man and animals. Thus, to study the effect of trampling, two sites one along the footpath and the other away from it were selected for representing trampled and untrampled areas respectively. Both the sites were free from grazing and cutting.

In each of the two sites, density, leaf area and aboveground biomass were estimated for both the species in the month of July.

T. repens showed greater value for density, leaf area

Table 2.3: Growth of T. repens and P. dilatatum as influenced by soil fertility (average value/m² ± S.E.).

Parameters	High fertility site		Low fertility site	
	<u>T. repens</u>	<u>P. dilatatum</u>	<u>T. repens</u>	<u>P. dilatatum</u>
Density	30±6	180±6	1468±87	133±9
Leaf area (sq. cm.)	210±29	4721±93	6132±165	1751±91
Aboveground biomass (g)	1.61±0.29	77.81±4.97	30.31±4.39	35.21±3.07

Table 2.4: Growth of T. repens and P. dilatatum as affected by trampling (average value/m² ± S.E.).

Parameters	Trampled		Untrampled	
	<u>T. repens</u>	<u>P. dilatatum</u>	<u>T. repens</u>	<u>P. dilatatum</u>
Density	1236±92.38	156±17.32	120±11.55	210±32.33
Leaf area (sq. cm.)	5861±219.9	1561±150.7	341±86.6	2968±682.4
Aboveground biomass (g)	28.61±3.23	20.61±9.01	1.20±0.26	80.31±17.67

and aboveground biomass on trampled site than on untrampled site. The legume grew better on trampled site than the grass while the latter showed better growth on untrampled site.

Growth of two leaf morph populations of *T. repens* in various field situations

T. repens exhibits white markings of different shapes on its leaflets. In the grasslands of Shillong two populations of *T. repens* could be easily distinguished on the basis of leaf marking. In one population the white 'V' shaped marking occurs on the leaflets and the second population does not have any such marking. These two populations (white marked and unmarked) have been considered for studying inter-population competition (Chapters 8 and 9).

Effect of grazing on two leaf morph populations of *T. repens*:
(Table 2.5)

For studying the effect of grazing on two leaf morph populations of *T. repens*, two sites - one representing heavily grazed and the other moderately grazed area were selected near the university campus. The grassland sites selected for this study, contained both the populations. The field observations with respect to frequency, density and abundance of the two leaf morphs were taken in the month of May. Besides, leaf area, aboveground biomass and seed output of the two populations were also determined.

Table 2.5: Growth of the two leaf morph populations of T. repens as affected by grazing pressure (average values/m² + S.E.).

Parameters	Heavily grazed		Moderately grazed	
	White marked	Unmarked	White marked	Unmarked
Frequency %	100	67	67	100
Density	455.97 ± 50.81	132.0 ± 17.32	296.0 ± 17.32	450.0 ± 103.93
Abundance	478.0 ± 36.61	194.32 ± 144.34	336.0 ± 69.28	489.0 ± 104.50
Leaf area (sq. cm)	1826.0 ± 901.27	421.0 ± 32.33	1569.9 ± 259.82	2695.0 ± 693.42
Aboveground biomass (g)	18.21 ± 2.89	2.18 ± 0.93	14.61 ± 2.09	20.16 ± 3.24
Seed output	4155 ± 92.38	156 ± 34.06	3581 ± 670.28	4561 ± 165.13

Frequency, density and abundance of the two leaf morph populations were estimated by using 50 cm² quadrats on both the sites. Leaf area was determined with the help of graph paper. For the determination of aboveground biomass, the aboveground parts were harvested, sorted out into marked and unmarked populations and dried in an oven at 80°C for 2 days and weighed. Seed output was computed by multiplying average number of seeds/fruit by average number of fruits per 50 cm². However, all the values have been expressed in terms of 1 m² area.

The marked population (with white marking on the leaflets) showed higher values on heavily grazed site than on moderately grazed site for various parameters while the unmarked population showed greatly suppressed growth on the heavily grazed site.

Effect of soil fertility on two leaf morph populations of *T. repens*: (Table 2.6)

In order to study the effect of soil fertility on growth performance of the two populations, two sites - one situated quite near to the heap of compost manner representing the high soil fertility and the other with low soil fertility situated in the grasslands of the University campus, were selected.

The observations pertaining to frequency, density, leaf area, aboveground biomass and seed output of the two leaf morphs were recorded on both sites in May following the methods outlined under the studies of grazing effect.

Table 2.6: Growth of two leaf morph populations of T. repens in relation to soil fertility (average value/m² + S.E.).

Parameters	High fertile site		Low fertile site	
	White marked	Unmarked	White marked	Unmarked
Frequency %	100	33	67	67
Density	889.56±92.87	105.00±17.71	556.61±69.63	765.11±148.84
Leaf area (sq. cm)	8735.48±501.15	670.95±75.06	3261.00±75.41	4861.00± 92.38
Aboveground biomass (g)	45.61±2.81	6.31±1.33	12.08±5.17	40.18± 2.92
Seed output	12332 ±727.48	938 ± 161.66	2560±554.27	6832±461.89

The white marked population showed greater density, leaf area, aboveground yield and seed output under high soil fertility level, while the unmarked population behaved just the reverse. At high fertility level the difference between the two populations was more obvious than at low fertility level. Thus the white marked population seems to dominate over unmarked population on fertile soil (Plate 6).

Plate 6: Showing the abundance of marked and unmarked populations of T. repens beside the heap of compost manure representing high fertile soil. Note the dominance of marked over unmarked population.



PLATE 6

CHAPTER 3

EFFECT OF SIMULATED GRAZING ON THE GROWTH PERFORMANCE OF
TRIFOLIUM REPENS AND PASPALUM DILATATUM IN FIELD SITUATION

INTRODUCTION

Trifolium repens L. and Paspalum dilatatum Poir are the sympatric species occurring abundantly in the local grassland vegetation. These grasslands are exposed to frequent grazing, cutting and other biotic disturbances. The grass-legume behaviour in relation to grazing and cutting has been studied by various workers (Davies, 1958; Reid, 1966; Frame, 1976; Litav and Zeligman, 1977). Some workers (Robinson and Sprague, 1947; Cowling and Green, 1956; Stern and Donald, 1962a) have shown the aggressiveness of grasses over legumes although in nitrogen deficient soils legumes have been reported to do relatively better, but no work seems to have been done on the mechanism of co-existence of T. repens and P. dilatatum in nature. The grasses have also been observed to differ in the magnitude of competition which they offer to T. repens (Myers and Garber, 1942; Ahlgren, Smith and Nielson, 1945; Chestnut and Lowe, 1970; Hill, 1977). However, T. repens forms a positive association with many grass species and negative with other legumes (Turkington, Cavers and Aarssen, 1977).

We find T. repens growing quite profusely in the disturbed grasslands of Shillong while it shows relatively poor growth in protected sites. It was suspected that the clover might be suppressed if the grazing pressure was relaxed. Thus a field experiment was performed to study the comparative response of T. repens and P. dilatatum to simulated grazing and to see if

the two species could co-exist in the absence of grazing and cutting.

MATERIALS AND METHODS

In the present study grazing has been simulated by the periodic herbage removal using exclosure technique (Brown, 1954). A patch of sward of 5m^2 was fenced to exclude the external disturbances on the study site. The fenced area was divided into two equal parts. The first part was kept as control and the other was subjected to herbage removal at 3 months interval over one year period starting from the month of May 1978. The herbage was removed at the ground level. Each time, when the herbage was removed, the plants were allowed to grow for 3 consecutive months and the growth was measured at the end of the third month. The density, total leaf area, total herbage yield and the number of reproductive shoots of the two species growing in control as well as treated plots were estimated. The shoot having root system at each node was considered to be an individual plant in case of T. repens and the tillers of P. dilatatum were considered as individuals for the purposes of density estimation. For recording data, 3 permanent quadrats of 50cm^2 were marked on each site. For density estimation the quadrats were further subdivided into small quadrats of 10cm^2 to facilitate counting and to ensure accuracy. The leaf area was determined using graph paper and the dry matter yield was determined by harvesting the aboveground herbage from three quadrats of 30cm^2 and drying it in an oven at 80°C for 2 days.

The experiment was conducted in the natural sward growing in the experimental garden of the Department of Botany, North-Eastern Hill University, Shillong.

RESULTS

The density of Trifolium repens is greatly reduced in the undisturbed sward as compared to its density in the treated plot (Fig. 3.1). The first cutting in the month of May brought about a considerable increase in density of T. repens, possibly due to relaxed competition from the grasses after herbage removal and favourable climatic conditions. The density of T. repens, however, declines after subsequent cuttings showing the lowest value in the month of February presumably due to low temperature prevailing in winter months. The magnitude of reduction in density at successive observation periods was much greater in protected plot where luxuriantly growing P. dilatatum was able to suppress the growth of legume to a great extent.

There was an increase in density of T. repens after February in the treated plot while in the protected plot further reduction in density of the legume occurred after February as indicated by the decrease in density from February to May. Finally, in the month of August the clover seemed to be completely eliminated in the control plot. This decrease in density of the legume in control set may be attributed to competition offered by the grasses which are allowed to grow without any disturbance although T. repens shows an active growth during the

period of March to August.

In general, T. repens showed a remarkable increase in density after herbage removal. It may be mentioned that P. dilatatum does not show any difference in density values recorded in treated and control plots in the month of November which indicates that during the period of August to November, which is the active growth period of P. dilatatum, the grass recovers rapidly from the herbage removal. In general, the grass, however, tends to exhibit a reduction in its density in the treated plot.

Like density, the leaf area per m^2 of T. repens showed greater values in the clipped plot as compared to the protected plot. On the contrary, P. dilatatum showed lesser leaf area in the treated plot (Fig. 3.2). This may be due to the stunted growth and marked reduction in the leaf area per plant of the grass (Table 3.1). In time sequence, leaf area of T. repens gradually decreased from May onwards. In the control plot, the leaf area of T. repens showed further decrease during February to August, 1979, when the value was found to be negligible. Possibly, the reasons are same as have been given for differential changes in the density values in the control and treated plots.

There was also a great reduction in dry matter accumulation by T. repens in the control plot where the grasses overtopped the legume (Table 3.2). P. dilatatum, however, produced

Fig. 3.1: Periodic changes in density per m^2 of T. repens and P. dilatatum as affected by herbage removal. T. repens, control (●—●) and treated (O---O); P. dilatatum, control (x—x) and Treated (x---x).

Fig. 3.2: Effect of herbage removal on total leaf area per m^2 of T. repens and P. dilatatum. T. repens, control (●—●); and treated (O---O); P. dilatatum, control (x—x) and treated (x---x).

Fig. 3.1

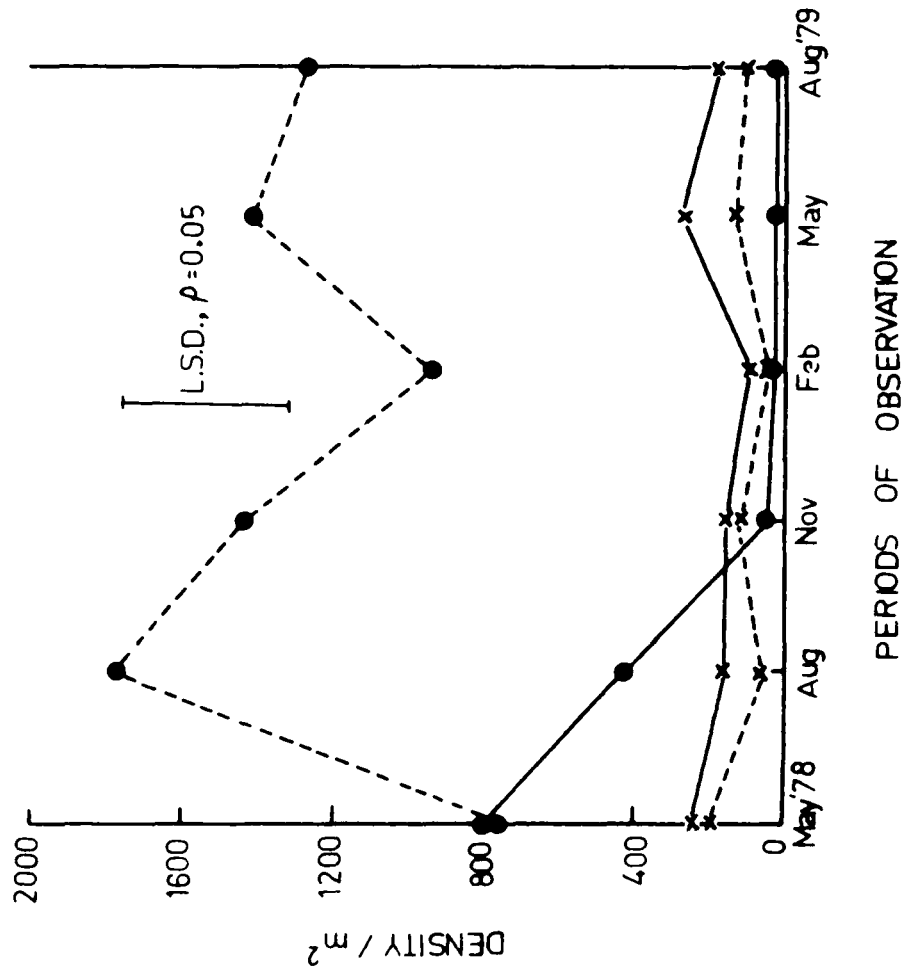


Fig. 3.2

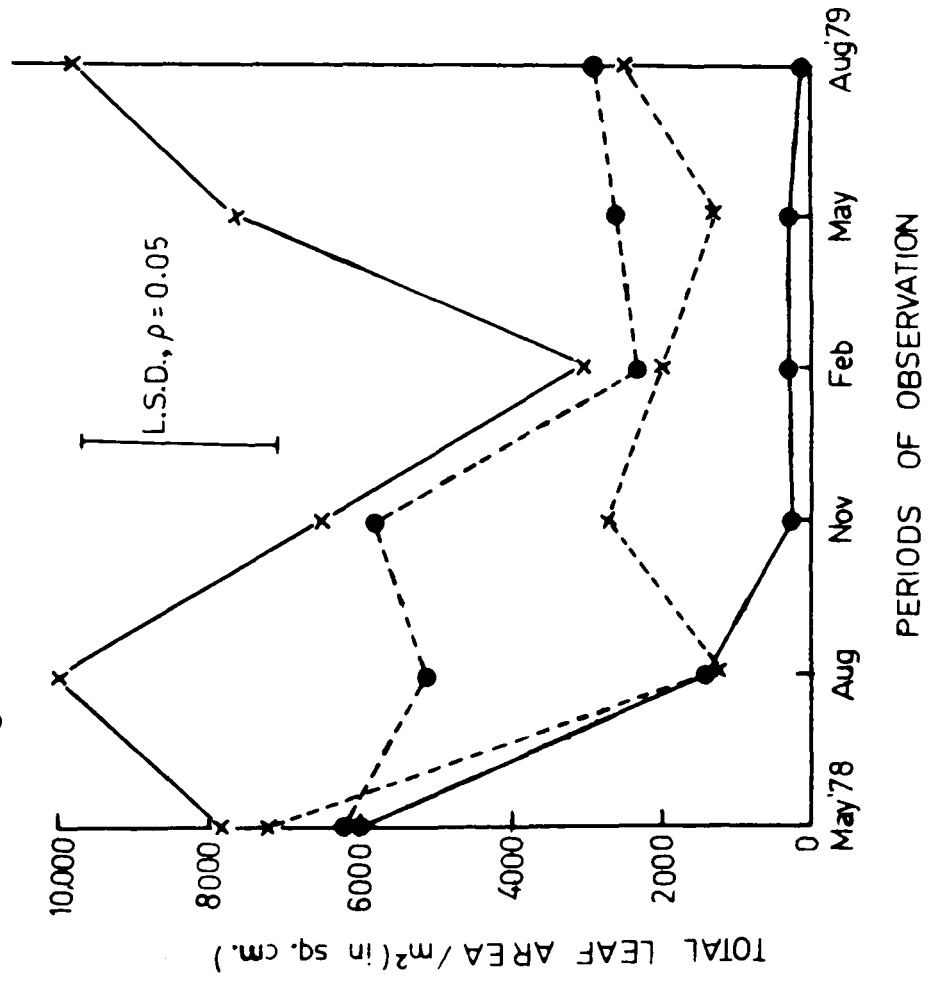


Table 3.1: Effect of herbage removal on leaf area per plant of T. repens and P. dilatatum (average values \pm S.E.).

Species	Treatment	Leaf area/plant (sq. cm.)					
		May '78	Aug.	Nov.	Feb.	May	Aug. '79
<u>T. repens</u>	Control	7.49 \pm .14	3.34 \pm .28	6.31 \pm .52	2.88 \pm 1.44	3.14 \pm 1.57	1.39 \pm 1.38
	Treated	8.12 \pm 1.28	2.87 \pm .03	6.83 \pm .39	2.23 \pm .03	1.83 \pm .03	2.37 \pm .04
<u>P. dilatatum</u>	Control	32.74 \pm .88	65.43 \pm 7.64	44.64 \pm 2.69	38.06 \pm 1.31	28.04 \pm 3.65	64.93 \pm 2.52
	Treated	31.92 \pm 2.91	91.13 \pm 3.01	20.61 \pm .07	10.80 \pm 3.14	11.36 \pm 1.05	29.76 \pm 2.77

Table 3.2: Effect of herbage removal on total aboveground yield/m² of T. repens and P. dilatatum (average value \pm S.E.).

Species	Treatment	Total aboveground yield/m ² (g)				
		Aug. '78	Nov.	Feb.	May	Aug. '79
<u>T. repens</u>	Control	15.66 \pm 4.20	1.26 \pm .85	.51 \pm .04	.39 \pm .03	.15 \pm .02
	Treated	31.37 \pm 5.28	29.86 \pm 12.81	16.39 \pm 7.23	15.18 \pm 3.16	6.99 \pm 3.51
<u>P. dilatatum</u>	Control	121.66 \pm 49.48	58.14 \pm 20.52	30.05 \pm 8.72	100.74 \pm 22.32	240.55 \pm 25.70
	Treated	26.07 \pm 9.44	40.67 \pm 16.29	15.18 \pm 6.56	10.80 \pm 3.14	44.44 \pm 5.39

greater phytomass in protected plot. The highest phytomass of the grass was recorded in the month of August which may be due to its active growth phase during this period.

The percentage of reproductive shoot in T. repens was also reduced to nil presumably due to intense competition from the grasses in the undisturbed plot (Table 3.3). There was much reduction in the percentage of reproductive shoots in P. dilatatum in the clipped plot which may be due to removal of well grown shoots before they could flower. In the treated plot the percentage of flowering shoot in the grass was about 4% in August, 1979 which is also substantially low as compared to the unclipped plot.

DISCUSSION

The poor growth of T. repens in the undisturbed sward as evident from the results is due to the luxuriant growth of P. dilatatum which is an erect rhizomatous grass attaining a height of more than 1m, if left undisturbed. Thus, the grass reduces the availability of light to the prostrate growing T. repens. This is in conformity with the results of Donald (1963) that the reduced light intensity at the clover leaf canopy caused a reduction in its growth. The grass on the other hand, suffers a set back in the plot subjected to herbage removal, which may be due to overall reduction in the photosynthetic surface. Sometimes, the density of the grass is,

Table 3.3: Effect of herbage removal on reproductive behaviour of T. repens and P. dilatatum (average values \pm S.E.).

Species	Treatment	% Reproductive Shoot					
		May '78	Aug.	Nov.	Feb.	May	Aug. '79
<u>T. repens</u>	Control	36.78 ± 5.41	(negligible)	-	-	-	-
	Treated	32.75 ± 2.79	.82 $\pm .06$.18 $\pm .06$	-	1.3 $\pm .20$.15 $\pm .14$
<u>P. dilatatum</u>	Control	-	21.48 $\pm .72$	-	-	-	49.85 ± 12.49
	Treated	-	-	-	-	-	3.75 ± 3.0

however, increased on cutting as numerous rametes are produced from the rhizome after cutting the aboveground parts. These shoots, of course become stunted due to repeated herbage removal and during its active growth phase the grass quickly recovers from the cutting treatment and produces some reproductive shoots too.

The production of reproductive shoots, aboveground biomass and total leaf area of T. repens, all showed drastic reduction in the protected plot. This was mainly due to competition for light which was not allowed to reach the level of photosynthetic surface of T. repens on account of profuse growth of P. dilatatum and other erect growing plant species in absence of herbage removal. However, the data also suggest that the percentage of reproductive shoot and other growth parameters of the grass were recorded low in periodically clipped plot. This may be attributed to reduction in photosynthetic tissue on account of frequent removal of aboveground herbage close to ground. This is in accordance with the result of Maclusky and Morris (1964), who found that the maximum dry matter yield of grasslands are obtained with a combination of long periods of uninterrupted regrowth and low cutting height. Ryegrass and ryegrass plus clover swards gave higher yields with 3 cuts than with 6 cuts per year (Anonymous, 1963).

It is evident from the study that frequent herbage removal changes the sward structure in such a manner that it

becomes legume dominated (Fig. 3.1), while in the absence of cutting the grass dominates over the legume and the growth of the latter is greatly suppressed and its population size is substantially reduced owing to competition offered by P. dilatatum and other plant species with erect habit.

There are clear indications that in absence of disturbances like grazing and cutting for longer duration, T. repens will be altogether eliminated from the local grasslands. The grass, on the other hand flourishes in undisturbed situation. In the grasslands frequently exposed to grazing, cutting and trampling, P. dilatatum and T. repens grow together without one succeeding at the expense of the other although the growth of the grass happens to be quite poor as compared to its growth in protected situations. Under local conditions, T. repens grows most actively during March to May whilst the grass shows most active growth during June to August. Thus the growth cycles of the two species are asynchronous and the resource competition, therefore, is never so crucial as to cause complete suppression of any of the two species in natural situation.

The co-existence of the species has been attributed to the asynchronous growth of the associates (Harper and Clatworthy, 1963; Turkington and Harper, 1979a). However, in our studies, we found that in spite of their asynchronous growth, T. repens and P. dilatatum cannot manage to co-exist in the grasslands fully protected from the biotic disturbances. Thus, it may be assumed

with considerable degree of certainty that T. repens and P. dilatatum owe their co-existence to biotic disturbances like grazing, cutting and trampling as prevalent in the local grasslands.

C H A P T E R 4

EFFECT OF SEASON ON COMPETITIVE BEHAVIOUR OF TRIFOLIUM REPENS
AND PASPALUM DILATATUM GROWN IN PURE AND MIXED STANDS

INTRODUCTION

Two or more species simultaneously requiring similar resources may undergo an intense competition which may lead to the ousting of one species by the other. But, by virtue of differences in phenology, growth form or nutritional needs, the species may evade such a direct competition or struggle for existence and 'interniche' in such a way that they persist and co-exist together in nature. The co-existence of the two species of Trifolium, T. fragiferum and T. repens, is a very interesting case studied by Harper and Clatworthy (1963). Both the species strongly compete for light but they manage to co-exist in nature owing to the difference in their morphological characteristics and asynchronous growth period. Turkington and Harper (1979a), have found that Trifolium repens and Lolium perenne are intimately associated and have a close cohabitation which has been argued by them to be possible due to the looser tussock of L. perenne and the marked asynchrony of growth cycle of these two species. Scarisbrick and Ivines (1970) showed that competitive interactions between pasture plants are influenced by seasonal weather conditions. They observed that Lolium perenne, which commences growth in early spring (Blackman, 1933) is more successful in competition. However, during July and August a depression in growth of L. perenne occurs (Anslow, 1965) coinciding with the periods when conditions are optimal for the growth of T. repens (Blackman, 1933). Lieth (1960) showed that T. repens and L. perenne form a mobile mosaic in

which low clover density areas are invaded by grass and vice-versa. Besides asynchronous growth of the species in grasslands contributing to their co-existence, the biotic disturbances like grazing and cutting are also vital factors influencing the co-existence (Pradhan and Tripathi, 1980) under field conditions. The legume shows active growth during February-March to July-August showing peak growth in April while the active growth of the grass occurs during April to September showing peak growth during May-June. Thus the two species may be able to avoid intense competition for the resources due to the difference in their growth periods. However, the two species come in direct contact with each other in some part of their growth periods. Thus, the effect of season on the competitive success of the two species was studied by raising their pure and mixed populations, under controlled conditions, in three distinct seasons.

MATERIALS AND METHODS

Four days old seedlings of T. repens and P. dilatatum were transplanted on 12 July 1979 to the plastic pots of 21.0 cm diameter and 19.0 cm depth filled with sandy loam soil mixed with compost manure in the ratio of 5:1. The amount of soil plus manure per pot was ca. 7.0 kg. The pure and mixed populations of the two species were raised in the following manner so as to give de Wit's 'replacement series' (de Wit, 1960), maintaining an overall density of 8 plants per pot:

- 1) 0% T. repens (T) + 100% P. dilatatum (P)
- 2) 50% T + 50% P
- 3) 100% T + 0% P

The experimental design consisted of 3 proportions x 3 replicates x 3 harvest times. The three harvests H₁, H₂, and H₃ were respectively taken in time sequence at 4, 8 and 12 months after planting.

Besides the above experiment which continued for one year, two short-term experiments each of 4 months duration were also set up. The first short term experiment commenced from 12 November 1979 and the second from 12 March 1980. Various growth characters of the two species were measured after 4 months i.e. at the time of termination of the short term experiments. The harvest time of the first and second short-term experiments coincided with H₂ and H₃ experiments of one year duration.

The short-term experiments were also set up in accordance with 'de Wit's replacement series' with the same proportions and density, as used in the long-term experiment. The short-term experiments consisted of 3 proportions x 3 replicates x 1 harvest.

At each harvest in both the long and short-term experiments, the number of stolons or rhizomes, number of leaves, total leaf area, dry matter yield, allocation of dry matter to aboveground plant parts, and fertile shoot production were

estimated. The dry matter yield was estimated by drying the plant material in an oven at 80°C for 2 days.

The experiments were conducted in an unheated glass house. The minimum temperature in the glass house was recorded to be 6.2°C in January 1980 and maximum (29.5°C) in April 1980. The pots were randomized inside the glass house using the table of random numbers (Fisher and Yates, 1963). An equal amount (500 ml) of water was added in each pot at 3 days interval. A dilute solution of 'cythion' (0.2%) was sprayed regularly on the plants to avoid attack by slugs and larvae.

EXPERIMENTAL RESULTS

Number of stolons and tillers (Table 4.1);

T. repens produced greater number of stolons in pure than in mixed stands in long-term as well as short-term experiments. Although there was a progressive increase in stolon production in pure and mixed stands with time, the difference between the pure and mixed stands widened with the passage of time. Number of stolons produced was the same in the short-term experiments set up in November and March. However, at the time of first harvest of the long-term experiment which may be treated as equivalent to another short-term experiment commencing from July the number of stolons produced was comparatively very high. P. dilatatum, on the other hand, produced more tillers in mixed than in pure stand in long-term experiment and

Table 4.1: Number of stolons per plant of T. repens and tillers per plant of P. dilatatum grown in pure and mixed stands after 4 (H₁), 8 (H₂) and 12 months (H₃) from planting in long-term and after 4 months growth in short-term experiments.

Nature of stand	Long-term experiment			Short-term experiment no.			
	H ₁	H ₂	H ₃	F:variance ratio	I	II	F:variance ratio
<u>T. repens</u> (Pure)	17.65	21.33	33.56	15.01*	6.17	6.00	0.84 NS
<u>T. repens</u> (Mixed)	12.00	19.45	18.00	4.42 NS	3.22	2.84	0.99 NS
<u>P. dilatatum</u> (Mixed)	6.53	12.67	19.56	57.22**	2.11	8.33	799.34**
<u>P. dilatatum</u> (Pure)	5.21	11.67	17.67	32.05**	2.34	6.33	61.26*
F:Variance ratio	36.47**	106.28**	5.52**		19.89**	45.28**	

** indicate significant differences at P = 0.01

* indicates significant differences at P = 0.05

NS: Not significant

short-term experiment set up in March. However, in the short-term experiment commencing from November, the tiller production by the grass in mixture was slightly lower than in the pure stand (Table 4.1).

Leaf area (Table 4.2):

Leaf area per plant of T. repens was also lower in mixed stand than in pure in the long-term experiment while in the short-term experiment leaf area was greater in pure stand. P. dilatatum, on the other hand, produced more leaf area in mixture than in monoculture except in the experiment set up in November where there was not much difference in leaf area produced in pure and mixed stands. Leaf area of both the species was substantially low when grown during winter while in the short-term experiment commencing from March and in the long-term experiment which was started in July the leaf area was quite high. In long-term experiment, P. dilatatum generally showed a progressive increase in leaf area with time, while in case of T. repens there was a decline in leaf area after 8 months growth. The magnitude of reduction in leaf area of the legume was much greater in mixture than in pure stand of the long-term experiment. In T. repens, the maximum leaf area was observed at H_2 of the long-term experiment in both pure and mixed stands. There was a reduction in leaf area of the grass from H_1 to H_2 , but the value increased considerably at H_3 (Table 4.2).

Table 4.2: Total leaf area (sq. cm) per plant of T. repens and P. dilatatum grown in pure and mixed stands after 4 (H₁), 8 (H₂) and 12 months (H₃) from planting in long-term and after 4 months growth in short-term experiments.

Nature of stand	Long-term experiment			Short-term experiment no.			
	H ₁	H ₂	H ₃	F:variance ratio	I	II	F:variance ratio
<u>T. repens</u> (Pure)	424.27	972.78	822.90	7.59*	8.99	283.77	98.35*
<u>T. repens</u> (Mixed)	297.57	949.85	146.08	67.45**	7.45	132.25	45.66*
<u>P. dilatatum</u> (Mixed)	531.89	401.91	1292.22	9.96*	7.36	1031.15	258.37**
<u>P. dilatatum</u> (Pure)	302.58	289.98	731.82	6.65*	7.28	668.27	227.24**
F:variance ratio	2.54 ^{NS}	182.21**	13.83**		3.38 ^{NS}	100.52*	

** indicate significant differences at P = 0.01

* indicates significant differences at P = 0.05

NS: Not significant.

Dry matter yield (Table 4.3):

Dry matter yield of T. repens was greater in pure than in mixed stands but a reverse trend was exhibited by the grass. The latter showed a progressive increase in dry weight per plant in time sequence in the long-term experiment. T. repens also showed a similar behaviour in pure but in mixture the increase was conspicuous from H_1 to H_2 but at H_3 , there was slight decrease in yield. The dry matter production of the grass was much greater in the short-term experiment set up in March and also in the long-term experiment where the first harvest was taken after 4 months duration.

P. dilatatum accumulated more biomass than T. repens both in pure and mixed stands. The difference in the mixture yield and the pure stand yield of P. dilatatum increased with the passage of time (Fig. 4.1a and b).

Fertile shoot (%):

T. repens showed some flowering in the short-term experiment harvested in July in pure stand but did not show any in the mixed stand showing thereby that the grass is more favoured by the climatic conditions prevailing during this period and its luxuriant growth suppresses the flowering of T. repens in mixture. This is also evident from the long term-experiment where the flowering of T. repens was much lesser in mixed than in pure stand. In the long-term experiment, T. repens showed flowering

Table 4.3: Dry weight (g) per plant of T. repens and P. dilatatum grown in pure and mixed stands, after 4 (H₁), 8 (H₂) and 12 months (H₃) from planting in long-term and after 4 months growth in short-term experiments.

Nature of stand	Long-term experiment			Short-term experiment no.			
	H ₁	H ₂	H ₃	F:variance ratio	I	II	F:variance ratio
<u>T. repens</u> (Pure)	2.34	6.86	7.40	15.87*	0.08	1.73	25.0*
<u>T. repens</u> (Mixed)	1.94	3.57	3.35	1.41 ^{NS}	0.07	0.47	22.02*
<u>P. dilatatum</u> (Mixed)	9.57	15.93	21.89	6.43 ^{NS}	0.08	11.42	50.54*
<u>P. dilatatum</u> (Pure)	5.03	10.98	18.02	14.60*	0.10	5.93	11.95 ^{NS}
F:variance ratio	41.85**	52.62*	12.74*		2.84 ^{NS}	22.69*	

** indicate significant differences at P = 0.01

* indicates significant differences at P = 0.05

NS Not significant.

Fig. 4.1(a): Replacement diagram based on total biomass/pot of T. repens (—●—) and P. dilatatum (—○—) grown in pure and mixed stands after 4 (H_1), 8 (H_2) and 12 months (H_3) from planting. The combined yield per pot (---x---) is also given.

Fig. 4-1(a)

Long term experiments

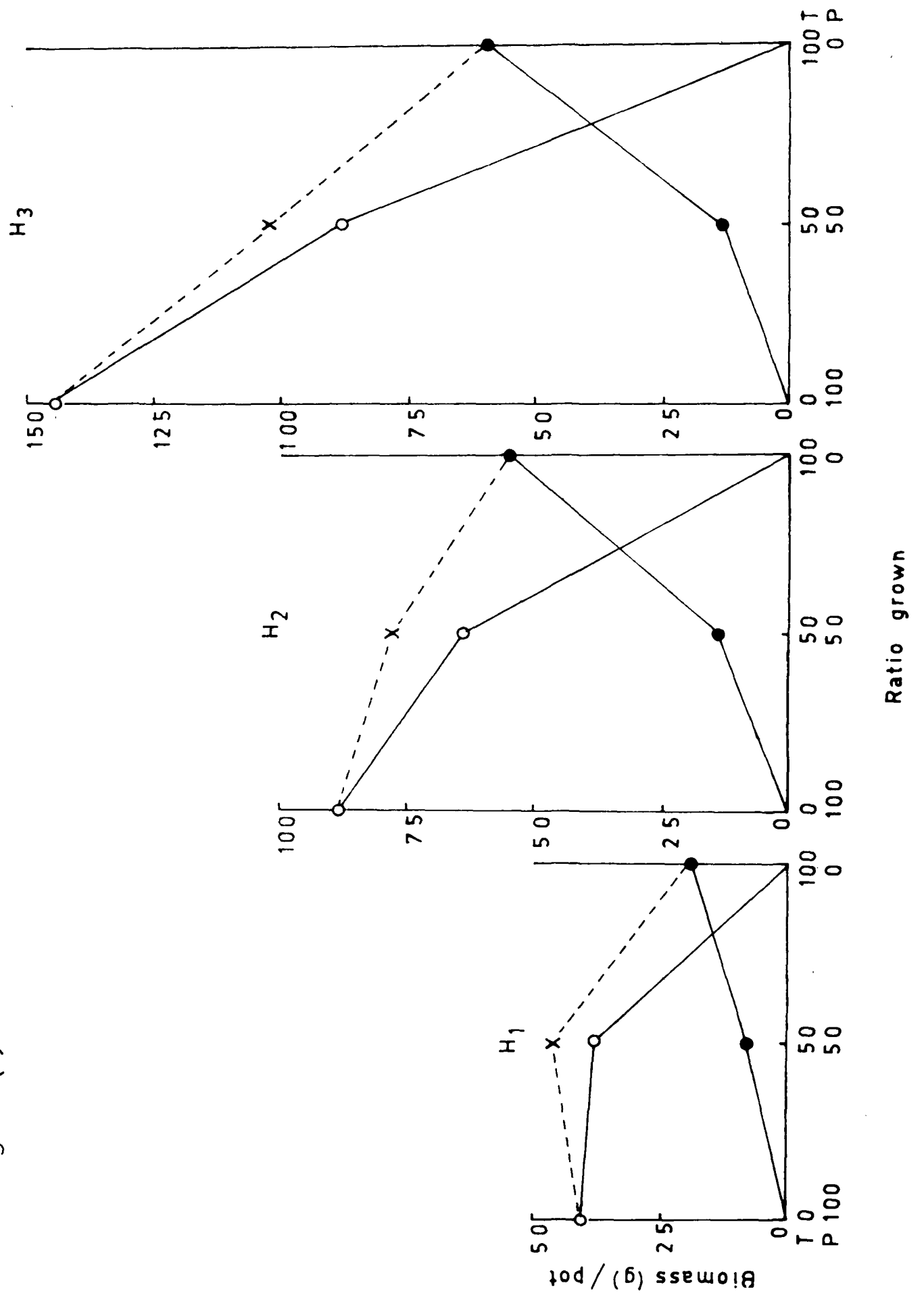
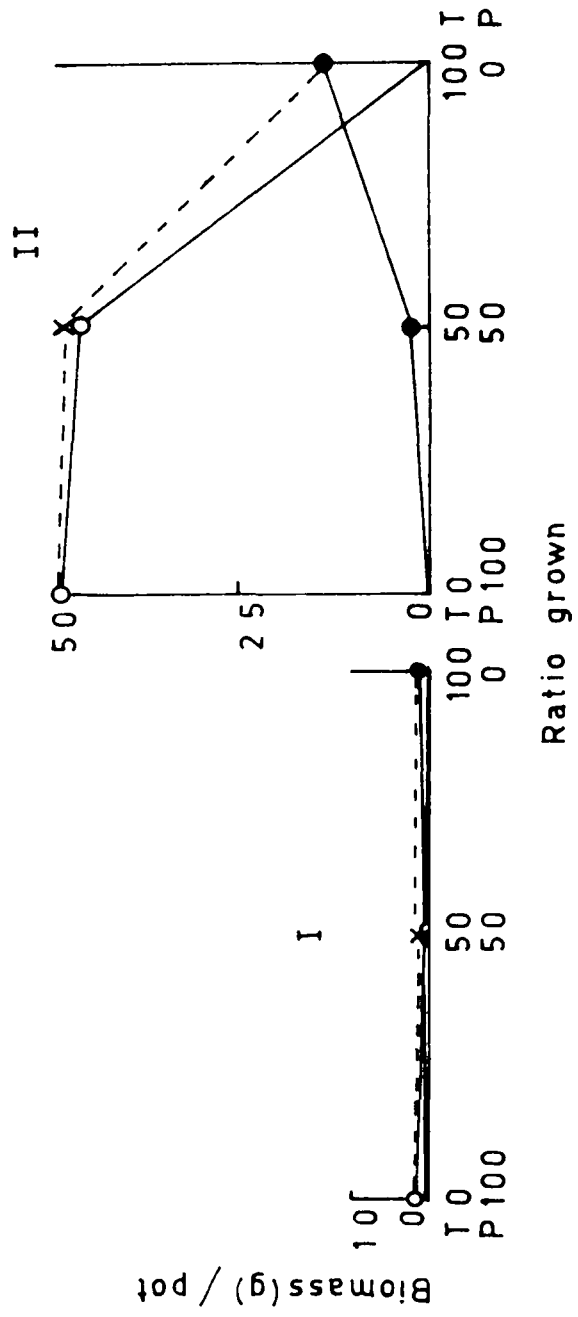


Fig. 4.1(b): Replacement diagram based on total biomass/pot of T. repens (—●—) and P. dilatatum (—○—) grown in pure and mixed stands after 4 months from planting. The combined yield per pot (---x---) is also given.

Fig. 4.1(b) Short-term experiments



after 8 months growth at H_2 i.e. in March. Here again the percentage of fertile shoots was considerably higher in pure stand than in mixture. P. dilatatum, on the other hand, suffers more from intra-specific competition and so with decrease in number of the grass plants as is the case in mixed stands, percentage of fertile shoots increases. Percentage fertile shoots in the grass was quite high at H_1 , but at H_2 the grass did not show any flowering indicating that environmental conditions between H_1 and H_2 are not favourable for its reproductive growth. However, with the onset of warm weather conditions the grass again showed flowering at H_3 (Table 4.4).

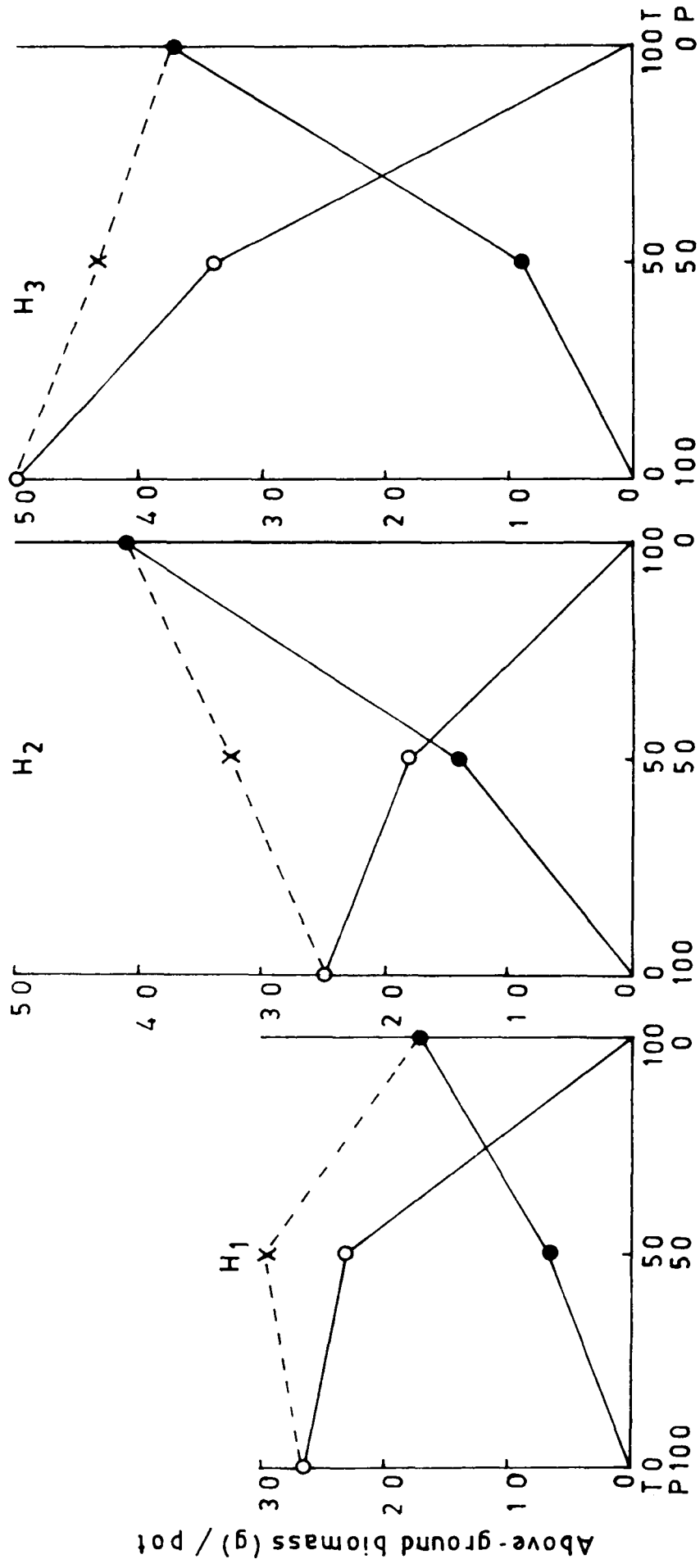
T. repens generally showed higher aboveground yield in pure stand than in mixture, while P. dilatatum behaved just the reverse in both long-term and short-term experiments. However, both the species showed very poor growth during winter as is apparent from the results of short-term experiment set up in November, and so, the differences due to species or due to nature of stands was not discernible. This, however, indicates that the suppression in growth of T. repens which is generally caused by the luxuriant growth of the grass no longer occurs during winter months characterized by unfavourable weather conditions.

The data on aboveground yield per pot of the two species also confirm this point (Fig. 4.2a and b).

Fig. 4.2(a): Replacement diagram based on total aboveground biomass/pot of T. repens (—●—) and P. dilatatum (—○—) grown in pure and mixed stands after 4 (H_1), 8 (H_2) and 12 months (H_3) from planting. The combined aboveground yield per pot (---x---) is also given.

Fig. 4.2(a)

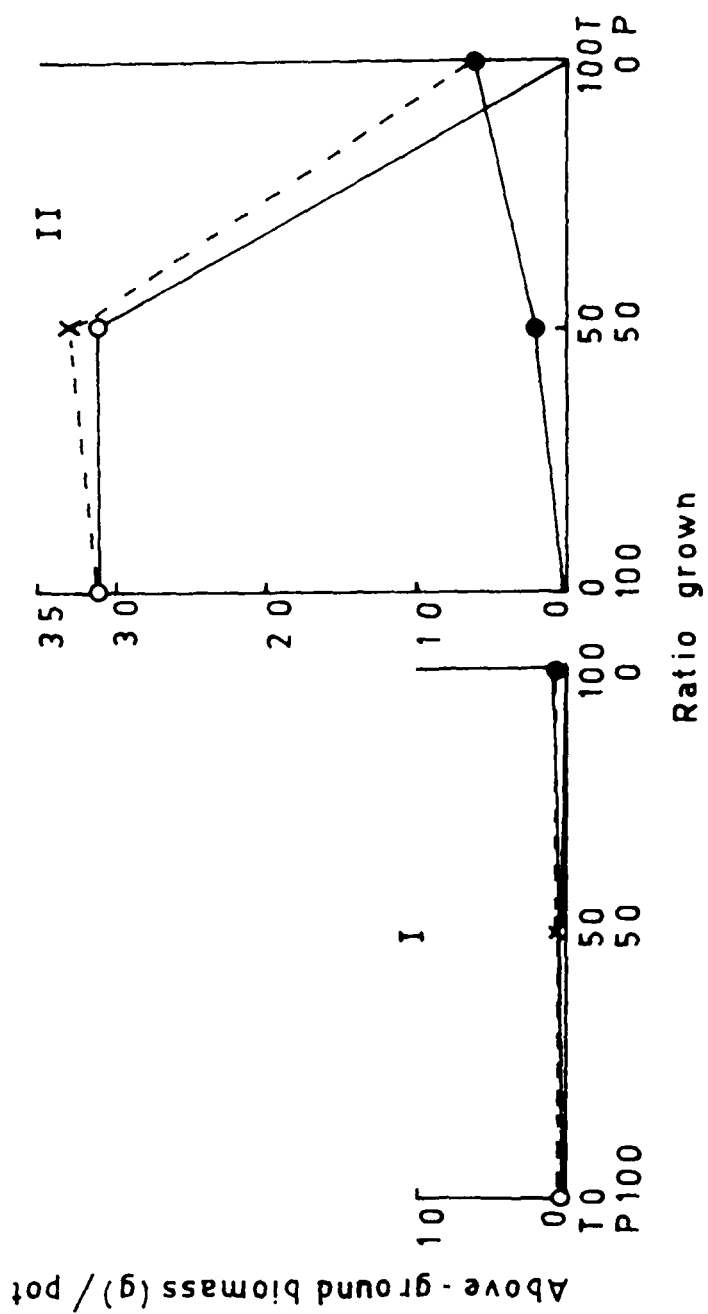
Long-term experiment



Ratio grown

Fig. 4.2(b): Replacement diagram based on total aboveground biomass/pot of T. repens (—●—) and P. dilatatum (—○—) grown in pure and mixed stands after 4 months from planting. The combined yield per pot (—x—) is also given.

Fig. 4.2(b) Short term experiments



DISCUSSION

The growth of P. dilatatum and T. repens in pure and mixed stands shows that the grass is a better competitor than the legume. However, it seems to suffer more from intra-specific competition, while in inter-specific competition the legume suffers miserably, in spite of the asynchronous growth pattern of the two species. However, during November to March, the grass failed to suppress the growth of T. repens as the grass itself showed quite poor growth due to unfavourable conditions prevailing during the period. Compared with the yield of the two species in other experiments the reduction in growth of P. dilatatum during winters was reduced to a very great extent while the magnitude of reduction was not that high in T. repens, which is a temperate species and so it may probably withstand low temperature conditions better.

In the experiments where the two species were allowed to grow during relatively warm period, the grass invariably gets an upper hand which is shown by its better growth in the mixed population, and the legume growth is suppressed on account of severe competition offered by fast growing P. dilatatum. The time taken between planting to flowering is longer in T. repens than in the grass (Table 4.4). Thus the grass completes its flowering before winter season which represents a period of inactive growth for the grass. The plants of T. repens grown in July (long-term experiment), however, showed flowering even

Table 4.4: Percentage fertile shoots of T. repens and P. dilatatum grown in pure and mixed stands after 4 (H_1), 8 (H_2) and 12 months (H_3) from planting in long-term experiment and after 4 months period from planting in short-term experiments.

Nature of stand	Long-term experiment			Short-term experiment no.	
	H_1	H_2	H_3	I	II
<u>T. repens</u> (Pure)	0	9.56	4.98	Nil	0.15
<u>T. repens</u> (Mixed)	0	2.31	0.40	"	0
<u>P. dilatatum</u> (Mixed)	35.68	0	11.15	"	14.05
<u>P. dilatatum</u> (Pure)	38.39	0	8.00	"	4.00

Table 4.5: Relative yield of T. repens and P. dilatatum grown in pure and mixed stands after 4 (H_1), 8 (H_2) and 12 months (H_3) from planting in long-term experiment and after 4 months period from planting in short-term experiments. Quotient of relative yield of T. repens to P. dilatatum is also given.

	Long-term experiment			Short-term experiment no.	
	H_1	H_2	H_3	I	II
Relative yield <u>T. repens</u>	0.42	0.26	0.23	0.44	0.40
<u>P. dilatatum</u>	0.95	0.73	0.61	0.44	0.40
Quotient of relative yield of <u>T. repens</u> to <u>P. dilatatum</u>	0.44	0.36	0.38	3.14	0.43

during winter which again indicates that the legume can manage to grow relatively better than the grass during winter months, although in short-term experiment set up immediately before the onset of winters the legume also did not show any flowering until March. With the rise in temperature after winter months, the grass once again shows active growth and starts flowering at H₃ of the long-term experiment. Further, the increase in dry matter yield from H₂ to H₃ both in pure and mixed populations was much greater in the grass in comparison with the legume. It may, therefore, be generalized that P. dilatatum grows better than the legume during most of the year except in winter season.

Competitive outcome in favour of the grass is also confirmed by the relative yield values of the two species (Table 4.5). The quotient of relative yield of T. repens to P. dilatatum which was always $\ll 1$ suggests that the legume invariably loses to the grass in competitive situations. The only exception to this generalization is the competitive behaviour of the two species grown during winters. Donald (1963) showed that shading caused by tall growing grass species suppresses the growth of legumes. In the present study as well, the growth of the legume in mixed population suffers on account of shade caused by the tall growing P. dilatatum.

Kershaw (1959) showed a positive association of Trifolium repens with Lolium perenne and negative with Dactylis glomerata

and Agrostis tenues. Turkington and Harper (1979a) found a close cohabitation of T. repens and L. perenne and they attributed it to looser tussock of the grass. In field conditions, the two species show asynchronous growth pattern. with T. repens starting its active growth phase much earlier than the grass, but once the grass comes onto the scene the legume faces a very tough competition due to rapid growth of the grass.

As indicated by the competitive behaviour, the species probably cannot co-exist for long duration in spite of their asynchronous growth. It is observed that the grasslands at Shillong are dominated by the legume (T. repens) during March to May and by the grass (P. dilatatum) during August to November. An earlier study (Pradhan and Tripathi, 1980) has shown that the growth of P. dilatatum in protected areas free from grazing and other biotic disturbances results into virtual elimination of T. repens. This has been attributed to poor availability of light, on account of luxuriant growth of P. dilatatum to the legume which occupies the lowest stratum in the grassland vegetation. Their co-existence in field conditions, owes to the biotic disturbances like grazing, cutting and trampling which are so common in the local grasslands.

CHAPTER 5

COMPETITIVE INTERACTIONS BETWEEN TRIFOLIUM REPENS AND PASPALUM
DILATATUM IN RELATION TO SOIL NITROGEN

INTRODUCTION

The importance of grazing on the co-existence of Trifolium repens L. and Paspalum dilatatum Poir, in nature has been stressed in Chapter 3. T. repens being a legume can exploit the atmospheric nitrogen; P. dilatatum on the other hand, depends on soil nitrogen alone although certain grasses have also been reported to fix atmospheric nitrogen to some extent with the help of bacteria living in the rhizosphere (Ruinen, 1974; Dobereiner, 1977). Thus it would be interesting to study the grass legume interaction at different nitrogen levels. It is expected that the legume (T. repens) might suppress the grass (P. dilatatum) at low nitrogen regime. It may also be argued that when grown in mixture in nitrogen deficient soil, atmospheric nitrogen fixed in the root nodules of the legume may be incorporated in soil and it could possibly be utilized by the grass.

Competition for nutrients has been stressed by many workers (King, 1971; Snaydon, 1971; Eagles, 1972) and the effect of nutrient competition may be substantial as has been demonstrated by Hall (1971). A lot of study has been done on grass-legume interaction in relation to soil nitrogen, and it has been shown that the grasses benefit more from the increase in nitrogen supply as compared to the suppression caused to them by the legumes due to competition (Walker et al., 1954; Russell, 1961; Bryan, 1962), although legumes may sometimes reduce the

uptake of nitrogen by grass (Willoughby, 1954; Davies, 1964; Simpson, 1965; Whitney et al., 1967; Vallis et al., 1977).

The present study was made to examine the competitive effect of T. repens and P. dilatatum on each other in relation to soil nitrogen. The experimental procedure has been so adopted as to give some idea regarding the utilization of nitrogen fixed in the root nodules of the legume by the grass.

MATERIALS AND METHODS

The seeds of Trifolium repens and Paspalum dilatatum were washed thoroughly and kept in running water for 24 hours, as a preliminary study on seed germination of P. dilatatum indicated that such a treatment enhances the seed germination. In order to avoid any variation due to water treatment, the seeds of T. repens were also given similar treatment. The washed seeds were sown in sterilized, acid washed sand having pH range from 6.5 to 7.5 in two separate trays in an unheated glass house of the Department of Botany, North-Eastern Hill University, Shillong, where temperature ranged from 12.5°C (Min.) in March to 28°C (Max.) in May, 1980. The seeds of P. dilatatum germinate after 4 - 5 days from sowing, while T. repens seeds can germinate after 2 days. So, the seeds of grass were sown on 26th March 1980 and those of legume on 28th March 1980 so as to ensure germination simultaneously. The seedlings of T. repens having two cotyledonary leaves and a trifoliate leaf and the

grass seedlings having one leaf were transplanted in the experimental pots filled with sterilized, acid washed sand on April 12, 1980.

Preparation of Sand:

River sand was collected from a river bed and passed through 0.2 to 0.02 mm sieve to get fine sand. The fine sand thus obtained was sterilized with Conc H_2SO_4 for one hour. The acid treated sand was then kept in running tap water till the acid was washed off. This took about 24 hours. The sand was further washed 5 - 6 times with deionized water. The pH of the sand suspension was measured and it was found in the range of 6.5 to 7.5.

Experimental procedure:

The experimental pots of 10 cm. diameter and 15 cm. depth were filled with equal amount (c.1 kg) of sterilized sand. The pots were provided with a hole on the bottom, which was plugged with glass wool to avoid water logging and to ensure proper aeration.

The seedlings of T. repens and P. dilatatum were transplanted in the pots in such a manner as to give de Wit's replacement series (de Wit, 1960). The growth of the two species was studied in pure and mixed stands at three different nitrogen levels (described below) at the same over-all density

(4 plants per pot). The species had the following three proportions:

- 1) 0% T. repens (T) + 100% P. dilatatum (P)
- 2) 50% T + 50% P
- 3) 100% T + 0% P

Composition of nutrient solutions:

The nutrient solution was prepared in deionized water separately for three solutions to give three different nitrogen levels referred to as N_0 , N_1 and N_2 in the text. The nutrient solutions of E.G. Bollard cited in Hewitt (1966) was used.

Molar concentration of reagents used to obtain nil (N_0), half (N_1) and 2 fold (N_2) standard concentration of nitrogen is as follows :

Reagents	(-N)	($\frac{1}{2}$ N)	(2N)
K_2HPO_4	0.001	0.001	0.001
NH_4NO_3	-	-	0.012
$(NH_4)_2SO_4$	-	0.002	0.002
K_2SO_4	0.001	0.001	0.001
$MgSO_4$	0.002	0.002	0.002
$CaSO_4$	0.002	-	-
$Ca(NO_3)_2$	-	0.002	0.002

Standard levels of elements and compounds in the nutrient solutions were: K = 156 ppm, Mg = 48 ppm, Ca = 80 ppm, PO_4 = 95 ppm, SO_4 = 480 ppm and N_2 = 0, 112 and 448 ppm for N_0

N₁ and N₂ respectively.

The micronutrients were added using Hewitt (1966) micronutrient composition as follows:

Reagents	Concentration %	Milligram equivalent/ litre	ppm conc.
NnSO ₄ · 4H ₂ O	2.23	0.02	0.55
CuSO ₄ · 5H ₂ O	0.25	0.002	0.064
ZnSO ₄ · 7H ₂ O	0.29	0.002	0.065
H ₃ BO ₃	3.10	0.05	0.54
Na ₂ MoO ₄ · 2H ₂ O	0.121	0.003	0.048
CoSO ₄ · 6H ₂ O	0.053	0.0004	0.012
Fe citrate 5H ₂ O	6.70	0.30	5.60

Nutrient solution was prepared in deionized water separately for the three nitrogen levels. 100 ml of each of the nutrient solution representing N₀, N₁ and N₂ was added to each of the pot for three nitrogen levels separately every after 4 days beginning from 12th April 1980 till the experiment was terminated.

The three harvests H₁, H₂ and H₃ were taken for growth measurements on 14th June, 26th July and 27th September 1980, corresponding to 9, 15 and 24 weeks from planting. At each harvest, the number of tillers or stolons, number of leaves, total leaf area, number of fertile shoots, seed output and dry matter allocated to different plant parts (viz. root, rhizome or stolon, stem with sheath, leaves and inflorescence with seeds) were measured. The

plant parts were kept in an oven at 80°C to constant weight for dry matter estimation. In case of legume the number of root nodules and its dry weight was also estimated.

The chlorophyll content of the fresh leaves and nitrogen content of the aboveground plant parts of both species grown under different treatments were also determined. Chlorophyll content was determined by the method outlined by Allen (1974) and nitrogen content of the plant material was estimated by Micro-kjeldahl method outlined by Misra (1968).

The experiment comprised of 3 nitrogen levels x 3 proportions x 3 replicates x 3 harvest times involving in all 81 pots. The pots were randomized in the glass house and the position of each pot was changed from one place to another every alternate day. The algal growth was checked by scraping off the surface layer of sand but in spite of constant care some blue-green algae did appear in the pots.

EXPERIMENTAL RESULTS

Number of stolons and tillers:

The number of stolons produced by T. repens was greater in pure than in mixed stands at N₀ and N₁ nitrogen levels, but at N₂, the number of stolons was more in mixed than in pure stand and it increased progressively from H₁ to H₃. P. dilatatum, on the other hand, showed an increased number of tillers in mixture than in pure at all the nitrogen levels, although at N₀ the

tiller production was less than that of N_1 and N_2 (Table 5.1).

Number of stolons produced per pot by T. repens was also higher in mixture than in pure at N_0 (Fig. 5.1). P. dilatatum, on the other hand, showed this trend at high nitrogen level. Number of stolons per pot produced by T. repens decreased in mixture with the increase in soil nitrogen. In pure, however, it increased from N_0 to N_1 but with further increase in soil nitrogen the number decreased. In pure stand, P. dilatatum also showed similar response in respect of tiller production. In mixture some increase was noticed from N_0 to N_1 but any further addition of nitrogen did not affect the tiller production. The stolon production by T. repens plus tiller production by P. dilatatum in mixture was greater than the stolon or tiller production in the corresponding pure stands at N_0 . At N_2 , however, the combined value in mixture was lower than stolon production of T. repens in pure stand. At low nitrogen level stolon production by T. repens and tiller production by P. dilatatum in pure was more than their total production in mixture. There was gradual decrease in number of stolons of T. repens plus tillers of P. dilatatum in mixture with increase in soil nitrogen (Fig. 5.1).

Number of leaves and leaf area:

At N_0 T. repens produced more leaves in mixture than in pure stand. But at N_1 and N_2 the trend was reversed (Table 5.2). P. dilatatum, on the other hand, produced more leaves in mixture

Table 5.1: Stolon and tiller production per plant of T. repens and P. dilatatum respectively, grown in pure and mixed stands at three varying nitrogen regimes taken after 9 (H₁), 15 (H₂) and 24 weeks (H₃) from planting.

Nature of stand	Harvests									L.S.D.		
	H ₁			H ₂			H ₃					
	N ₀	N ₁	N ₂	L.S.D.	N ₀	N ₁	N ₂	L.S.D.	N ₀		N ₁	N ₂
<u>Pure Trifolium</u> (100%)	1.00	4.17	5.00	2.45	4.25	5.67	6.75	1.08	5.42	11.00	8.53	1.20
<u>Mixed Trifolium</u> (50%)	2.00	3.17	3.00	0.25	9.50	2.33	2.83	1.06	11.67	1.33	0.87	2.06
<u>Mixed Paspalum</u> (50%)	1.00	3.00	3.00	1.26	1.00	5.67	5.33	0.96	1.17	10.00	10.00	2.07
<u>Pure Paspalum</u> (100%)	1.00	2.17	2.33	1.84	0.83	3.75	3.42	0.42	0.67	6.75	6.17	2.34
L.S.D.	0.49	0.81	0.47		0.72	1.23	1.41		1.57	2.77	2.33	

L.S.D. at P = 0.05

Fig. 5.1: Replacement diagram based on stolon production per pot by T. repens and tiller production per pot by P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes (N_0 , N_1 and N_2) after 24 weeks (H_3) from planting. The symbols $\text{---}\bullet\text{---}$, $\text{---}o\text{---}$ and $\text{---}\blacksquare\text{---}$ stand for T. repens, P. dilatatum and combined yield per pot respectively.

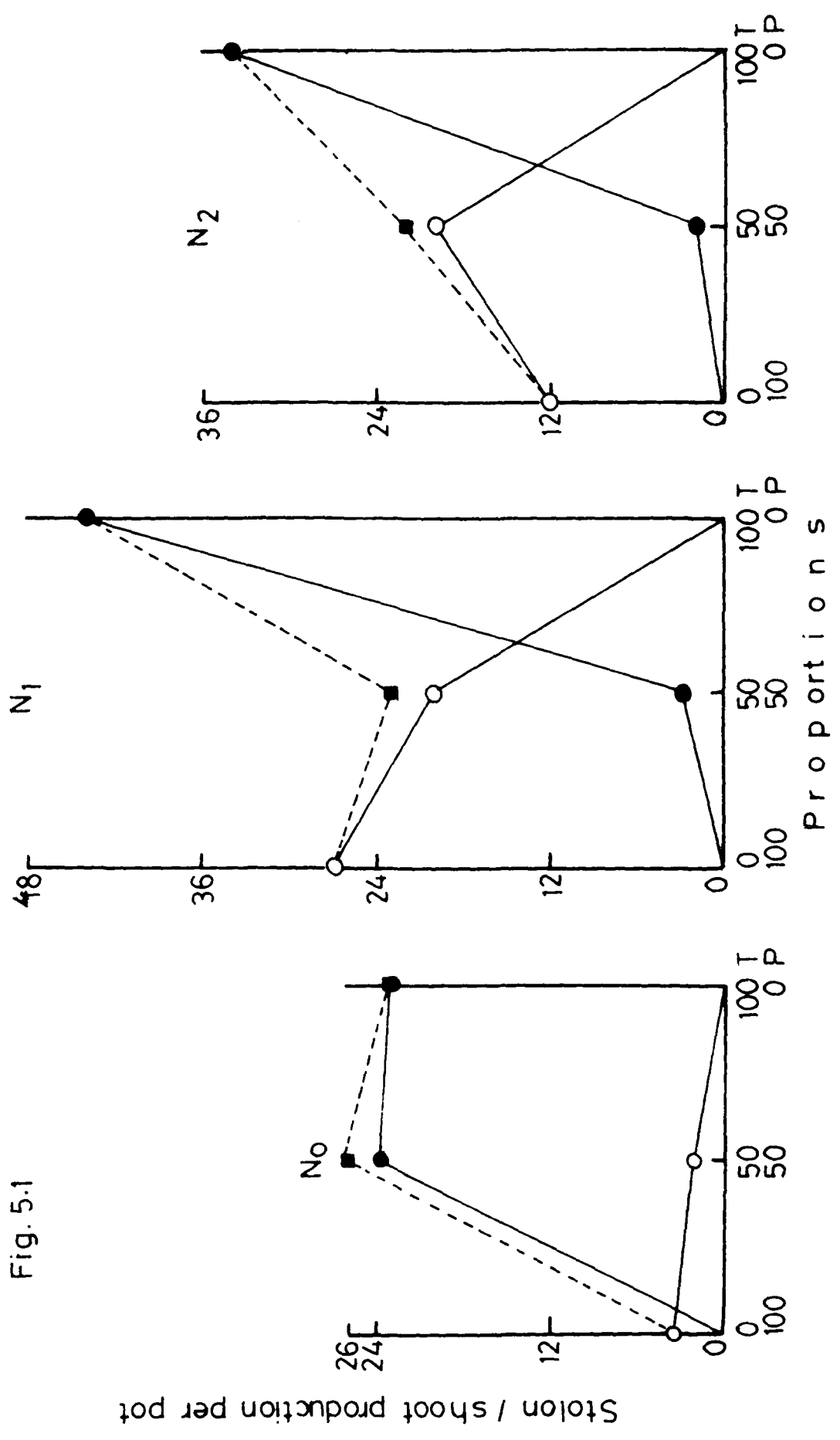


Fig. 5.1

Stolon / shoot production per pot

Table 5.2: Leaf production per plant of T. repens and P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes after 9 (H₁), 15 (H₂) and 24 weeks (H₃) from planting.

Nature of stand	Harvests											
	H ₁				H ₂				H ₃			
	N ₀	N ₁	N ₂	L.S.D.	N ₀	N ₁	N ₂	L.S.D.	N ₀	N ₁	N ₂	L.S.D.
<u>Pure Trifolium</u> (100%)	3.50	21.50	26.60	2.80.	28.58	35.75	38.67	8.52	23.83	59.08	52.06	3.42
<u>Mixed Trifolium</u> (50%)	5.17	15.67	14.67	5.02	56.83	2.67	3.33	7.24	56.83	3.08	3.00	0.99
<u>Mixed Paspalum</u> (50%)	3.00	7.83	10.00	1.67	3.67	17.83	18.50	0.93	1.44	29.33	34.17	4.66
<u>Pure Paspalum</u> (100%)	3.17	6.00	7.83	0.78	2.17	13.83	10.92	3.14	1.00	16.13	15.67	1.89
L.S.D.	1.42	5.11	9.38		4.94	3.65	3.22		12.72	14.90	3.43	

L.S.D. at P = 0.05

than in pure at all nitrogen regimes. The magnitude of increase in mixture was more pronounced at high nitrogen level. The total leaf area per plant of the two species also showed similar pattern (Fig. 5.2).

Total biomass:

Total biomass per plant of T. repens was greater in mixture than in pure at N_0 , but at high nitrogen regime the trend was reversed. P. dilatatum, on the other hand, produced more biomass per plant in mixture at all the nitrogen levels and its yield in mixture was magnified with increase in nitrogen levels (Table 5.3). The grass generally showed a gain in total yield in time sequence both in pure and mixed stands at all the nitrogen levels except the pure stand yield at N_0 from H_1 to H_2 (Table 5.4). T. repens also showed increase in yield with time in pure stand but in mixture except at N_0 the yield was progressively reduced at N_1 and N_2 . The yield of T. repens in mixture showed considerable increase over its pure stand yield at N_0 (Table 5.5) while at N_1 and N_2 there was decrease in yield in mixture with respect to monoculture. P. dilatatum, on the other hand, showed increase in yield per plant in mixture with respect to its pure stand at all nitrogen levels but the increase was particularly high at N_0 after 15 - 24 weeks from planting.

At N_0 , the per pot yield of the legume and grass was greater in mixture than pure stand (Fig. 5.3). P. dilatatum

Fig. 5.2: Total leaf area per plant of T. repens and P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes (N_0 , N_1 and N_2) after 9 (H_1), 15 (H_2) and 24 weeks (H_3) from planting.

(Closed columns (■), pure T. repens; hatched columns (▨) mixed T. repens; dotted columns (▤) pure P. dilatatum and open columns (□) mixed P. dilatatum. Vertical lines (I) represent L.S.D. at $P = 0.05$).

Fig. 5.2

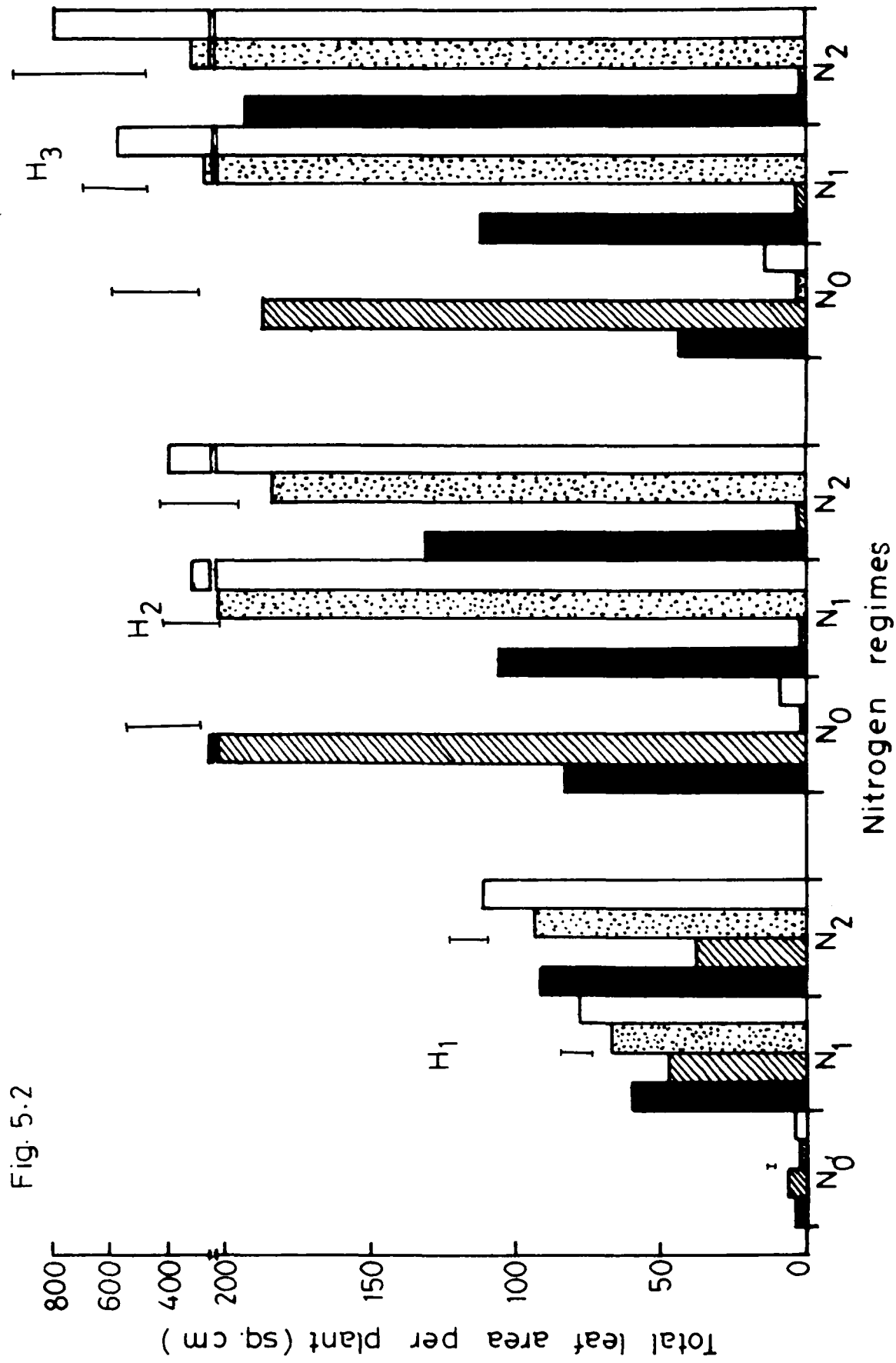


Table 5.3: Total biomass (g) per plant of T. repens and P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes after 9 (H₁), 15 (H₂) and 24 weeks (H₃) from planting.

Nature of stand	Harvests														
	H ₁				H ₂				H ₃						
	Nitrogen regimes		L.S.D.		Nitrogen regimes		L.S.D.		Nitrogen regimes		L.S.D.				
N ₀	N ₁	N ₂	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂	L.S.D.
Pure <u>Trifolium</u> (100%)	0.01	0.29	0.34	0.14	0.45	0.74	0.82	0.17	0.29	0.88	0.93	0.39			
Mixed <u>Trifolium</u> (50%)	0.06	0.26	0.21	0.26	1.34	0.14	0.09	0.38	1.20	0.18	0.16	0.47			
Mixed <u>Paspalum</u> (50%)	0.01	0.60	0.67	0.48	0.07	3.38	4.30	1.08	0.22	6.90	8.59	3.20			8
Pure <u>Paspalum</u> (100%)	0.01	0.37	0.52	0.11	0.01	2.45	2.83	0.24	0.03	3.65	4.28	1.22			
L.S.D.	0.15	0.22	0.12	0.03	0.45	0.69	0.15	0.94	1.56						

L.S.D. at P = 0.05.

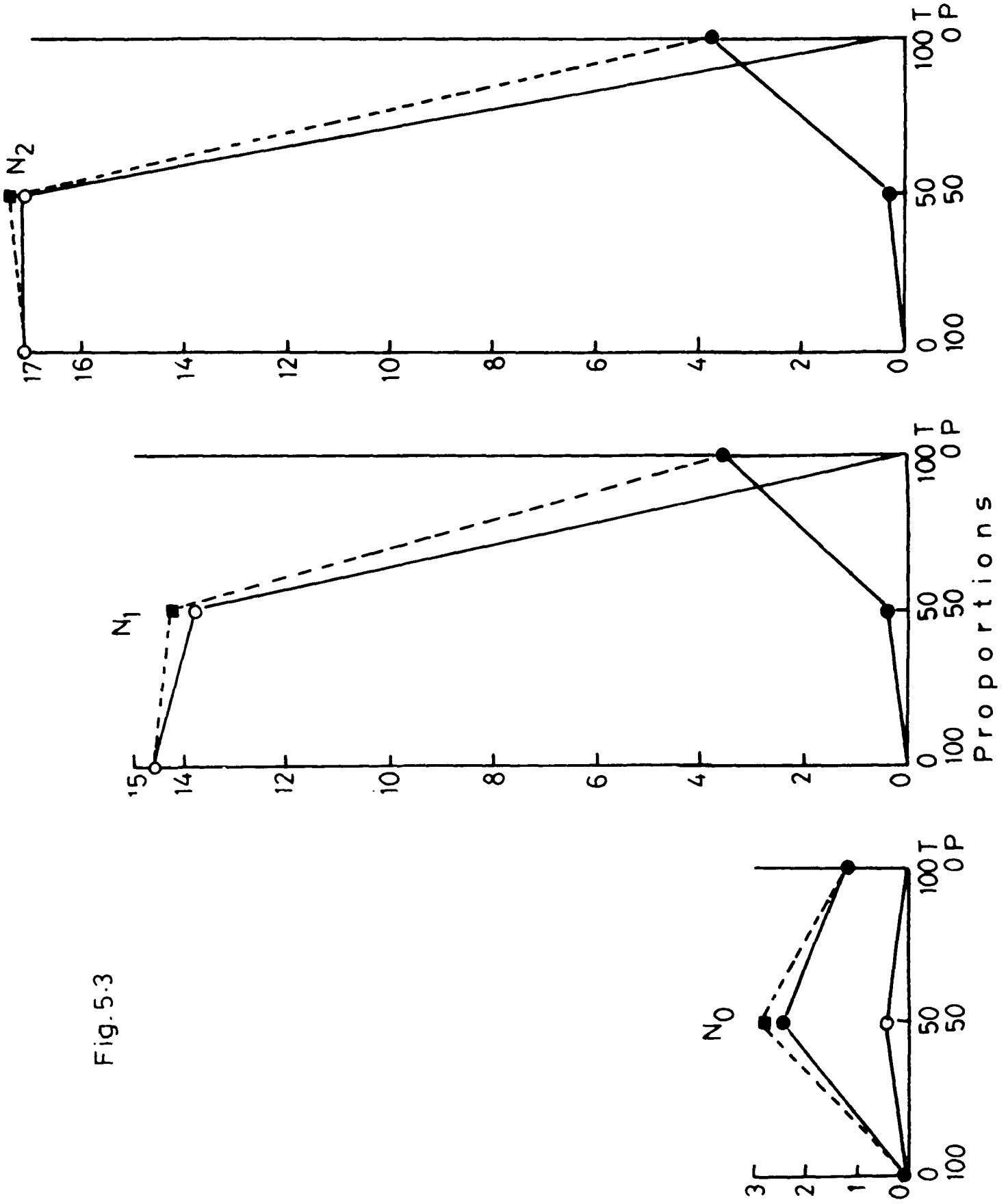
Table 5.4: Percentage increase (+) or decrease (-) in total yield per plant of T. repens and P. dilatatum with time in pure and mixed stands at three varying nitrogen regimes (N_0 , N_1 , & N_2) after 15 (H_2) and 24 (H_3) weeks from planting (% increase or decrease calculated on the basis of total yield of plant after 9 weeks (H_1) from planting).

Nature of stands	Harvests					
	H_2		H_3			
	N_0	N_1	N_2	N_0	N_1	N_2
Pure <u>Trifolium</u> 100%	97.78(+)	60.81(+)	58.54(+)	96.55(+)	67.05(+)	63.44(+)
Mixed <u>Trifolium</u> 50%	95.52(+)	85.71(-)	133.33(-)	95.00(+)	144.44(-)	31.25(-)
Mixed <u>Paspalum</u> 50%	85.71(+)	82.25(+)	84.42(+)	95.45(+)	91.30(+)	92.20(+)
Pure <u>Paspalum</u> 100%	0	84.90(+)	81.63(+)	66.67(+)	89.86(+)	87.85(+)

Fig. 5.3: Replacement diagram based on total biomass per pot of T. repens and P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes (N_0 , N_1 and N_2) after 24 weeks (H_3) from planting. The symbols $\text{---}\bullet\text{---}$, $\text{---}o\text{---}$ and $\text{---}\blacksquare\text{---}$ stand for T. repens, P. dilatatum and combined yield per pot in mixture respectively.

Total biomass (g) per pot

Fig. 5.3



generally maintained this trend at N_1 and N_2 nitrogen levels, whilst T. repens was suppressed in mixture to a great extent with increase in soil nitrogen. The mixture yield per pot is found to be high at N_0 and N_2 , while at N_1 the mixture yield is found to be lesser than the pure stand yield of P. dilatatum. The contribution of T. repens to the combined yield in mixture at N_1 and N_2 was negligible and the major contribution was made by the grass. At N_0 , on the contrary, the legume contributed much more to the mixture yield than the grass.

Relative yield and relative yield total (RYT): (Table 5.6)

The relative yield of T. repens was higher in the beginning but it decreased with time indicating an increased severity of competition offered by P. dilatatum with passage of time. The increase in competitive superiority of the grass is also reflected by increase in its relative yield from H_1 to H_3 . A remarkably high relative yield of the legume at H_1 and of the grass at H_2 and H_3 at N_0 level is also noteworthy. The values of relative yield total (RYT) at N_0 was higher than that of N_1 and N_2 and increased progressively from H_1 to H_3 , while at N_1 it decreased from H_1 to H_3 . But at N_2 it showed an increase from H_1 to H_3 , although the increase was less as compared to the values at N_0 .

Nodule formation:

The number of root nodules produced by T. repens was

Table 5.5: Percentage increase (+) or decrease (-) in total yield per plant of T. repens and P. dilatatum in mixture with respect to pure stand at three varying nitrogen regimes (N_0 , N_1 and N_2), after 9 (H_1), 15 (H_2) and 24 weeks (H_3) from planting.

Species	Harvests								
	H_1			H_2			H_3		
	N_0	N_1	N_2	N_0	N_1	N_2	N_0	N_1	N_2
<u>T. repens</u>	500(+)	10.35(-)	38.24(-)	197.78(+)	81.08(-)	89.02(-)	313.79(+)	79.55(-)	82.80(-)
<u>P. dilatatum</u>	0	62.16(+)	28.85(+)	600.00(+)	37.96(+)	51.94(+)	633.33(+)	89.04(+)	100.70(+)

71

Table 5.6: Relative yield (based on total biomass) of T. repens and P. dilatatum grown at three varying nitrogen regimes after 9 (H_1), 15 (H_2) and 24 weeks (H_3) from planting. The values of Relative yield total (RYT) is also given.

	Nitrogen regimes								
	N_0			N_1			N_2		
	H_1	H_2	H_3	H_1	H_2	H_3	H_1	H_2	H_3
<u>T. repens</u>	6.00	2.98	4.14	0.90	0.19	0.21	0.62	0.11	0.17
<u>P. dilatatum</u>	1.00	7.00	7.33	1.62	1.38	1.89	1.29	1.52	2.01
RYT	7.00	9.98	11.47	2.52	1.57	2.10	1.91	1.63	2.18

higher at N_0 than at N_1 and N_2 both at pure and mixed stands. The nodule production decreased with increase in soil nitrogen. The number showed remarkably higher increase from H_1 to H_2 at N_0 showing its extensive formation from 9 to 15 weeks from planting. At N_1 , the formation of nodule was high at H_3 in both pure and mixed stands. Both at N_0 and N_1 the nodule production was higher in mixture than in pure stand, while at N_2 it was suppressed in both the stands. The dry weight of nodule also showed similar pattern (Table 5.7).

Resource allocation:

The resource allocation pattern shows that T. repens allocates its resources equally to sink (root and stolons) and source (leaves) at the early stage of growth (H_1) in pure stand of all the nitrogen treatments. But with the passage of time the allocation to leaves decreases in all the nitrogen treatments and especially at nil nitrogen level (Fig. 5.4). The root allocation also follows similar pattern but allocation to stolons increases with the passage of time. Similar pattern was exhibited in mixed stand, but the magnitude of reduction in resource allocation to leaves and roots was much greater at N_1 and N_2 nitrogen levels as compared to N_0 . P. dilatatum on the other hand, showed higher allocation to source tissue (leaves, sheath and stem) than roots and rhizomes in both pure and mixed stands at N_1 and N_2 , while at N_0 resource allocation to the belowground parts was relatively higher. At N_0 , no rhizomes

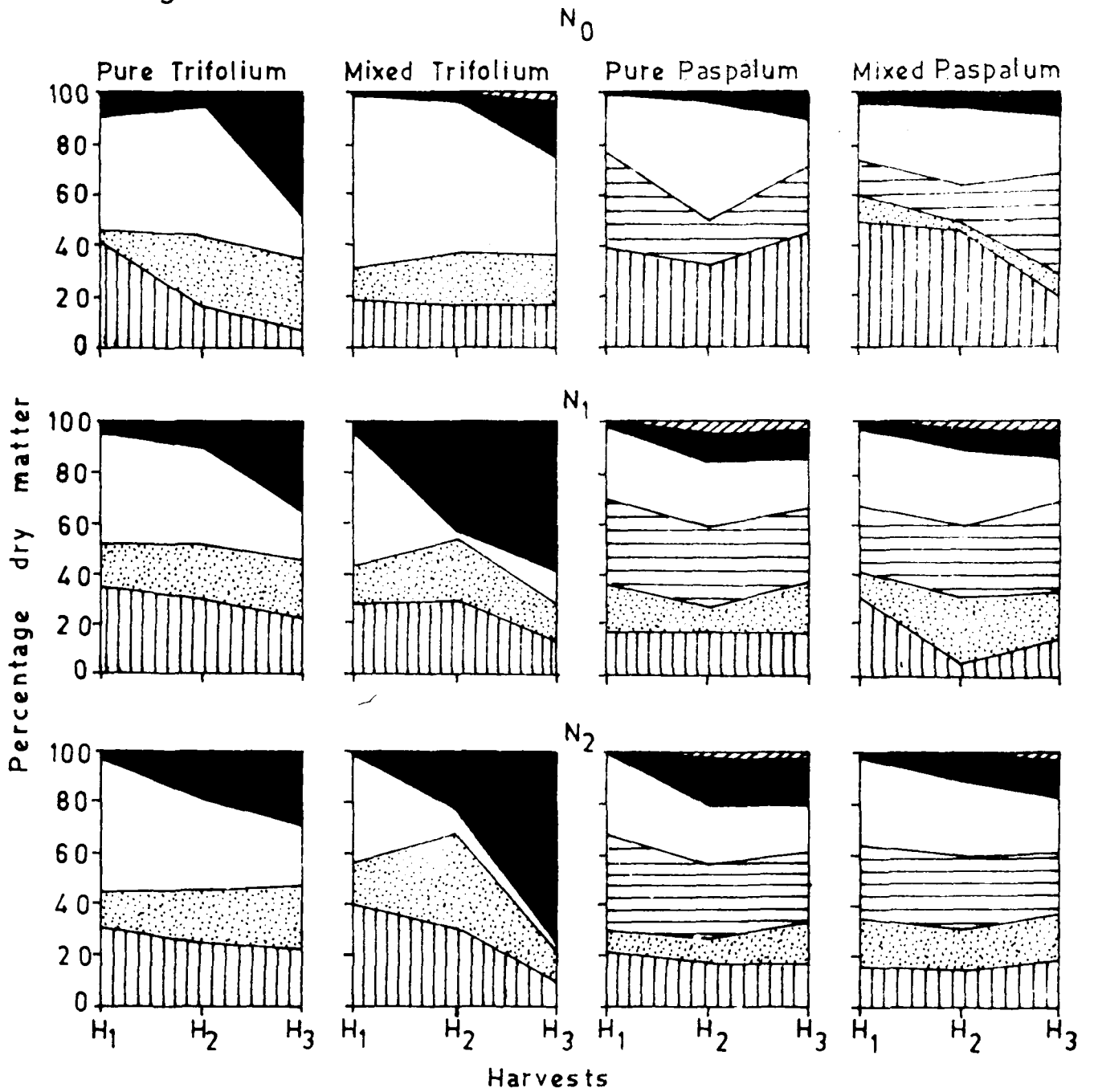
Table 5.7: Number of nodules and its weight (g) produced by T. repens in pure and mixed stands at three varying nitrogen regimes (N₀, N₁ & N₂) after 9 (H₁), 15 (H₂) and 24 (H₃) weeks from planting.

Nodule character	Nature of stand					
	Pure <u>Trifolium</u> (100%)			Mixed <u>Trifolium</u> (50%)		
	Nitrogen regimes			Nitrogen regimes		
	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂
Number						
H ₁	2.17	4.00	0	5.33	3.33	1.50
H ₂	39.50	5.17	0	49.17	3.50	0
H ₃	20.50	14.33	2.50	42.67	18.67	0
Weight						
H ₁	0.0003	0.0037	0	0.008	0.081	0.001
H ₂	0.0187	0.0008	0	0.0329	0.0013	0
H ₃	0.0021	0.0008	0.0002	0.0203	0.0071	0

Difference in number and weight of nodules between pure and mixed stands is significant at 1% and between harvests significant at 5% level.

Fig. 5.4: Dry matter allocation to various plant parts of T. repens and P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes (N_0 , N_1 and N_2) after 9 (H_1), 15 (H_2) and 24 weeks (H_3) from planting.

Fig.5.4



Root
 Stolon / Rhizome
 Stem & sheath
 Leaves (leaflets & petiole in case of *T. repens*)
 Standing dead
 Inflorescence with seeds.

were formed in pure stand but it allocated ca. 10% of its resources to rhizomes in mixtures. However, at N_1 and N_2 nitrogen levels the allocation to rhizome varies from 10 to 25% and greater allocation was observed in the mixed stands. A small percentage of resources (up to 3%) was also allocated to sexual reproduction at N_1 and N_2 . Maximum allocation to flowers and seeds was found to be at moderate nitrogen level (N_1). Conversely, T. repens failed to allocate resources to flowers and seeds at N_1 and N_2 but it did allocate some resources (upto 2%) for sexual reproduction at N_0 in mixed stand. Allocation to dead parts increased considerably in mixed situation at N_1 and N_2 in case of T. repens.

Nitrogen uptake by the two species:

Percentage nitrogen content and total nitrogen of the plant material of T. repens was generally higher in mixture than in pure at N_0 but at N_1 and N_2 nitrogen levels, the legume showed greater nitrogen content in pure. P. dilatatum, however, showed higher values in mixed stands than in pure at all the nitrogen levels (Tables 5.8 and 5.9). The percentage increase or decrease in total nitrogen content of shoots of the two species in mixed stands over the corresponding pure populations also confirm this point (Table 5.10). At nil nitrogen level (N_0) total nitrogen content of T. repens shoots was substantially higher than P. dilatatum both in pure as well as mixed stands.

Table 5.8: Percentage nitrogen content of the dried aboveground plant material of T. repens and P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes after 9 (H₁), 15 (H₂) and 24 (H₃) weeks from planting (average value ± S.E.).

Nature of stand	H ₁		H ₂		H ₃		
	H ₀	N ₁	N ₀	N ₁	N ₀	N ₁	N ₂
Pure <u>Trifolium</u> (100%)	0.33 ±0.09	2.90 ±0.26	1.25 ±0.09	2.63 ±0.12	2.00 ±0.03	2.38 ±0.19	2.88 ±0.25
Mixed <u>Trifolium</u> (50%)	0.75 ±0.14	2.55 ±0.29	2.18 ±0.06	2.50 ±0.09	2.45 ±0.14	2.38 ±0.22	2.38 ±0.35
Mixed <u>Paspalum</u> 50%	0.38 ±0.06	5.30 ±0.12	1.60 ±0.20	5.40 ±0.72	1.93 ±0.22	5.00 ±0.09	3.70 ±0.52
Pure <u>Paspalum</u> 100%	0.10 ±0.03	3.83 ±0.46	0.15 ±0.03	4.33 ±0.22	0.14 ±0.03	2.22 ±0.12	2.40 ±0.25

Table 5.9: Total nitrogen content (mg) of shoots per plant of T. repens and P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes taken after 9 (H_1), 15 (H_2) and 24 weeks (H_3) from planting (average value \pm S.E.).

Nature of stand	Harvests								
	H_1		H_2		H_3				
	N ₀	Nitrogen regimes N ₁ N ₂	N ₀	Nitrogen regimes N ₁ N ₂	N ₀	Nitrogen regimes N ₁ N ₂			
<u>Pure Trifolium</u> (100%)	0.02 \pm 0.01	5.12 \pm 0.51	6.71 \pm 0.70	4.18 \pm 1.21	10.81 \pm 1.21	11.25 \pm 1.45	2.81 \pm 0.47	9.01 \pm 1.74	12.93 \pm 1.21
<u>Mixed Trifolium</u> (50%)	0.08 \pm 0.02	4.20 \pm 0.06	3.03 \pm 0.18	23.15 \pm 1.84	0.95 \pm 0.14	1.05 \pm 0.15	17.40 \pm 1.25	1.11 \pm 0.05	0.05 \pm 0.02
<u>Mixed Paspalum</u> (50%)	0.02 \pm 0.01	20.88 \pm 1.41	24.90 \pm 2.89	0.54 \pm 0.133	143.15 \pm 12.32	177.40 \pm 5.01	2.28 \pm 0.12	258.65 \pm 17.71	210.52 \pm 9.46
<u>Pure Paspalum</u> (100%)	0.01 \pm 0.01	10.11 \pm 1.89	5.08 \pm 0.22	0.02 \pm 0.01	74.04 \pm 13.86	85.60 \pm 3.23	0.02 \pm 0.01	55.47 \pm 6.17	69.18 \pm 2.24

Table 5.10: Percentage increase (+) or decrease (-) in total nitrogen content of the shoots of T. repens and P. dilatatum in mixture with respect to pure stand, at three varying nitrogen regimes (N₀, N₁ & N₂) after 9 (H₁), 15 (H₂) and 24 weeks (H₃) from planting.

Species	Harvests								
	H ₁			H ₂			H ₃		
	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂
<u>T. repens</u>	300(+)	17.97(-)	54.84(-)	453.83(+)	91.21(-)	90.67(-)	519.22(+)	87.68(-)	99.61(-)
<u>P. dilatatum</u>	100(+)	106.53(+)	390.16(+)	2600.00(+)	93.34(+)	107.24(+)	111.88(+)	366.29(+)	359.67(+)

Chlorophyll content:

T. repens showed greater chlorophyll content in mixed stands, than in pure at nil nitrogen level (N_0) but at N_1 and N_2 levels the chlorophyll content was more in pure. P. dilatatum, on the other hand, generally had more chlorophyll in mixture than in pure at all the nitrogen levels (Table 5.11). T. repens in both pure and mixed stands showed progressive increase in chlorophyll content from H_1 to H_3 at N_0 , but no such trend was observed at N_1 and N_2 . P. dilatatum also showed a similar trend. However, the pure stand of grass population at N_0 , suffered from chlorophyll deficiency while no chlorosis was observed in mixed stand of the same nitrogen treatment (Plate 7).

DISCUSSION

An increase in number of tillers and leaves in mixed stands of P. dilatatum over the values in pure stand suggests that the grass is more competitive than the legume. Although increase in soil nitrogen stimulated the leaf production, but tillering was not affected. This is in contrast to the findings of Langer (1959), that the N fertilizer increased tillering but not the number of leaves per tiller in timothy (Phleum pratense). There was increase in tillering with increase in nitrogen from N_0 to N_1 but further increase in nitrogen (i.e. at N_2) number of tillers per plant did not show any increase. This may be due to an intense intraspecific competition at high nitrogen regime.

Table 5.11: Chlorophyll content (mg/g) of fresh leaf material of T. repens and P. dilatatum grown in pure and mixed stands at three varying nitrogen regimes (N₀, N₁ and N₂) taken after 9 (H₁), 15 (H₂) and 24 weeks (H₃) from planting (Mean value ± S.E.).

Nature of stand	Harvests											
	H ₁			H ₂			H ₃			H ₃		
	Nitrogen regimes			Nitrogen regimes			Nitrogen regimes			Nitrogen regimes		
	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂	N ₀	N ₁	N ₂
Pure <u>Trifolium</u> (100%)	2.79 ±0.06	16.09 ±0.15	20.45 ±2.47	6.51 ±0.53	55.08 ±2.92	20.40 ±4.19	10.44 ±0.16	28.26 ±0.04	23.05 ±4.95	37.30 ±0.00	18.01 ±0.06	29.45 ±0.29
Mixed <u>Trifolium</u> (50%)	12.83 ±4.43	5.85 ±0.11	4.55 ±0.33	14.90 ±0.01	7.79 ±2.06	9.09 ±1.28	17.95 ±0.46	24.27 ±0.21	41.32 ±0.02	1.92 ±0.18	15.52 ±0.01	28.53 ±3.33
Mixed <u>Paspalum</u> (50%)	0.07 ±0.06	19.26 ±0.48	20.62 ±0.88	0.15 ±0.01	19.48 ±0.06	14.22 ±0.20	0.68 ±0.01	18.18 ±0.06	41.32 ±0.02	0.07 ±0.06	19.26 ±0.48	20.62 ±0.88

Sukatchev (1928); White and Harper (1970); and Bazzaz and Harper (1976); also reported that the mortality of individuals undergoing self thinning, is increased under high fertility level. T. repens, on the other hand, produced more stolons per plant in mixed stand as compared to pure stand at N_0 while at N_1 and N_2 its trend was reversed. This may be due to intense competition offered by P. dilatatum which grows very luxuriantly at high fertility level and brings about tremendous suppression in growth of the legume in mixture.

This is also confirmed by the yield of the two species in pure and mixed stands at various nitrogen levels. The data indicated that an increase in soil nitrogen favours the grass more than the legume and this is also reflected in much reduced growth of T. repens in mixture with increase in soil nitrogen. Blackman and Templeman (1938) studied the effect of competition in mixed stands of T. repens and grass species by varying light intensity and rates of applied nitrogen and concluded that the competition of grasses reduced the growth of clover when additional nitrogen was applied. Blaser and Brady (1950) also found that when nitrogen was applied to mixed stands of legumes and grasses the growth of legumes was reduced.

At N_0 , the yield of P. dilatatum in mixture was much greater than in pure stand which may be attributed to possible transfer of nitrogen fixed by the legume to the grass. The nitrogen content of grass was found to be more in mixed stands

than in pure. Haystead and Lowe (1977) also reported that the nitrogen content of the grass growing with the clover was higher but using isotope technique (N^{15}) reported that the transfer of N from white clover to associated perennial ryegrass was not detected. However, a number of studies have shown the contribution made by white clover to nitrogen economy of grass-clover swards in glass house situation (Henzell, 1962; Simpson, 1965) and in field (Walker et al., 1954; Cowling, 1961; Bastiman, 1969; Munro and Davies, 1974). Gasser (1969) also reported that ryegrass proved to be a dominant species in ryegrass/white clover sward in soil supplied with nitrogen fertilizer.

The relative yield of grass and legume reveals that the legume competes better with the grass at early growth stage in the absence of nitrogen, but later on (i.e. at H_3), the grass shows better growth than the legume indicating the possible addition of atmospheric nitrogen fixed by the legume to the soil and its subsequent utilization by the grass. A substantial increase in number and weight of nodules at H_2 and H_3 (Table 5.7) also confirms this point.

The difference in energy allocation to different plant parts can be interpreted as an essential aspect of overall life cycle strategies of plant species. Both the species reproduce vegetatively as well as through seeds. Dry matter allocation to stolons of T. repens after 6 months was more at N_0 than at N_1

and N_2 in mixed stands indicating that increased soil nitrogen makes the grass more competitive as compared to the legume. An increased proportion of dead tissue in T. repens at N_1 and N_2 also indicates that the grass exercises a strong suppressive effect on the legume (Fig. 5.4; Plate 8). T. repens could produce some seeds only at N_0 in mixed stand where P. dilatatum showed extremely poor growth due to nitrogen deficiency. The failure of flowering and seed setting by the legume in monoculture may be attributed to severity of intra-specific competition, and in mixtures at N_1 and N_2 , to increased competition offered by luxuriantly growing P. dilatatum. The grass, on the other hand, did not allocate any resources to sexual reproduction at N_0 in either pure or mixed stands, while at N_1 and N_2 a part of energy was channelized to seed production. This is in contrast to the observation made by Harper and Ogden (1970) and Andel and Vera (1977) who found reproductive allocation to be independent of nutrient level in Senecio vulgaris and S. sylvaticus respectively. At N_0 , P. dilatatum did not produce any rhizome in pure stand while in mixed stand a part of the total resources was allocated to rhizomes. This indicates that the presence of legume in mixed stand presumably adds some nitrogen to the soil through atmospheric nitrogen fixation by the nodule bacteria and so the grass might utilize it for its growth. This is confirmed by the higher nitrogen content of the grass in mixture as compared to pure stand.

It could be assumed that soil nitrogen in a pot culture

Plate 7: T. repens and P. dilatatum grown in pure and mixed stands at nil (N_0) nitrogen level after 24 weeks growth. T. repens is growing well in both pure and mixed stands, while P. dilatatum, is showing chlorosis in pure but in mixed stand it does not show chlorosis and grows better.

Plate 8: T. repens showing growth in mixture at nil (N_0), $\frac{1}{2}$ (N_1) and 2 (N_2) nitrogen levels. Note the substantial reduction in legume growth at N_1 and N_2 and relatively much better growth at N_0 level.



PLATE 7

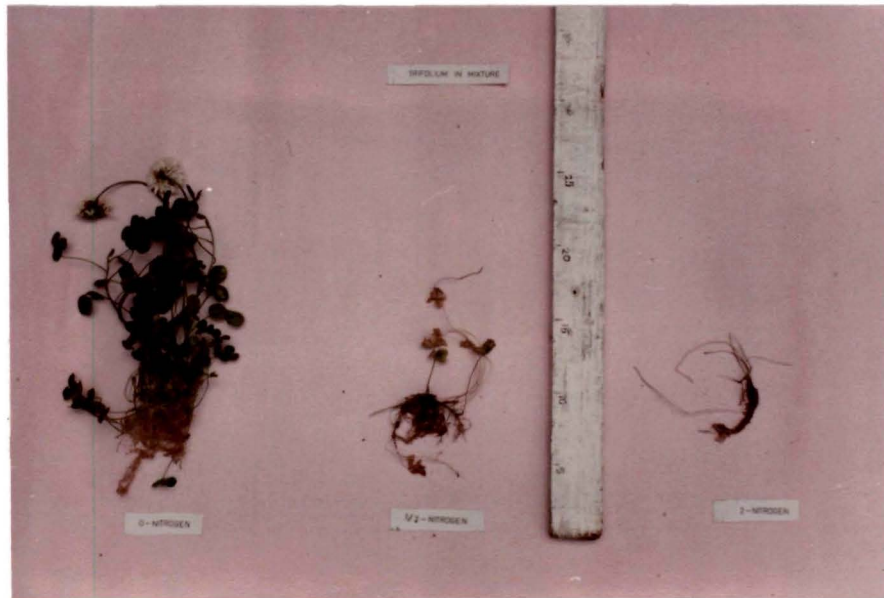


PLATE 8

would be available to both the species but depending on their comparative uptake abilities, their rates of root elongation, total absorbing surface and efficiency of their roots, different quantities of soil nitrogen would be taken up by the two species. Relatively higher total nitrogen content of shoots of the grass (Table 5.9) indicates that the nitrogen uptake by the grass is much greater as compared to the legume in spite of more energy allocated to roots by the legume (Fig. 5.4); which shows that the root system of the grass is more efficient in exploiting available soil nitrogen. However, at N_0 where the grass showed much reduced growth, the uptake of nitrogen by the legume seems to be greatly increased as indicated by much greater amount of nitrogen in the legume as compared to the grass in mixed situation. It seems that the restricted growth of grass in N_0 treatment is, in some way, helping the legume in realizing its full potential of nitrogen utilization. This is in conformity with the findings of Vallis et al. (1977) who also observed that uptake of nitrogen by legumes (L. bainesii and T. repens) was to the extent of 100% of the total ^{15}N applied at spring harvest when growth of associated tropical grasses was limited by low temperature.

The data in nodule population and weight also confirm that with increase in nitrogen level, the nodulation in T. repens is considerably reduced (Table 5.7). The much decreased quantity of nitrogen in shoots of the legume at N_1 and N_2 relative to N_0 treatment shows that from the soil rich in nitrogen, the grass

is able to utilize maximum amount of nitrogen and shows lush growth while the legume suffers miserably in grass-legume mixture. Bartholomew (1965); MacAuliffe et al. (1958) etc. have also found that on fertilizer application, nitrogen fixation by nodules is inhibited and nodulation is suppressed.

Besides failure to utilize enough nitrogen by the legume, another factor which might contribute to greatly suppressed growth of the legume in mixture, is the shade caused by fast growing P. dilatatum. The growth suppression and consequent elimination of T. repens from the protected grassland vegetation free from grazing and other disturbances also confirm the competitive superiority of P. dilatatum over the legume, which might be due to deep shade cast by the fast growing canopy of the grass in protected situation. The reduction in chlorophyll content of T. repens in mixed stands relative to monoculture at N_1 and N_2 , where P. dilatatum grows luxuriantly also indicate that availability of nitrogen and light to the legume is curtailed in mixed stands as the chlorophyll content is directly related to nitrogen uptake by plants (Nevins and Loomis, 1970; Natr, 1972) and availability of light (Franck and Kenney, 1955; Blackman, 1968).

At N_0 , the grass growing in pure stands showed chlorosis while in mixture with T. repens it synthesized chlorophyll pigments (Table 5.1) and showed better growth suggesting once again that in mixed situation the grass probably gets some supply of nitrogen due to presence of T. repens.

C H A P T E R 6

GROWTH OF TRIFOLIUM REPENS AND PASPALUM DILATATUM AS AFFECTED
BY SIMULATED TRAMPLING

INTRODUCTION

The grassland species are subjected to varying degree of trampling, by grazing animals and man. The 'stress' of trampling may affect the plants directly by causing injury to them or indirectly by changing the physical properties of soil or by differentially affecting the plant species thereby changing their competitiveness in a community. Several studies have been made, using both glass house and field experiments, to assess individual plant response to trampling (Liddle, 1975a,b; Canaway, 1975; Blom, 1976; 1977; 1978a, b). It has been found that the plant species exposed to trampling vary in their tolerance and response to such treatment. The growth of certain species may be stimulated under light trampling stress. The prostrate growth forms of Plantago major and Poa annua have been reported to withstand clipping and trampling damage better than the corresponding erect growth forms (Warwick and Briggs, 1978 α ,b, 1980; Warwick, 1980).

The two species in the present study are found growing luxuriantly in the grasslands of Shillong and are subjected to intense trampling along with other biotic disturbances like grazing and cutting. Of the two species P. dilatatum has an erect growth form while T. repens is of prostrate nature. Thus the trampling stress may exercise an influence on competitive behaviour of the two species and their success in nature.

MATERIALS AND METHODS

The seeds of T. repens and P. dilatatum after washing thoroughly in running tap water were sown in the experimental pots. The seeds of P. dilatatum were sown on 20th March 1980 and those of T. repens on 23rd March 1980 to synchronise the seedling emergence time. The grass seeds took 4-5 days and the legume 2 days for germination after sowing. The seedlings of T. repens having two cotyledonary leaves and a trifoliate leaf and the grass seedlings with one leaf were transplanted on 28th March 1980 in experimental pots of 21.0 cm diameter, filled with sandy loam soil mixed with compost manure in the ratio of 5:1. The pots were kept in the net house covered with polythene sheet, where the temperature ranged from 13.5°C (min.) in April to 30.0°C (max.) in May 1980. The legume and grass seedlings were planted in the following manner so as to give de Wit's replacement series (de Wit, 1960).

- 1) 0% T. repens (T) + 100% P. dilatatum (P)
- 2) 50% T + 50% P
- 3) 100% T + 0% P

In case of pure stand, 6 seedlings of a particular species were transplanted while in case of mixed stand 3 seedlings each of T. repens and P. dilatatum were transplanted alternately in a circular manner at an equal distance from each other. Thus the growth of two species was studied in pure and mixed stands at the same overall density (6 plants per pot).

The experimental design consisted of 3 trampling treatments x 3 proportions x 3 replicates x 2 harvest times, thus involving in all 54 pots.

The trampling effect was simulated by dropping a heavy metallic plate of 19 cm diameter having 0.8 cm thickness, weighing 1.5 kg, over the plants in the pots. The metallic plate bore a hole in the centre to allow its free movement along an iron rod (Plate 9a and b). At the time of treatment the rod was fixed in the centre of the pot and the plate was released along the iron rod from a height of 1.0 m, giving a pressure of 8187.82 dynes/cm² on the plants by a single drop of the plate. The dropping of the plate was repeated for 10 times at the time of treatment, thus the plants were subjected to simulated trampling treatment. The time schedule of the simulated trampling treatment was as follows:

Control - No trampling treatment.

T_M - Monthly trampling treatment given on 2nd of each month commencing from April 1980.

T_F - Fortnightly trampling treatment given on 2nd and 16th of each month commencing from April 1980.

The pots were kept in the net house of the experimental garden in the Department of Botany, School of Life Sciences, North-Eastern Hill University, Shillong, and were randomised with the help of table of random numbers. The position of pots was changed regularly at 3 days intervals.

Plate 9: Showing the simulation of trampling treatment by dropping a heavy metallic disc over the plants in an experimental pot. (a) The metallic disc held at 1 m height and (b) the disc has been dropped over the plants.



a



b

PLATE 9

The observations on growth of the two species were recorded after 15 and 24 weeks from planting. The observation period are referred to as 'harvest 1' (H₁) taken on 11th July 1980 and 'harvest 2' (H₂) taken on 12th September 1980, in the text. At each harvest, the number of tillers or stolons, number of leaves, total leaf area, number of fertile shoots and biomass of the two species were estimated. For dry matter estimation the plant materials were kept in an oven at 80°C to constant weight.

EXPERIMENTAL RESULTS

Number of stolons and tillers:

Productions of stolons by T. repens was reduced in mixture in control but in the other two treatments where trampling was done more stolons were produced in mixture than in pure (Table 6.1). With the increase in the intensity of trampling stolon production in pure stand was reduced. However, T. repens generally produced more stolons in mixed stands subjected to trampling treatment as compared to control. On the other hand, tiller production by P. dilatatum in both pure and mixed stands decreased with the increased intensity of trampling. The grass showed better tillering in mixture as compared to the corresponding pure stands. In general, the increase in mixture over the corresponding monoculture was of higher magnitude in control.

Table 6.1: Effect of trampling on number of stolons per plant and shoots per plant of P. dilatatum grown in pure and mixed stands.

Nature stand	Harvest 1				Harvest 2			
	Control	TM	TF	F:variance ratio	Control	TM	TF	F:variance ratio
<u>Pure Trifolium</u> (100%)	4.67	4.44	4.11	3.39 ^{NS}	14.78	10.56	6.00	6.97*
<u>Mixed Trifolium</u> (50%)	2.89	5.11	5.50	9.60*	9.67	11.56	7.33	2.51 ^{NS}
<u>Mixed Paspalum</u> (50%)	7.45	6.89	5.67	3.82 ^{NS}	9.33	8.22	5.66	3.94 ^{NS}
<u>Pure Paspalum</u> (100%)	6.33	6.29	5.33	1.28 ^{NS}	7.83	7.89	3.78	9.39*
F:variance ratio	31.32**	6.52*	1.76 ^{NS}		8.12*	4.76*	1.03 ^{NS}	

** indicate significant differences at P = 0.01

* indicates significant differences at P = 0.05

NS Not significant

The differences between Harvests is significant at 5% level.

Number of leaves and leaf area:

In control set, the leaf production by T. repens was greater in pure than in mixed stand while the plants subjected to trampling produced more leaves in mixture (Table 6.2). In mixed stands, the leaf production by the legume seems to be stimulated by trampling treatment whilst in pure stands leaf production decreased as the intensity of trampling increased. The total leaf area per plant also exhibited a similar trend (Fig. 6.1). P. dilatatum, on the other hand, showed greater leaf production in mixture than in pure stand. Leaf production in pure stand as well as in mixture decreased due to trampling at H₁. At H₂, however, leaf production decreased from T_M to T_F although moderate trampling stimulated leaf production.

Total leaf area per plant of P. dilatatum also showed higher values in mixture than in pure stand. Generally, there was decrease in leaf area in both pure and mixed stands with the increase in the intensity of trampling.

Total biomass:

Like stolon and leaf production, the biomass per plant of T. repens was also found to be higher in pure than in mixed stands in control but trampling treatment caused reversal in this trend (Table 6.3). As a result the yield of T. repens increased with increase in the intensity of trampling (Table 6.4). On the other hand, P. dilatatum produced greater

Table 6.2: Number of leaves per plant of T. repens and P. dilatatum grown in pure and mixed stands as influenced by trampling treatment.

Hature of stand	Harvest 1				Harvest 2			
	Control	TM	TF	F:variance ratio	Control	TM	TF	F:variance ratio
Pure <u>Trifolium</u> (100%)	50.56 14.57	20.44	20.00	16.05*	54.00	31.28	28.22	7.88**
Mixed <u>Trifolium</u> (50%)	14.57	25.17	26.17	11.37*	19.67	36.67	41.89	7.19**
Mixed <u>Paspalum</u> (50%)	28.33	24.11	21.67	6.08 ^{NS}	30.11	34.17	14.67	4.48 ^{NS}
Pure <u>Paspalum</u> (100%)	22.89	21.67	18.78	14.46**	19.78	26.11	14.67	1.89 ^{NS}
F:variance ratio	10.72**	6.41*	5.08*		6.94*	1.21 ^{NS}	10.60**	

** indicate significant differences at P = 0.01

* indicates significant differences at P = 0.05

NS Not significant.

The difference between the harvests are significant at P = 0.05 level.

Fig. 6.1: Total leaf area per plant of T. repens and P. dilatatum grown in pure and mixed stands treated with three varying trampling treatments (C, T_M and T_F) after 15 (H₁) and 24 weeks (H₂) from planting.

Dotted columns (◻) pure T. repens; solid columns (■) mixed T. repens; hatched columns (▨) pure P. dilatatum; and open columns (□) mixed P. dilatatum. Vertical lines (I) represent L.S.D. at P = 0.05 .

Fig.6-1

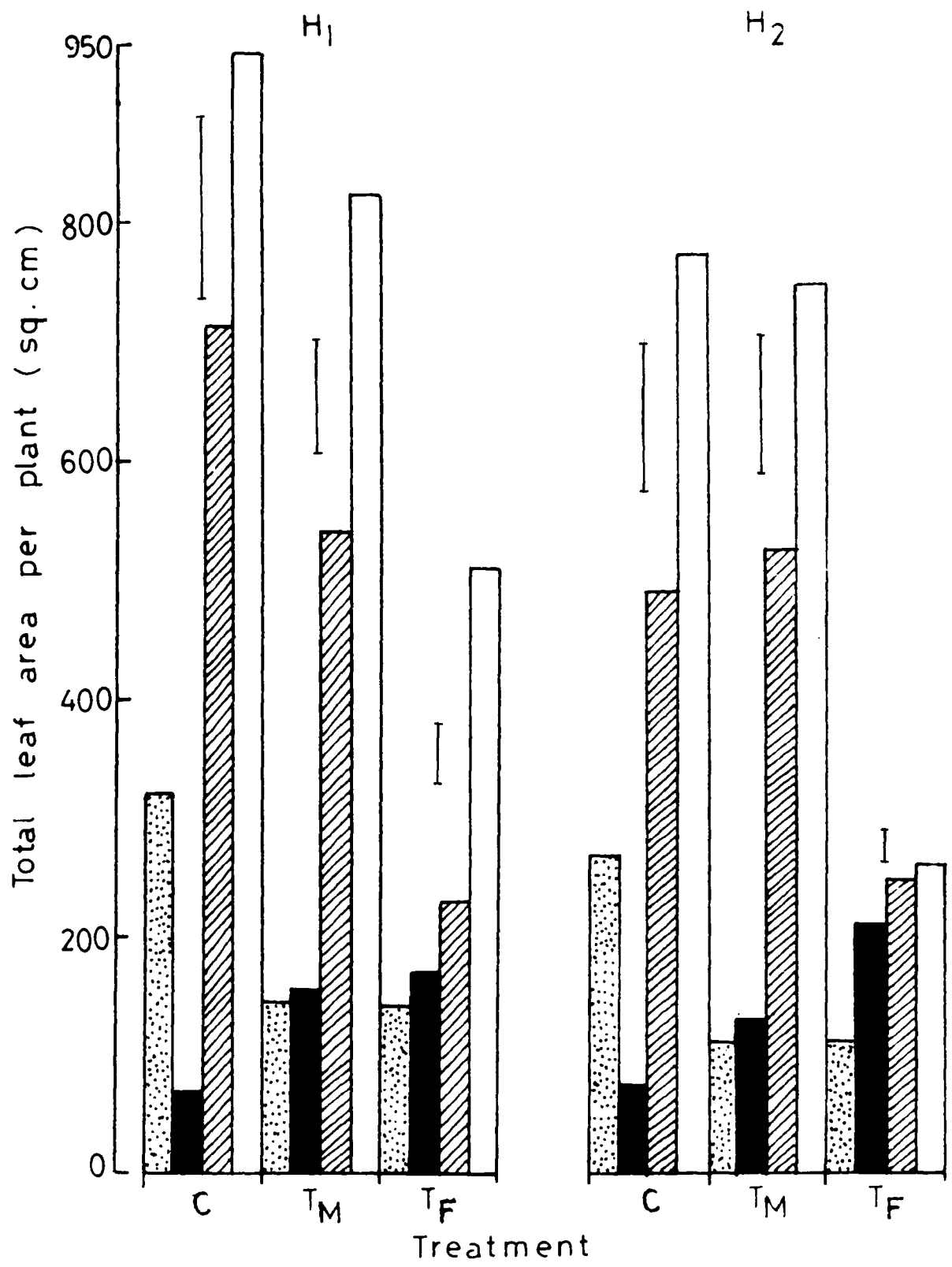


Table 6.3: Dry weight (g) per plant of T. repens and P. dilatatum grown in pure and mixed stands as influenced by trampling treatment.

Nature of stand	Harvest 1				Harvest 2			
	Control	TM	TF	F:variance ratio	Control	TM	TF	F:variance ratio
Pure <u>Trifolium</u> (100%)	0.67	0.53	0.45	1.77 ^{NS}	1.78	0.72	0.57	7.61 [*]
Mixed <u>Trifolium</u> (50%)	0.28	0.58	0.91	40.23 ^{**}	0.75	1.00	1.43	1.91 ^{NS}
Mixed <u>Paspalum</u> (50%)	6.02	4.19	3.17	6.33 ^{NS}	16.55	9.66	2.88	65.26 ^{**}
Pure <u>Paspalum</u> (100%)	5.52	3.89	2.67	15.15 [*]	13.05	9.48	2.42	64.89 ^{**}
F:variance ratio	104.77 ^{**}	12.37 ^{**}	514.79 ^{**}		228.41 ^{**}	60.45 ^{**}	8.71 ^{**}	

** indicate significant differences at P = 0.01

* indicates significant differences at P = 0.05

NS Not significant

The difference between Harvest 1 and Harvest 2 of T. repens is significant at 5% while the difference between Harvest 1 and Harvest 2 of P. dilatatum are significant at 1% in control and TM but at TF it is not significant.

biomass in mixture as compared to pure stand at both the harvest times. The biomass per plant of P. dilatatum decreased both in mixture and monoculture with the increase in the intensity of trampling (Tables 6.3 and 6.5).

Total biomass per pot of P. dilatatum after 24 weeks of growth showed a drastic reduction both in pure and mixed stands due to trampling while biomass production by legume increased in the mixtures subjected to trampling treatment although in pure stand the legume also exhibited the same trend as the grass. In mixture, trampling treatment seems to weaken the grass and favour the legume, but in any case, a greater proportion of the combined total biomass is contributed by the grass (Fig. 6.2). However, the percentage contribution by the grass decreases with the increase in trampling pressure (Table 6.6).

Relative yield:

The relative yield of P. dilatatum was greater than that of the legume in the absence of trampling but with the increase in trampling frequency, the relative yield of T. repens increased so much so that under fortnightly trampling treatment its relative yield became more than 1. The relative yield total of the two species was found to be lesser than 1 in absence of trampling but it increased and exceeded 1 under trampling treatment (Table 6.7).

Table 6.4: Percentage increase (+) or decrease (-) in yield of T. repens due to trampling in pure and mixed stands.

Nature of stand	Harvest 1		Harvest 2	
	TM	TF	TM	TF
Pure (100%)	20.90(-)	32.84(-)	59.55(-)	67.98(-)
Mixed (50%)	107.14(+)	225.00(+)	33.33(+)	90.67(+)

Table 6.5: Percentage decrease (-) in yield of P. dilatatum due to trampling in pure and mixed stands.

Nature of stand	Harvest 1		Harvest 2	
	TM	TF	TM	TF
Pure (100%)	29.53(-)	51.63(-)	27.63(-)	81.46(-)
Mixed (50%)	30.40(-)	47.34(-)	41.63(-)	82.60(-)

Table 6.6: Percentage contribution of T. repens and P. dilatatum in mixture and total combined yield per unit area (m^2) as affected by trampling grown in pure and mixed stands.

	Harvest 1			Harvest 2		
	Control	TM	TF	Control	TM	TF
<u>T. repens</u>	4.44	12.16	22.30	4.34	9.38	33.18
<u>P. dilatatum</u>	95.56	87.84	77.70	95.66	90.62	66.82
Combined yield	182.27	138.32	118.32	501.70	309.14	124.99

Fig. 6.2: Replacement diagram based on dry weight per pot of T. repens and P. dilatatum grown in pure and mixed stands after 24 weeks from planting as influenced by trampling treatment. The symbols —●—, —○— and ----□---- stand for T. repens, P. dilatatum and combined yield respectively.

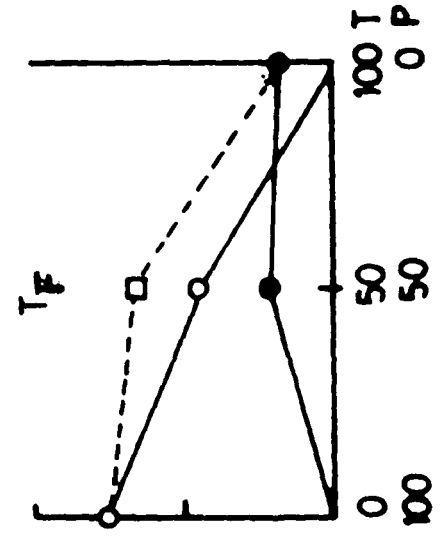
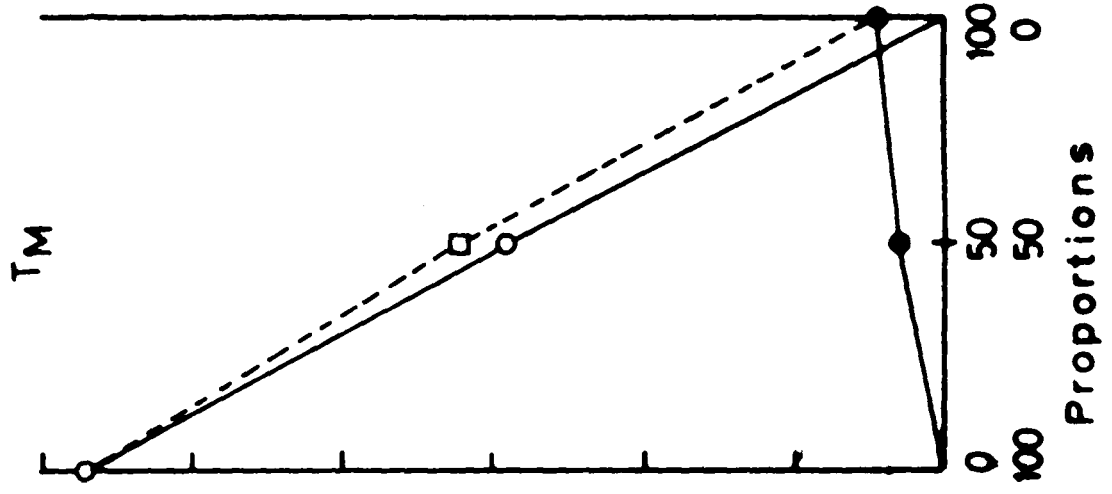
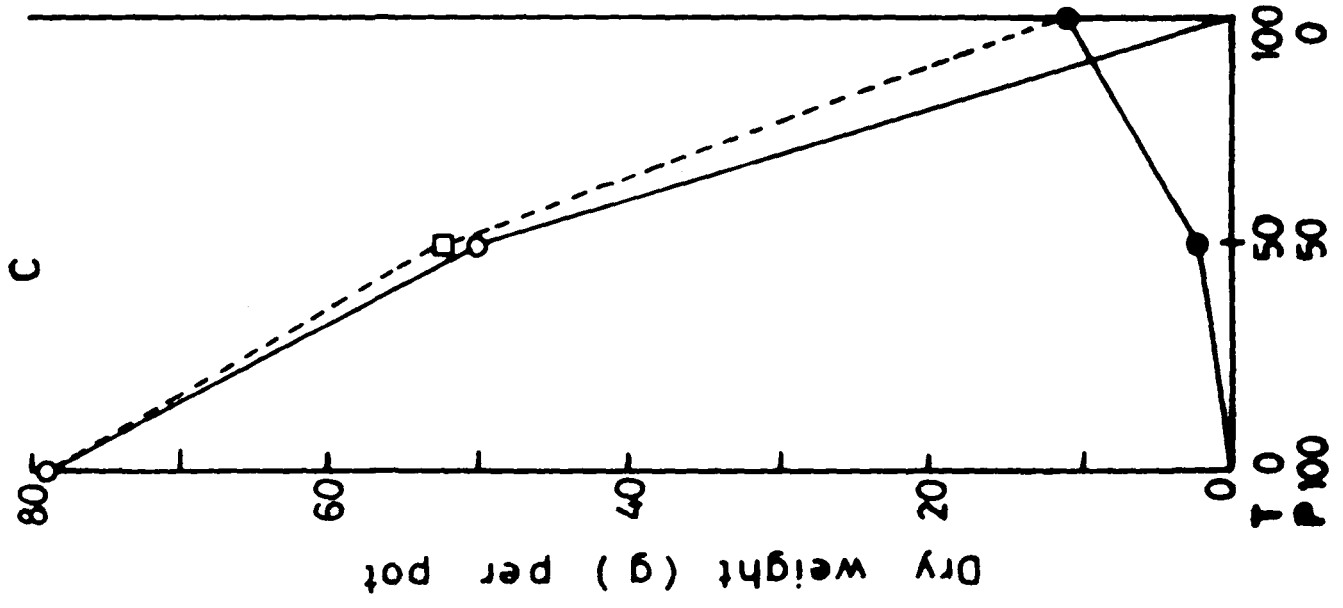


Fig. 6.2

Fertile shoot production:

P. dilatatum produced more fertile shoots in mixture than in pure stands, although in both the stands, there was decrease in fertile shoot production with the increase in trampling pressure (Table 6.8). T. repens, on the other hand, could produce fertile shoots either in pure stand in control or in mixture under fortnightly trampling where the growth of grass was too suppressed to offer intense competition to the legume.

DISCUSSION

An increase in number of stolons and leaves and dry matter yield of T. repens in mixed stands exposed to trampling treatment indicates that, it becomes competitive in the situation where vegetation undergoes severe trampling, while in absence of trampling, it fails to compete successfully with P. dilatatum. It may be mentioned that due to erect growth form the grass is more severely affected by trampling treatment and such a differential effect relaxes the intensity of competition which would have otherwise been offered to the legume by P. dilatatum. This is clear by the strong suppressive influence of the grass on the legume in mixed situation under control treatment. Comparatively better growth of the grass in mixtures than in the corresponding monocultures suggests that the grass suffered more from intraspecific competition. However, leaf production and tillering in the grass was adversely affected by

Table 6.7: Fertile shoots (%) of T. repens and P. dilatatum grown in pure and mixed stands as influenced by trampling treatment at final harvest (H₂).

Nature of stand	Trampling treatments		
	Control	TM	TF
Pure <u>Trifolium</u> (100%)	2.27±2.00	0	0
Mixed <u>Trifolium</u> (50%)	0	0	2.32±0.67
Mixed <u>Paspalum</u> (50%)	34.10±2.61	28.14±6.82	5.83±3.33
Pure <u>Paspalum</u> (100%)	19.80±1.20	13.50±5.68	0

Table 6.8: Relative yield based on total biomass per pot of T. repens and P. dilatatum grown in pure and mixed stands as influenced by trampling treatment after 15 (H₁) and 24 weeks (H₂) from planting. Relative yield total (RYT) is also given.

	Trampling treatment					
	Control	TM H ₁	TF	Control	TM H ₂	TF
Relative yield <u>T. repens</u>	0.21	0.56	1.01	0.21	0.69	1.25
Relative yield <u>P. dilatatum</u>	0.55	0.54	0.59	0.63	0.51	0.60
Relative yield total	0.76	1.10	1.60	0.84	1.20	1.85

trampling both in pure and mixed stands. This is in contrast to the result of Liddle (1975a), who showed that the number of leaves/tillers were hardly affected in Festuca rubra L. by trampling, although the tiller length, leaf length and dry weight were reduced.

Total leaf area per plant of P. dilatatum was also reduced due to trampling treatment which is in conformity with the findings of Speight (1973); Dale and Weaver (1974); Davidson and Fox (1974) and Liddle (1975a) who reported that the vegetation cover is reduced by trampling, although some plants are more resistant to trampling than the others. T. repens was also adversely affected by trampling in pure stand, but in mixed stand under trampling treatment the total leaf area of the legume was greater as compared to the corresponding pure stands. The prostrate habit of T. repens makes it relatively less susceptible to trampling. Besides this, in mixed situation some amount of protection is also afforded to it by erect growing P. dilatatum which absorbs the trampling pressure and suffers considerably. The damage caused to the grass also helps the legume growing with it through reduced competition from the grass. Plantago major and Poa annua having prostrate growth form have also been reported by Warwick (1980) to withstand trampling damage better than their populations having erect growth form. The differential effect of trampling on the two species makes their co-existence possible in nature. In absence of trampling, grazing and other biotic disturbances the legume

is totally eliminated from the grasslands as reported by Pradhan and Tripathi (1980).

The reduction in biomass production of the grass under trampling treatment may be due to the wear and tear of its aboveground parts. The quantitative effects of wear and tear on vegetation by trampling have also been shown by other workers (Bell and Bliss, 1973; Liddle, 1975a; Liddle and Greig Smith, 1975; Rogova, 1976). However, the growth of T. repens in the grass-legume mixture is enhanced with trampling pressure and this may largely be attributed to the damage caused by trampling to P. dilatatum which is an aggressive competitor.

The poor competitive ability of T. repens in undisturbed situation is also reflected by its low relative yield in control. Gradual increase in relative yield of the legume and decreased relative yield of the grass under trampling treatment clearly indicates that under heavy trampling, T. repens may compete successfully with P. dilatatum. T. repens showed flowering either in pure stand in absence of trampling or in mixed stand subjected to fortnightly trampling and under monthly trampling treatment no flowering could be observed in both pure and mixed stands. This behaviour may also be attributed to reduced competition from the grass under fortnightly trampling treatment or to complete absence of competition from the grass in pure stand of legume in absence of trampling. In the grass, however, increase in trampling pressure caused reduction in flowering.

Blom (1978b) found that moderate trampling had a positive effect on the number of spikes of Plantago coronopus and P. major, but increase in compaction and trampling caused reduction in numbers of spikes of P. lanceolata and P. coronopus.

C H A P T E R 7

COMPETITION BETWEEN TRIFOLIUM REPENS AND PASPALUM DILATATUM
UNDER TWO LIGHT REGIMES

INTRODUCTION

It has been found in the previous experiment that T. repens and P. dilatatum co-exist in nature in presence of biotic disturbances (Chapter 3) and the shade cast by the grass to the legume results into complete elimination of the latter from the swards in protected situation. It has been shown by many workers that if the competition for water and nutrients ceases, then light becomes the sole limiting factor to production (Donald, 1951; Blackman and Black, 1959).

Several studies have been done on the effect of light on grass-legume interaction, showing that the legume suffers due to competition for light (Donald, 1951; Stern and Donald, 1962b). Some field studies involving the effect of light, grazing, defoliation and fertilizer levels have also been done (Armitage and Templeman, 1964; Maclusky and Morris, 1964; Wilson, 1964).

T. repens and P. dilatatum have different growth habit and occupy different strata in the grassland. The grass with erect habit occupies the higher stratum while the legume grows prostrate. The legume suffers due to competition from the grass presumably because of reduction in light intensity caused by the interception through the grass canopy. However, the reaction of the grass to reduced

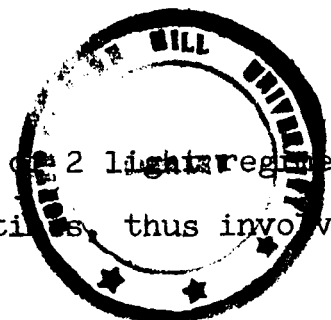
light intensity needs to be investigated. Thus, the growth of the two species was studied in pure and mixed stands under two different light regimes.

MATERIALS AND METHODS

Four days old seedlings of T. repens and P. dilatatum were transplanted to the experimental pots of 21.0 cm diameter, filled with sandy loam soil mixed with compost manure in the ratio of 5:1 on 25th May 1980. The pots were kept in a net house with its roof covered with polythene sheet for protection against rain. The net house was divided into two equal parts. In one part of the net house shade was created by putting a muslin cloth below the polythene roofing and also on east and west side of the net house. The other half was not covered with muslin cloth. The light available in the first half was reduced to ca. 50% of that in the other half. These two situations represent the two light regimes under which the plants were grown. Pure and mixed populations of T. repens and P. dilatatum were raised in the experimental pots according to de Wit's replacement series (de Wit, 1960) in the following manner:

- 1) 0% T. repens (T) + 100% P. dilatatum (P)
- 2) 50% T + 50% P and
- 3) 100% T + 0% P

The experimental design consisted of 2 light regimes x 3 proportions x 3 replicates x 3 harvest times, thus involving



in all 54 pots. In the pure stand, 6 seedlings of a particular species were transplanted while in the mixed stands 3 seedlings each of T. repens and P. dilatatum were transplanted so as to maintain an overall density of 6 plants per pot. The seedlings were planted at an equal distance from each other in a circular manner. In case of mixed stands the seedlings of the two species were alternately planted.

The experiment started on 25th May 1980. The three harvest H_1 , H_2 , and H_3 were taken after 45, 90, and 135 days from planting. At each harvest, the number of leaves, tiller or stolon production, leaf area and dry matter yield were determined. Besides, dry matter allocation to different plant parts, was also estimated. For dry matter estimation the plant materials were kept in an oven at 80°C to constant weight.

The leaf area ratio, leaf weight ratio, relative growth rate and net assimilation rate were also calculated.

The leaf area ratio (LAR) representing leaf area per unit plant dry weight was calculated by using the following formula:

$$\frac{L_A}{W}$$

where L_A and W are the total leaf area and total plant dry weight respectively.

The leaf weight ratio (leaf weight per unit plant dry weight) was calculated by using the formula $\frac{Lw}{W}$ where Lw and W

are the total leaf weight and total plant dry weight respectively.

The relative growth rate (RGR) was calculated by the formula developed by Fischer (1921) and described by Evans (1972) as follows:

$$\text{RGR} = \frac{\text{Log}_e 2^W - \text{Log}_e 1^W}{2^T - 1^T}$$

where 1^W and 2^W are the total plant dry weights at times 1^T and 2^T respectively at the beginning and end of the period.

The net assimilation rate (NAR) was calculated using the formula described by Williams (1946) as:

$$\text{NAR} = \frac{(W_2 - W_1) (\text{Log}_e L_2 - \text{Log}_e L_1)}{(t_2 - t_1) (L_2 - L_1)}$$

where W_1 and W_2 are the plant dry weights and L_1 and L_2 are the leaf areas of plants at the times t_1 and t_2 respectively.

RESULTS

Number of stolons/tillers per plant:

T. repens produced more stolons in pure than in mixed stands under high light regime. But at low light intensity it generally produced more stolons in mixed than in pure stand. P. dilatatum, on the other hand, produced more tillers in mixed than in pure stand (Table 7.1).

Leaf production and leaf area:

T. repens produced greater number of leaves in pure than in mixed stand at high light intensity while in shade more leaves were produced in mixed stand upto H₂. P. dilatatum, on the other hand, generally produced more leaves in mixed than in pure stand under both light regimes. Leaf production in both species was reduced at low light intensity (Table 7.2).

The above trend was observed in the leaf area per plant as well under reduced light, however, there was no significant difference between pure and mixed stands in both the species (Fig. 7.1).

Leaf area ratio and leaf weight ratio:

The leaf area ratio of T. repens was higher in pure than in mixed stand under high light regime but in shade it was higher in mixed stand (Table 7.3). P. dilatatum also showed higher value in mixture at low light intensity. At high light intensity, however, the mature plants of the grass showed greater ratio in pure stand but the differences were insignificant between open and shade situations.

Both the species produced higher leaf weight ratio in shade than under high light intensity both in pure and mixed stands (Table 7.4). T. repens generally showed higher leaf weight ratio in mixed than in pure stand under both light

Table 7.1: Effect of light on stolon production/plant of T. repens and tiller production/plant of P. dilatatum grown in pure and mixed stands after 45 (H_1), 90 (H_2) and 135 days (H_3) from planting.

Nature of stand	Open			Shade		
	H_1	H_2	H_3	H_1	H_2	H_3
<u>T. repens</u> (Pure)	4.11	9.33	14.19	1.00	1.11	2.11
<u>T. repens</u> (Mixed)	4.89	8.78	4.89	1.00	2.11	2.22
<u>P. dilatatum</u> (Mixed)	2.44	4.89	10.00	1.00	1.00	3.22
<u>P. dilatatum</u> (Pure)	1.88	2.89	6.50	1.00	1.00	1.83

Difference between open and shade significant at 1% and between ratio at 5% in both the species.

Table 7.2: Effect of light on leaf production/plant of T. repens and P. dilatatum grown in pure and mixed stands after 45 (H_1), 90 (H_2) and 135 days (H_3) from planting.

Nature of stand	Open			Shade		
	H_1	H_2	H_3	H_1	H_2	H_3
<u>T. repens</u> (Pure)	21.45	51.64	96.84	5.44	5.67	10.94
<u>T. repens</u> (Mixed)	23.56	45.44	14.11	6.33	13.67	8.78
<u>P. dilatatum</u> (Mixed)	10.66	20.45	25.78	5.11	7.22	12.33
<u>P. dilatatum</u> (Pure)	8.55	12.78	17.17	5.89	7.00	9.17

Difference between open and shade significant at 1% and between ratio at 5% in both the species.

Fig. 7.1: Total leaf area per plant of T. repens and P. dilatatum grown in pure and mixed stands at two light regimes after 45, 90 and 135 days from planting. The symbols —●— and ---o--- stand for T. repens in pure and mixed stands and —▲— and ---△--- stand for P. dilatatum in pure and mixed stands respectively.

Fig. 7.1

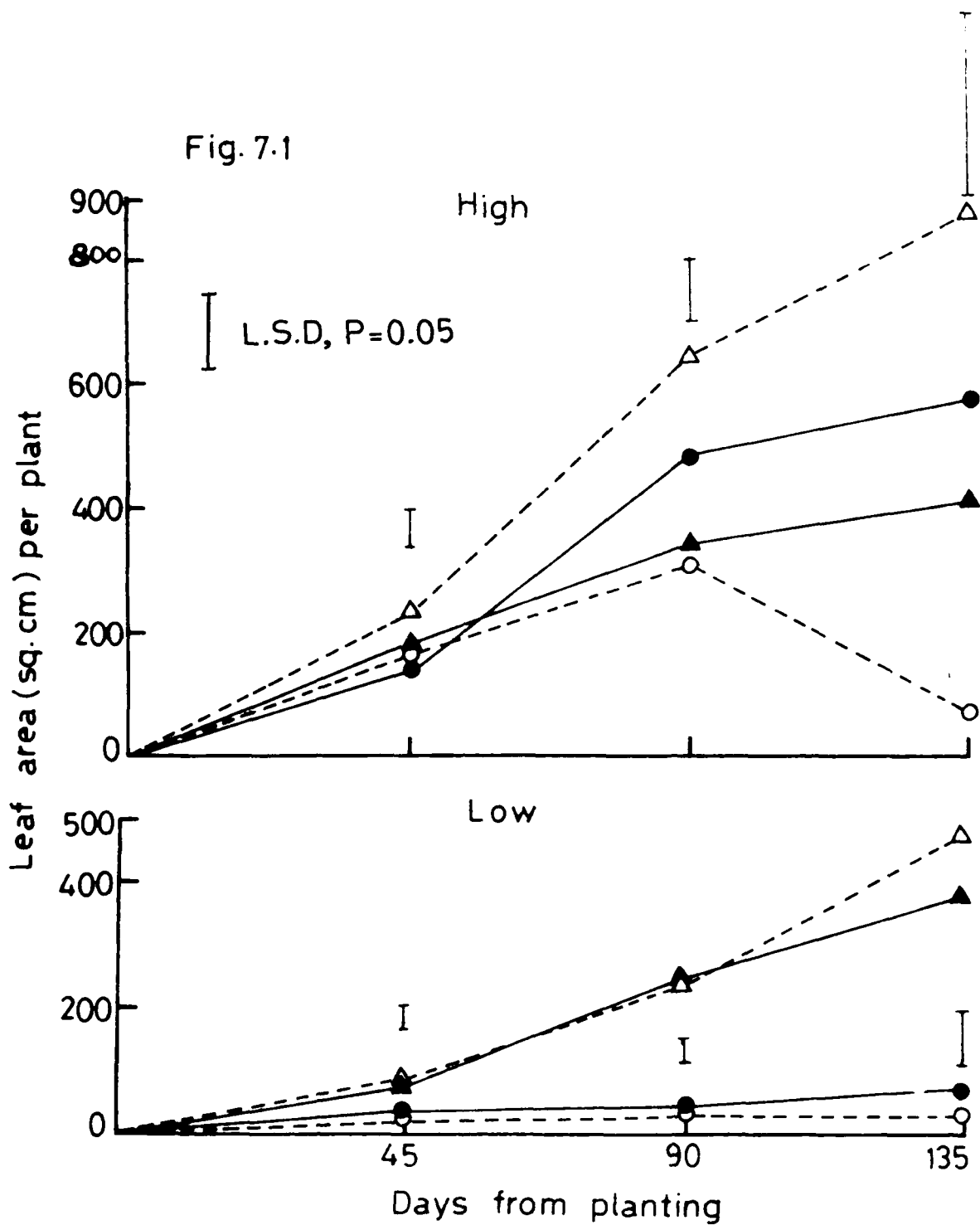


Table 7.3: Effect of light on biomass (g) per plant of T. repens and P. dilatatum grown in pure and mixed stands after 45 (H_1), 90 (H_2) and 135 days (H_3) from planting.

Nature of stand	Open			Shade		
	H_1	H_2	H_3	H_1	H_2	H_3
<u>T. repens</u> (Pure)	0.35	1.95	2.77	0.13	0.12	0.31
<u>T. repens</u> (Mixed)	0.46	1.38	0.61	0.08	0.08	0.13
<u>P. dilatatum</u> (Mixed)	0.84	6.66	10.21	0.19	0.92	2.26
<u>P. dilatatum</u> (Pure)	0.61	3.36	4.65	0.24	1.17	2.12

Difference between open and shade and between ratio significant at 5% in both the species.

Table 7.4: Leaf area ratio (LAR) (cm^2/g) of T. repens and P. dilatatum after 45 (H_1), 90 (H_2) and 135 days (H_3) of growth from planting grown in pure and mixed stands under two light regimes.

Nature of stand	Open			Shade		
	H_1	H_2	H_3	H_1	H_2	H_3
<u>T. repens</u> (Pure)	410.63	245.23	205.92	190.00	332.67	230.45
<u>T. repens</u> (Mixed)	350.85	221.15	137.24	246.94	377.38	301.92
<u>P. dilatatum</u> (Mixed)	274.50	95.19	85.42	435.68	263.05	215.18
<u>P. dilatatum</u> (Pure)	242.62	100.22	88.62	332.04	215.80	182.10

conditions. P. dilatatum, on the other hand, did not show much difference between pure and mixed stands at high light intensity but in shade the ratio was relatively higher in mixture than in monoculture.

Biomass per pot:

The legume generally produced greater biomass in pure than in mixed stand. The grass, however, produced greater biomass in mixture under high light regime and monoculture was more productive at low light intensity upto H₂ (Table 7.5). Better light condition stimulated biomass accumulation in both the species.

T. repens produced lesser biomass per pot than P. dilatatum under both light regimes (Fig. 7.2a&b). The grass showed better growth in mixture whilst the legume growth was suppressed in comparison to corresponding monocultures under high light intensity. With passage of time the suppression caused by the grass over legume was further exaggerated. The total combined yield per pot in mixture was higher than the monoculture yields of both species. The yield data also suggest that the grass is more sensitive to intra-specific competition and the legume suffers more from inter-specific competition.

The reduced light resulted into substantial decrease in yield of both species (Fig. 7.2a&b). The legume, however, showed much greater reduction (Table 7.6). The reduction in yield of the grass at low light regime was more pronounced in mixture

Table 7.5: Leaf weight ratio (g/g) of T. repens and P. dilatatum after 45 (H_1), 35 (H_2) and 135 days (H_3) of growth from planting grown in pure and mixed stands under two light regimes.

Species under different stands.	Open			Shade		
	H_1	H_2	H_3	H_1	H_2	H_3
<u>T. repens</u> (Pure)	0.28	0.29	0.12	0.43	2.73	0.25
<u>T. repens</u> (Mixed)	0.39	0.24	0.35	0.82	0.99	0.32
<u>P. dilatatum</u> (Mixed)	0.51	0.22	0.19	0.61	0.55	0.45
<u>P. dilatatum</u> (Pure)	0.51	0.21	0.24	0.44	0.53	0.40

Table 7.6: Relative yield of T. repens and P. dilatatum grown in pure and mixed stands under two light regimes after 45 (H_1), 90 (H_2) and 135 days (H_3) from planting. The RYT value is also given.

Species	Open			Shade		
	H_1	H_2	H_3	H_1	H_2	H_3
<u>T. repens</u>	0.66	0.35	0.09	0.09	0.33	0.21
<u>P. dilatatum</u>	0.67	0.99	1.09	0.40	0.39	0.53
RYT	1.33	1.34	1.18	0.49	0.72	0.74

Fig. 7.2a: Replacement diagram based on biomass per pot of T. repens and P. dilatatum grown in pure and mixed stands at high light regime after 45 (H_1) 90 (H_2) and 135 days (H_3) from planting. The symbols $\text{---}\bullet\text{---}$, $\text{---}\blacktriangle\text{---}$ and $\text{---}x\text{---}$ stand for T. repens, P. dilatatum and combined yield respectively.

Fig. 7.2a

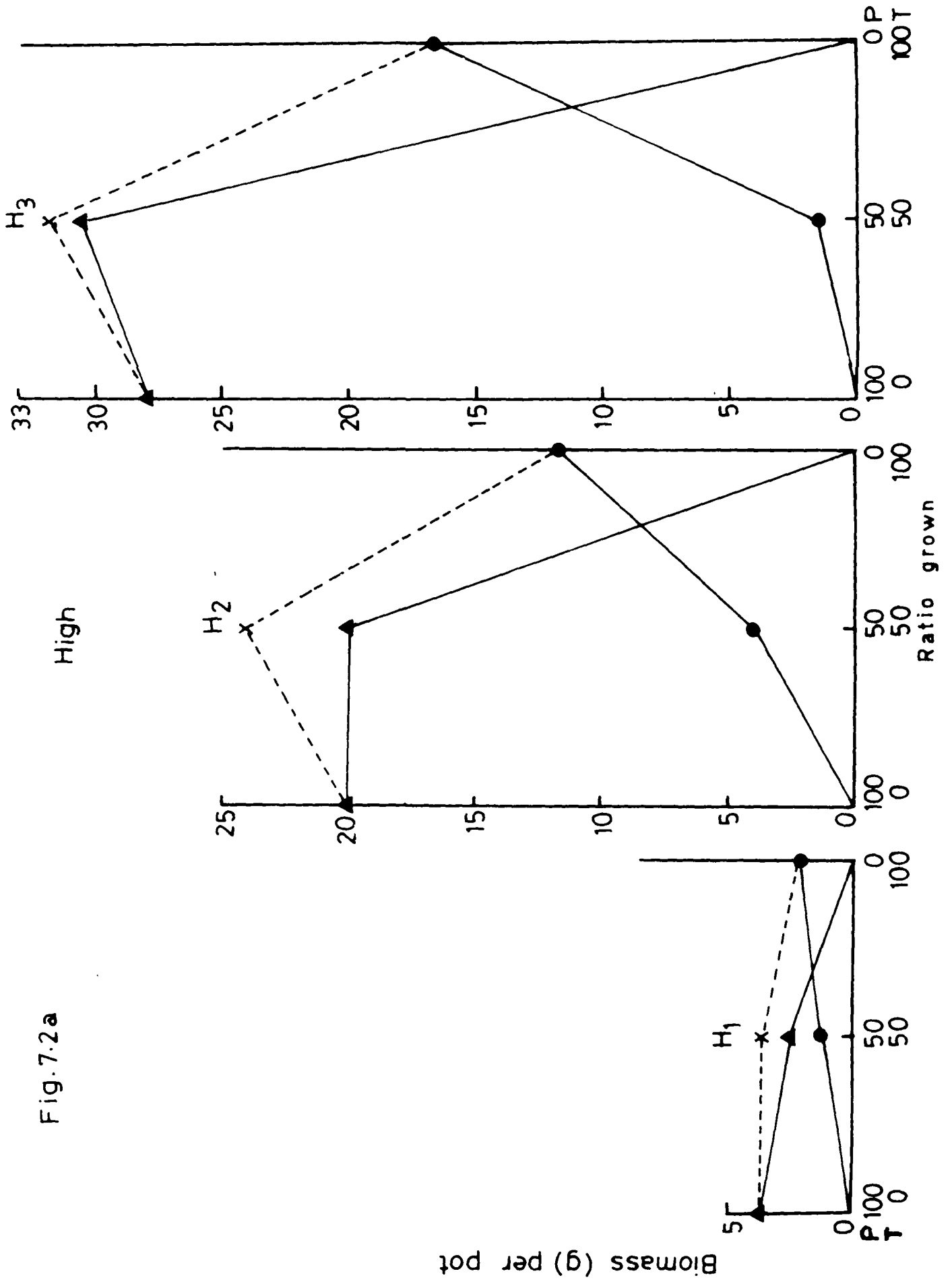
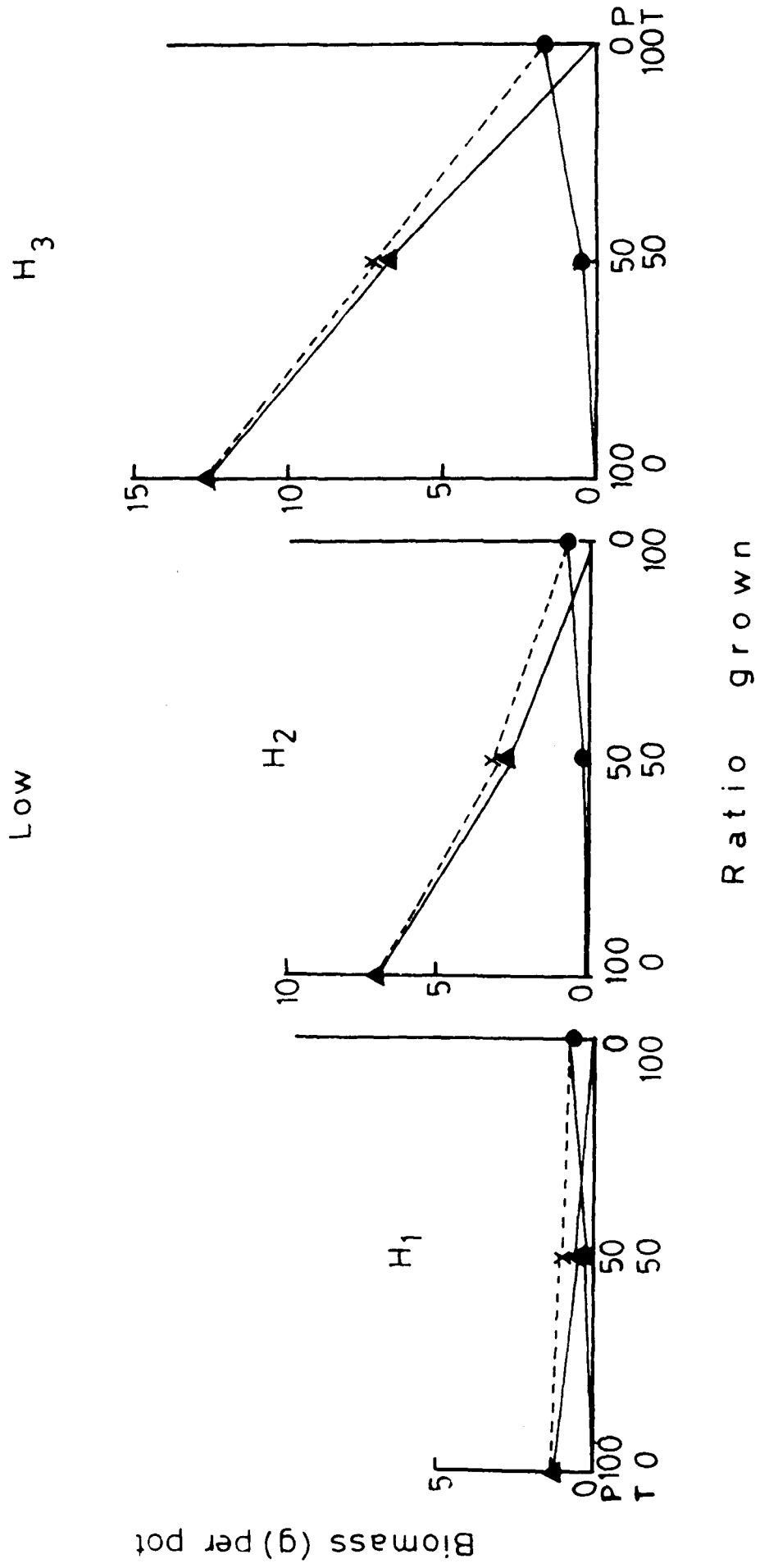


Fig. 7.2b: Replacement diagram based on biomass per pot of T. repens and P. dilatatum grown in pure and mixed stands at low light regime after 45 (H_1), 90 (H_2) and 135 days (H_3) from planting. The symbols $\text{---}\bullet\text{---}$, $\text{---}\blacktriangle\text{---}$ and $\text{---}x\text{---}$ stand for T. repens, P. dilatatum and combined yield respectively.

Fig. 7.2b



than in monoculture. The yield of P. dilatatum was higher in monoculture than in mixture under shade while at high light regime the grass did much better in mixture. Under both light conditions the contribution by P. dilatatum to the combined yield was much higher than that of T. repens.

Relative yield and quotient of relative yield:

At high light intensity, the relative yields of the two species were equal in the early stage of growth, but with passage of time the relative yield of P. dilatatum increased so much that at the final harvest it exceeded 1, while the value of T. repens was reduced to 0.09 at H₃ from 0.66 at H₁. But in shade, relative yield of both the species was lower in the beginning and increased at the later harvests. Relative yield values of both species were much lesser under low light regime than under high light intensity (Table 7.7). The value of RYT was greater than one at high light intensity while in shade RYT was always less than one (Table 7.7).

The quotient of relative yield of T. repens over P. dilatatum also showed higher value in the early stage of growth at high light intensity, while in shade it was lesser in the later stages of growth with maximum value at H₂ (Fig. 7.3) which shows that P. dilatatum offers more severe competition to the legume under high light regime than under low light regime.

Table 7.7: Relative growth rate (mg/mg/day) of T. repens and P. dilatatum grown in pure and mixed stands at two light regimes after 45 (H₁), 90 (H₂) and 135 days (H₃) from planting (mg/mg/week) is given in parenthesis).

Species under different stands	Open			Shade		
	H ₁ (0-45 days)	H ₂ (45-90 days)	H ₃ (90-135 days)	H ₁ (0-45 days)	H ₂ (45-90 days)	H ₃ (90-135 days)
<u>T. repens</u> (Pure)	0.1302 (0.9114)	0.0382 (0.2674)	0.0078 (0.0546)	0.1082 (0.7574)	-0.0018 (-0.0126)	0.0211 (0.1477)
<u>T. repens</u> (Mixed)	0.1362 (0.9534)	0.0244 (0.1708)	-0.0222 (-0.1554)	0.0973 (0.6811)	0 (0)	0.0109 (0.0763)
<u>P. dilatatum</u> (Mixed)	0.1496 (1.0472)	0.0460 (0.3220)	0.0096 (0.0672)	0.1167 (0.8169)	0.0349 (0.2443)	0.0200 (0.1400)
<u>P. dilatatum</u> (Pure)	0.1424 (0.9968)	0.0380 (0.2660)	0.0073 (0.0511)	0.1218 (0.8846)	0.0351 (0.2457)	0.0133 (0.0981)



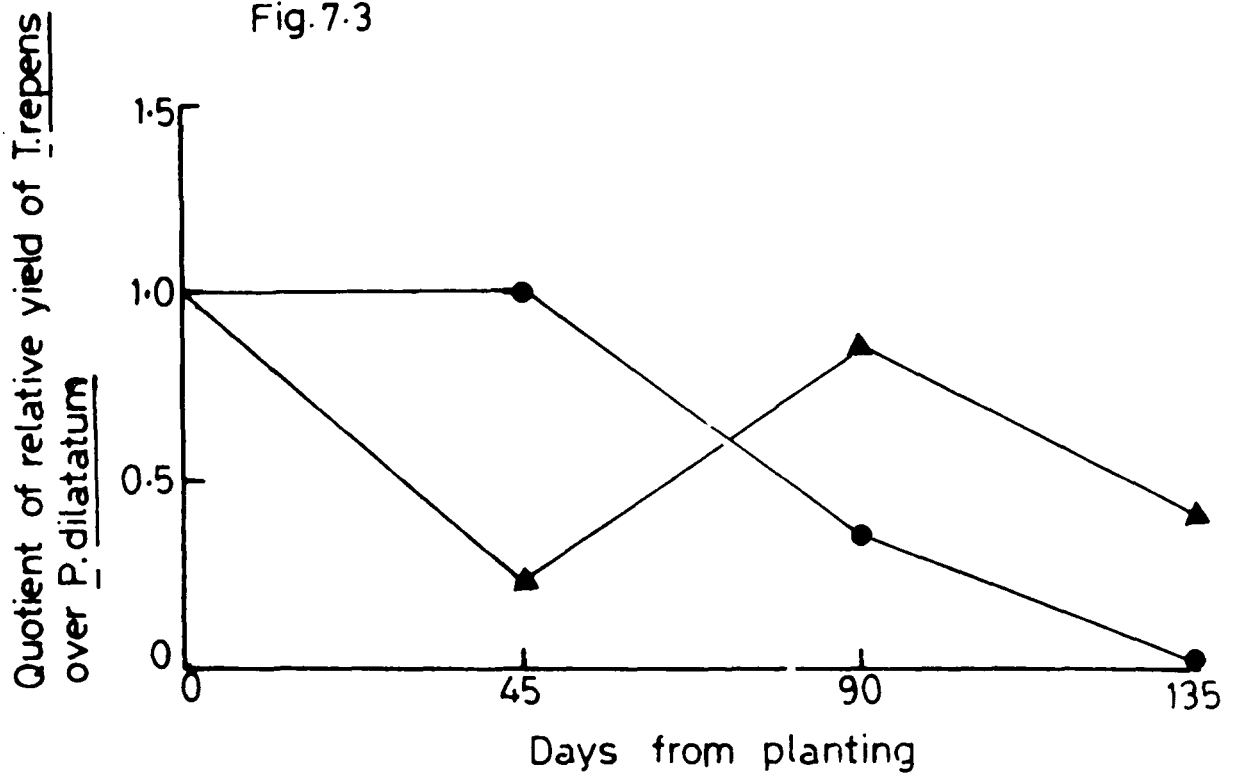
Fig. 7.3: Quotient of relative yield of T. repens and P. dilatatum grown in pure and mixed stands at two light regimes after 45, 90 and 135 days from planting. The symbols  and  stand for open and shade situations respectively.

Fig.7.3



Relative growth rate:

The relative growth rate (RGR) of P. dilatatum was higher than that of T. repens in both pure and mixed stands under both light conditions. Further, the RGR of the grass was more in mixed than in pure stand. T. repens, on the other hand, generally showed higher RGR in monoculture than in mixture (Table 7.8).

Net assimilation rate:

The net assimilation rate (NAR) of P. dilatatum was higher than that of T. repens under high light regime both in pure and mixed stands, but under shade no definite trend could be observed. At high light intensity, T. repens showed greater NAR in mixture than in monoculture in the early stage of growth but at later stages NAR was higher in monoculture. At low light regime, however, its NAR was higher in pure than in mixed stand. P. dilatatum, on the other hand, showed greater NAR in mixed than in pure stand at high light intensity, while under reduced light, it was higher in pure than in mixed stands at H_1 and H_2 (Table 7.8).

The NAR of P. dilatatum decreased with reduction in light intensity. T. repens also showed similar response in mixed populations while in monoculture its NAR was greater under reduced light.

Table 7.8: Net assimilation rate ($\text{mg}/\text{cm}^2/\text{day}$) of T. repens and P. dilatatum grown in pure and mixed stands at two light regimes after 45 (H_1), 90 (H_2) and 135 days (H_3) from planting ($\text{mg}/\text{cm}^2/\text{week}$ is given in parenthesis).

Species under different stands	Open			Shade		
	H_1	H_2	H_3	H_1	H_2	H_3
<u>T. repens</u> (Pure)	0.2689 (1.8820)	0.0894 (0.6257)	0.0056 (0.0394)	0.3751 (2.6256)	-0.0027 (-0.0187)	0.0344 (0.2408)
<u>T. repens</u> (Mixed)	0.3220 (2.2541)	0.0426 (0.2982)	-0.4068 (-2.8473)	0.2613 (1.8293)	0	0.0074 (0.0519)
<u>P. dilatatum</u> (Mixed)	0.4300 (3.0097)	0.2063 (1.4444)	0.0289 (0.2020)	0.2253 (1.5768)	0.0719 (0.5033)	0.0172 (0.1205)
<u>P. dilatatum</u> (Pure)	0.4577 (3.2039)	0.1492 (1.0443)	0.0140 (0.0983)	0.2930 (2.0510)	0.0944 (0.6608)	0.0169 (0.1181)

Allocation of dry matter:

In the early stage of growth, T. repens allocated greater dry matter to leaves, while P. dilatatum allocated more to the stem and leaves. But, at subsequent harvests, allocation to sink (root + stolon or rhizome) was increased under high light regime (Fig. 7.4a) the magnitude of increase was, however, greater in T. repens than P. dilatatum. Further, increase in allocation to stolons in the legume was more in pure than in mixed stand. In case of grass there was reduction in allocation to sink tissue (roots + rhizome) and increase in leaf allocation under shade (Fig. 7.4b). Reproductive allocation in both species was nil under shade. At high light intensity, however, the grass allocated some resources to reproductive structures in both pure and mixed stands while the legume reproduced only in pure stand.

T. repens showed somewhat increased allocation to sink tissue in pure than in mixed stand under high light regime, while under shade allocation to sink tissue was almost same in pure and mixed stands.

Under low light regime, the allocation to sink tissue in T. repens was far less but here also as was the case under high light regime, the allocation to sink tissue increased with passage of time but the magnitude of increase was smaller than what was observed under high light regime.

The legume allocated much greater proportion of

Fig. 7.4(a): Allocation of dry matter (%) to different plant parts of T. repens and P. dilatatum grown in pure and mixed stands at high light regime after 45 (H_1), 90 (H_2) and 135 days (H_3) from planting.

Fig. 7-4 (a)

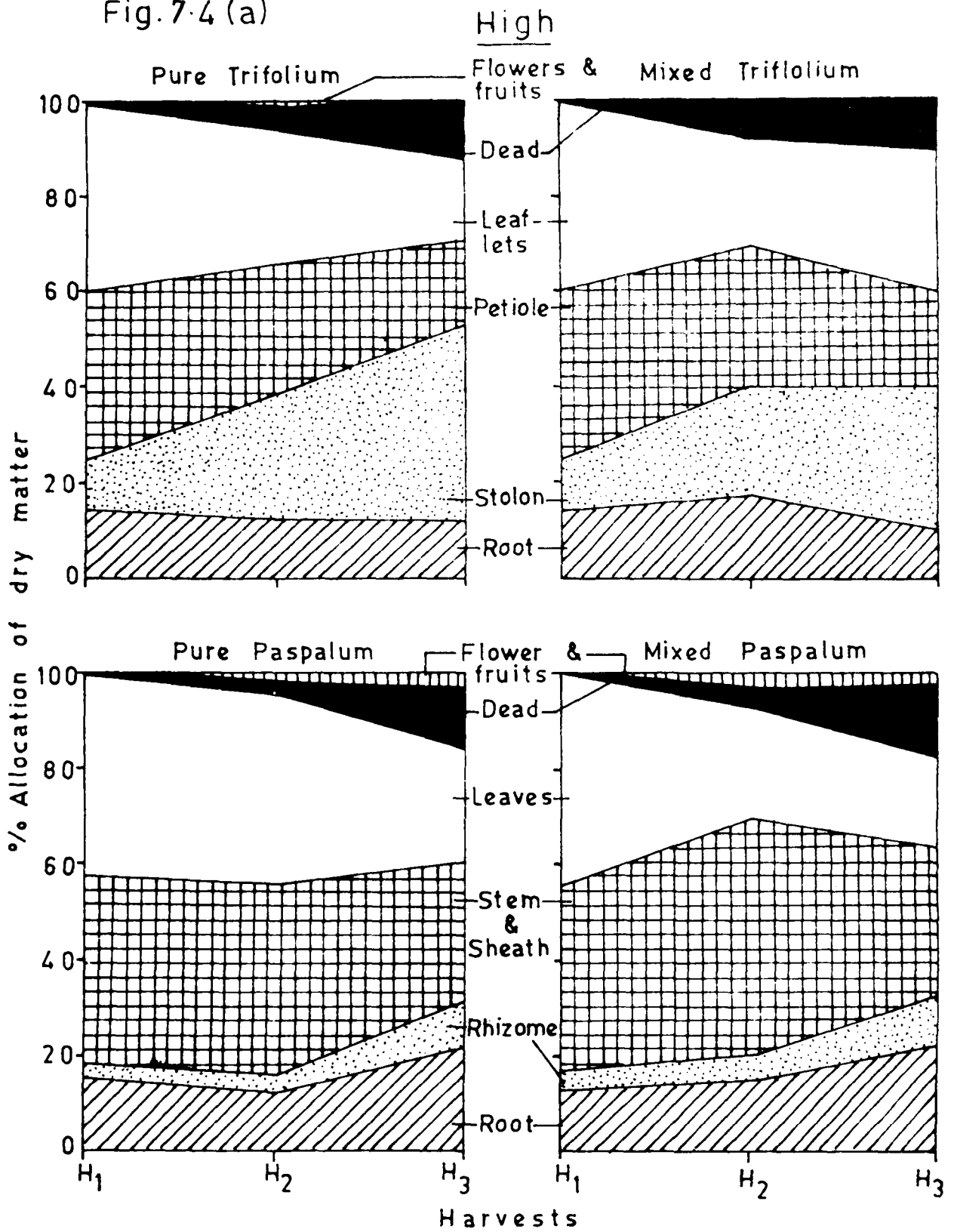
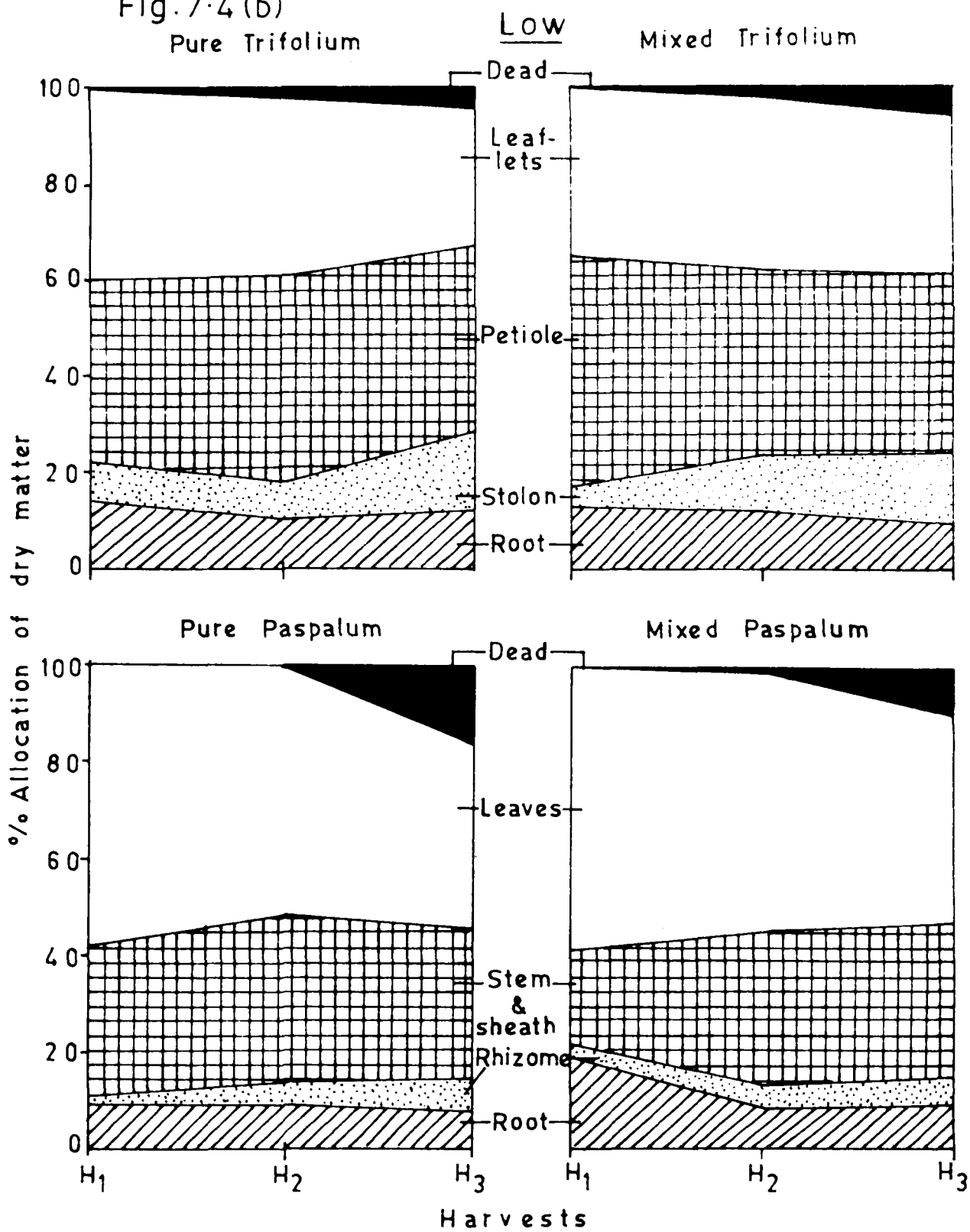


Fig. 7.4(b): Allocation of dry matter to different plant parts of T. repens and P. dilatatum grown in pure and mixed stands at low light regime after 45 (H_1), 90 (H_2) and 135 days (H_3) from planting.

Fig. 7.4 (b)



resources to the root and stolon as compared to allocation of resources to root and rhizome by the grass and the difference was particularly pronounced under high light regime.

Allocation to standing dead was not affected by light conditions in the grass, whereas the legume showed greater allocation to standing dead at high light intensity.

DISCUSSION

The growth analysis of T. repens and P. dilatatum in pure and mixed stands under two different light regimes indicates that the legume shows substantial reduction in growth in mixture, while the grass grows better in mixture than in monoculture. This shows that the legume suffers heavily due to competition from the grass while the latter is more susceptible to intra-specific competition under both light regimes. This is in contrast with the results of Ennik (1960), who found that in Lolium perenne and Trifolium repens mixture under high light intensity the grass tended to become extinct, while at low light intensity the two tended to attain an equilibrium - mixture with excess grass tending to increase its clover content and those with excess of clover tending to increase in grass. Van den Bergh and de Wit (1960) working on Phleum pratense and Anthoxanthum odoratum and Lieth (1960) on Lolium perenne and Trifolium repens under field situations have also found that the patches dominated by one species tend to be invaded by the

other attaining an equilibrium. However, P. dilatatum, in the present study seems to be a very strong competitor for the legume and it is expected that under all circumstances it might maintain the competitive superiority.

Both the species show suppressed growth under shade showing that competitive effects become more pronounced when light intensity is reduced. It has been shown by many workers that if the competition for water and nutrients ceases, then light becomes the sole limiting factor for production (Donald, 1951; Blackman and Black, 1959); although some recent studies indicate that 'competition for nutrients' is of greater importance than 'competition for light' (King, 1971; Snaydon, 1971; Eagles, 1972).

The relative yield total (RYT) value > 1 under high light intensity shows that either one or both the species are gaining in mixed culture. Very low relative yield of the legume suggests that it suffers heavily in competition with the grass which alone gains in mixture. Under low light intensity, however, the RYT value was lesser than one showing that both the species probably suffers while competing under low light intensity. It appears that further reduction in legume growth under reduced light intensity, might affect the growth of grass as well. It could be assumed that the nitrogen fixation which is directly related with the growth of the legume as reported by earlier workers (Strong and Trumble, 1939; Buttler et al., 1959) who found that shading causes a

loss of root and nodule tissue in white clover. Thus reduced growth of the legume under low light regime might result into more severe competition for nutrients particularly nitrogen. Cowling (1961) found that the better growth of legume (T. repens) under wet climatic conditions produced better herbage yield of cocksfoot/white clover sward, while depressed clover growth did not produce good mixture yield. In the present work also, the mixture yield at high light intensity was greater than pure stand yield of either species while under low light regime the mixture yield was far less (Fig. 7.2a and b). This indicates that suppression in growth of the legume which was quite pronounced results under low light regime into overall yield of the grass-legume mixture.

The leaf area ratio (LAR) of the legume was higher in pure under high light intensity but under low light the ratio was higher in mixture. As revealed by their growth in field conditions both the species seem to be adapted to bright light but their LAR values were higher under low light regime. This is in contrast with the earlier reports (Blackman and Wilson, 1951; Pandey and Sinha, 1977) that the species adapted to low light intensity show an increase in leaf area ratio under shade. Higher leaf area ratio of the two species under low light intensity indicates that a larger photosynthetic area is needed for producing a unit weight of dry matter.

Although the leaf weight ratio of the two species did

not differ much, the higher RGR and NAR values of P. dilatatum in mixture under both the light regimes may confer competitive advantage to the grass as also revealed by the relative yield values. However, it may be pointed out that the competitive ability of a species depends not only on how quickly it grows but also on how it allocates the assimilates to different plant parts (Williams, 1970). But in the present study, the data on various growth parameters also show that the grass is more aggressive than the legume.

The competition afforded by the grass to the legume is so severe that the legume failed to reproduce sexually when grown mixed with the grass while in the absence of P. dilatatum, it could allocate some of its resources for the formation of flowers and fruits under high light regime. This clearly shows that the severe competition offered by the grass hampers the sexual reproduction of the legume while the grass remains unaffected in mixed stand. Both species, however, suffer due to reduction in light intensity and failed to allocate resources towards sexual reproduction.

The adverse effect of reduced light intensity on allocation to stolons in T. repens has an important bearing on success of this species as in absence of seed, stolon alone contributes to population growth. The reduced allocation to stolons in mixed stands where the grass grew luxuriantly, may also partly be due to low availability of light to the legume.

Putwain and Harper (1970) have also suggested that under established grassland situation the maintenance of different population is mostly with the help of vegetative reproduction. Further, the species with lower seed production compensates with the production of higher number of vegetative propagules (Tripathi and Harper, 1973).

T. repens, although suffers both due to reduced light intensity as well as the competition from the grass, it has a subtle way of utilizing its resources with its increasing tendency for the production of stolons. However, the legume is found to be eliminated from the grassland protected from disturbance and grazing for longer period of growth (Pradhan and Tripathi, 1980), on account of severe competition from luxuriantly growing P. dilatatum. This indicates that the stolon production which occurs to a limited extent under stressed condition may not maintain the population of the legume if the stress is allowed to continue for a longer period.

C H A P T E R 8

INTERFERENCE BETWEEN TWO POPULATIONS OF TRIFOLIUM REPENS IN
RELATION TO SOIL NITROGEN

INTRODUCTION

The white leaf markings in Trifolium repens are very distinct and can be used to identify the individual clones (Harberd, 1963). Several studies have been done to show the role of predation on the dominance of one clone over the other (Charles, 1968; Walton et al., 1970; Crawford - sidebotham, 1972; Angseesing, 1974; Cahn and Harper, 1976b). Some studies have been done involving edaphic ecotypes of T. repens occurring on calcareous and acid soils (Snaydon, 1962), and altitudinal ecotypes differing in photosynthetic CO₂ fixation products (Machler, Nosberger and Erismann, 1977). However, no serious attempt seems to have been made to investigate the competitive behaviour of the clones of T. repens in relation to soil nitrogen status although grass-legume interactions have been studied at different nitrogen regimes (Stern and Donald, 1962a; Whitehead, 1970; Litav and Zeligman, 1978).

MATERIALS AND METHODS

The stolons of the two populations of Trifolium repens differing in leaf morphs were collected from the natural swards of Shillong.

The two populations wherever they occur, form a mosaic in the local swards. The morph with conspicuous 'V' shaped white mark on the leaflets can be easily distinguished from the one with no mark on the leaflets, in the field situation. The stolons

of the two morphs were cut into 2 cm pieces of 0.2 cm diameter, each with a node in the middle to serve as propagules for raising the populations. The dry matter of the stolon pieces of both the morphs was found to be in the range of 14-15 mg (average value based on 10 measurements). The stolon pieces of the two morphs were sown on 27 November 1978 in separate pots filled with garden loam soil. The stolon pieces sprouted after 1-3 weeks after sowing. The sprouts of uniform size (with one leaf) were selected and 8 of such sprouted pieces of each morph raised the pure populations. The sprouts were grown at a distance of 2 cm from each other in a circular manner. In the case of mixed stands, 4 sprouted pieces of each of the two morphs were planted per pot. The pieces of the two morphs were planted alternating with each other in circular fashion maintaining 2 cm distance between any two pieces. The planting and thinning dates were same as on the pure stands.

The pure and mixed populations of the two morphs were grown at two soil nitrogen regimes. The low nitrogen regime represented the garden soil (%N in the garden soil = 0.27%) and in the case of the high soil nitrogen regime two doses each of 600 mg of nitrogen per pot (equivalent to c. 270 kg/ha) in the form of NaNO_3 were added to the original garden soil after 12 and 17 weeks from the planting dates. The low nitrogen regime represented by the garden soil was equivalent to c.80 kg/ha. There were 3 replications for each of the two nitrogen treatments in case of the pure and mixed populations of the two morphs.

The experiment was conducted in plastic pots of 21 cm diameter, kept in an unheated net house roofed with polythene sheet. The maximum temperature (30°C) was recorded in May and minimum temperature (4°C) in January. The first harvest (H₁) was taken after 14 weeks from planting as the growth of the two populations was restricted due to low temperature in winter months. The second (H₂) and third (H₃) harvests were taken after 23 and 32 weeks of growth. The experiment was terminated on August 1, 1979. At each harvest, the stolon length, leaf area per plant, number of fertile shoots and dry weight of different plant parts viz. root, stolon, leaves (leaflets and petioles) and flowers and fruits were estimated. The dry weight was determined by drying the plant material in an oven at 80°C to constant weight.

Chlorophyll content of the fresh leaves and nitrogen content of the above ground plant parts of T. repens were determined. Chlorophyll extraction was done in acetone and its content was determined by the method outlined by Allen (1974) and nitrogen by micro-kjeldahl method as outlined ^{by} Misra (1968).

RESULTS

Leaf area:

The total leaf area per plant of the white morph was greater in mixture than in pure at low N regime while at high N regime the reverse was generally true (Fig. 8.1). The leaf area per plant of the unmarked morph was, however, greater in pure

than in mixture (significant at 5%). The average size per leaf of the white morph was greater in mixture at low nitrogen level while at high nitrogen level there was reduction in leaf size in the mixed stands (Table 8.1). The unmarked population was also characterised by a decrease in leaf size in the mixture at high nitrogen level at H₃. At low nitrogen level, however, the reduced leaf size in mixture was apparent only at initial growth stage (significant at 5%, $t = 2.65$).

Length of stolon:

The total stolon length per plant in both the clones was significantly greater in the mixed stands than in pure after 32 weeks of growth at low nitrogen (Fig. 8.2). The stolon production by the white morph was stimulated by the addition of nitrogen (significant at 5%, $t = 3.40$) whereas the unmarked morph behaved differently particularly in mixture. After 32 weeks of growth, the stolon production by the unmarked morph was higher as compared to the corresponding pure and mixed stands of the white leaf morph at low nitrogen regime (significant at 5%), while at high nitrogen there was no significant difference.

Dry matter production:

The unmarked morph after 32 weeks of growth was found to accumulate more dry matter per plant than the white marked morph at the low nitrogen level irrespective of the nature of stand ($p < 0.05$). The white leaf morph responded better to the addition of nitrogen by accumulating greater amount of dry matter at high

Table 8.1: Average size (sq. cm.) per leaf of the two populations of Trifolium repens grown in pure and in mixture under high and low nitrogen regimes (average values \pm S.E.).

Nature of stand	Nitrogen regimes					
	High			Low		
	H ₁	H ₂	H ₃	H ₁	H ₂	H ₃
White marked in pure	4.97 \pm 1.26*	5.46 \pm 0.73	7.64 \pm 1.07*	2.16 \pm 0.10	4.64 \pm 0.80	4.65 \pm 0.25
White marked in 50:50 mixture	1.19 \pm 0.16*	4.91 \pm 0.20	5.29 \pm 0.17*	2.19 \pm 0.24	5.48 \pm 0.02	5.35 \pm 0.33
Unmarked in 50:50 mixture	1.66 \pm 0.61	3.80 \pm 1.15	4.98 \pm 0.07*	1.64 \pm 0.20*	5.10 \pm 0.16	4.98 \pm 0.19
Unmarked in pure	1.55 \pm 0.16	4.72 \pm 0.74	5.49 \pm 0.15*	2.38 \pm 0.11*	5.71 \pm 0.25	4.79 \pm 0.12

The values at H₁ are significantly different (at 5% level) from those at the later harvests whilst the difference between the data at H₂ and H₃ are insignificant.

The data marked with an asterisk in pure of a given morph are significantly different at 5% from those marked with an asterisk in mixture of the same morph.

Fig. 8.1: Total leaf area per plant of the two populations of T. repens after 14, 23 and 32 weeks from planting under two nitrogen regimes. White marked in pure (●—●) and in mixture (○---○) and unmarked in pure (▲—▲) and in mixture (△---△).

Fig. 8.1

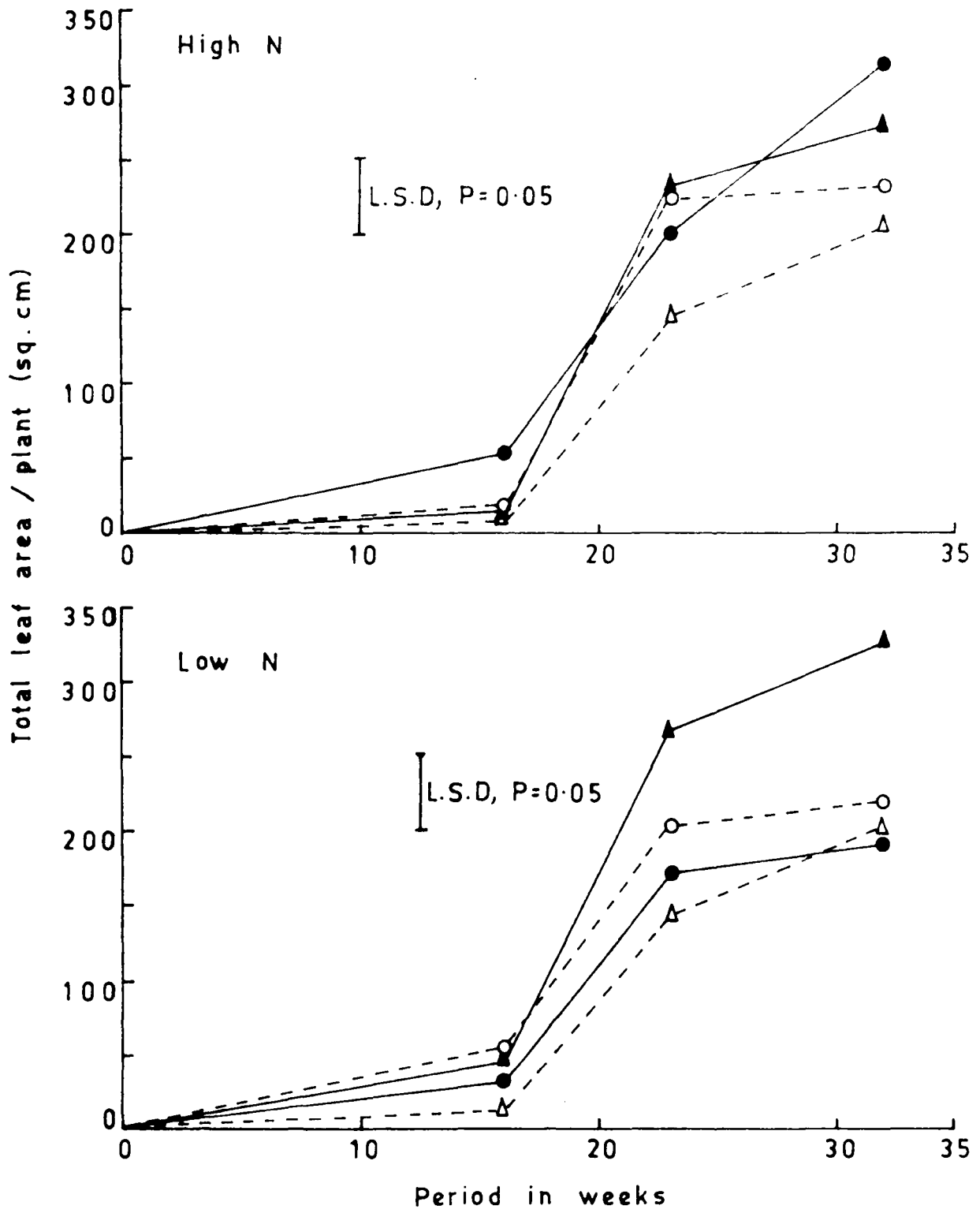
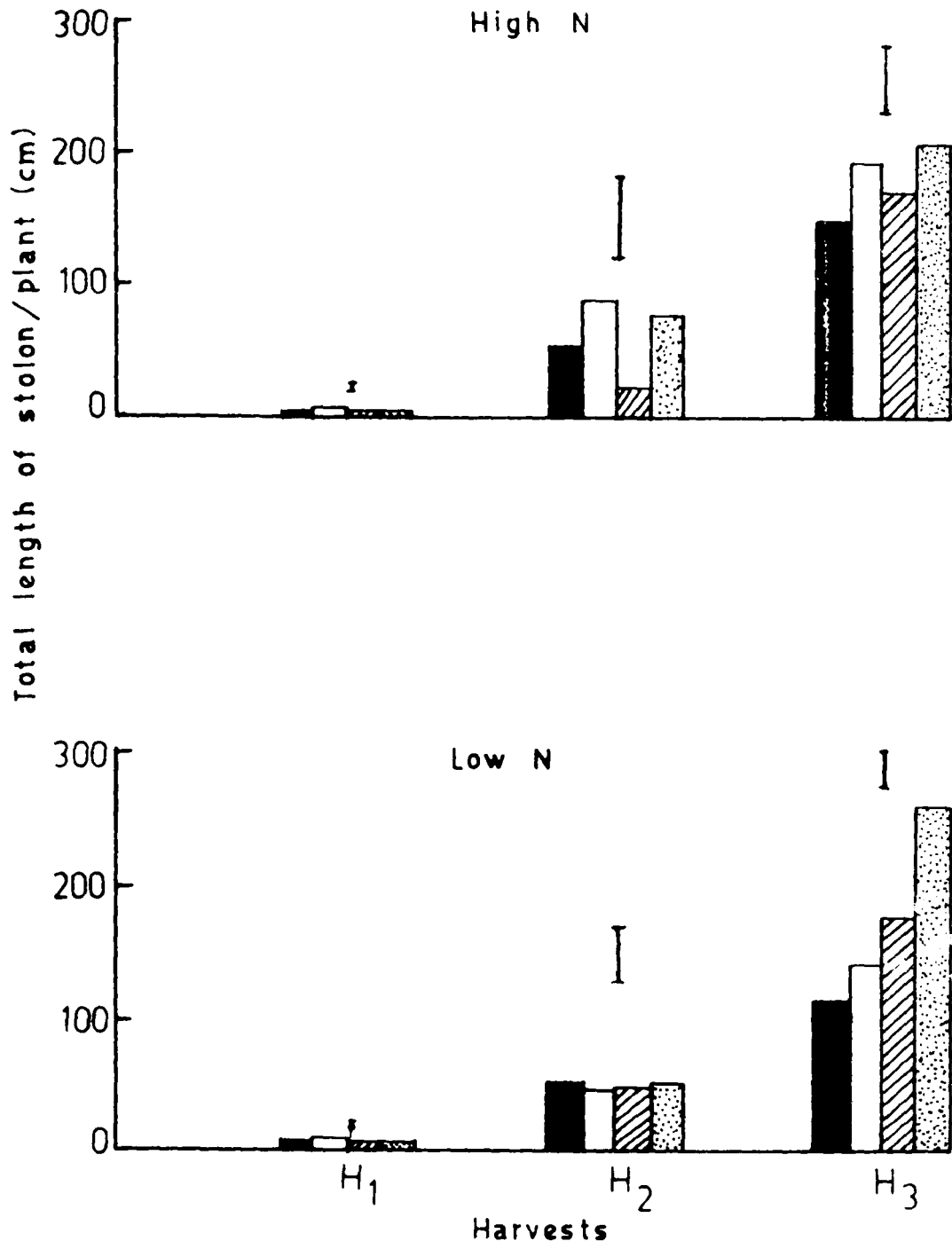


Fig. 8.2: Total length of stolon per plant of the two populations of T. repens after 14 (H_1), 23 (H_2) and 32 weeks (H_3) under two nitrogen regimes. White marked grown in pure (■) and in mixture (□); unmarked grown in pure (▨) and in mixture (▩). Vertical lines (I) indicate L.S.D. at $P = 0.05$.

Fig. 8·2



nitrogen level as compared to its dry matter at low nitrogen level (significant at 5%, $t = 2.42$). At high nitrogen level, both the morphs showed an increase in dry weight in mixed stands relative to their corresponding pure stand yields whilst the reverse trend was observed at low nitrogen regime although the differences were insignificant (Fig. 8.3). The white leaf morph showed higher mixture yield at high nitrogen level than at low N level, and the difference in yield of the two morphs was narrowed down at high nitrogen regime. The mixture yield of the white morph at high N regime was greater than its pure yield while at low N level the mixture yield was lesser which indicates that the outcome of competition is dependent on the soil nitrogen level.

The relative performance of the two morphs in mixture:

The total yield per pot in mixture at both the N levels was intermediate between the pure stand yield of the two morphs. An increase in soil nitrogen resulted in greater yield per pot of the white morph both in pure and mixture but the unmarked morph was almost unaffected by the addition of nitrogen (Fig. 8.4).

The relative yield of the two clones and the quotient of their relative yield (Table 8.2) were calculated to compare the competitive success of the two morphs. At the high nitrogen regime, the relative yield of the unmarked morph seems to be higher in the early stage of growth, but at later harvests white marked morph wins over the former, which is also indicated by the

Fig. 8.3: Dry weight per plant of the two morphs of *T. repens* after 14, 23, and 32 weeks from planting under two nitrogen regimes. White marked grown in pure (●—●) and in mixture (○---○); unmarked grown in pure (▲—▲) and in mixture (Δ---Δ). Vertical lines (I) indicate L.S.D. at $P = 0.05$.

Fig. 8.3

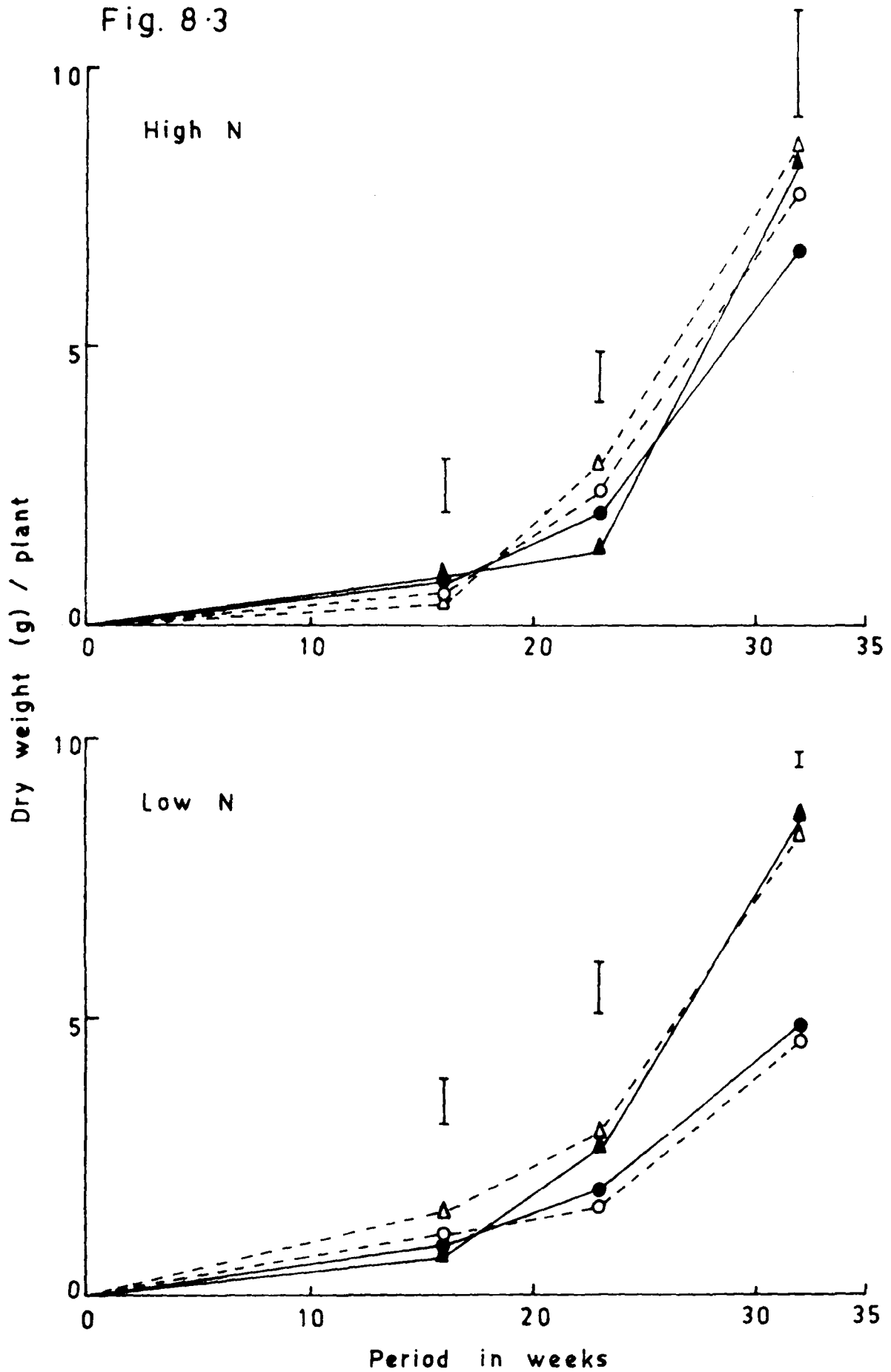


Fig. 8.4: Replacement series diagram based on total biomass per pot (g) of two morphs of T. repens at final harvest grown at two soil nitrogen levels. The symbols, (—●—) and (—○—), represent the yield of white marked and unmarked populations respectively. The total yield per pot in mixture (---○---) is also given.

Fig. 8.4

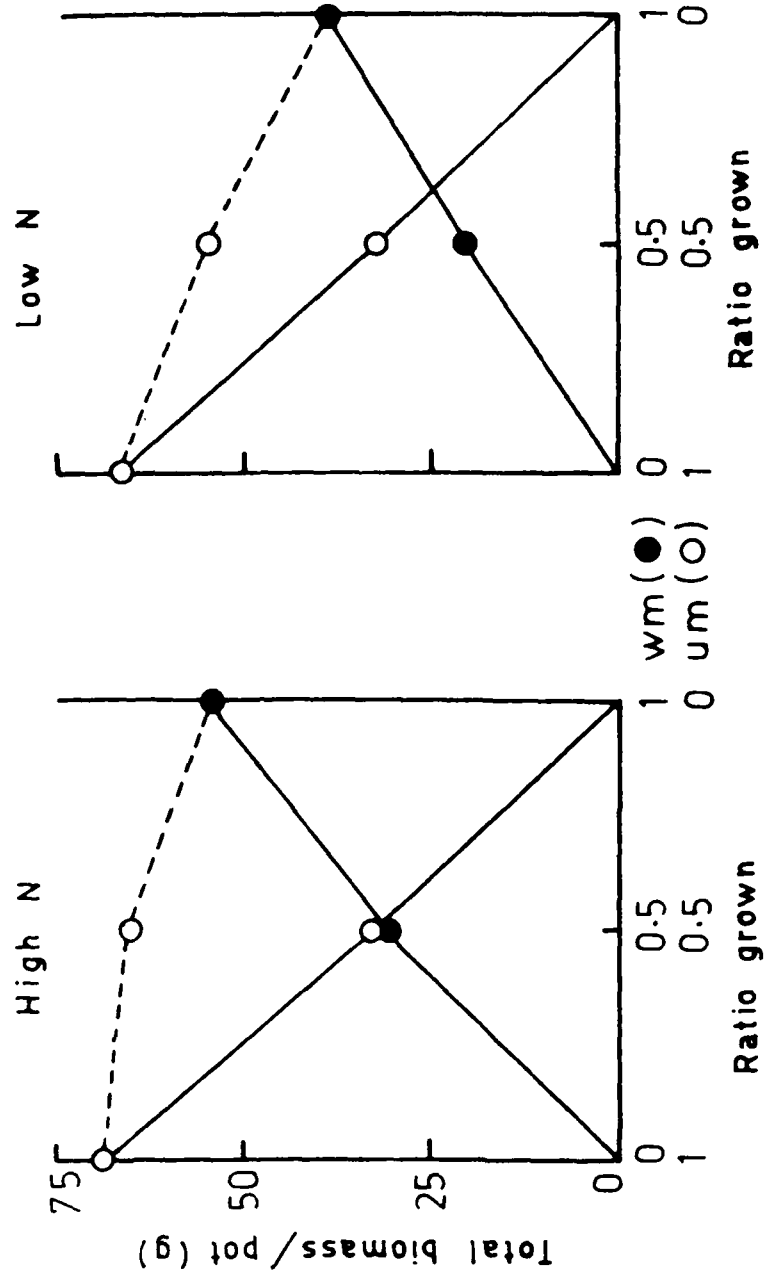


Table 8.2: The relative yield of the two morphs and quotient of their relative yield at the three harvests under high and low nitrogen regimes.

	High N			Low N		
	Harvests					
	H 1	H 2	H 3	H 1	H 2	H 3
White marked	0.78	1.20	1.14	1.10	0.78	1.05
Relative yield						
Unmarked	0.89	0.46	0.95	0.54	0.97	0.98
Quotient of relative yield of white marked to unmarked	0.87	2.60	1.20	2.03	0.80	1.07

quotient of relative yield. This competitive behaviour of the two morphs is, however, reversed at the first two harvests under low nitrogen regime although at H₃, almost the same trend was observed at both the nitrogen regimes.

The allocation of resources:

The allocation pattern in white marked morph seems to be unaffected due to competitive interaction between the two morphs at low N regime (Fig. 8.5b), while the unmarked morph allocates more of its resources to the sexual reproductive parts (Flowers and fruits) in the mixture as compared to the pure stand where the allocation to leaf was found to be higher. It seems that the white marked morph allocates relatively greater proportion of its resources to leaves while the unmarked morph allocates more food reserves to the sink tissue (root and stolon). The allocation to the leaf decreases with age whilst there was increased allocation to the roots and stolons with passage of time.

The allocation pattern of white marked morph gets slightly changed due to added soil nitrogen, particularly at the early stage when the allocation towards leaves was much less and to stolons much greater than the corresponding values at low N level (Fig. 8.5a). The allocation to the leaves and to the flowers and fruits by the white marked morph at high nitrogen level was greater in pure stand than in mixture. At both the nitrogen levels there was a tendency for greater allocation towards stolons at H₃ while the allocation to leaves decreased considerably at

Fig. 8.5a: Dry matter allocation to various plant parts of the two populations of T. repens grown in pure and in mixture under high N regime at three harvests taken after 14 (1), 23 (2) and 32 weeks (3) from planting.

Fig. 8.5a

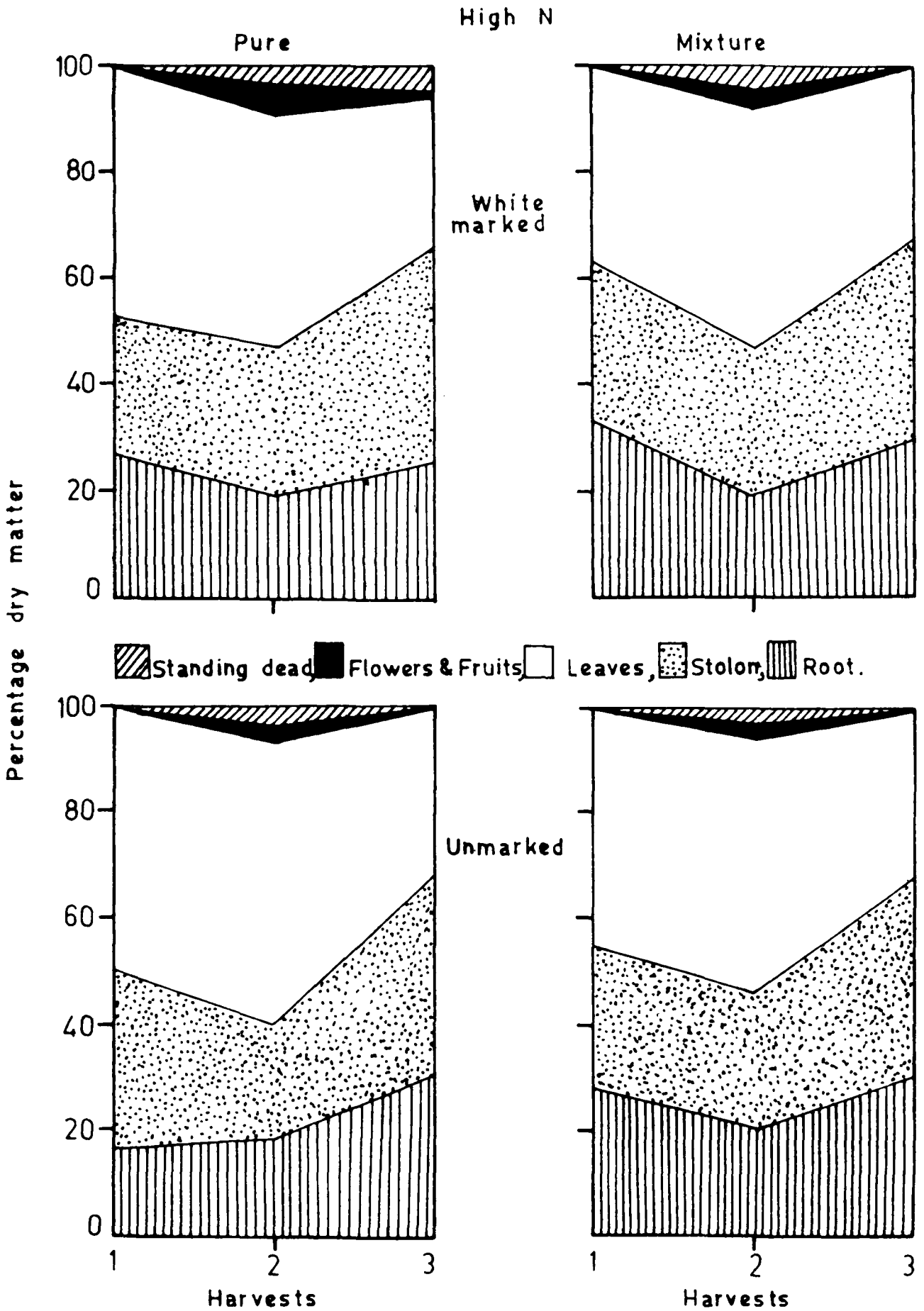
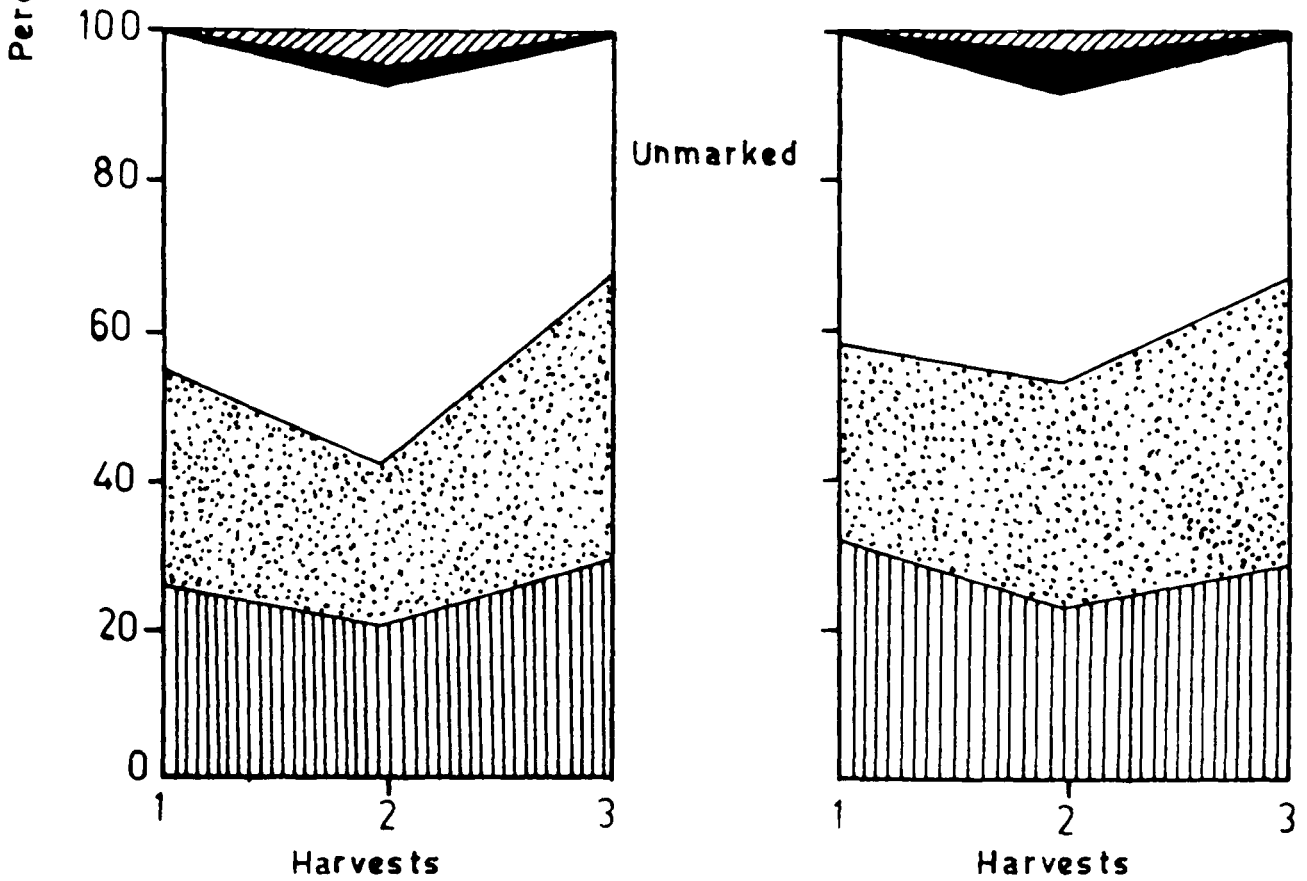
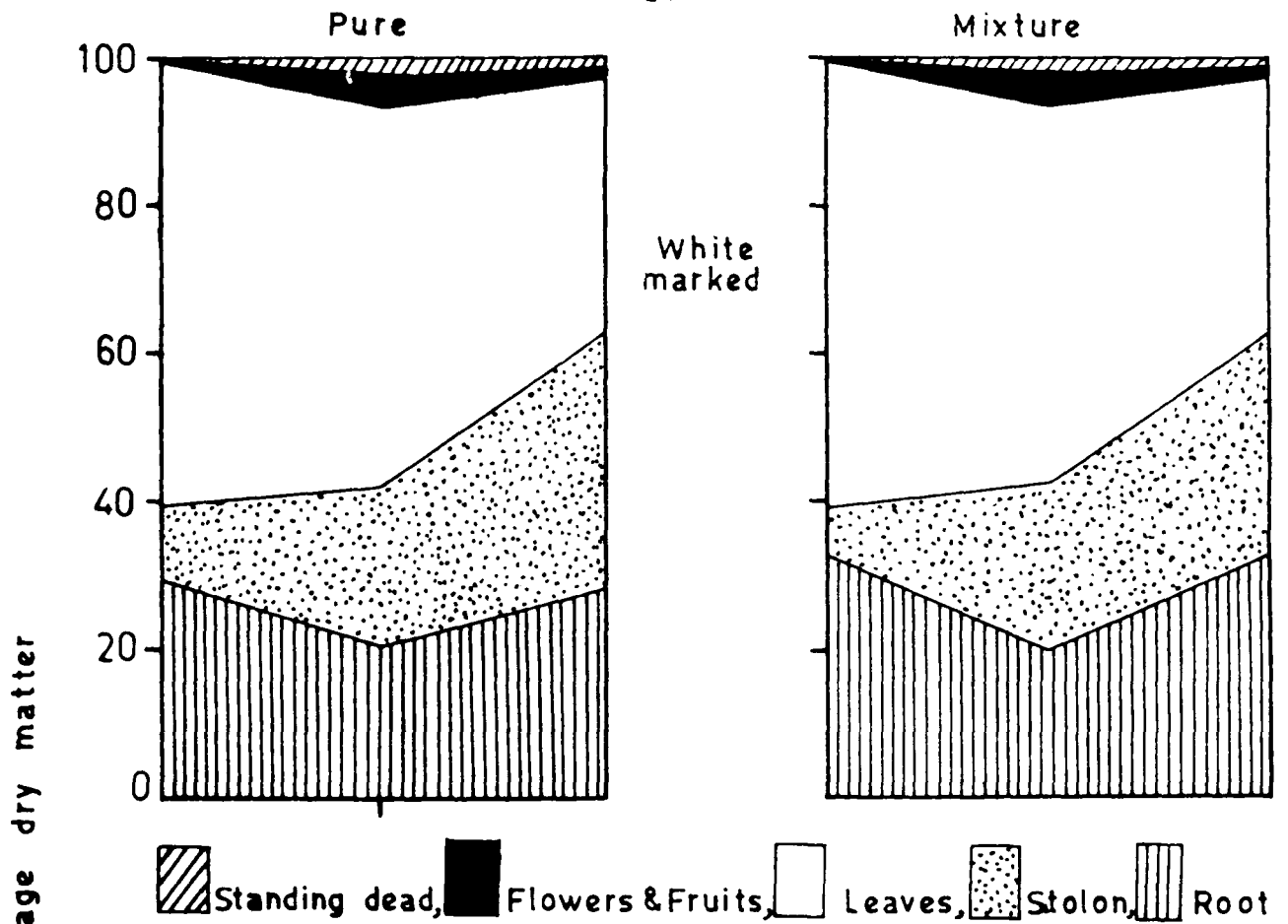


Fig. 8.5b: Dry matter allocation to various plant parts of the two populations of T. repens grown in pure and in mixture under low N regime at three harvests taken after 14 (1), 23 (2) and 32 weeks (3) from planting.

Fig. 8.5 b

Low N



this harvest. However, the magnitude of increase in energy allocation to stolons from H_1 to H_3 was much greater in case of white marked morph at low nitrogen level. It seems that the interaction between the two morphs does not affect the energy allocation pattern.

Chlorophyll content:

In the marked population, chlorophyll content was greater in mixture than in pure stand at both the nitrogen regimes. However, no definite trend was observed in the unmarked population. At both the nitrogen regimes, leaves of the unmarked population generally contained more chlorophyll compared to the marked population (Table 8.3). Chlorophyll content was highest at H_2 in both the populations.

Nitrogen content:

The percentage nitrogen content of marked population in the above ground parts was greater in mixture than in the pure stand at high nitrogen regime. This trend was, however, reversed at low nitrogen regime. The nitrogen content of the aboveground parts of the marked population at low nitrogen did not show significant difference between pure and mixed stands. The unmarked population, on the other hand contained less nitrogen in mixture than in pure stand at high nitrogen regime, but at low nitrogen regime no definite trend was observed (Table 8.4).

Flowering and seeding behaviour:

Both the marked and unmarked populations produced more

Table 8.3: Chlorophyll content (mg/g of fresh leaves) of the two populations of T. repens grown in pure and mixed stands under two nitrogen regimes.

Nature of stand	High N			Low N			F:variance ratio
	H ₁	H ₂	H ₃	H ₁	H ₂	H ₃	
White marked in pure	2.63	24.73	15.91	2.00	16.23	11.84	336.25**
White marked in 50:50 mixture	2.45	41.02	22.35	2.78	36.86	22.17	95.60**
Unmarked in 50:50 mixture	3.41	66.35	15.44	1.93	77.67	25.31	37.85
Unmarked in pure	3.73	48.40	21.09	2.53	26.16	20.74	54.47
F:variance ratio	1.06 ^{NS}	38.18**	7.05*	1.51 ^{NS}	28.26**	15.94	

The values of white marked population at H₂ and H₃ under high N regime are significantly different (5% level) from those of low N regime, while the difference due to harvests in unmarked population are insignificant.

- ** indicate significant differences at P = 0.01
- * indicates significant differences at P = 0.05
- NS Not significant.

Table 8.4: Nitrogen content (%) of the aboveground parts of the two populations of T. repens grown in pure end mixed stands at two nitrogen regimes.

Nature of stand	High N			Low N			F:variance ratio	
	H ₁	H ₂	H ₃	F:variance ratio	H ₁	H ₂		H ₃
White marked in pure	1.16	1.68	1.64	2.73 ^{NS}	2.38	2.35	1.75	20.70 ^{**}
White marked in 50:50 mixture	1.96	2.21	2.42	11.64 [*]	0.99	2.35	1.75	63.58 ^{**}
Unmarked in 50:50 mixture	1.11	1.27	1.28	1.76 ^{NS}	2.98	2.03	1.83	22.01 ^{**}
Unmarked in pure	1.95	2.04	2.73	34.90 ^{**}	0.75	2.07	1.74	52.93 ^{**}
F:variance ratio	66.64 ^{**}	11.82 ^{**}	15.93 ^{**}		27.83 ^{**}	6.82 [*]	0.25 ^{NS}	

The values of both the populations under high nitrogen regimes are significantly different at 5% level from those of the low nitrogen regime.

** indicate significant differences at P = 0.01

* indicates significant differences at P = 0.05

NS Not significant.

fertile shoots in mixture at high nitrogen regime while at low nitrogen more fertile shoots were produced in monoculture (Table 8.5). In white marked population the number of fertile shoots increased at high soil nitrogen regime both in pure and mixed stands. The unmarked population also showed similar response in mixture but in pure stands, fertile shoot production was reduced at high nitrogen level.

Per pot seed production in the white marked population in mixture was more than in pure at low nitrogen regime whilst at high nitrogen regime seed production in pure stand yield was more than in mixture as well as that of the monoculture of unmarked morph (Fig. 8.6). In pure, the seed output of the marked population was higher than that of the unmarked population at high nitrogen regime, but the unmarked population did not show any significant increase due to soil nitrogen.

DISCUSSION

The accumulation of dry matter in the mixed stands by the white marked morph was lesser than in the pure stand at low N level in spite of greater leaf area in pure stand. Similarly, in the unmarked morph as well, the wide difference in leaf area values in the pure and mixed stands is not reflected in dry matter yield which is almost equal in the two types of stands (Fig. 8.3). At high N level, the dry matter yield of the marked morph at H₃ was higher in mixture than in pure whereas the photosynthetic area was greater in pure stand. The same trend

Fig. 8.6: Replacement diagram based on total seed output per pot of the two populations of T. repens after 32 weeks from planting. The symbols $\text{---}\bullet\text{---}$, $\text{---}x\text{---}$ and $\text{---}o\text{---}$ stand for marked population, unmarked population and combined seed output respectively.

Fig 8.6

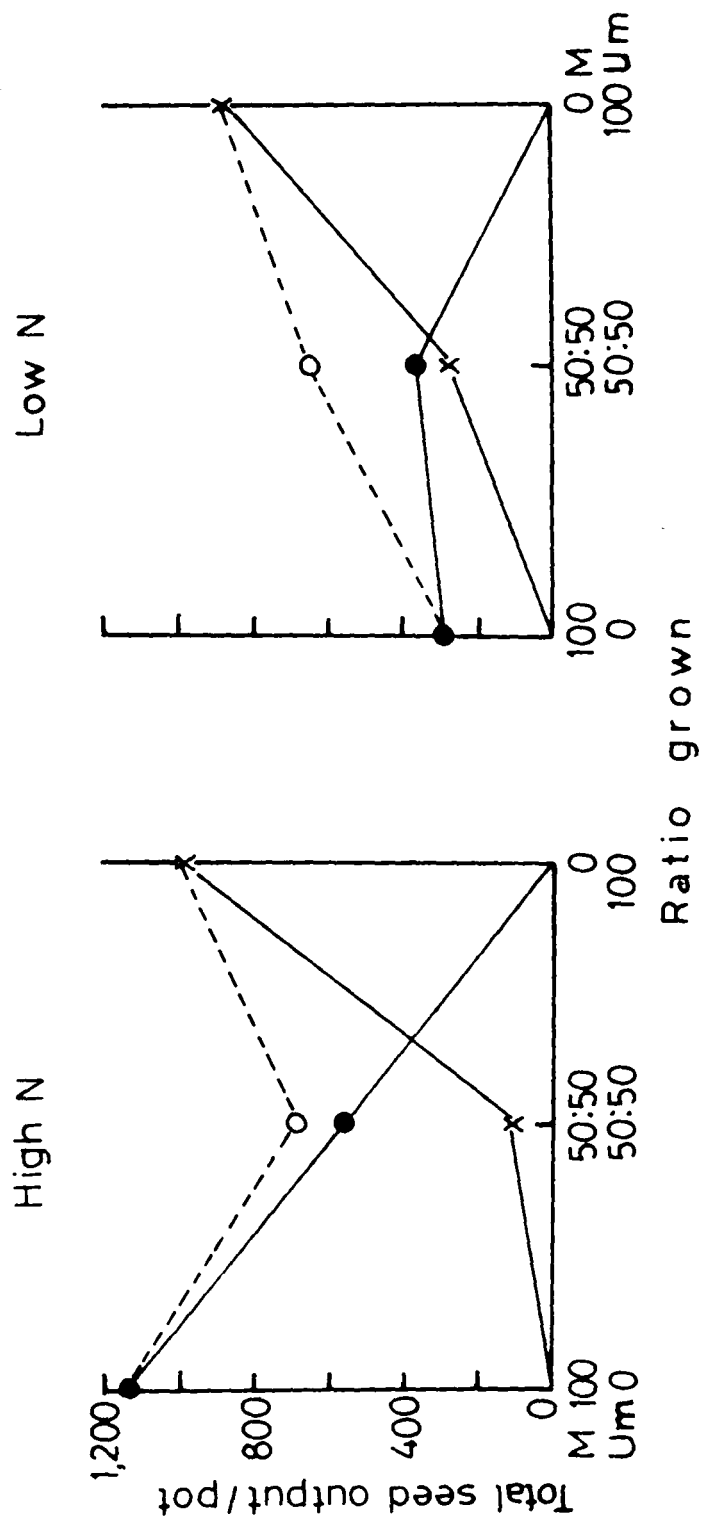


Table 8.5: The degree of flowering as indicated by the percentage of fertile shoots to the vegetative shoots (each node with a leaf and root system was considered as an individual shoot) of the two populations of T. repens after 24 weeks (H_3) from planting grown in pure and mixed stands at two nitrogen regimes (average value \pm S.E.).

Nature of stand	Nitrogen regimes	
	High N	Low N
Pure marked (100%)	10.01 \pm 0.60	12.90 \pm 0.25
Mixed marked (50%)	14.72 \pm 2.0	6.37 \pm 1.56
Mixed unmarked (50%)	7.22 \pm 0.33	7.10 \pm 1.0
Pure unmarked (100%)	6.31 \pm 0.50	10.60 \pm 1.10

was repeated by the unmarked morph also at high N level. It appears, therefore, that the efficiency of resource utilization increases in the mixed stands. Similarly, lesser chlorophyll content of the marked population in pure than mixed stand suggests that this population suffers from intra-population competition in respect of resource utilization for the synthesis of chlorophyll in the plant body while the unmarked population does not suffer to the same extent in pure stand (Table 8.3). Lower chlorophyll content of the marked population may be attributed to the air spaces present within the palisade tissue. However, increased soil nitrogen appears to have stimulated chlorophyll synthesis in the marked population, both in pure and mixed stands. Chlorophyll content of leaves in the unmarked population was not affected by soil nitrogen.

The stolon length of the two morphs at both the nitrogen regimes was relatively greater in the mixture than in monoculture which indicates that the interference amongst the individuals of the same population causes greater suppression in stolon production. The increase in stolon length in the mixture is much higher at high N regime particularly at H₂ which shows that the intensity of competition in the monocultures is more severe under increased soil nitrogen. At H₃ the unmarked morph showed greater increase in stolon length in mixture at low N level.

Allocation pattern shows that a greater proportion of the assimilates is allocated to leaf tissue at low nitrogen

level in the white marked morph. In spite of this, the dry matter yield of this morph is much lower than that of the unmarked morph (Fig. 8.3), which may be attributed to the presence of lesser amount of 'sink' tissue (Stolon in this case) in the white marked morph (Fig. 8.5b). The difference in the dry matter yield of the two morphs as exhibited at low nitrogen regime is considerably narrowed down at high nitrogen regime (Fig. 8.3) where the allocation to 'sink' tissue in the two morphs is also not much different from each other in both pure and mixed stands (Fig. 8.5a) indicating that the energy allocation to different structures is also modified by the soil nitrogen.

The dry matter data suggest that the competitive success of the two morphs is controlled, at least in part, by the soil nitrogen regime. This is revealed by the poor competitive ability of white marked morph at low nitrogen level and its better performance at high N level (Fig. 8.3). The relative yield values also confirm this fact (Table 8.2). In spite of accumulating more dry matter, the unmarked morph seems to be a weak competitor than the white marked morph indicated by the data on relative yield and quotient of relative yield at the final harvest (Table 8.2). Thus, the aggressiveness of the two morphs may be greatly modified by the soil nitrogen. The increased soil nitrogen caused considerable increase in yield of the white marked morph both in pure and mixed populations whilst yield of the unmarked morph was practically unaffected.

Thus, the present study is partly in contrast to the findings of Cowling (1961) who reported that the nitrogen fertilizer does not result in the increased yield of the white clover. The yield response of the white marked morph of T. repens to applied nitrogen is, however, in conformity with the results reported by Dilz and Mulder (1962) in case of red clover growing in acid soils and by Drysdale (1966) in white clover. It is clear that the nitrogen requirement of the white marked morph is greater than the unmarked morph. This is also reflected in the nitrogen content (%) of the two populations. At high soil nitrogen, nitrogen content of the marked population had more nitrogen in mixture than in monoculture showing its competitive superiority over the unmarked population at high soil nitrogen regime. Conversely, the unmarked population suffers more from inter-population competition at high soil nitrogen regime, although at low soil nitrogen regime the nitrogen content of this population was greater in mixed than pure stand. It could be argued that the nitrogen uptake by a given population of T. repens depends not only on the soil nitrogen level but also on competition from the other population. Vallis et al. (1977) found that the uptake of nitrogen by the legumes (Lotononis bainesii and Trifolium repens) increased considerably when competition from the grasses (Digitaria decumbens and Chloris gayana) was reduced.

An increase in flowering of both the populations in mixture at high nitrogen regime and a decrease at low nitrogen

level indicate the modifying influence of soil nitrogen on competitive interaction. The magnitude of increase or decrease in mixture over the corresponding monoculture was more pronounced in the marked population thus indicating differential response of the two populations to competition at different soil nitrogen levels.

T. repens reproduces both vegetatively and sexually and has both 'r' and 'K' strategies (Turkington and Cavers, 1978). Reproduction by seeds permits long distance dispersal although at a very high risk for propagules while the vegetative reproduction places daughters close to the parents with low risk. At low nitrogen level, the reproductive allocation in the marked population was always greater in mixture than in pure stand, while allocation to the other population in pure and mixed stands was almost same. It could be argued that under nutrient-stressed situation the unmarked population may be more successful in mixed stands in terms of reproductive allocation which may confer an advantage on this population in the maintenance and spread of its population. Incidentally the field observations on relative abundance of marked and unmarked populations also indicate that the former occurs more abundantly in fertile soils (Chapter 2).

The chlorophyll content in the marked population was comparatively less than in the unmarked population but it appears that the marked population has a subtle way of utilizing resources and owing to its greater allocation to stolons it might be able to regenerate rapidly in the established swards.

Cahn and Harper (1976b) have shown that animal grazing may be one of the factors for the failure of unmarked morph to dominate over the marked morph. The present study, however, shows that the competitive success of the two morphs may be determined by the soil nitrogen as well.

C H A P T E R 9

GROWTH OF TWO LEAF MORPH POPULATIONS OF TRIFOLIUM REPENS IN
RELATION TO THEIR PROPORTION IN MIXTURE

INTRODUCTION

It is quite evident from the previous experiment (Chapter 8) that the dominance of 'white marked' population of T. repens over that of 'unmarked' population is partly controlled by soil nitrogen regime, although some other studies (Charles, 1968; Cahn and Harper, 1979b) have shown that their dominance is controlled by predation. Cahn and Harper (1979b) have further shown that the white mark on the leaflets of T. repens protect it from the grazing animals like sheep, indicating thereby that the presence of white marks on the leaflets is of adaptive significance.

It is expected that these two populations of T. repens differing in leaf character exist with different proportion in the grassland situations. Thus both the populations are expected to undergo intense competition from increasing density of each other. Hence the present study has been carried out to investigate the effect of different proportions of two populations of T. repens distinguishable by the presence or absence of 'V'-shaped marking on the leaflets, on their competitive behaviour.

MATERIALS AND METHODS

The stolons of the two clones of Trifolium repens differing in leaf character, one with 'V'-shaped conspicuous white markings on the leaflets and the other with no such

markings were collected. The stolons of the two morphs were cut into 2 cm pieces of 0.2 cm diameter, each with one trifoliate leaf to serve as propagule for raising the populations. The cuttings were sown to give a replacement series of marked to unmarked in the ratio of 100/0, 75/25, 50/50, 25/75 and 0/100. For this a total of 24 cuttings was sown on 23rd April 1979 in each of the pots filled with garden soil mixed with compost manure in the ratio of 5:1. After sprouting, the population was thinned down on 30th April to the desired density of 8 plants/pot for pure stands, where each plant was arranged at a distance of 2 cm from the other in a circular manner. In case of mixed stands of 50:50 ratio, 12 pieces of each of the two populations were sown per pot and on sprouting, the thinning was done in such a manner that each pot of the mixed stand contained 4 plants of each of the two populations, which were arranged alternately at a distance of 2 cm from each other in a circular manner. In case of the mixed stands of marked to unmarked, in the ratio of 25/75 and 75/25, a total of 6 marked and 18 unmarked and 18 marked and 6 unmarked stolon pieces were respectively sown in each pot. After sprouting it was later thinned down to a desired density of 8 plants/pot constituting 2 marked + 6 unmarked and 6 marked + 2 unmarked arranged in a circular manner with two stolons of the same population in the opposite direction facing each other and on either side of the population, three stolon pieces of the other population were arranged in such a manner that the distance between any two stolons was 2 cm.

The experiment was conducted in the plastic pot of 21 cm diameter kept in an unheated net house roofed with polythene sheet in the premises of the Department of Botany, North-Eastern Hill University, Shillong. The experiment was started on 23rd April and terminated on 30th July, 1979. The first harvest (H_1) was taken after 8 weeks from the commencement of the experiment and the second harvest (H_2) was taken after 14 weeks of growth. At each harvest the total stolon length, number of fertile shoot and dry weight of belowground and stolon and other aboveground parts were estimated. The total leaf area per plant could be accurately estimated only at first harvest, and so, the data based on the first harvest only have been presented for this parameter.

The dry weight was determined by drying the plant material in an oven at 80°C to constant weight.

RESULTS

The total leaf area per plant of the marked population was greater in pure stand than in mixture while the unmarked population behaved just the reverse. The marked population grown in the mixture with greater proportion of the unmarked population showed reduction in its leaf area (Table 9.1).

Although the unmarked population showed an increased leaf area in the mixture, the stolon length and stolon weight did not show any increase in mixture at H_1 . However, the values

obtained at H₂ for these two parameters were higher than the pure stand values. The marked population, on the other hand, generally produced greater stolon length and put more weight in stolon in mixed stands than in pure at both the harvests. With increase in proportion of unmarked population, stolon length and weight of the marked population in mixture tended to increase at H₁, while the reverse was true in case of unmarked population (Table 9.2). The same trend was followed at H₂ but the marked population in 50:50 mixture produced lesser dry weight than its pure stand. In the mixture with 25% marked to 75% unmarked populations, the dry weight produced by the former was, however, higher than its pure stand yield.

The marked population accumulated more dry matter in mixture as compared to the corresponding pure stand (Table 9.3). The unmarked morph showed just the reverse. Also with increase in proportion of the unmarked population in mixture the dry matter production of the marked population increased. The trend exhibited at H₁ by the two populations was maintained at the final harvest. The total yield per pot in mixture was intermediate between the monoculture yield of the two leaf morph populations (Fig. 9.1).

The marked population showed an increased dry matter allocation to belowground parts in the mixture with 25% marked and 75% unmarked population (Fig. 9.2a). Conversely, the unmarked population showed reduced allocation to belowground

Table 9.1: Total leaf area per plant (sq. cm) of the two populations of Trifolium repens grown in pure and mixed after 2 months of growth.

		% Ratio of Marked to Unmarked					
Pure Marked	Marked + Unmarked	Marked + Unmarked	Marked + Unmarked	Pure Unmarked			
	75%	50%	25%	75%			
351.08	270.38	289.71	255.81	286.15	192.56	201.60	161.73

Difference due to ratio in both the marked and unmarked populations are significant at 5% level, but due to species insignificant.

Table 9.2: Stolon length (cm) and stolon weight (g) per plant of the two populations of Trifolium repens grown in pure and mixed stands.

		Mixed stands with % ratio of marked to unmarked population						
Parameters	Pure Marked	Marked + Unmarked	Marked + Unmarked	Marked + Unmarked	Pure Unmarked			
	75%	25%	50%	25%	75%			
Harvest I								
Stolon length (cm)	45.13	55.33	78.42	64.42	51.17	93.75	64.17	59.08
Stolon weight	0.21	0.39	0.57	0.42	0.53	0.47	0.67	0.28
Harvest II								
Stolon length (cm)	134.25	184.25	160.33	226.00	186.00	233.67	201.50	206.17
Stolon weight	3.18	3.23	2.19	2.01	2.54	3.31	2.50	3.17

Difference due to harvests in both the populations in both stolon length and its weight significant at 1% and due to ratio at 5%, but due to species insignificant.

Table 9.3: Total yield (g) per plant of the two populations of T. repens grown in pure and mixed stands.

Harvests	Mixed stands with % ratio of marked to unmarked populations						
	Pure marked	Marked + Unmarked	Marked + Unmarked	Marked + Unmarked	Pure Unmarked	Pure Unmarked	
	75%	25%	50%	50%	25%	75%	
Harvest I	0.75	1.35	1.31	2.01	0.92	2.28	2.74
Harvest II	6.56	6.43	9.39	7.36	9.27	7.17	8.88

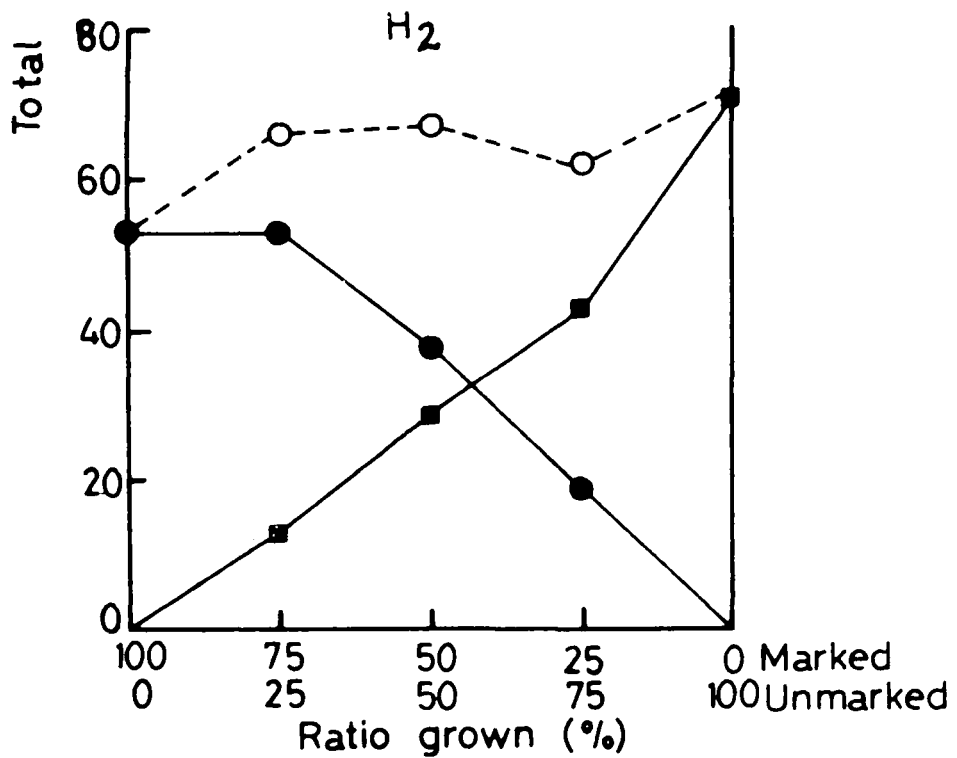
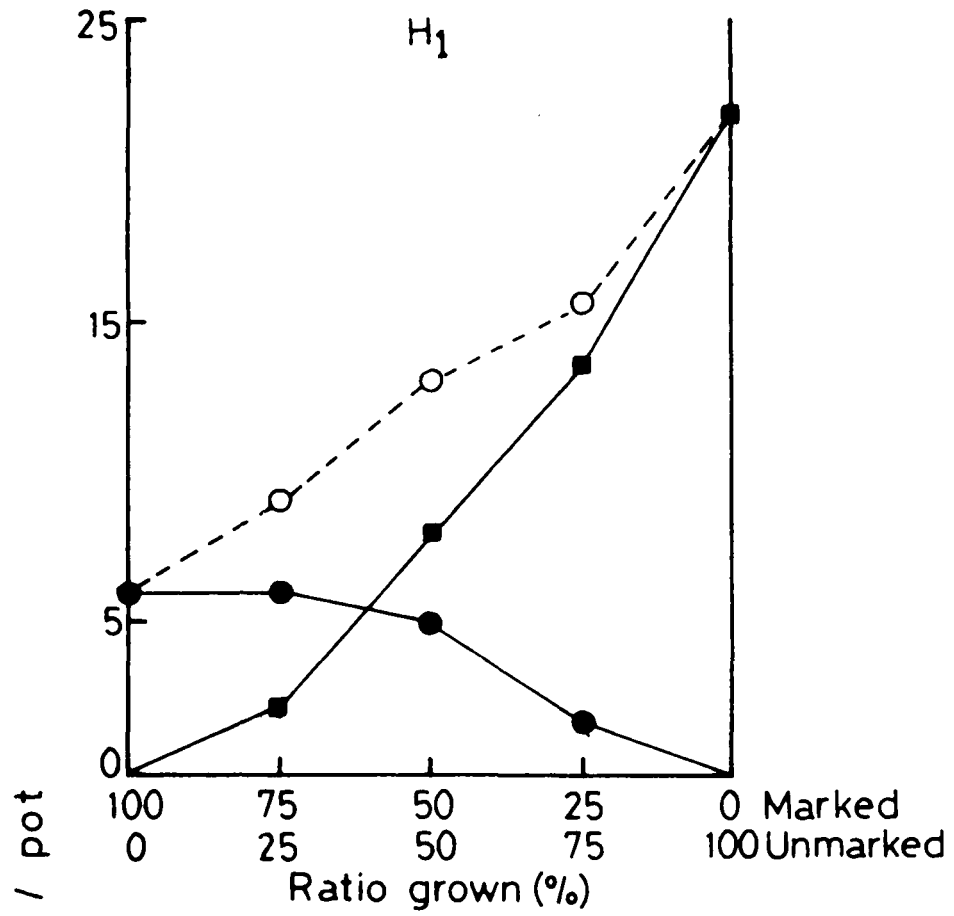
Difference due to harvests in both the species significant at 1%, due to ratio at 5% and due to species at 5% at H_1 but at H_2 the difference is insignificant.

Table 9.4: Number of fertile shoots per pot of two populations of T. repens grown in pure and mixed stands at maturity (average value \pm S.E.).

Pure Marked	Mixed stands with % ratio of marked to unmarked populations						
	Marked + Unmarked	Marked + Unmarked	Marked + Unmarked	Marked + Unmarked	Pure Unmarked	Pure Unmarked	
	75%	25%	50%	50%	25%	75%	
4.0 \pm 1.0	3.0 \pm 1.0	4.0 \pm 1.0	6.0 \pm 1.0	10.0 \pm 1.0	6.0 \pm 1.0	4.0 \pm 1.0	6.0 \pm 2.0

Fig. 9.1: Replacement diagram based on total yield/pot of the two populations of T. repens at two harvests grown in pure and mixed stands. The symbols —●—, —■—, and ---o--- stand for marked population, unmarked population and combined yield respectively.

Fig. 9.1



parts in the mixtures at H_1 . At the final harvest, however, the allocation pattern did not show any definite trend (Fig. 9.2b). The marked population showed an increased allocation to the belowground parts both in pure and mixed stands with time and so was the case with the unmarked population in the mixtures. The allocation to below and aboveground parts remained unchanged from H_1 to H_2 in pure stand of the latter population.

Both the leaf morph populations showed maximum flowering and seed setting in 50:50 mixture (Table 9.4, Fig. 9.3). The total number of fertile shoots per pot in mixture was always higher in the monoculture of both the populations. The marked population also produced maximum number of seeds per pot in 50:50 mixture, while in case of the unmarked population maximum seed production (number of seeds per pot) was observed in pure stand (Fig. 9.3). Per pot seed production was observed to be the highest in the mixture 50:50 marked and unmarked population and with increase or decrease in proportion of the two leaf morph populations in mixture resulted in reduced seed output per pot.

DISCUSSION

The white marked population showed greater stolon length and weight in mixture than in monoculture while the unmarked population suffered in mixture indicating that the marked population is a better competitor. This is also confirmed by dry weight production data in mixture and monocul-

Fig. 9.2(a): Percentage allocation of dry matter to aboveground and belowground parts of the two populations of T. repens after 8 weeks from planting in pure and mixed stands.

Fig. 9.2 (a)

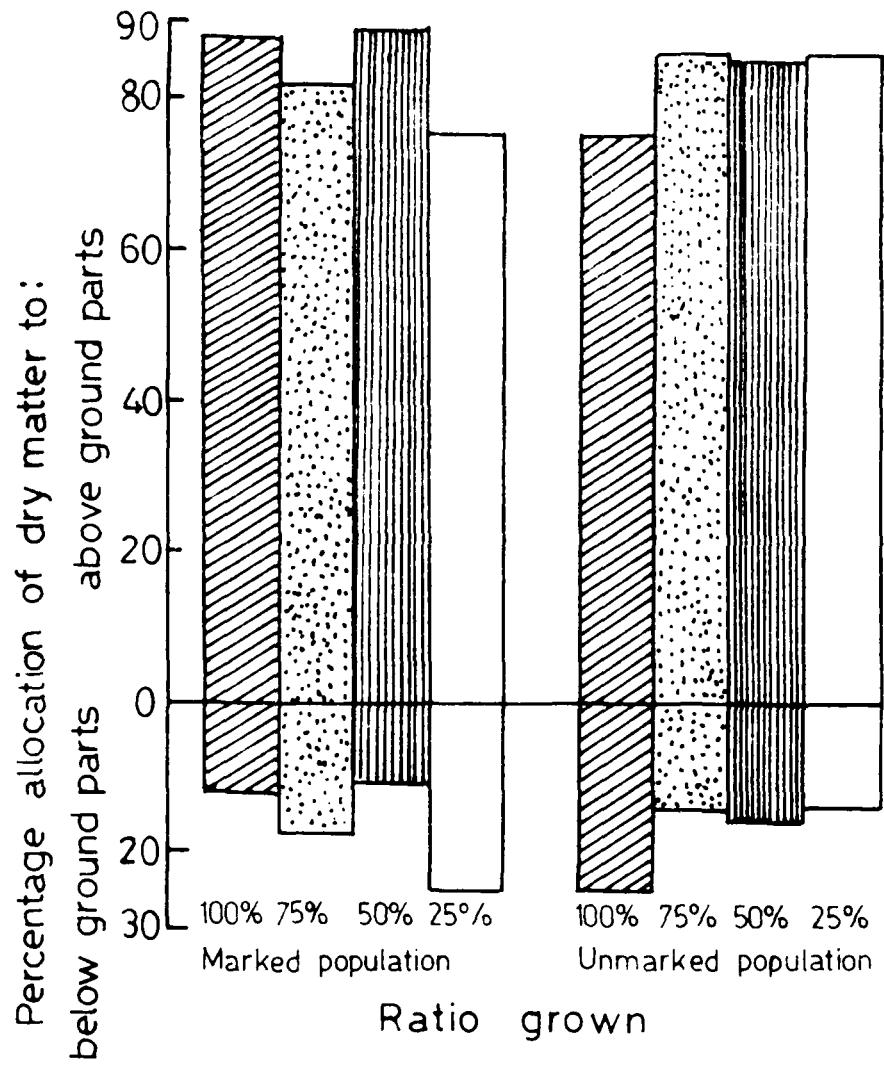


Fig. 9.2(b): Percentage allocation of dry matter to above-ground and belowground parts of the two populations of T. repens after 14 weeks from planting in pure and mixed stands.

Fig. 9.2 (b)

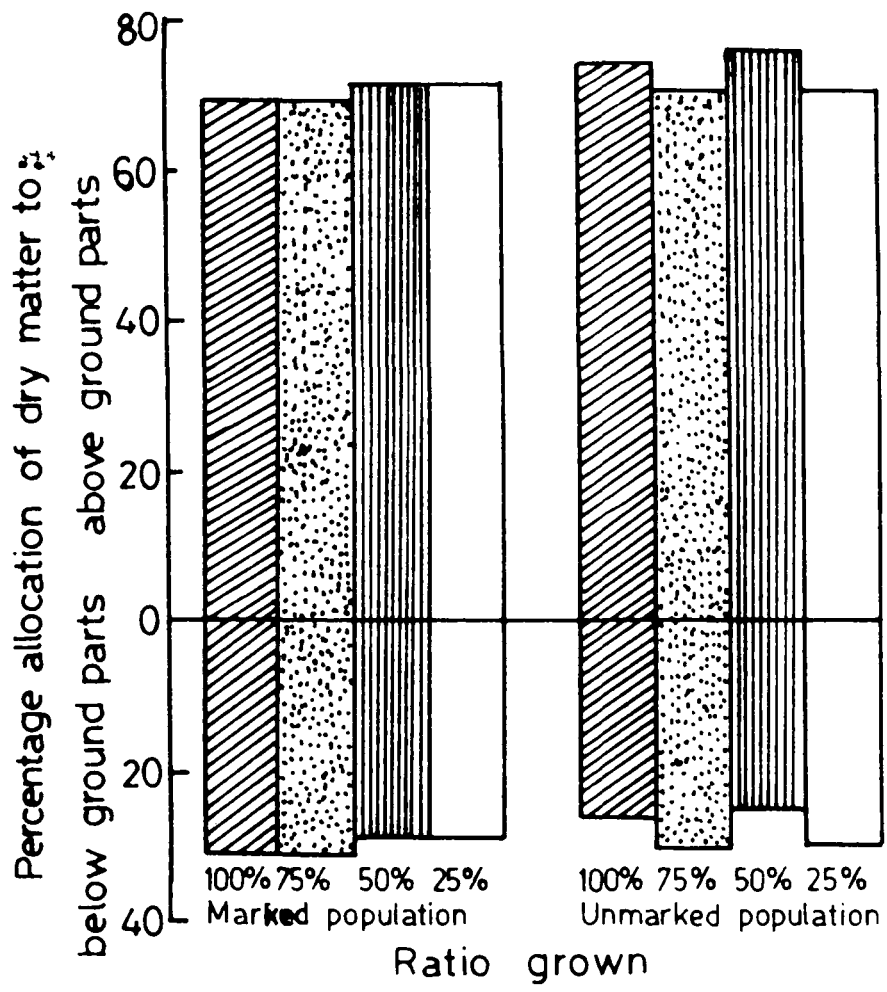
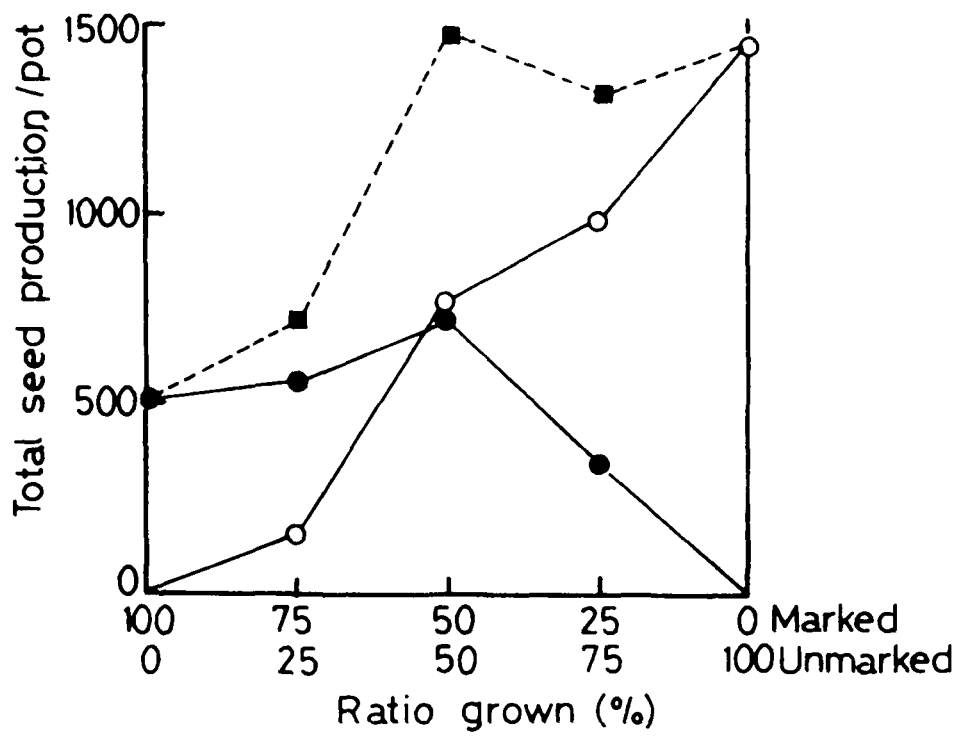


Fig. 9.3: Replacement diagram based on total seed production per pot of the two populations of T. repens grown in pure and mixed stands after 14 weeks from planting. The symbols $\text{---}\bullet\text{---}$, $\text{---}\circ\text{---}$ and $\text{---}\blacksquare\text{---}$ stand for marked population, unmarked population and combined seed production respectively.

Fig. 9.3



ture (Table 9.3) of the two populations. The total yield per pot of the marked population in the ratio of 75% marked + 25% unmarked mixture was higher than its pure stand yield showing that 6 plants in the above mixture could accumulate greater biomass than 8 plants in monoculture. This indicates that the marked population is more sensitive to self-crowding, whilst the unmarked population seems to be more susceptible to inter-clonal competition. Although the unmarked population had greater leaf area in the pure stands, the yield did not show any increase in mixture. In fact, the pure stand yield was rather higher in the unmarked population, indicating thereby that the dry matter production is not a function of leaf area alone. Probably, some role in photosynthetic assimilation may also be attributed to the stolons particularly in young stages. Thus, the marked population with greater stolon length manages to assimilate better although the leaf area value happens to be lower in this case.

The marked population produced more fertile shoots and seeds in mixture as compared to the monoculture. Also the marked population did better in terms of flowering and seeding in comparison to the unmarked population in the mixed stands. The mixed stand yields of the per unit area which further confirms the competitive superiority of the marked population, although the pure stand yields of the unmarked population was relatively higher.

There was some effect of interference between the two populations in the allocation of resources to the above and the belowground parts at H_1 . The higher allocation to belowground parts in the marked population in mixed stands in the early stage of growth may contribute to better exploitation of belowground resources by the marked population. Conversely, the unmarked population allocates more dry matter to belowground parts in pure stand showing that the presence of the marked population in mixture probably brings about a reduction in allocation of resources to the root system. Thus it appears that the marked population adopts a strategy of diverting more resources to the root system when it grows in mixture with other clone making it more efficient in the capture of belowground resources. Further, the greater accumulation of dry matter in the stolons of the marked population in mixture might stimulate the production of more rametes due to increased translocation of assimilates towards stolons.

The inputs of new genotypes through seedling establishment appear to be extremely rare for various perennial species as reported by Sagar and Harper (1960) in Plantago species and Putwain and Harper (1970) in Rumex acetosa and R. acetosella. Similarly, the production of seedlings in T. repens is very rare in the established grasslands (Cahn and Harper, 1976a) and the stolons are mainly responsible for population growth in sward situation. Thus, the population of T. repens which allocates greater biomass to stolons is likely to prove more

successful in resource competition.

Incidentally, the seed ~~production~~ by the marked population in the mixed stand also happens to be greater as compared to the other clone. This may presumably confer an advantage to the marked population in mixed situation under the conditions that may permit population growth even through genets.

C H A P T E R 10

GENERAL DISCUSSION

The data contained in various chapters indicate that the growth of T. repens greatly suffers when it grows in mixture with P. dilatatum, while the latter shows better growth in mixture. Thus the legume is a weak competitor than the grass. Data also reveal that T. repens is more susceptible to interspecific competition, while the grass suffers more from competition among its own individuals. In the experiment that was aimed at studying the influence of various levels of soil nitrogen on the competitive interaction, it was found that in absence of soil nitrogen (N_0), the grass depends completely on the legume for its nitrogen requirement. In monoculture, the grass failed to make any substantial growth in soil devoid of nitrogen. However, in mixture, the grass not only showed some growth but could even allocate a certain proportion of its resources for the formation of rhizome (Fig. 5.4), which plays an important role in the maintenance of its population in established swards, where seedlings have very little chance for survival.

However, irrespective of soil nitrogen levels, T. repens grew better in monocultures where it was not facing competition from the grass (Tables 5.3, 5.6 and Fig. 5.3). Although in mixture, it suffered invariably and its growth suppression was particularly evident under high soil nitrogen level. Obviously, greater soil nitrogen availability, helps the grass more than the legume whose growth is further suppressed due to competition

offered by the vigorously growing grass. This is also supported by relatively better growth of the grass in fertile soil as compared to growth of the legume (Table 2.3).

P. dilatatum is a tall growing grass with an erect habit and thus it casts shade over the legume, as a consequence of which the legume growth suffers considerably in mixed populations. It seems that competition for light is quite crucial for the legume in T. repens - P. dilatatum interaction. In earlier studies on legume-grass interaction (Donald, 1958; Stern and Donald, 1962a,b) also, a greater emphasis has been laid on the effect of light. Both species showed reduced growth due to decrease in light intensity. Leaf weight ratio (LWR) relative growth rate (RGR) and net assimilation rate (NAR) of both the species were also reduced under low light condition (Tables 7.5, 7.7 and 7.8) although effect was more severe on the legume than the grass. It appears that reduction in light intensity imposed restrictions on the utilization of other factors too that may be in abundant supply. Thus the shortage of one of the vital factors may limit the growth of plants. Donald (1958) showed that the failure of, say, the root to acquire sufficient nitrogen caused leaf development to suffer. This in turn reduced the supplies of assimilates to the root which grew less and so were less able to compete for nitrogen.

The pattern of dry matter allocation in both species changed due to low light intensity, nitrogen deficiency and

competitive stress (Figs. 7.4a,b and 5.4). This is in contrast to the findings of Harper and Ogden (1970); Abrahamson (1975); Abrahamson and Harshey (1977); Andel and Vera (1977); who observed that the allocation of resources to different plant parts remains constant under different environmental conditions. In the present study, the allocation pattern was, however, modified by the prevailing conditions which is in conformity with Hickman's observations (Hickman, 1975) that under water stressed conditions, the resource allocation in Polygonum cascadense shows plastic response. Similar results have been reported by Singh (1980) in Eupatorium adenophorum and E. riparium and by Trivedi and Tripathi (1981) in Spergula arvensis and Plantago major.

P. dilatatum showed reduction in the allocation of dry matter to belowground parts (root and rhizomes) under reduced light intensity (Fig. 7.4b). Although, at nil nitrogen level the grass and legume both failed to produce any seed, the grass in mixed stand could allocate a small proportion of its resources for rhizome formation while in pure stand the rhizomes could not be formed. This shows that the presence of the legume might be beneficial to the grass particularly in nitrogen deficient soils. T. repens, on the other hand, under nil nitrogen level could allocate a part of its resources for the formation of flowers and fruits, in both mixed and pure stands, but under high nitrogen regime, it produced seeds only in pure while in mixed stand it suffered miserably (Fig. 5.4). This indicates

that at high nitrogen level, the grass grows luxuriantly and suppresses the legume in mixed populations so much that flowering and fruiting do not occur at all. Thus, the allocation pattern not only depends on the supply of nutrients but also on the interference caused by the neighbouring species. Thus, the earlier conclusion by Harper and Ogden (1970) and Andel and Vera (1977) that the reproductive allocation is independent of nutrient level, is not applicable to T. repens and P. dilatatum.

The two species have asynchronous growth periods. T. repens shows active growth earlier than P. dilatatum, and thus having established earlier, the legume is expected to exercise controlling influence on the grass seedlings which come up later. Milthorpe (1961), showed that the establishment of plants from seeds in vegetation occurs only in bare areas arising from the death of previous occupants or from incomplete coverage. Similarly, Miles (1972) has shown that the seedling establishment within undisturb Callunetum was very poor as compared with that on bare ground.

In the grasslands under study, however, open patches do exist here and there, which could provide suitable ecological niche for the grass seedlings. Even in such places where T. repens grows, suitable conditions for seedling establishment could be created after the senescence of the legume. In any case, once the grass gets chance to establish, it grows fast and being a strong competitor (as suggested by the experimental results) can

substantially suppress the legume growth. In nature, however, P. dilatatum makes sufficient growth usually after the flowering and seeding of the legume is over. It appears that in spite of tremendous growth suppression that could be caused to the legume due to strong competitive influence of the grass, the two species manage to co-exist in nature.

It is clear that aggressiveness of the competing species often depends on the stage of growth of plants. This has also been confirmed by earlier studies (de Wit and Van den Bergh, 1965; Van den Bergh, 1968). In the present study although the two species differ in their active growth periods which certainly helps in avoiding intense competition between them, their perennial habit does afford opportunity for interference during some part of the year. After seeding, the legume becomes rather less active and the grass grows actively. Thus, the interference between the grass and the legume occurs at the expense of the legume growth (Table 4.4) and in the protected field situation where the tall growing P. dilatatum is not grazed or cut for long period, T. repens is altogether eliminated (Tables 3.2, 3.3 and Figs. 3.1 and 3.2). But, a short-term experiment set up during spring season suggests that the legume grows well and is also able to compete with the grass in mixed population during this period. Presumably, the environmental conditions, prevailing during spring are not conducive for the growth of the grass and so, the legume growth

does not suffer from competitive suppression. However if the two species are allowed to grow together for longer period, the grass seems to eliminate the legume in spite of the fact that the legume makes better growth in early stages during spring season. There are reports that the species arriving late in already established vegetation show very low densities as compared to the species arriving at an early period (Tamm, 1956; Sagar and Harper, 1960; Cavers and Harper, 1967; Putwain, Machin and Harper, 1968). But in the present case, the grass is so vigorous and aggressive that it manages to gain dominance over the legume in the grasslands.

It has also been suggested that the species showing seedling emergence earlier have an advantage in capturing the light energy over those species which arrive later (Sagar and Harper, 1961; Lazenby, 1961; Tripathi, 1969; Ross and Harper, 1972; Gupta, 1977). However, in the present study although the seedling emergence in T. repens is much earlier than the grass and it is also able to make sufficient vegetative growth before the grass enters the arena, the legume fails to compete successfully with the grass. Not only this, the legume is totally eliminated from the grasslands that are protected from the biotic disturbances for longer duration (Chapter 3) possibly due to intense competition offered to the legume due to unchecked growth of the grass.

Under nitrogen deficient soil, however, the legume grows

better than the grass in monocultures due to atmospheric nitrogen fixation in its root nodules. The nitrogen fixed in root nodules of the legume is also likely to be exploited by the grass in mixed population as evident from better growth of the grass in mixture than in monoculture particularly in nitrogen deficient medium (Table 5.5, Fig. 5.3). The nitrogen contents of the grass grown in mixture and monoculture indicate that there is a transfer of nitrogen from the legume to the grass in mixed situation (Tables 5.8, 5.9, 5.10). Thus, it would appear that presence of the legume is beneficial to the grass. This coupled with better competitive ability of the grass, makes the latter more aggressive and in spite of differences in growth habit and periods of peak growth, the factors which may help the competing species in co-existence (Lieth, 1960; Harper and Clatworthy, 1963; Turkington and Harper, 1979b), T. repens and P. dilatatum fail to co-exist if the grasslands are protected from biotic disturbances as indicated by the field experiment involving "exclosure technique" (Chapter 3). It was observed that T. repens is more resistant to trampling when grown with P. dilatatum (Chapter 6). The trampling pressure was, presumably, absorbed by tall growing P. dilatatum, giving a protection to the prostrate growing T. repens from being injured by trampling pressure. The protective role of the grass in mixture is clear by the greater damage caused to the legume in monoculture. This is in agreement with the findings of Warwick and Briggs (1978a, 1980); Warwick (1980); who reported that the species with prostrate growth form are more resistant

to clipping and trampling than the erect growing species.

P. dilatatum exercises a very strong competitive influence on T. repens but its competitive superiority is reduced by the prevailing frequent cutting, grazing and trampling which affects the grass more adversely than the legume. Although the grass suppresses and eliminates the legume, from the undisturbed grasslands, it also protects T. repens from severe biotic disturbances. Thus, the presence of the grass helps the legume in the situations exposed to intense grazing, cutting and trampling while T. repens is helpful to the grass by supplying nitrogen specially when growing on nitrogen-deficient soils (Table 5.10).

It is evident that T. repens and P. dilatatum derive benefit from each other when growing as mixed populations under certain sets of condition. As the results reveal the competitive superiority of the grass, has an over-riding influence on the legume, but the two species co-exist in the grasslands which are frequently disturbed by biotic agents. The grassland communities of Shillong and adjoining areas predominated by T. repens and P. dilatatum thus seem to have evolved due to the intense biotic pressure.

Besides the grass-legume interaction studies, an attempt has also been made to analyse the competitive interaction between the two leaf morph populations (white marked and unmarked) of T. repens, in order to assess their relative fitness in the local grassland vegetation. It was observed that the marked population

is a better competitor than the unmarked population, although the latter accumulates greater biomass than the former. The unmarked population suffers in presence of the marked population (Table 9.3, Fig. 8.1) which may be attributed to the greater stolon production by the latter in mixture (Table 9.2). It may be mentioned that the stolon production not only helps in the regeneration but also stimulates the production of photosynthate.

Increase in soil nitrogen confers further competitive advantage on the marked population (Table 8.4). Field observations on growth of the two leaf morph populations also indicated that the marked population grows better than the unmarked population in fertile soil (Table 2.6). Under high soil nitrogen regime, dry matter yield, stolon production and seed output of the marked population were greater than the unmarked population in mixed stands. As observed by Cahn and Harper (1976a), the establishment of plant through seedlings in T. repens is quite rare in the established grasslands, and the stolons are mainly responsible for population growth and regeneration. Further, a greater seed production of the marked population than the unmarked one may give an added advantage to the former in invading open areas.

It has been suggested that the unmarked morph is less grazed than the marked morph by the grazing animals, as the markings in the leaf, helps the animals to selectively graze the marked population (Charles, 1968; Wolton ~~et al~~ 1970). As revealed by the field observations (Table 2.5) which conforms with the

findings of Cahn and Harper (1976b) who reported that the grazing animals like sheep avoid the white leaf mark population of T. repens and graze mostly upon the unmarked population thereby restricting the dominance of the unmarked morph. In the present study, however, the marked population showed an edge over the unmarked one. In addition to the effect of grazing, the soil nitrogen also seems to decide the dominance of one population of T. repens over the other as shown by the pot culture experiment (Chapter 8), emphasising the need for further studies involving the combined effect of grazing and soil fertility.

The present work throws some light on certain aspects of the competitive interaction and co-existence of T. repens and P. dilatatum and relative fitness of the two leaf morph populations of T. repens in the grasslands of Shillong and adjoining areas; but further work on the following aspects could also be done in order to understand the competitive biology of these species better.

- a) T. repens and P. dilatatum are capable of reproducing both from seeds and vegetative propagules (rhizomes in case of the grass and stolons in the legume). Thus, a study involving the reaction of the individuals raised from seeds on those from the rametes of the same or different species might be interesting.
- b) The response of the seedling population of the two species to different field conditions could also be studied.
- c) In the grass-legume mixtures under field conditions, the

predators like slugs and catterpillers are found to cause an extensive damage to the legume, because of its greater palatability. This might affect the botanical composition of the local swards, tilting the balance in favour of the grass. So, a study relating to the predators on these two species in mixed and pure cultures may form an important aspect that may be taken up in future.

d) A detailed study on the behaviour of the two leaf morph populations of T. repens as related to altitudinal variation, grazing and other biotic factors may also be undertaken for better understanding of the biology of these micro-populations.

SUMMARY

The thesis embodies the results pertaining to the studies on grass-legume interaction. The species selected for the present study are Paspalum dilatatum (a grass) and Trifolium repens (a legume). Both species are perennial and grow abundantly in the grasslands of Shillong and adjoining regions, and have good fodder value. They represent a sympatric pair of species but differ in growth habit.

P. dilatatum has an erect habit and T. repens is prostrate growing. Besides, their growth is somewhat asynchronous and one of them, T. repens, is capable of exploiting atmospheric nitrogen. Thus, the competition studies between them under varied ecological conditions prevailing in their natural habitats were carried out. A summary of the results of the field and culture pot experiments is given below:

Effect of simulated grazing and cutting:

The response of the two species to simulated grazing was studied using 'exclosure technique' in the field condition where both the species were growing together. The herbage was removed at the ground level at three months interval for a year beginning from May 1978. The data on density, total leaf area, total herbage yield and the number of reproductive shoots of the two species were recorded in both the treated and control plots.

The density of T. repens was much greater in the treated than in the control set, while P. dilatatum showed

the reverse trend. Both species seemed to maintain an equilibrium in density in the treated plot. Leaf area and dry matter yield also showed a trend similar to density. Although, P. dilatatum showed slightly stunted growth in the treated plot, it quickly recovered from the herbage removal treatment and was able to produce some flowering shoots, but the reproductive potential was greatly reduced due to the treatment. T. repens, on the other hand, showed substantially reduced density, and growth in the protected plot. The severe competition offered by the grass which grew luxuriantly in absence of herbage removal, suppressed the legume substantially. It was concluded that the co-existence of the two species in the grassland of Shillong is possibly due to constant grazing and biotic disturbances operating in nature.

Effect of season:

Pure and mixed populations of T. repens and P. dilatatum were raised in different seasons to study the effect of season on their competitive interaction. Besides these short-term experiments, a long-term experiment was also conducted to study competitive behaviour of the two species over a period of one year.

At each observation period, in both the long- and short-term experiments, the number of stolons or rhizomes, number of leaves, total leaf area, dry matter yield, allocation of dry matter to above- and below-ground plant parts and number

of fertile shoots were estimated.

T. repens produced more stolons in pure than in mixed stands while P. dilatatum produced more tillers in mixture than in pure stand under long-term experiment. Similar trend was exhibited by leaf area and dry matter yield.

In long-term experiment the flowering of T. repens was much lesser in mixture than in monoculture while P. dilatatum produced more fertile shoots in mixed than in pure stand both in the long- and short-term experiments.

Both species showed poor growth in winter, but immediately after the winter season i.e. during March-April, T. repens showed much better growth. It also showed profuse flowering in April-May when P. dilatatum was still in the seedling stage. This asynchronous active growth period of the two species might be helpful in minimizing the severity of competition between them. However, they failed to co-exist in nature for longer period in such situations where herbage removal and biotic disturbances did not exist.

Competition at varying nitrogen levels:

Sand culture experiment was carried out using 3 levels of nitrogen to study the effect of soil nitrogen on competitive behaviour of the two species by growing them in pure and mixed stands at the same over-all density.

Both the species suffered due to nitrogen deficiency of soil in the beginning. But with passage of time, the legume (T. repens) showed comparatively greater yield and produced more stolons and leaves and even could allocate a part of its resources for sexual reproduction (flowers and fruits) in the mixed stand. The better performance of T. repens in mixture at nil nitrogen level could be attributed to relaxed competition from the grass which suffered severe setback due to nitrogen deficiency in the growth medium. At higher nitrogen regimes, however, the legume grew better in monoculture than in mixture.

At lowest nitrogen level (N_0) the growth of P. dilatatum was greatly suppressed in pure stand but in mixed stand it showed comparatively better growth. Thus it appears that in mixed situation the grass benefits from the legume in terms of nitrogen supply. This is also evident from the higher nitrogen content of the grass in mixture as compared to pure stand. At higher nitrogen levels, P. dilatatum grew very luxuriantly particularly in the mixed stands where the legume showed much reduced growth indicating that the grass is a stronger competitor than the legume if the supply of nitrogen was not limited.

Effect of simulated trampling:

Under field conditions, the two species are subjected to varying degree of trampling by man and grazing animals. In order to know whether trampling influences the competitive behaviour of P. dilatatum and T. repens, their pure and mixed

populations grown at the same overall density were subjected to simulated trampling treatment.

Trampling treatment had more severe effect on P. dilatatum than T. repens and so, the competitive effect of the grass on the legume was minimized where the mixed populations were subjected to trampling treatment. An analysis of growth of T. repens in pure and mixed populations in relation to trampling clearly reveals this fact. Although P. dilatatum showed better growth in mixture than in monoculture, its growth in mixture was particularly better in absence of trampling. While the grass always contributed more to the combined yield in mixture the percentage contribution by the grass decreased with increase in trampling pressure. The relative yield and fertile shoot production also showed similar trend.

Competitive interaction as affected by light regimes:

The two species were grown in pure and mixed stands at the same overall density under two light regimes to examine the effect of light on competition between T. repens and P. dilatatum.

Under high light regime, the legume produced more stolons in pure than in mixture while at low light intensity stolon production was more in mixed stand. P. dilatatum, however, produced more tillers in mixture as compared to pure stand under both the light conditions. Growth of both the species was retarded under decreased light intensity but the decrease in

growth of the legume was more pronounced. Under both the light regimes, the contribution by the grass to the combined yield was much greater than that of T. repens and the R.G.R. and N.A.R. values were also higher for the grass.

Under high light intensity, the legume allocated a part of its resources to reproductive structures in pure stand but in mixed populations no flowering was observed. The relative yield values of both species and their RYT were much lesser under low light regime. Besides decrease in light intensity, the competition offered by the grass further contributes to the reduction in growth of the legume.

Interaction between the two leaf morph populations of T. repens:

Two distinct leaf morph populations of T. repens were observed to occur in the local grasslands. One population is characterised by having 'V' shaped white marking on the leaflets (white marked population) while the other population has no such leaf marking (unmarked population). The field observations suggest that the two leaf morph populations have differential nitrogen requirement and they grow mixed together in varying proportions. Thus, an attempt was also made to analyse the competitive behaviour of the two populations of T. repens as influenced by soil nitrogen and their proportion in mixed stands.

Effect of soil nitrogen:

The two leaf morph populations of T. repens were grown

in pure and mixed stands in the experimental pots according to de Wit's replacement series under high and low nitrogen regimes. The measurements were made in respect of stolon length, leaf area, number of fertile shoots, dry weight and allocation of dry matter to different plant parts. Besides, chlorophyll content in the leaves and nitrogen content in the aboveground plant parts were also determined.

Both the morphs produced more stolons in mixture than in monoculture at low nitrogen regime. The stolon production by the white morph was stimulated by the addition of nitrogen while the unmarked morph did not show such a behaviour. However, the leaf area per plant of the unmarked morph was greater in mixture at low nitrogen level while under high nitrogen regime, the plants grown in pure stand produced larger leaf area.

Yield of the white morph both in pure and mixed stands increased under high soil nitrogen regime, while the unmarked morph was unaffected by the addition of soil nitrogen. The dry matter allocation pattern of the white marked population was slightly changed due to added soil nitrogen, particularly in the early stages, when the allocation towards leaves was much less and to stolons much greater than the corresponding values at low nitrogen level.

Chlorophyll and nitrogen content, flowering and seed production of the white marked population increased with increase in soil nitrogen. Thus the nitrogen requirement of the white

marked population seems to be higher than that of the unmarked population. The quotient of relative yield values showed that the white marked population was more competitive as compared to the other morph. This confirms the field observations with regard to greater abundance of the white marked population than the unmarked population on fertile soils.

Growth of the two populations of *T. repens* in relation to their proportion in mixture:

The two leaf morph populations of *T. repens* were grown in monoculture and mixed stands in different proportions (25, 50, and 75%) at an overall density of 8 plants per pot.

It was observed that the marked population produced greater leaf area in pure than mixed stand, while the unmarked population produced larger photosynthetic area in the mixed stands. However, stolon length and weight of the marked population showed an increase in mixture over the corresponding monoculture values.

Similarly, the dry matter yield of the marked population was also more in mixture than in pure stand. Further, with increase in proportion of the unmarked population in mixture dry matter yield of the marked population increased indicating that the latter population is probably more sensitive to intra-morph competition.

The maximum number of seeds/pot was produced by the

marked population in mixture having equal proportion of the two populations, while the unmarked population produced maximum number of seeds in pure stand. Thus it seems that besides soil nitrogen controlling the abundance of the two morphs, the relative proportion of the two morphs in mixture may also largely decide the outcome of competition between the two leaf morph populations.

Results of the various experiments on competitive interaction between the grass and legume indicate that T. repens, although a weak competitor, plays a significant role in the growth and maintenance of Paspalum dilatatum - Trifolium repens grassland community at Shillong particularly on less fertile soils where the grass may depend, to some extent, for nitrogen supply on the legume. P. dilatatum, being a strong competitor, is capable of completely suppressing the growth of T. repens in the grasslands protected from biotic disturbances. In field situation, the grass, however, absorbs most of the grazing, trampling and cutting pressure, and is rendered weak to offer severe competition to the legume, which therefore can manage to co-exist with the grass under disturbed conditions prevailing in the grassland vegetation at Shillong.

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ON THE CO-EXISTENCE OF *TRIFOLIUM REPENS* L. AND *PASPALUM DILATATUM* POIR IN THE GRASSLANDS OF SHILLONG

P. PRADHAN AND R. S. TRIPATHI

*Department of Botany, School of Life Sciences
North-Eastern Hill University, Shillong - 793014*

ABSTRACT

Trifolium repens L. and *Paspalum dilatatum* Poir occur abundantly in the grassland vegetation of Shillong and adjoining areas. An attempt has been made in the present paper to understand the mechanism of their co-existence in nature. The data obtained through the exclosure technique revealed that *T. repens* is almost eliminated from the protected site where the lush growth of *P. dilatatum* offered an intense competition to the legume, whilst both species grow well in grazed situation, indicating that the biotic disturbance is one of the major factors responsible for their co-existence in nature.

TRIFOLIUM *repens* L. and *Paspalum dilatatum* Poir are the sympatric species occurring abundantly in the local grassland vegetation. These grasslands are exposed to frequent grazing, cutting and other biotic disturbances. The grass-legume behaviour in relation to grazing and cutting has been studied by various workers (Davies, 1958; Reid, 1966; Frame, 1976; Litav and Zeligman, 1977). Some workers (Robinson and Sprague, 1947; Cowling and Green, 1956; Stern and Donald, 1962) have shown the aggressiveness of grasses over legumes, although in nitrogen deficient soils legumes have been reported to do relatively better. No work seems to have been done on the mechanism of co-existence of *T. repens* and *P. dilatatum* in nature. The grasses have also been observed to differ in their competitive effects on *T. repens* (Myers and Garber, 1942; Ahlgren, Smith and Nielsen, 1945; Chestnut and Lowe, 1970; Hill, 1977). However, *T. repens* has been shown to be positively associated with many grass species and negatively associated with other legumes (Turkington *et al.* 1977).

T. repens grows quite profusely in the disturbed grasslands of Shillong while it shows relatively poor growth in protected sites. It was suspected that

the clover might be suppressed if the grazing pressure was relaxed. Thus a field experiment was performed to study the comparative response of *T. repens* and *P. dilatatum* to simulated grazing and to see if the two species could co-exist in the absence of grazing and cutting.

MATERIAL AND METHODS

In the present study grazing has been simulated by periodic herbage removal using enclosure technique (Brown, 1954). A patch of sward, 5m² in area, was fenced to exclude external disturbances on the study site. The fenced area was divided into two equal parts. The first part was kept as control, while the other was subjected to herbage removal at 3 months interval over a one year period starting from May, 1978. The herbage was removed at the ground level. Each time, after the herbage removal plants were allowed to regrow for 3 consecutive months and the growth was measured at the end of this period. The density, total leaf area, total herbage yield and the number of reproductive shoots of the two species growing in control as well as in treated plots were estimated. The shoot having roots system at each node was considered to be an individual plant in the case of *T. repens*, and the tillers of *P. dilatatum* were considered as individuals for the purpose of density estimation. For recording data, 3 permanent quadrats each of 50 cm², were marked on each site. For density estimation the quadrats were further sub-divided into small quadrats of 10 cm² to facilitate counting and to ensure accuracy. The leaf area was determined by harvesting the above-ground herbage from three quadrats, each of 30 cm², and drying it in an oven at 80°C for 2 days.

The experiment was conducted in the natural sward occurring in the experimental garden of the Department of Botany, North-Eastern Hill University, Shillong.

RESULTS

The density of *Trifolium repens* is greatly reduced in the undisturbed sward (control) compared to that in the treated plot (Fig. 1). The first cutting in May brought about a considerable increase in density of *T. repens* possibly due to relaxed competition from the grasses after herbage removal and favourable climatic conditions. The density of *T. repens*, however, declines after subsequent cuttings showing the lowest value in the month of February presumably due to low temperatures of winter months. The magnitude of reduction in density at successive observations was markedly greater in the protected plot where luxuriantly growing *P. dilatatum* was able to suppress the growth of legume to a great extent.

There was an increase in the density of *T. repens* after February in the

treated plot, while in the protected plot further reduction in density of the legume occurred after February as indicated by the decrease in density from February to May. Finally, in August the clover seemed to be completely eliminated in the control plot. This decrease in density of the legume in control

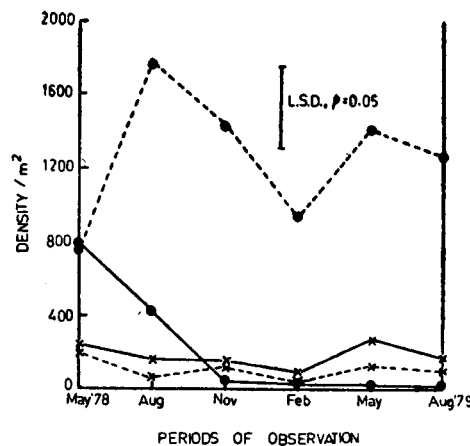


Fig. 1. Periodic changes in density per m^2 of *T. repens* and *P. dilatatum* as affected by herbage removal. *T. repens*, control (o — o) and treated (o — — o) ; *P. dilatatum*, control (x — x) and treated (x — — x)

set may be attributed to competition offered by the grasses which are allowed to grow without any disturbance.

In general, *T. repens* shows a remarkable increase in density after herbage removal. It may be mentioned that *P. dilatatum* does not show any difference between density values recorded for treatment and control plots in the month of November. This indicates that during August to November, which constitutes the active growth period for *P. dilatatum*, the grass recovers rapidly from the herbage removal. However, the grass tends to exhibit a reduction in its density in the treated plot.

Like density, the leaf area per m^2 of *T. repens* was higher in the clipped plot as compared to the protected plot. On the contrary, *P. dilatatum* showed lesser leaf area in the treated plot (Fig. 2). This may be due to stunted growth and marked reduction in the leaf area per plant of the grass (Table 1). In time sequence, leaf area of *T. repens* gradually decreased from May onwards. In the control plot, the leaf area of *T. repens* showed further decrease during February

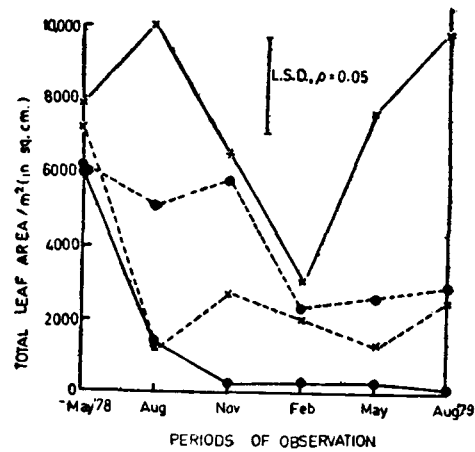


Fig. 2. Effect of herbage removal on total leaf area per m² of *T. repens* and *P. dilatatum*. *T. repens*, control (o—o) and treated (o—o); *P. dilatatum*, control (x—x) and treated (x—x)

to August, '79, when the value was found to be negligible. Possibly, the reasons are same as have been given for differential changes in the density values in the control and treated plots.

Table 1. Effect of herbage removal on leaf area per plant of *T. repens* and *P. dilatatum*. (average values \pm S.E.)

Species	Treatment	Leaf area/plant (sq. cm.)					
		May '78	Aug.	Nov.	Feb.	May	Aug. '79
<i>T. repens</i>	Control	7.49 ± 1.14	3.34 ± 0.28	6.31 ± 0.52	2.88 ± 1.44	3.14 ± 1.57	1.39 ± 1.38
	Treated	8.12 ± 1.28	2.87 ± 0.03	6.83 ± 0.39	2.23 ± 0.03	1.83 ± 0.03	2.37 ± 0.04
<i>P. dilatatum</i>	Control	32.74 ± 0.88	65.43 ± 7.64	44.64 ± 2.69	38.06 ± 1.31	28.04 ± 3.65	64.93 ± 2.52
	Treated	31.92 ± 2.91	19.13 ± 3.01	20.61 ± 0.07	10.80 ± 3.14	11.36 ± 1.05	29.76 ± 2.77

There was also a great reduction in dry matter accumulation by *T. repens* in the control plot where the grass overtopped the legume (Table 2). *P. dilatatum*, however, produced greater biomass in the protected plot. The highest biomass of the grass was recorded in the month of August probably due to the active growth phase during this period.

Table 2. Effect of herbage removal on total aboveground yield/m² of *T. repens* and *P. dilatatum*. (average value \pm S.E.)

Species	Treatment	Total aboveground yield/m ² (g)				
		Aug. '78	Nov. '78	Feb. '78	May '79	Aug. '79
<i>T. repens</i>	Control	15.66 gm. ± 4.20	1.26 $\pm .85$.51 $\pm .04$.39 $\pm .03$.15 $\pm .02$
	Treated	31.37 ± 5.28	29.86 ± 12.81	16.39 ± 7.23	15.18 ± 3.16	6.99 ± 3.51
<i>P. dilatatum</i>	Control	121.66 ± 49.48	58.14 ± 20.52	30.05 ± 8.72	100.74 ± 22.32	240.55 ± 25.70
	Treated	26.07 ± 9.44	40.67 ± 16.29	15.18 ± 6.56	10.80 ± 3.14	44.44 ± 5.39

The percentage of reproductive shoots in *T. repens* was also reduced to nil presumably due to intense competition from the grass in the undisturbed plot (Table 3). There was much reduction in the percentage of reproductive shoots in *P. dilatatum* in the clipped plot which may be due to removal of well grown shoots before they could flower. In the treated plot the percentage of flowering shoots in the grass was about 4% in August, '79 which is also substantially low as compared to that in the unclipped plot.

DISCUSSION

The poor growth of *T. repens* in the undisturbed sward as evident from the results is due to the luxuriant growth of *P. dilatatum* which is an erect rhizomatous grass attaining a height of more than 1 m, if left undisturbed. Thus, the grass reduces the availability of light to the *T. repens* which has a prostrate growth form. This is in conformity with the results obtained by Donald (1963) that the reduced light intensity at the clover leaf canopy caused a reduction in its growth. The grass on the other hand, suffers a set back in the plot subjected to herbage removal, which may be due to overall reduction in the photosynthetic

Table 3. Effect of herbage removal on reproductive behaviour of *T. repens* and *P. dilatatum* (average values \pm S.E.)

Species	Treatment	% Reproductive Shoot					
		May '78	Aug. '78	Nov. '79	Feb. '79	May '79	Aug. '79
<i>T. repens</i>	Control	36.78 ± 5.41	(negligible)	—	—	—	—
	Treated	32.75 ± 2.79	.82 $\pm .06$.18 $\pm .09$	—	1.3 $\pm .20$.15 $\pm .14$
<i>P. dilatatum</i>	Control	—	21.48 $\pm .72$	—	—	—	49.85 ± 12.49
	Treated	—	—	—	—	—	3.75 ± 3.0

surface. Sometimes, the density of the grass is increased on cutting, however, as numerous rametes are produced from the rhizome after cutting the above-ground parts. These shoots, of courses, become stunted due to repeated herbage removal and during its active growth phase the grass quickly recovers from the cutting treatment and produces some reproductive shoots too.

The production of reproductive shoots, aboveground biomass and total leaf area of *T. repens*, all showed drastic reduction in the protected plot. This was mainly due to the fact that enough light was not allowed to reach the level to photosynthetic surface of *T. repens* on account of profuse growth of *P. dilatatum* and of other erect growing plant species in the absence of herbage removal. However, the data also suggest that the percentage of reproductive shoots and other growth parameters of the grass were reduced in periodically clipped plot. This may be attributed to reduction in photosynthetic tissue on account of frequent removal of aboveground herbage close to the ground. This is in accordance with the result of Maclusky and Morris (1964), who found that the maximum dry matter yield of grasslands are obtained with a combination of long periods of uninterrupted regrowth and low cutting height. Ryegrass and ryegrass plus clover swards gave higher yields with 3 cuts than with 6 cuts per year (Anonymous, 1963).

It is evident from the study that frequent herbage removal changes the sward structure in such a manner that it becomes legume dominated (Fig. 1), while in absence of cutting the grass dominates over the legume and the growth

of the latter is greatly suppressed and its population size is substantially reduced owing to competition offered by *P. dilatatum* and other plant species with erect habit.

There are clear indications that in the absence of disturbances due to grazing and cutting for longer duration, *T. repens* will altogether be eliminated from the local grasslands. The grass, on the other hand, flourishes in undisturbed situation. In the grasslands frequently exposed to grazing, cutting and trampling, *P. dilatatum* and *T. repens* grow together without one succeeding at the expense of the other, although the growth of the grass happens to be quite poor as compared to its growth in protected situations. Under local conditions, *T. repens* grows most actively during March to May whilst the grass shows most active growth during June to August. Thus, the growth cycles of the two species are asynchronous and the resource competition, therefore, is never so crucial as to cause complete suppression of any of the two species in natural situation.

The co-existence of species has been attributed to the asynchronous growth of the associates (Harper and Clatworthy, 1963; Turkington and Harper, 1979). However, in our studies, we found that in spite of their asynchronous growth, *T. repens* and *P. dilatatum* cannot manage to co-exist in the grasslands fully protected from the biotic disturbances. Thus, it may be assumed that *T. repens* and *P. dilatatum* owe their co-existence to biotic disturbances like grazing, cutting and trampling as prevalent in the local grasslands.

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