

**STUDIES ON ECOLOGICAL STRATEGIES OF
OXALIS CORNICULATA LINN. AND *O. LATIFOLIA* H.B.K.**

By

ALLANA ROSE LALOO

THESIS
SUBMITTED
IN

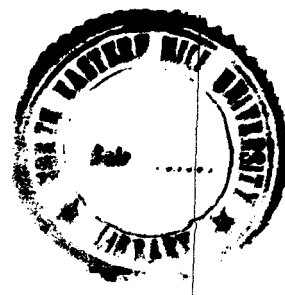
FULFILMENT OF THE REQUIREMENT OF THE DEGREE OF
DOCTOR OF PHILOSOPHY IN BOTANY



NORTH-EASTERN HILL UNIVERSITY

SHILLONG (INDIA)

MARCH, 1990



DS
583.216045
LAL

~~XXXXXXXXXXXXXXXXXXXX~~
Ac: 102717
A:
Da: *[Signature]*
Cl:
Su:
Ent:
~~Transfer to 01/18/96~~



North-Eastern Hill University

DEPARTMENT OF BOTANY


Dr. R. S. Tripathi
Professor of Ecology

Gram : NEHU
Phone (office) : 23390

School of Life Sciences
SHILLONG 793 014, INDIA

March 15, 1990.

I certify that the thesis entitled "Studies on ecological strategies of Oxalis corniculata Linn. and O. latifolia H.B.K.", submitted by Mrs. Allana Rose Laloo, 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 her under my supervision. She has been duly registered and the thesis presented is worthy of being considered for the award of the Ph.D. Degree. The work has not been submitted for any Degree of any other University.


Signature of the Supervisor

Forwarded
Y.S. Clarke
15.3.90

Recd
Department of Botany
School of Life Sciences
N.E.H.U., Shillong.

ACKNOWLEDGEMENTS

I am indebted to Professor R.S. Tripathi, Department of Botany, N.E.H.U., Shillong for his able guidance, constant encouragement and inspiration throughout the course of this study for which I express my deep sense of gratitude to him.

I am grateful to the Head of the Department of Botany for extending laboratory and other facilities. I thank Dr. H.N. Pandey, Reader in Ecology, Department of Botany for his valuable suggestions and comments.


I am thankful to Dr. M.L. Khan, Dr. A.K. Das, Dr. (Miss) B. Wankhar and Dr. (Miss) M.S. Dkhar for the help rendered by them in various ways. I thank Miss P. Rao and Mr. R.S. Lepcha for helping me in drawings. I also thank Mr. P. Pradhan, Mr. S.K. Barik, Miss S. Rynjah and Miss J. Mishra for their kind cooperation.

My special thanks are due to the Principal St. Mary's College, Shillong and my colleagues in the Department of Botany for their encouragement and cooperation.

The help rendered by Miss R. Sunabi in typing out the thesis and Mr. B.K. Das in photography is thankfully acknowledged.

Last but not the least, I am most grateful to my parents, my husband and children, my uncle and my sisters for their constant inspiration, encouragement and support.

March 15, 1990.


(ALLANA ROSE LALOO)
Lecturer in Botany
St. Mary's College
Shillong

CONTENTS

CHAPTER I	General Introduction	... 1
CHAPTER II	Review of Literature	... 9
CHAPTER III	Climate, soil and vegetation of the area and biology of <u>O.corniculata</u> and <u>O.latifolia</u> 21
CHAPTER IV	Effect of associated vegetation on growth of <u>O.corniculata</u> and <u>O. latifolia</u> 30
CHAPTER VA	Growth of <u>O.corniculata</u> raised from seeds and stolon cuttings in pure and mixed stands.	... 38
CHAPTER VB	Growth of <u>O.latifolia</u> as affected by bulb size.	... 46
CHAPTER VI	Effect of light on the competitive interaction between <u>O.corniculata</u> and <u>O.latifolia</u> 57
CHAPTER VII	Effect of NPK and moisture regimes on competition between <u>O.corniculata</u> raised from seedlings and cuttings and <u>O.latifolia</u> raised from bulbs.	... 76
CHAPTER VIII	Effect of clipping and 2, 4-D application on the growth of <u>O.corniculata</u> and <u>O.latifolia</u> in pure and mixed stands.	... 96
CHAPTER IX	General Discussion	... 115
	Summary	... 124
	References	... 130

CHAPTER I

General Introduction

Plant populations are generally exposed to continuous changing environment. However, weeds represent the most successful and stable populations and can successfully occupy large areas. Many weed species utilize breeding systems adapted for inbreeding to produce stable duplicates of successful genotypes and as a result, weeds are very good colonisers (Allard 1965, Baker 1974, Young & Evans 1976). Moreover, they possess multiple propagation mechanism and are prolific reproducers. Salisbury (1961) predicts that, "casual weeds of today are likely to become noxious weeds of tomorrow". The weedy species seem to adopt different strategies to persist in natural populations and expand their range of distribution. Thus a proper understanding of the ecological strategies of weeds would be helpful in designing effective control measures.

The characteristics of weeds that ensure their survival and population growth under varied environmental conditions may be grouped under 'adaptive strategy'. As argued by Tripathi and Trivedi (1984), these characteristics contribute to successful exploitation of available resources and continued persistence and proliferation of weedy species. The reproductive strategy as a part of the total adaptive strategy of weeds assumes a special significance as the weed population growth is, in all probability, a direct function of the reproductive success under a given set of environmental conditions (Tripathi & Trivedi 1984). Studies on resource allocation to reproductive structure under different ecological habitats,

therefore, constitute an important aspect of the analysis of ecological strategies of weeds.

Cody (1966) used 'r'- and 'K'- strategies in his attempt to study geographic variation in avian clutch size. He observed that birds in seasonal environments allocate more resources to reproduction but in less seasonal environments, populations are nearer to carrying capacity, and more resources are consequently allocated to competitive activities.

MacArthur and Wilson (1967) described the theory of strategies in the light of r- and K- selection. K- selection consists of organisms which allocate more energy to vegetative activities for increased competitive ability. Under r- selection, evolution promotes productivity, high rates of resource exploitation and high reproductive output. These two types of selection lie on the two opposite poles in the evolutionary spectrum. It is now widely accepted that the majority of organisms fall between the extremes of r- and K- selection. More recent evidence suggests that genetic variation may cause populations of the same species to occupy different positions along the r-K continuum (Gadgil & Solbrig 1972).

Grime (1977) proposed that during the course of evolution of plants three basic forms of natural selection known as C-S-R selection occurred. C-S-R strategy model comprise competitive (C), stress tolerant (S) and ruderal (R) strategies. Grime suggests that the ruderal and stress-tolerant strategies correspond, respectively to the

extremes of r- and K- selection and that highly competitive species occupy an intermediate position. The C-S-R strategy model differs from the r-K continuum in the recognition of stress tolerant as a distinct strategy evolved in intrinsically unproductive habitats or under conditions of extreme resource depletion induced by the vegetation itself.

Kaul (1985) observes that annual plants generally exhibit the syndrome of 'r' selection. They occupy ephemeral habitats, show high mortality and short lifespans, develop rapidly and recolonize often, reproduce early in their lives and produce numerous small seeds, allocate greater energy and materials to reproduction, and their populations are spatially and temporally variable. Perennials often exhibit 'K' selection, a syndrome whose features are the opposites of 'r- selected' species. Similar observations were made by Pitelka (1977) and Primack (1979). A comparison of the growth strategies of annuals, biennials and perennials showed that biennials are better adapted for exploiting resources in sites that are available only intermittently (Hart 1977).

Stearns (1976) argued that in fluctuating environments, early maturity, production of numerous small young and large reproductive efforts, which are characteristics of r-selected species, are favoured, while in stable environments, late maturity, few seeds and small reproductive efforts are favoured (K-selected species).

Allocation of resources to various parts of the plant is an important aspect in studying the ecological strategies of plants. Bazzaz et al. (1987) suggest that at an evolutionary level, allocation involves balancing fecundity against survival probability through the lifespan and the effects of this balance on fitness. At an ecological level, allocation includes the relationship between investment in one function and investment in others, such as the relationship between defence and growth. At a physiological level, allocation entails the partitioning of resources within the plant and the consequences of this partitioning for resource gain or loss.

Harper (1967) emphasized the evolutionary importance of life histories and reproductive allocations of plants. Hickman (1975) suggests that all functions of organisms are ultimately focussed towards maximizing successful reproduction. Studies on the adaptive nature of resource allocation in plants have been undertaken by various workers (Gadgil & Solbrig 1972, Abrahamson & Gadgil 1973, Tripathi & Harper 1973, Ogden 1974, Trivedi & Tripathi 1982a, 1982b, Jurik 1983, Bazzaz & Reekie 1985, McCrea & Abrahamson 1987, Reekie & Bazzaz 1987). Kawano (1981) stressed the significance of ecological distribution, dispersal, survival patterns and mortality factors in addition to measurements of reproductive effort to assess life-history strategies.

Allocation patterns in different plant populations under different competitive regimes have been studied by various workers

(Solbrig & Simpson 1974, Law et al. 1977, Wilken 1977, Grace & Wetzel 1981, Trivedi & Tripathi 1982a, Tripathi & Yadav 1982, Rai & Tripathi 1983, Zangerl & Bazzaz 1983). These studies suggest that plant populations in 'closed' habitats are different from populations in 'open' habitats, allocating more to persistence and competition and less to the production of propagules for dispersal. In the light of 'r'- and 'K'- selection, it may be said that populations from open habitats show 'r'- selection and those from closed habitats are 'K'-selected.

The allocation pattern of a plant defines the ecological roles and is, therefore, an important factor in understanding plant distribution and adaptation. Moreover, continued improvement of agronomic species is likely to draw insights obtained through ecological studies of allocation in wild species (Bazzaz et al. 1987).

Plant form may also confer an important adaptive advantage to different plant species. A prostrate habit permits maximum ground cover at minimum cost as the requirement for supporting tissue is reduced (Lovell & Lovell 1985). Moreover, it encourages vegetative spread because these organs are prolific producers of adventitious roots (Lovell & White 1986) essential for the establishment of independent ramets.

The study of ecological strategies of weeds would be primarily concerned with such aspects as the growth responses to different

environmental conditions, competitive behaviour, energy allocation to different plant parts and the production of seeds and vegetative propagules.

Several exotic weeds have undergone tremendous range expansion in north-eastern India and many of them have become important pests of agriculture and plantation crops (Tripathi 1985). Oxalis corniculata and Oxalis latifolia represent two such exotic weeds. They are sympatric perennial species belonging to the family Oxalidaceae. They occur in wastelands, arable lands, kitchen gardens, lawns and grow with potted ornamental plants. O. corniculata is a prostrate stoloniferous, creeping herb which reproduces vegetatively by rooting at nodes and by seeds which are dispersed forcefully from the capsules away from the parent plant (Robertson 1975, Holm et al. 1977).

O. latifolia is a bulbous perennial which undergoes a state of dormancy during the cold and dry winter months with the underground bulbs serving as perennating organs. The bulbs germinate only in late spring. The plant reproduces mainly by vegetative propagation through the production of daughter bulbs. Therefore the bulbs act as perennating organs as well as the organs for vegetative reproduction.

The difference in their life form and differential emphasis placed by them on vegetative and sexual modes of reproduction make

them interesting material for the analysis of ecological strategies.

The ecological strategies of these two weeds have been analysed in terms of their growth response and reaction to different ecological conditions. The aspects that have been considered are as follows :

- I. Growth of the two Oxalis species in relation to the selective removal of associated vegetation.
- II. A comparative growth of O. corniculata raised from seeds and cuttings in pure and mixed stands.
- III. Growth of O. latifolia as affected by bulb size.
- IV. Effect of light intensity on the competitive interaction between O. corniculata and O. latifolia.
- V. Competition between O. corniculata and O. latifolia at two NPK levels under two moisture regimes.
- VI. Effect of clipping and 2, 4-D application on competitive interaction between O. corniculata and O. latifolia.

The basic structure of the dissertation is outlined below:-

1. General Introduction (Chapter I) sets out objectives of the thesis.
2. Review of Literature (Chapter II).

3. Description of the study site and biology of the two species of Oxalis selected for the study (Chapter III).
4. Analysis of the ecological strategies of the selected species to varied ecological conditions (Chapter IV - VIII).
5. General Discussion (Chapter IX).

Most of the experimental data collected during the study period have been presented in Chapters IV - VIII and the data contained in each one of them have been discussed in the corresponding chapters. The major results of the entire study however, have been briefly discussed in an integrated manner in "General Discussion" which is followed by "Summary" of the thesis. The references cited in the thesis have been listed at the end.

CHAPTER II

Review of Literature

In order to understand the basic features of their ecology it is necessary to examine the strategies adopted by plants during their life histories (Grime 1979). Weeds appear to have evolved certain strategies which enable them to grow successfully in various types of ecological habitats. It is important to recognize their major ecological strategies and to relate these strategies to their success in nature.

The concept of r- and K- strategies is the most widely accepted theory of selection. The first explicit reference to r- and K- selection appears to have been made by MacArthur's student, M. Cody (1966) who credits the idea to MacArthur. Cody (1966) used r- and K- in his attempt to explain patterns of geographic variation in avian clutch size. He argued that in seasonal environments, density independent mortality lowers the mean population size, thus reducing competition among survivors. Therefore, birds in seasonal environments have more resources to allocate to reproductive functions, including clutch size. In contrast, in less seasonal environments, populations are nearer to carrying capacity, and more resources are subsequently allocated to competitive activities.

According to MacArthur and Wilson (1967) in an initially colonized population, r- selection would predominate for a time, but ultimately the population would come under K- selection. They argued that under r- selection, evolution promotes productivity,

high rates of resource exploitation and high reproductive output, while under K- selection, genotypes which can at least replace themselves with a small family at the lowest food level will win, the food density being lowered so that large families cannot be fed. Evolution here favours efficiency of conversion of food into offspring (MacArthur & Wilson 1967).

Pianka (1970) assumed that increased population density will result in decreased juvenile survivorship and consequently, the optimal reproductive effort should decrease with increasing population size (Pianka 1972, Schaffer & Gadgil 1975, Horn 1978). Based upon this over-generalization, he generated a table that lists what he claims as life history correlates of r- and K- selection. For example, r- selected taxa mature early, exhibit high levels of reproductive effort and parental care. K- selected forms should somehow have the opposite traits, such as delayed breeding, low level of reproductive effort and parental care. Since the appearance of Pianka's table, r- selection has been equated with high reproductive potential and K- selection with low reproductive potential (Stearns 1976, Parry 1981).

Southwood (1977) developed a very different interpretation of r- and K- selection. According to him, the permanence of habitats or 'habitat durational stability' can clearly influence longevity and the potential for density dependence. On the other hand, Parry (1981) argued that to imply exact synonymy between habitat durational

stability and r- and K- selection will only obscure the actual selective forces that operate in different habitats.

Grime (1979) proposed a C-S-R strategy model for plant life histories. The first of these (C-selected) has involved selection for high competitive ability which depends upon plant characteristics which maximize the capture of resources in productive and relatively undisturbed conditions. The second (S-selection) has brought about reductions in both vegetative and reproductive vigour, adaptations which allow endurance of continuously unproductive environments. The third (R-selection) is associated with a short life span and with high seed production and has evolved in severely disturbed but potentially productive environments.

The most substantial way in which the Grime's strategy model differs from that of the r-K continuum lies in recognition of stress-tolerance as a distinct strategy evolved in intrinsically unproductive habitats or under conditions of extreme resource depletion induced by the vegetation itself.

Competition from the neighbouring species plays an important part in plant growth and survival strategies. Numerous field experiments indicate significant reductions in plant growth or survival in the presence of neighbours (Putwain & Harper 1970, Pinder 1975, Allen & Forman 1976, Dwivedi & Tripathi 1980, Gross 1980, Fowler 1981, Silander & Antonovics 1982, Yadav & Tripathi 1984, Goldberg 1987). Co-existing plant species are those that are equivalent in

competitive ability for shared resources (Aarssen 1983, Agren & Fagerstrom 1984, Hubbell & Foster 1986). Competitive ability includes the response of individuals to the presence of competitors, and the ability to grow, survive and reproduce despite depletion of resource levels by neighbours (Goldberg & Werner 1983, Goldberg 1987).

In order to assess the relationship of a single species to groups of other species, some workers used either removal or addition experiments. Hartnett and Bazzaz (1985) observed that when clones of Solidago canadensis were grown experimentally with pure stands of different species, the neighbouring species had different effects on ramet shoot-growth, flower-head production and clonal growth. In general, S. canadensis shoot growth and flower production were greatest in the neighbourhood of Poa pratense and lowest among Aster pilosus, whereas clonal growth was greatest among ramets growing in the A. pilosus neighbourhood and lowest in the S. canadensis neighbourhood. Schmid (1985a) observed that rosette density of Bellis perennis was stable with time and little affected by the removal of either grasses or dicotyledonous species. On the other hand, Prunella vulgaris was influenced by the presence of other dicotyledonous species in the sward. Dwivedi and Tripathi (1980) observed that the interference from the associates caused 90.5% reduction in seed production of Alysicarpus monilifer and Indigofera enneaphylla, thus restricting the occupancy of ecological niches by the two species in subsequent generations.

Differences in range and habitat between sexuals and asexuals have been considered as a basis for understanding the adaptive significance of sex. From reviews by Levin (1975) of plants and by Glesener and Tilman (1978) of animals on the distributions of sexual and asexual organisms the following general pattern emerges. In contrast to sexual species, asexual species tend to occur in more disturbed environments, in habitats that are more xeric and at higher altitudes and latitudes. Asexual species have been described as 'weedy' (Wright & Lowe 1968) and proficient as colonizers (Stebbins 1950), but inferior as competitors (Cueller 1977). Williams (1975) advanced the hypothesis that the greater fecundity of asexual individuals may temporarily provide greater success, but that the evolution of superior, better adapted genotypes through outcrossing will eventually lead to dominance of sexuals.

Asexuality confers an adaptive advantage to asexuals as colonists. Firstly, because they do not require a mate and a single founding event can initiate and build a new population (Stebbins 1950, Soumalainen 1950, Manning 1981). Secondly, every offspring is female, and therefore the reproductive potential of an asexual colonizer will be higher than a sexual one (Stebbins 1950, Mayr 1963). Furthermore, if asexuals are superior colonists, then one can predict from classic life history theory (Stearns 1977) that asexuals should produce more, but smaller seeds (Smith & Fretwell 1974, Wilbur 1977); that asexual offspring should have lower survivorship (Gadgil & Bossert

1970); and that an asexual plant should have reduced allocation to growth and future reproduction (Williams 1966).

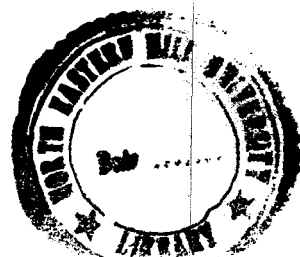
Tripathi and Harper (1973) studied the growth of mixed populations of Agropyron repens and A. canicum established from tillers and from seeds and observed that plants established from tillers proved more vigorous and aggressive than their counterparts produced from seeds. In mixtures, A. repens had a suppressive effect on A. canicum. Kushwaha et al. (1983) also observed that the plants of Imperata cylindrica raised from rhizomes proved to be more aggressive compared to plants raised from seeds, though the aggressiveness decreased with the passage of time.

Propagule size is important in determining the growth and survivorship of plant species (Harper & Obeid 1967, Werner 1975, Barkham 1980, Bourdot 1984, Stanton 1984). Spencer (1986) has shown that tuber size may be as important as environmental factors in regulating aquatic macrophyte population growth. Initial tuber size in Potamogeton pectinatus influenced the rate at which ramets were produced and larger tubers produced more ramets per clone than did the smaller tubers.

Brown et al. (1985) observed strong correlations between ramet size and certain phenological traits in Clintonia borealis and Aster acuminatus. Larger ramets of both the species tended to emerge earlier, mature more slowly, live longer, and die later. Size may both contribute to and be a partial consequence of long life.

Eriksson (1988) observed that the stolon production in Potentilla anserina ramets was positively correlated with the size of ramets. A similar tendency existed for the relation between size and the occurrence of flowering. This behaviour suggests that the initiation of stolons and probably of flowers also, occurs when the 'resource level' within ramets has passed some internal threshold. A similar size-related initiation of Viola spp. has been suggested by Thompson and Beattie (1981). Most organisms live in fluctuating environments. The phenotypic plasticity of life history traits in fluctuating environments may be considerable (Nichols, Conley & Tipton 1976). Phenotypic responses to environmental change are typically expected to occur in the same direction as that favoured by natural selection (Hickman 1975, Goodman 1979, Boyce & Daley 1980). Hume and Cavers (1982, 1983) observed that the genetic differences in resource allocation, reproductive strategy and life history among populations of Rumex crispus were, apparently, adaptations to native habitats. Environmental factors such as rainfall, moisture and soil particles size accounted for much of the variation that occurred with respect to mortality and dry matter allocation. Also colonizing species or populations tend to allocate greater proportions of their resources to reproduction than do longer-lived plants which are under more competitive stress. The longer-lived plants require more resources for self-maintenance (Harper 1977). McNaughton's (1975) findings in Typha species also supports this view. Abrahamson & Gadgil (1973) demonstrated

102717



that reproductive effort in some species of Solidago declined with community maturity.

Phenotypic flexibility may be responsible for the successful growth and distribution of different plant species e.g. Typha latifolia (Grace & Wetzel 1981), Rumex crispus (Hume & Cavers 1982), Polygonum pennsylvanicum (Zangerl & Bazzaz 1983), Clintonia borealis (Ashmun & Pitelka 1985) and Danthonia spicata (Scheiner & Teeri 1986). Clough et al. (1979, 1980) argued that flexibility of Solanum dulcamara in response to light environment was primarily based upon the ability of individual genotypes to adjust to different light levels. Therefore much of the photosynthetic variability is based on phenotypic plasticity (Garbutt et al. 1985). Plasticity in resource allocation to clonal growth and flowering is an important factor which allows the persistence of Aster acuminatus over a wide range of light conditions (Ashmun & Pitelka 1984).

Various studies have shown adaptive ecological divergence of plants in response to various ecological factors (Clausen et al. 1940, Jain & Bradshaw 1966, McNeilly 1968, Snaydon 1970, Antonovics et al. 1971, Davies & Snaydon 1973 a,b, Wu & Antonovics 1976, Antle-finger 1981, Chapin & Chapin 1981). Populations of a plant species in closed habitats are genetically different from populations in open habitats, the former allocating more resources to persistence and competition and less to the production of propagules for dispersal (Solbrig & Simpson 1974, Law et al. 1977, Wilken 1977, Grace & Wetzel

1981). Schwaegerle & Bazzaz (1987) observed significant difference among populations of Phlox in survival, vegetative growth and flowering in response to different levels of moisture, light, nutrients and competition.

Species or genotypes differ seasonally in their growth or physiology, and therefore, their relative abilities to compete for a resource may also vary with time of the year (Fowler & Antonovics 1981, McMaster, Jow & Kummerow 1982, Forcella 1984). According to Benner & Bazzaz (1985, 1987), resource variability is likely to be high in disturbed environments, and colonizing species should be opportunistic in their abilities to use resource at any time during the growing season.

Plants of Abutilon theophrasti showed an opportunistic response, being able to use nutrients supplied at different times (Benner & Bazzaz 1985). Parrish & Bazzaz (1985), observed that plants of A. theophrasti grown at higher nutrient levels were larger and produced bigger and more seeds than plants grown at lower soil nutrient concentrations. Low nitrogen supply inhibits the growth of Ammophila arenaria and Elymus mollis (Pavlik 1983). Eriksson (1987) observed that the number of ovules/flower increased in response to nutrient addition in Potentilla anserina. In their competition studies Heil & Bruggink (1987) observed that the growth of Calluna and Molinia increased following the addition of nutrients. However, the increase in biomass of Molinia was much larger than that of Calluna. Also

increased nutrient availability favours competitive vigor of Molinia in interaction with Calluna.

Tripathi & Gupta (1981) studied the competitive interaction between Dichanthium annulatum and Bothriochloa pertusa in relation to soil moisture regime and observed that the competitive ability of the two grasses varies with change in soil moisture content. Yadav & Tripathi (1985) observed that dry matter yield of Eupatorium adenophorum and E. riparium declined at low moisture regime, the reduction being more in E. riparium. Ong (1984) observed that water stress had a major influence in the partitioning of dry matter in groundnut. Plants of Sorghum bicolor showed stunted growth, reduced leaf area and dry matter production under low moisture and low nutrient supply (Kapuya et al. 1985).

The impact of defoliation on plant growth and vigour has been studied by various workers (Blaisdell & Pechanec 1949, Sackston 1959, Stickler & Pauli 1961, Jameson 1963, Davidson 1964, Begum & Eden 1965, Lucas & Asana 1968, Kulman 1971, Harlow & Hills 1972, Chawdhry & Sagar 1974a, Madgwick 1975, Tripathi & Gupta 1980, Archer & Tieszen 1983, Lane 1984, Giannopolitis 1986, Rai & Tripathi 1986, Wallace 1987, Holt & Chism 1988). In one of the few studies done on the interaction between defoliation and competition in North American range plants, Mueggler (1970, 1972, 1975) observed that herbage production and flower stalk numbers of Festuca idahoensis and Agropyron spicatum decreased with increasing levels of competi-

tion and intensity of clipping. Regardless of the severity of defoliation, plants under competition showed greater reductions in biomass and flower production and were slower to recover from defoliation, than were plants under reduced competition. Bentley and Whittaker (1979) found that moderate defoliation had no significant effect on plants of two Rumex species when competing intraspecifically, but it did alter competitive relationships between species when competing interspecifically. Archer & Detling (1984) showed that tillers of graminoids defoliated under full competition produced significantly less leaf biomass than tillers defoliated under reduced competition.

Chawdhry & Sagar (1974b) observed that the applications of herbicides normally kill the tops of Oxalis latifolia and O. pes-caprae but give only temporary control due to the capacity for regeneration by the subterranean organs. However, Esler (1962) has demonstrated the inability of O. latifolia to withstand frequent regular defoliation. According to Ivens (1967) and Fryer & Makepeace (1970), destruction of the foliage of O. latifolia only stimulates the ripening of the new bulbils, the food reserves in the tuber being transferred apparently as a consequence of defoliation. Austin (1968), working in Tanzania has claimed that many species of Oxalis disappear after repeated spraying with Paraquat, and most quickly if sprayed when still young.

Holt & Chism (1988) studied the herbicidal activity of NAA (1 - Napthaleneacetic acid) on creeping woodsorrel (Oxalis corni-

culata) and observed that phytotoxicity of NAA was related to plant age. As plant age increased at the time of treatment, the level of injury decreased. However, relatively high rates are required for acceptable control of mature creeping woodsorrel.

Some studies on the control of Oxalis species have been undertaken by various workers (Jackson 1962, Chawdhry & Sagar 1973, 1974 a & b, Holt & Chism 1988), however, a detailed study on the ecology of Oxalis species is lacking. Therefore, a study on the ecological strategies of Oxalis species was undertaken with a view to suggest effective weed management programme.

CHAPTER III

Climate, soil and vegetation of the area and biology
of O. corniculata and O. latifolia.

Study site :

The present investigation was carried out in Shillong (Lat. $25^{\circ}34'N$, Long. $91^{\circ}56'$ alt. 1500 m), the capital of Meghalaya in north-east India. Field and pot experiments were conducted on the campus of the School of Life Sciences, North-Eastern Hill University, Shillong. Pot experiments were carried out under net house condition.

Climate :

Meghalaya enjoys a monsoonic climate with an average annual rainfall of 2500 mm. Most of the precipitation is due to south west monsoon which blows over the state during summer (May to September). The winter is generally dry, although some occasional showers are received through north-east monsoon. The average temperature and rainfall data recorded during the study period are given in Fig.3.1a & b. In the spring season (March-April), the temperature increase is accompanied by occasional thunder showers. Summer (May-September) experiences, relatively hot weather with abundant rainfall and high humidity. Cold and relatively dry weather prevails in October and November. From December to February, the temperature drops considerably and the winter becomes severe. Overall the climate is conducive for luxuriant growth of plants except during winter months when the temperature is low and weather considerably dry. During winter, the temperature sometimes drops down to $3^{\circ}C$.

Fig. 3.1 Temperature (Fig. 3.1A) and Rainfall (Fig. 3.1B) data for the study area during January 1987 to December 1988. ○—○ , mean maximum temperature; ●—● , mean minimum temperature; ●—● , average rainfall.

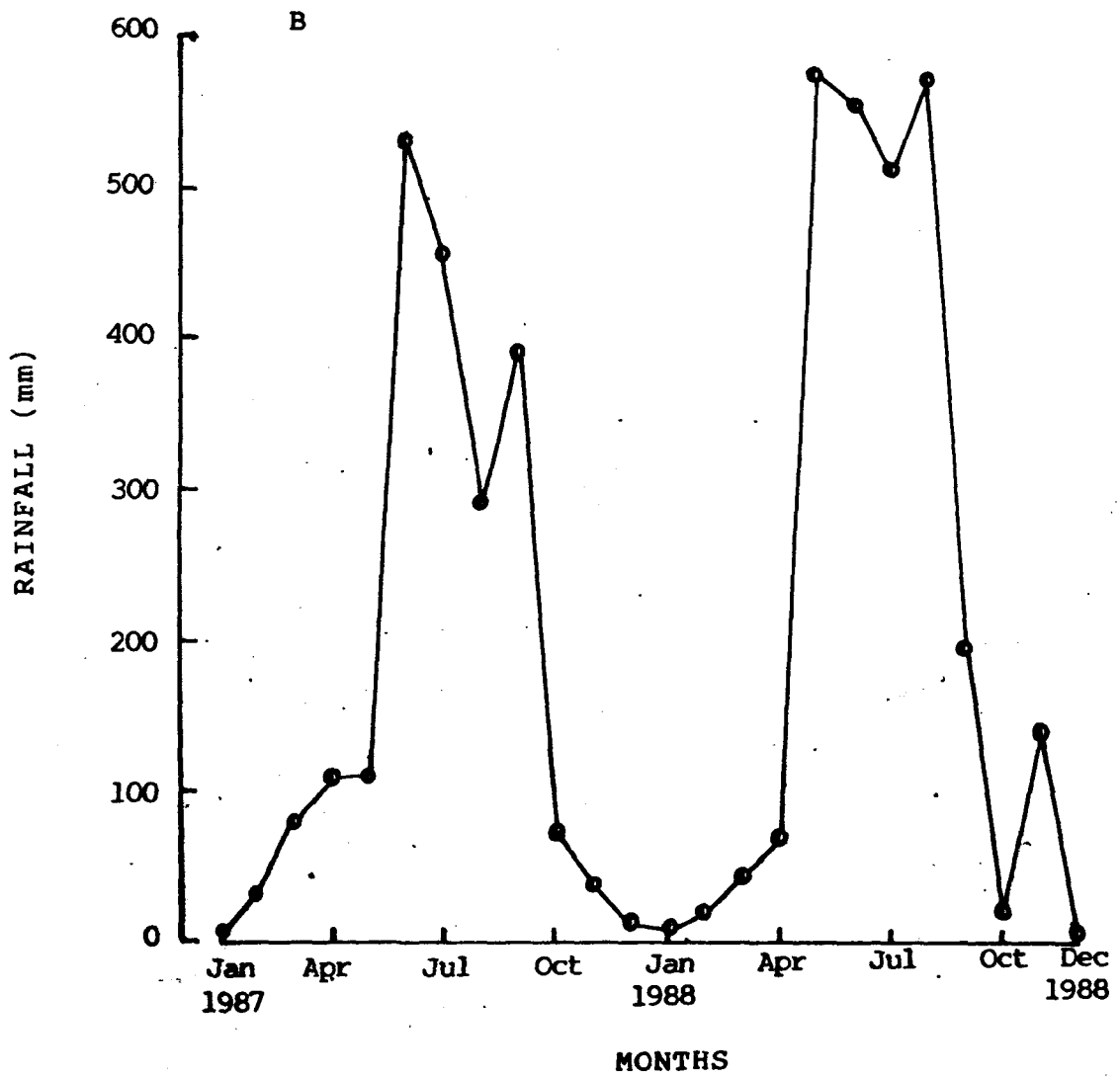
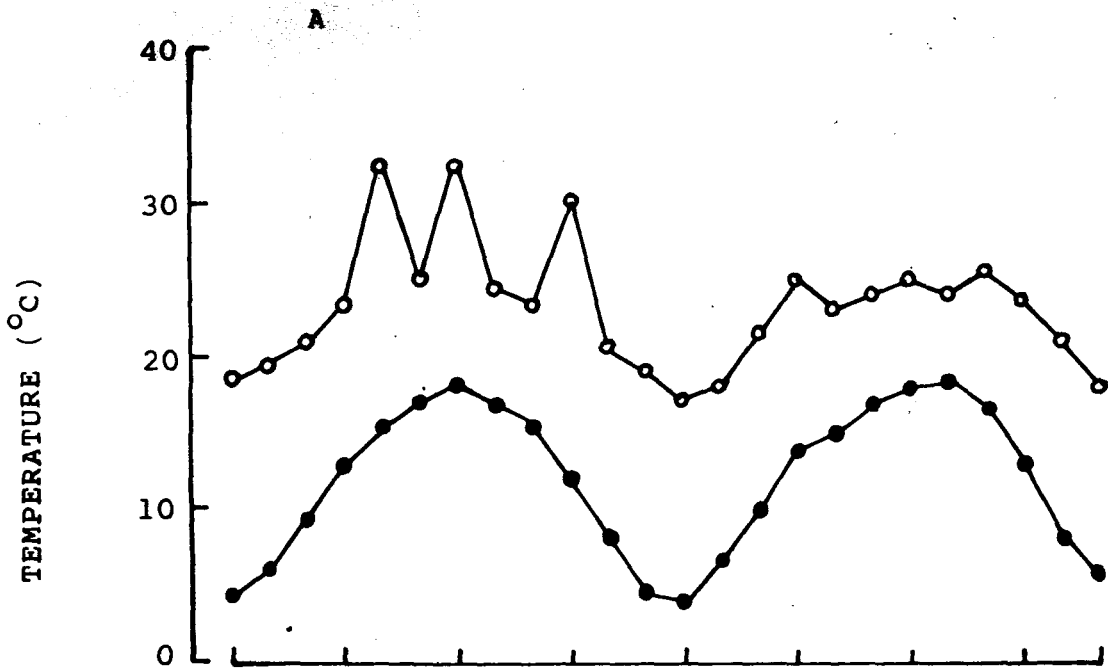


FIG. 3.1

Soil :

The Meghalaya plateau has an evolutionary history of emergence, submergence and peneplanation with several phases of erosion, sedimentation, diastrophism and intrusion movements of land and sea. The plateau has experienced the influence of an alternative phase of transgression and regression of the sea waters from mesozoic to earlier tertiary times. Major portion of the hill areas of Meghalaya plateau is covered with lateritic soil, developed under humid climate on a number of rock formations such as shales, granites, gneiss, granulites, conglomerates, quartzites etc. The soil is reddish brown in colour and clayey to sandy loam in texture. The soil of the study site is acidic with pH ranging from 5.2 to 6.5.

Vegetation :

The vegetation is predominantly evergreen being largely composed of Pinus kesiya - a coniferous tree endemic to Meghalaya. Degraded forests, jhum fallows richly colonised by ruderal weeds, savanna and patches of grasslands characterise the land scape of the area. Due to heavy rainfall, many types of mosses, lichens and epiphytes cover the branches of trees. The tribal people of the region generally practice shifting agriculture (locally called 'Jhum'), although they are now taking to settled agriculture in valleys and around the urban centres. The croplands are infested with large number of weeds, many of which are exotic and colonising very fast (Tripathi 1985). Oxalis corniculata and Oxalis latifolia, the two

TABLE 3.1. DENSITY PER m^2 (+ S.E.) OF O. corniculata AND O. latifolia
 BASED ON FIVE QUADRATS LAID RANDOMLY ON DIFFERENT HABITATS
 IN THE MONTH OF JULY, 1988.

Habitat	Density/ m^2	
	<u>O. corniculata</u>	<u>O. latifolia</u>
Open	35 \pm 3.1	31 \pm 1.2
Shaded	20 \pm 1.6	15 \pm 1.5
Cropland	25 \pm 1.7	35 \pm 3.0
Grassland	48 \pm 0.8	40 \pm 0.2
Roadside	54 \pm 3.7	60 \pm 4.0
Wasteland	38 \pm 1.8	28 \pm 2.5

perennial weeds which have been selected for study have assumed considerable importance in recent years due to their great abundance and luxuriant growth. They occur in shady places, open forests, croplands, lawns and wastelands, disturbed habitats, and roadsides. Densities of both the Oxalis species as determined by quadrat method (Misra 1968) on different habitats are given in Table 3.1. A few important plant species that generally occur with Oxalis spp. are Centella asiatica, Galinsoga ciliata, G. parviflora, Geranium nepalensis, Strobilanthes acrocephalus, Trifolium repens and grasses such as Panicum auritum, Pennisetum clandestinum and Setaria glauca.

Biology of the species

Oxalis corniculata L : (Plate 1)

Oxalis corniculata L., also known as creeping or yellow woodsorrel, belongs to the family Oxalidaceae. It is a spreading herbaceous perennial, native to Europe and America. It occurs in at least 17 crops in 44 countries around the world (Holm et al. 1977). Some of the important crops in Meghalaya in which the weed occurs are rice, maize, potato, groundnut, linseed and cauliflower (Plate 2).

Description of the plant :

O. corniculata is a creeping, stoloniferous, perennial herb, with aerial stems, often branching at the base and rooting at the nodes. The roots are fibrous in nature. The leaves are alternate and consist of three heart-shaped leaflets which are bright or pale green in colour and are borne on slender petioles with a winged-basal joint. In the evening, they fold down around the leaf stalk. Flowers are borne on axillary peduncles in a group of 1-6 on each stalk with the central flower developing first. Flowers are yellow in colour, funnel-shaped bending downwards as the fruits developed. Fruit is five-angled, linear, green and hairy capsule. Seeds are reddish brown, flattened and ovoid varying in number from 40-65 in one capsule.

Plate 1 - Photograph showing the growth habit of Oxalis corniculata.



PLATE 1

Plate 2 - Photograph showing the growth of O. corniculata and
O. latifolia in association with maize and potato
crops.



PLATE 2

Distribution and habitat :

O. corniculata has a cosmopolitan distribution occurring throughout temperate and tropical zone (Eiten 1963, Holm et al. 1977). Its presence on all continents and many islands indicates that its seeds are carried by birds. It is generally distributed to the east and west throughout the world on agricultural lands (Holm et al. 1977). It is found growing in the gardens, lawns, arable lands, pastures, and greenhouses (nurseries) where it is a serious pest (Eiten 1963, Holm et al. 1977, Lourteig 1979). It also grows on walls, roadsides and wastelands (Plate 3).

Biology of the plant :

Prolific reproduction of O. corniculata is one of the main factors contributing to its weediness. This stoloniferous herb reproduces both vegetatively (by rooting at nodes) and also by seeds which are dispersed forcefully from capsules away from the parent plants (Robertson 1975, Holm et al. 1977). Seed reproduction and dispersal are the primary means of invasion. The plant may grow and reproduce year-round indoors (Elmore, Humphrey and Hesketh 1979). In Meghalaya, seed production occurs throughout the year in field condition also. The broad range of germination requirement and slow rate of seed decay as reported by Holt (1987), are helpful in its persistence and spread wherever it occurs. O. corniculata is predominantly inbreeding, but it has retained the capacity to outcross (Holt 1987). This has contributed to its success as an aggressive

Plate 3 - Photograph showing the growth of O. corniculata and
O. latifolia in waste land.



PLATE 3

and colonizing weed in disturbed habitats (Ornduff 1972, Lovett Doust et al. 1981). O. corniculata showed chromosome numbers $n = 24$ (Khonglam 1982). Because of its prolific reproduction coupled with rapid spread, in some cases, the plants may serve as a valuable ground cover in preventing soil erosion in perennial crops such as tea or coconuts (Holm et al. 1977).

Oxalis latifolia H.B.K. (Plate 4a & b)

Oxalis latifolia, a native of South Africa and America, is widespread in occurrence. Some of the crops with which the weed is associated in Meghalaya are rice, potato, maize & cauliflower (Plate 2).

Description :

O. latifolia is a bulbous perennial plant. The stem is modified into bulb which consists of a central cone of stem tissue and two types of scales, termed membranous and true scales (Jackson 1960). Membranous scales may extend to form fully developed leaves and in their axils, inflorescences may be produced. The true scales cannot form leaves and from their axils underground laterals may be produced, which terminate in bulbils or daughter bulbs. At the base of the bulb is a thick tap root which contracts and pulls the bulb downwards at the onset of winter. Three leaflets arise laterally with pulvini at the junction of leaflets and petiole, which react to stimuli and cause leaflet movement. Semi-sheathing leaf-bases surround the stem apex. Flowers light purple or lilac in colour,

Plate 4a - Photograph showing the growth habit of O. latifolia.

Plate 4b - Photograph of O. latifolia showing germination of a newly formed daughter bulb in the same growing season.



PLATE 4a



PLATE 4b

are borne in umbels of five to ten or more on peduncles arising in the axils of foliage leaf.

O. latifolia reproduces mainly through bulbs and bulbils. Seeding is of rare occurrence (Young 1958, Jackson 1960, Robb 1962, Khonglam 1982). In the present study also, no seeding could be observed although flowering took place.

Distribution and habitat :

O. latifolia is widely distributed, occurring in many parts of the world, particularly in sub-tropical regions. It is a major weeds of gardens, nurseries, agricultural lands and causes serious inconvenience to farmers. It is also found growing on walls, roadsides and waste places (Plate 3).

Biology :

The growth of O. latifolia plants is seasonal. The bulbs germinate in late spring and the plants continue their growth in subsequent months, but during severe winter season the aboveground parts of the plants are killed. The underground bulbs undergo a state of dormancy and they serve as perennating organs. During the growth period of the plant, the tap roots and new bulbils or daughter bulbs serve as the principal storage organs (Chawdhry and Sagar 1973, 1974 a). A newly formed daughter bulb or bulbil may produce leaves in the same growing season (Plant 4b)

The widespread occurrence of O. latifolia is due to its prolific vegetative reproduction. The bulbils or daughter bulbs

are easily detached from the parent plant, get dispersed and sprout when conditions are favourable (Chawdhry & Sagar 1974b).

O. latifolia is tri-stylous species and the chromosome numbers showed $n = 14$ (Khonglam 1982). Besides, meiosis is highly irregular in nature and the pollen grains greatly vary in size and their fertility is very low.

CHAPTER IV

Effect of associated vegetation on growth of
O. corniculata and O. latifolia.

INTRODUCTION

The relative fitness of individuals in many plant communities is influenced mainly by the activity of other organisms, particularly neighbouring plants (Hartnett & Bazzaz 1985). The interference from the associated species as reported by Dwivedi and Tripathi (1980) exercise a strong influence on the ecological niches of Alysicarpus monilifer and Indigofera enneaphylla in restricting their growth to a smaller hyper-volume. Several studies have shown that the growth, survivorship and reproductive capacity of individual plants are determined, in large part, by the number, position and growth of neighbours (Putwain & Harper 1970, Mack & Harper 1977, Fowler 1984, Goldberg & Werner 1983, Yadav & Tripathi 1983, Hartnett & Bazzaz 1985, Goldberg 1987). The structure of a plant community therefore is determined to a large extent, by the relative suppressive effects of species on each other (Aarssen 1988).

Various workers have studied the relationship of a 'target' species to a group of other species in natural communities (Sagar & Harper 1961, Putwain & Harper 1970, Pinder 1975, Dwivedi & Tripathi 1980, Goldberg 1980, Gross 1980, Fowler 1981, Yadav & Tripathi 1984). Moreover, growth forms of the neighbouring species also affect the 'target' species. Werner (1977) analysed the effect of both individual species and growth forms (grasses, perennial dicots, shrubs) on the success of Dipsacus sylvestris experimentally sown into eight natural communities and found that success of Dipsacus is mainly

linked with growth forms rather than abundance of individual species. Dwivedi & Tripathi (1980) found that the aboveground yield and seed production of Alysicarpus monilifer and Indigofera enneaphylla were reduced considerably in the presence of grasses than in the presence of dicots. In view of the vital role of associated vegetation in the life of a 'target' species, a field study involving the effect of selective removal of associated plant species on the growth and biomass allocation of O. corniculata and O. latifolia HBK. was undertaken.

MATERIALS AND METHODS

The study was conducted on the campus of the School of Life Sciences, North-Eastern Hill University, Shillong. The experiment started in January 1988 and continued till December 1988.

Thirty six permanent quadrats of 50 x 50 cm size were marked in the field having uniform density of Oxalis spp. The areas was then properly fenced to prevent any disturbance and the following treatment plots were maintained.

- (i) O. corniculata grown alone.
- (ii) O. latifolia grown alone.
- (iii) The two Oxalis species grown together (all other plant species removed).
- (iv) O. corniculata grown with grasses (all non-graminaceous species removed).

- (v) O. latifolia grown with grasses (all non-graminaceous species removed).
- (vi) Oxalis spp. grown with all other plant species.

Three replications were maintained for each treatment. The plant samples of Oxalis spp. were taken for growth measurement from each treatment plot after 8 and 12 months, hereinafter referred to as H₁ and H₂ respectively. Leaf area, number of leaves, stolon/bulbs, flowers and seeds and dry matter yield per plant were determined. For dry weight estimation, the plants were thoroughly washed to remove the soil particles adhering to the roots. Plant parts were sorted out and oven-dried at 80°C to constant weight.

RESULTS

The associated plant species greatly influenced the growth of O. corniculata and O. latifolia. When the Oxalis spp. were allowed to grow free from competition by other plant species, they produced greater number of leaves, stolons, bulbs and flowers (also number of seeds in case of O. corniculata), leaf area and dry matter yield as compared to other treatment plots. Although the growth of Oxalis was reduced by all the associated plant species, the grasses played a major role in limiting the growth (Table 4.1, 4.2, Fig. 4.1 and Fig. 4.2).

In O. corniculata, allocation to roots was not affected by the presence of associates whilst allocation to stolon was greatly reduced specially by the presence of grasses. Allocation to leaves

TABLE 4.1. GROWTH OF O. corniculata AS AFFECTED BY VARIOUS ASSOCIATES IN FIELD CONDITION (+ STANDARD ERROR).

Parameters	Treatment Plots							
	OC - all species		OC + OL		OC + G		OC + all species	
	H ₁	H ₂	H ₁	H ₂	H ₁	H ₂	H ₁	H ₂
No. of leaves/Plant	25.42+5.12	43.22+6.31	20.33+9.75	38.75+7.41	7.5+0.70	15.0+0.49	10.5+0.70	20.0+2.52
No. of stolons/Plant	15.12+4.81	22.0 +3.52	10.0 +3.7	18.75+3.47	3.0+0.17	4.66+1.47	4.0+1.41	10.0+1.41
No. of flowers/Plant	4.13+1.53	10.02+2.31	1.66+1.08	4.75+1.19	0	0.5 +0.25	0.5+0.23	2.0+0.70
No. of seeds/Plant	150.0+9.32	318.0+10.55	103.5+3.50	209.0+16.7	0	0	0	120.0+2.8

OC - Oxalis corniculata

OL - O. latifolia

G - Grasses

TABLE 4.2. GROWTH OF O. latifolia AS AFFECTED BY VARIOUS ASSOCIATES IN FIELD CONDITIONS (+STANDARD ERROR).

Parameters	Treatment Plots							
	OL - all the species		OL + OC		OL + G		OL + all the species	
	H ₁	H ₂	H ₁	H ₂	H ₁	H ₂	H ₁	H ₂
No.of leaves/Plant	4.0 _± 1.32	5.3 _± 1.21	3.25 _± 0.28	4.5 _± 0.33	1.0 _± 0.26	1.0 _± 0.32	2.0 _± 0.14	3.0 _± 0.23
NO.of daughter bulbs/ Plant	2.0 _± 0.50	5.12 _± 1.53	1.5 _± 0.70	3.5 _± 0.33	0	1.13 _± 0.20	0	2.33 _± 0.40
No.of flowers/Plant	0	0	0	0	0	0	0	0

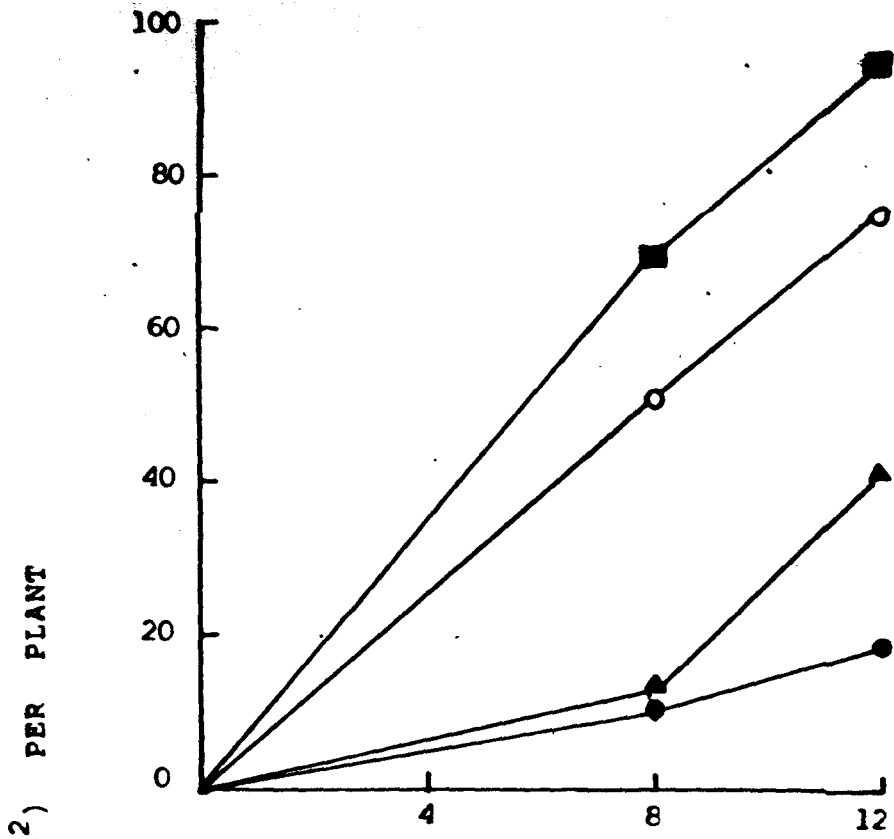
OL - O. latifolia

OC - O. corniculata

G - Grasses

Fig. 4.1 Leaf area per plant of O. corniculata and O. latifolia when grown with different associated species under field situation. ■—■, O. corniculata or O. latifolia grown alone; ○—○, Oxalis species grown with each other; ●—●, each of the Oxalis species grown with grasses and ▲—▲, each of the Oxalis spp. grown with all the species.

O. corniculata



O. latifolia

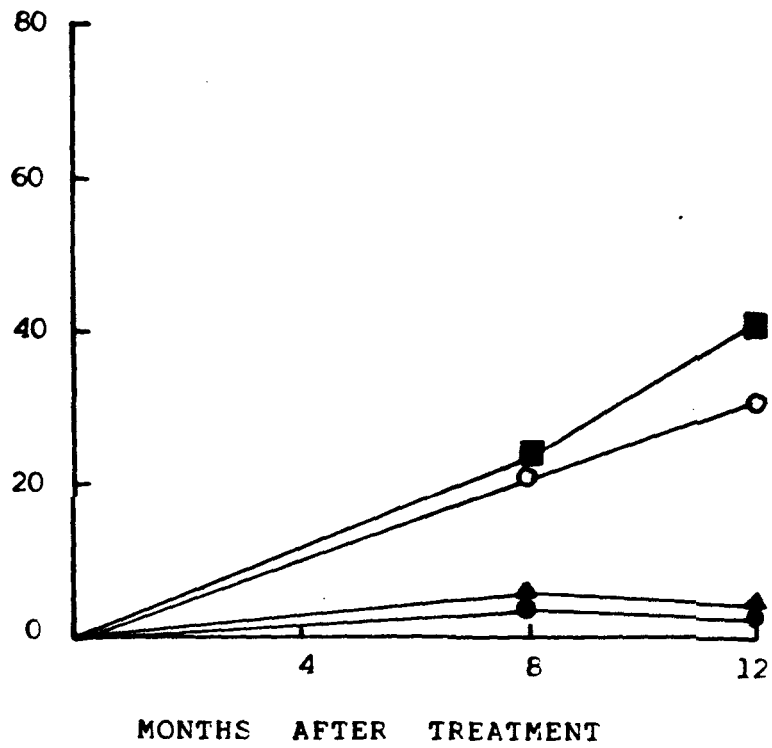


FIG. 4.1

Fig. 4.2 Dry matter yield (g) per plant of O. corniculata and O. latifolia when grown with different associated species under field condition. Symbols same as in Fig.4.1.

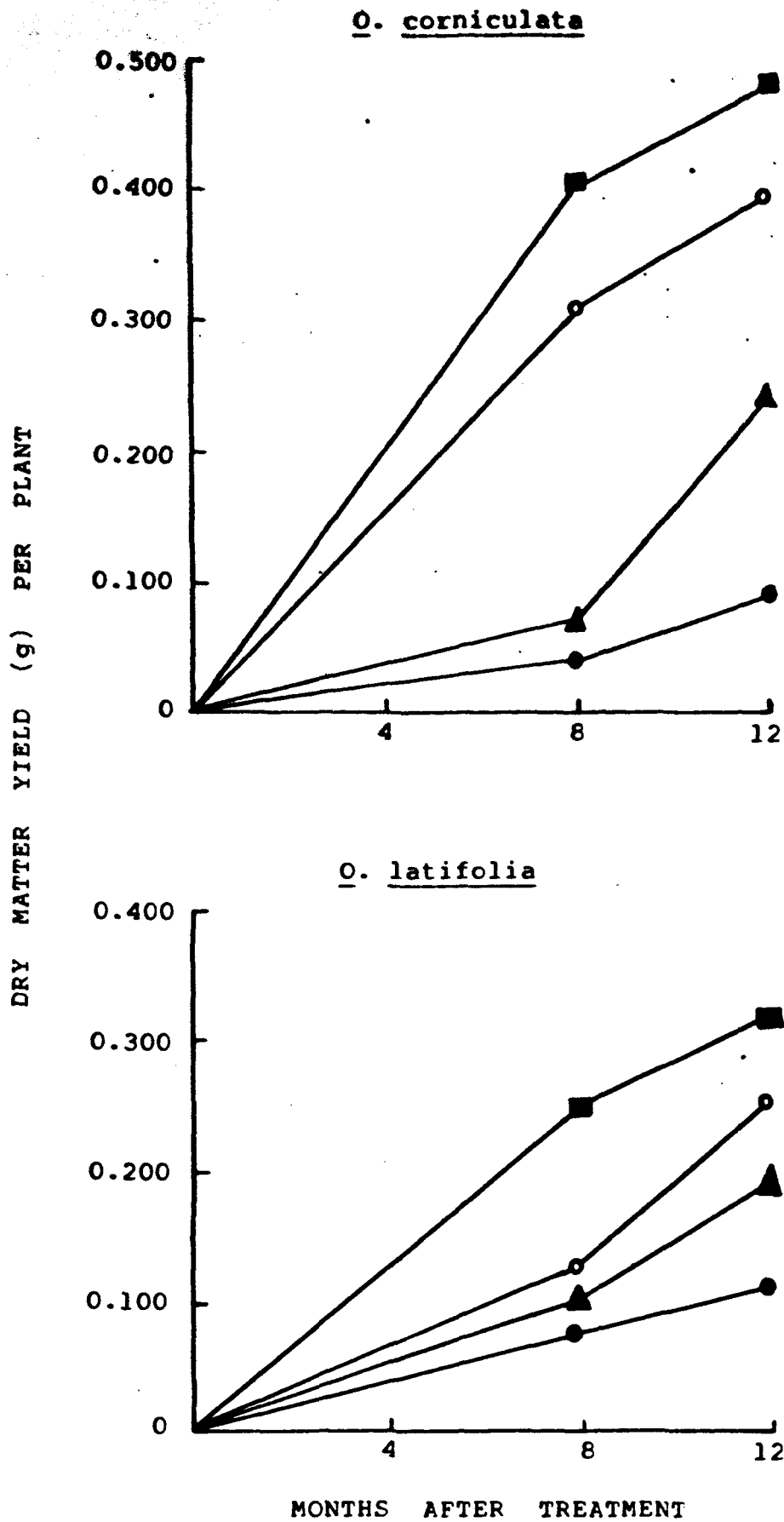


FIG. 4.2











Fig. 4.3A Percentage dry matter allocation towards roots  , stolon  , petiole  , leaves  , flowers & fruits  of O. corniculata in different treatment plots.

Fig. 4.3B Percentage dry matter allocation towards roots  , parent bulb  , daughter bulbs  , petiole  , & leaves  , of O. latifolia in different treatment plots.

Treatments : a = O. corniculata or O. latifolia grown alone.
 b = Oxalis species grown with each other.
 c = Each of the Oxalis species grown with grasses.
 d = Each of the Oxalis species grown with all the species.

was greater when O. corniculata was allowed to grow with grasses than when it grew alone, or with O. latifolia or with all other associated plant species. When grown alone, O. corniculata showed greater reproductive allocation and when grown with grasses, reproductive allocation was greatly reduced (Fig. 4.3a).

In O. latifolia, allocation to bulbils or daughter bulbs was reduced when grown with associated vegetation. However, allocation to parent bulb and leaves remained unaffected by the presence of associates (Fig. 4.3b). In O. latifolia, flower and seed production did not occur either when grown alone or with associates (Table 4.2). O. corniculata, however, showed flowering at the time of second harvest, but the seed production was absent when it was grown with grasses (Table 4.1). In general, the overall performance of O. corniculata in presence of the associates was better than O. latifolia, indicating that in field situation the former is less severely affected by the competition from the associated plant species.

DISCUSSION

The growth and reproduction of Oxalis corniculata and Oxalis latifolia are greatly affected as a result of competition from neighbouring species. Of the associated species, the grasses seem to play a major role in regulating the growth of Oxalis species. The suppressive effect of grasses on reproduction is in agreement with the findings of Tripathi and Dwivedi (1978) who found a 90.7% reduction in seed output of Alysicarpus monilifer when grown with grasses. The drastic reduction in growth of other species caused by the competition from grasses has also been reported by Sagar & Harper (1961) and Putwain and Harper (1970). Sagar (1970) reported that the chance of a seed producing a seedling or an established adult plant in case of Plantago lanceolata was greatly increased in grass-free plots.

Gupta and Tripathi (1979) reported that when Bothriochloa pertusa was introduced to already established population of Dichanthium annulatum, it showed reduced yield and complete suppression in reproductive growth. Flowering in Oxalis latifolia was totally absent when it grew in competition with grasses.

In O. corniculata, biomass allocation to roots did not change much due to the presence of associates. Greater allocation to leaves and decreased reproductive allocation in the presence of associates indicates that under competitive situations, the plant seems to concentrate more on vegetative growth.

In O. latifolia, allocation to parent bulb and leaves was not affected by the associates, but flowering did not occur and allocation to bulbils or daughter bulbs was greatly reduced, which indicates that greater emphasis is laid on the vegetative growth than on reproductive structures and this may be helpful in resource capture by this weed.

The study suggests that inter-specific competition is more crucial than intraspecific competition for both the species. The grasses have been found to exert strong suppressive effects on the vegetative and reproductive growth of the field population of O. corniculata and O. latifolia. As argued by Dwivedi & Tripathi (1980), the restrictions in the fundamental niches of the plant species in presence of associates may largely be attributed to the resource competition amongst various species populations. However, as revealed by the data, the two species respond to competition from the associates by concentrating more on vegetative growth. This is a useful strategy under competitive stress as it enables them to exploit the natural resources efficiently.

A comparison of the reactions of the two Oxalis species to the presence of the associated vegetation suggests that O. corniculata is a better competitor than O. latifolia.

CHAPTER V A

Growth of O. corniculata raised from seeds and stolon cuttings in pure and mixed stands.

INTRODUCTION

The response of different populations of a species over a similar habitat range reflects the adaptive nature of certain traits in plants (Turesson 1922, 1925, 1930; Mayr 1970, Corn & Hiessey 1973, Hume & Cavers 1983, Degennaro & Weller 1984). Selection acts upon the organism as a whole, favouring a balanced complex of genes that provides the best possible fitness to individuals (Gregor et al. 1936, Stebbins 1950, Waddington 1957, Glausen & Hiessey 1960, Bennett 1964, Lerner 1968, Mayr 1970, Hume & Cavers 1982, Schmid 1985b). Populations with high levels of variation will have broad niches and exploit a wider range of environmental variability (Zangerl & Bazzaz 1984). Wide ecological amplitude of perennial weedy species is correlated with the possession of several forms of regeneration (Grime 1978). Variation in ecological responses exists between seed-initiated and rhizome-initiated individuals (Tripathi & Harper 1973, Kushwaha et al. 1983, Lee et al. 1986). An indication of competitive ability of genets and ramets of the same species can be provided by growing them in mixtures and monocultures.

O. corniculata possesses both sexual and vegetative types of regeneration. Thus, in nature seed-initiated and stolon-initiated individuals occur together and compete for the available resources. The analysis of the growth of each in pure culture and in presence of the other may reveal their ecological fitness in the situations where O. corniculata occurs in abundance and other species are of

lesser importance. An experiment was, therefore, made to examine the growth response of the pure and mixed populations of O. corniculata raised from seeds and from stolon cuttings.

MATERIALS AND METHODS

The experiment was conducted in a net house provided with polythene sheet roofing. Stem cuttings of uniform size and weight (0.030 - 0.040 g) and seedlings of 2-3 leaf stage (0.010 - 0.015 g) were carefully selected. Stem cuttings and seedlings were collected from the natural populations. A constant density of 4 plants/pot was maintained in the experimental pots (21 cm diameter, 19 cm depth with a basal drainage hole). Pure and mixed populations of O. corniculata were raised from stem cuttings and seedlings by planting them in the ratios of 100 : 0; 50 : 50; and 0 : 100. The experiment was started on 30 June, 1988 and terminated on 29 September, 1988. The plants were harvested at fortnightly interval corresponding to 15, 30, 45, 60, 75 and 90 days after planting. At each harvest, stolon production, seed production, leaf area and dry matter yield were determined. Relative yield (RY), Relative yield ratio (RYR) and Relative yield total (RYT) (De wit and Van den Bergh 1965) were calculated from the yield data.

RESULTS

There exists a variation in the growth performance of plants raised from seeds and stolon cuttings. The plants raised from seeds

TABLE 5A.1. NUMBER OF STOLONS/PLANT OF O. corniculata RAISED FROM SEEDS AND CUTTINGS IN PURE AND MIXED STANDS.

Nature of stands	H A R V E S T S					
	H ₁	H ₂	H ₃	H ₄	H ₅	H ₆
<u>O. corniculata</u> raised from seeds (CS) (Pure stand)	-	-	-	3	8	15
<u>O. corniculata</u> (CS) mixed with CC	-	-	-	4	8	8
<u>O. corniculata</u> (CC) mixed with CS	-	2	3	10	10	12
<u>O. corniculata</u> raised from cuttings (CC) (Pure stand)	-	2	4	6	12	18

- indicates absence of stolons.

Fig. 5A.1. Replacement diagrams based on total leaf area/pot Cm^2 of the two populations of O. corniculata after 2 months and 3 months growth, ●—● , yield of pure population raised from seedlings (CS); ○—○ , yield of pure population raised from the stolon cuttings (CC); ----X----, yield of the mixed populations.

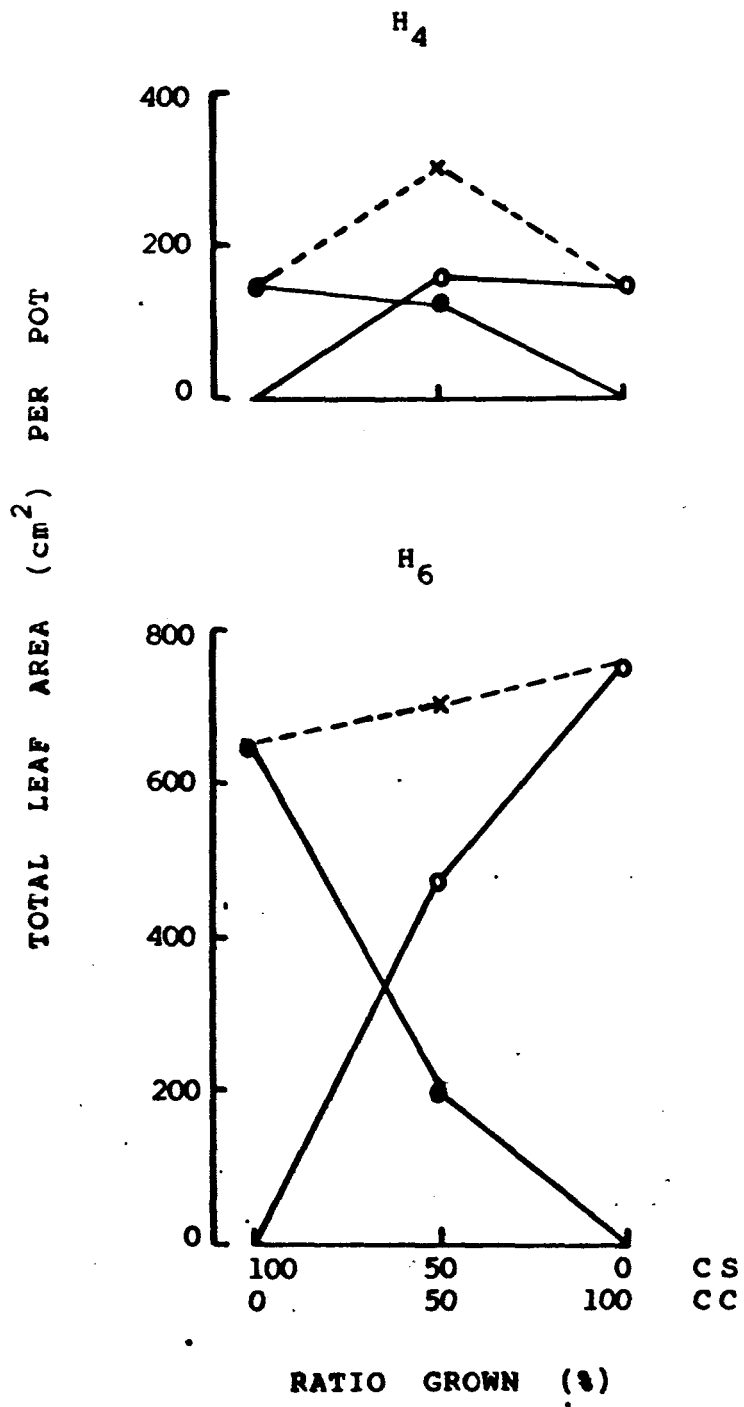


FIG. 5A.1

Fig. 5A.2. Replacement diagrams based on yield per pot (g) of the two populations of O. corniculata after 2 and 3 months growth. Symbols as in Fig. 5A.1.

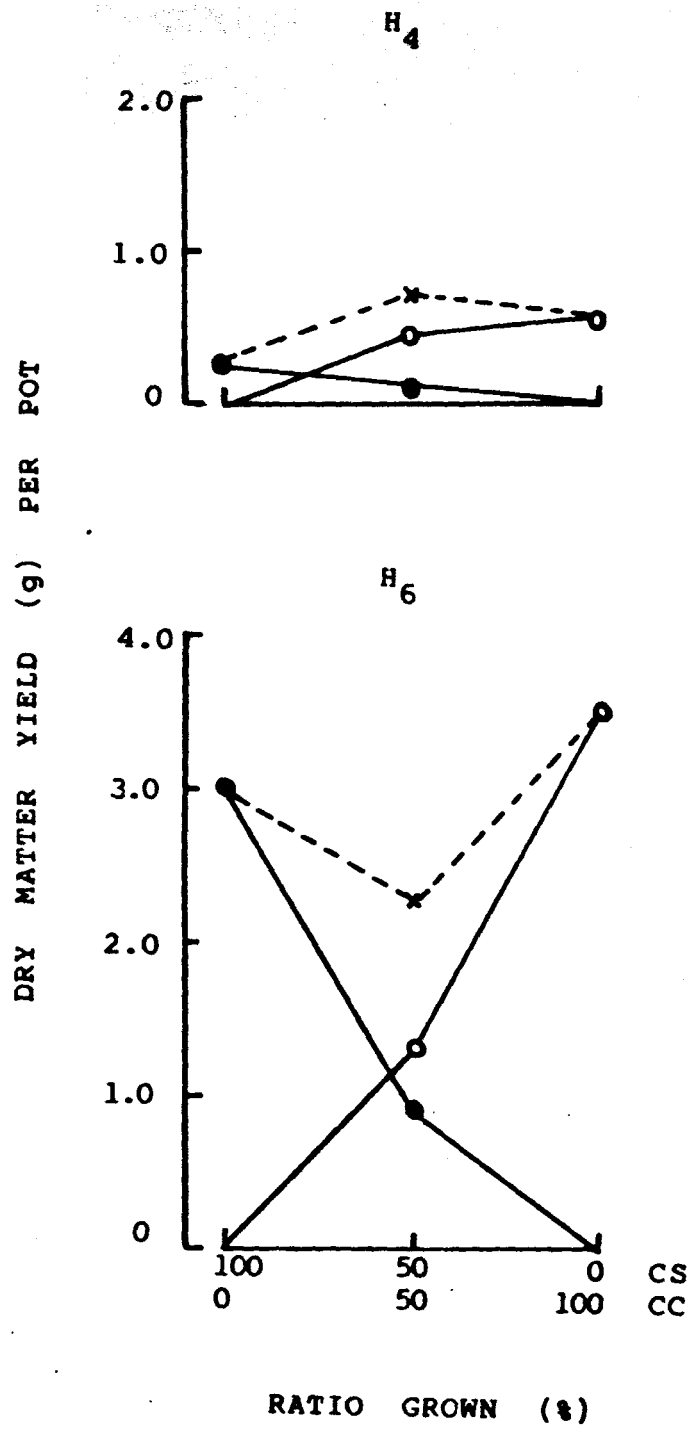








FIG. 5A.2

Fig. 5A.3. Percentage dry matter allocation towards roots  ,
stolons  , petiole  , leaf  , flowers
 , and seeds  , of O. corniculata in pure
and mixed stands raised from seedlings (CS) and stolon
cuttings (CC).

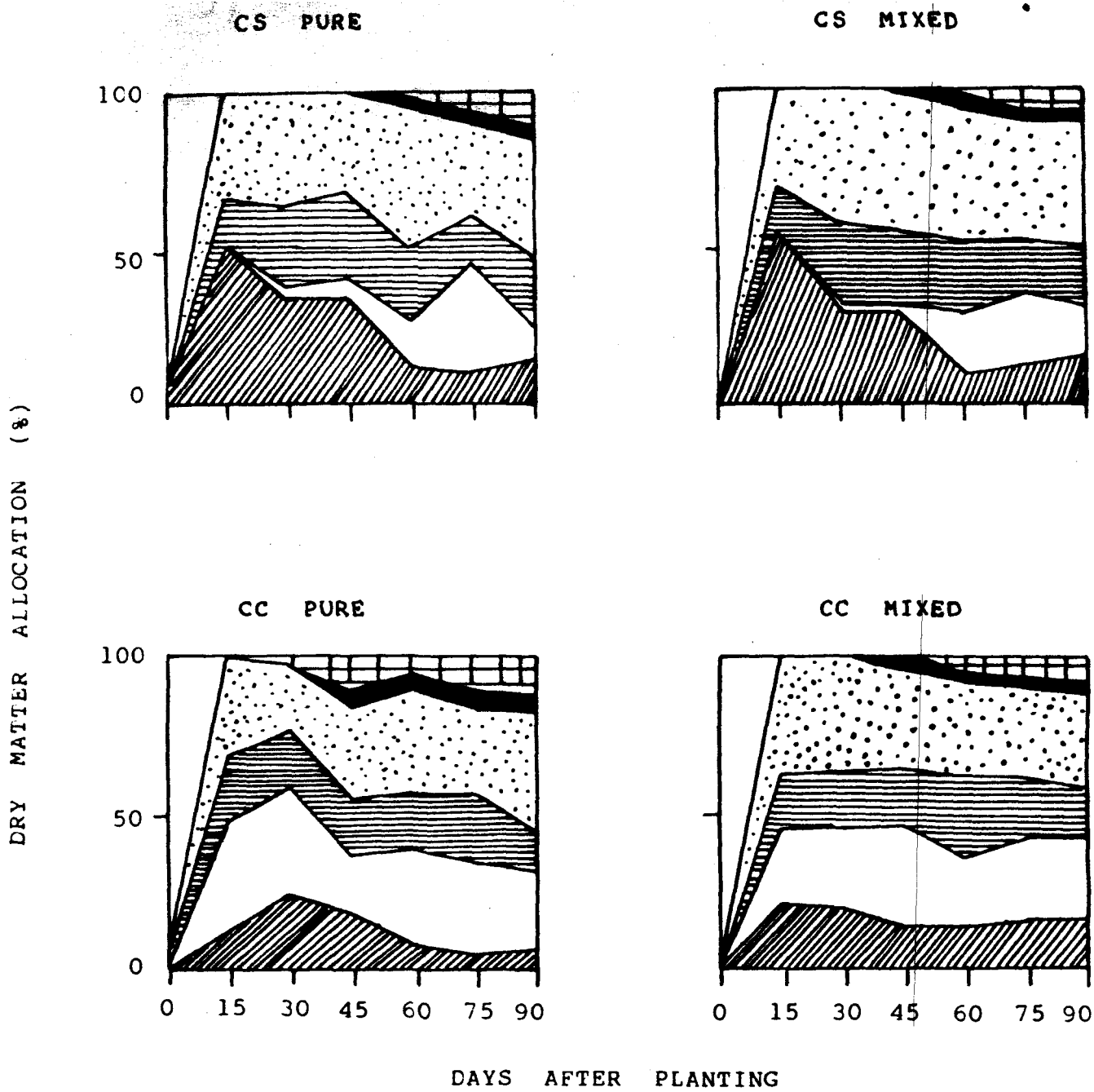


FIG. 5A.3

did not produce stolons even after 45 days from planting whereas those raised from the stolon cuttings produced stolons only after 15 days growth (Table 5A.1). The production of stolons was greater in monocultures than in mixtures. In general, the plants raised from cuttings produced greater number of stolons as compared to those raised from seeds.

Total leaf area and total yield of the plants raised from stem cuttings were generally greater than those raised from seeds. Growth of plants as indicated by leaf area and dry matter yield at the fourth harvest, was greater in mixtures than in monocultures (Fig. 5A.1 & 5A.2). Allocation of resources to roots was greater in plants raised from seeds, while the plants raised from cuttings allocated more resources to stolons, flowers and seeds. Allocation of resources to reproductive structures was greater in monocultures than in mixtures (Fig. 5A.3).

Relative yield of plants raised from cuttings was greater than those raised from seeds [Table 5A.2(a)]. RYT and RYR values were always greater than one [Table 5A.2(b) Fig. 5A.4].

Plants raised from cuttings produced more seeds compared to those raised from seedlings. However, at the last harvest, seed output was almost equal in the two categories of plants (Table 5A.3).

TABLE 5A.2(a). RELATIVE YIELD OF O. corniculata PLANTS RAISED FROM STOLON CUTTINGS AND SEEDLINGS AT SIX HARVESTS.

Nature of plants	Days after planting					
	15	30	45	60	75	90
<u>O. corniculata</u> raised from cuttings	0.60	1.29	0.57	1.95	1.12	1.89
<u>O. corniculata</u> raised from seeds	0.60	1.10	0.43	1.35	0.73	0.57

TABLE 5A.2(b). RELATIVE YIELD TOTAL OF O. corniculata PLANTS RAISED FROM CUTTINGS AND SEEDLINGS AT SIX HARVESTS.

	Days after planting					
	15	30	45	60	75	90
Relative Yield Total	1.20	2.39	1.00	3.30	1.85	1.46

Fig. 5A.4. Relative yield ratio of the population raised from stolon cuttings (CC) to that from seedlings (CS) at six harvests.

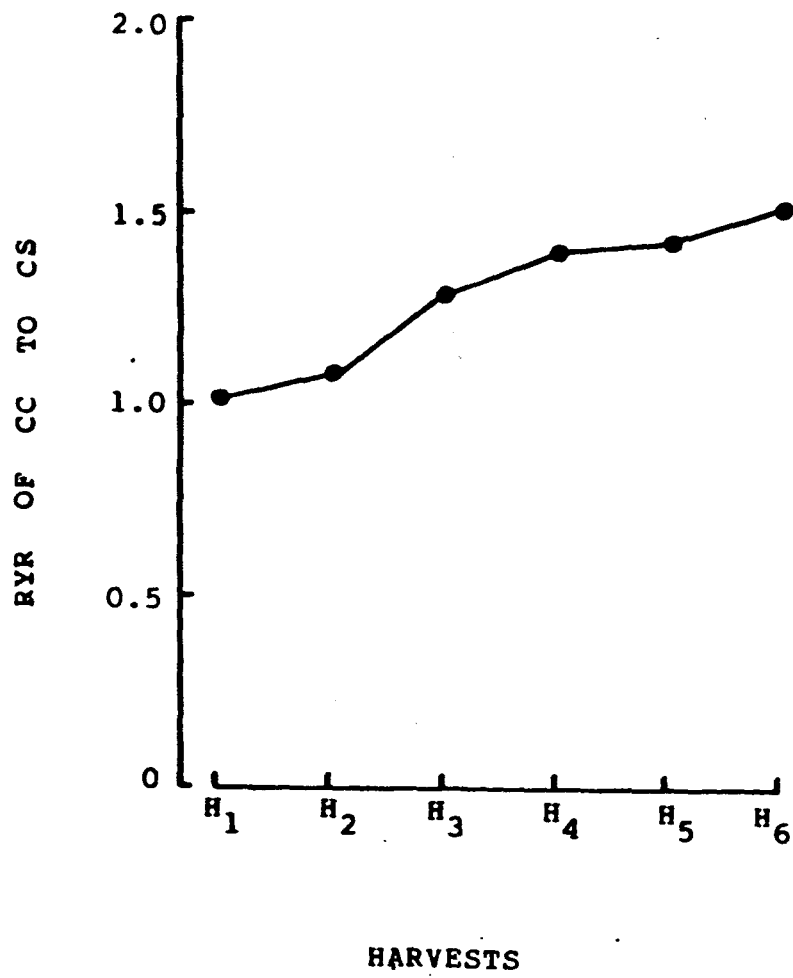


FIG. 5A.4

TABLE 5A.3. AVERAGE SEED OUTPUT/PLANT OF O. corniculata RAISED FROM SEEDS AND CUTTINGS IN PURE AND MIXED STANDS.

Nature of stands	Days after planting				
	30	45	60	75	90
<u>O. corniculata</u> (CS) Pure	-	-	50.0	275.0	660.0
<u>O. corniculata</u> (CS) Mixed with CC	-	-	-	190.0	385.0
<u>O. corniculata</u> (CC) Mixed with CS	-	-	111.0	220.0	400.0
<u>O. corniculata</u> (CC) Pure	55.0	100.0	160.0	350.0	660.0

DISCUSSION

O. corniculata plants raised from cuttings produced greater leaf area, more stolons and seeds, showed better growth and greater yield compared to those raised from seeds. The basis of differences may lie in the greater starting capital in stolons compared to seeds (Tripathi & Harper 1973, Turkington et al. 1979, Kushwaha et al. 1983, Zangerl & Bazzaz 1983), or it may also be due to ontogenetic niche variation (Parrish & Bazzaz 1985, Lee et al. 1986). At the fourth harvest the total yield in mixture was greater than the yield in monocultures (Fig. 5A.2), which indicates that at this growth stage the two populations exploit the resources with greater efficiency when grown in mixture than when grown in monoculture. It could also indicate the escape of each type from competition with the other, whereby the major growth phase of one type did not coincide with that of another, so that neither interfered so severely with the other. Although the two categories of plants do compete with each other, yet at a certain stage in their life cycles they offer no serious competition to each other allowing better growth in mixture. However, at the last harvest both the monocultures gave greater yield than the mixture. This type of interaction is of significant importance in the evolutionary strategies of plant populations.

Greater allocation of resources to roots, in seed-initiated plants indicates the need for greater absorptive surface for efficient exploitation of resources. Greater allocation of resources to stolons, flowers and seeds in stolon-initiated plants indicates that cuttings

lay more emphasis towards reproduction. The higher relative yield values of the plants raised from stem cuttings compared to the plants grown from seedlings indicates that they are more competitive than the latter. The RYR of CC to CS which was always greater than one also confirms that the cuttings are better competitors. The RYT values were always greater than one indicating that the competition between the two categories of plants is presumably not so severe (Harper 1977, Clay & Levin 1986). This indicates the possible co-existence of the two categories of populations which incidentally have been invariably observed to grow together in nature.

It is clear that inspite of differences in growth response and competitiveness of the two categories of plants, they have evolved the strategy of co-existence which is beneficial for the survival of interacting organisms.

CHAPTER V B

Growth of O. latifolia as affected by bulb size.

INTRODUCTION

The environment is in a continuous state of flux and many successful weedy species respond to such environmental variations by having different phenotypes produced from a single genotype. The ability of a genotype to produce a range of phenotypes is a crucial aspect of life history strategy (Cox & Ford 1987). Local environmental variation has direct effects on ramet size as has been demonstrated in the case of Aster acuminatus (Pitelka et al. 1980, Ashmun & Pitelka 1984). Plant or ramet size has been shown to be an important determinant of growth and survivorship and, therefore, an important component of fitness in many plant species (Werner 1975, Cook 1980, Bradbury 1981, Gross 1981, Solbrig 1981, Thompson & Beattie 1981, Caswell 1982, Brown et al. 1985, Pitelka et al. 1985 and Spencer 1986). Moreover, propagule size affect the growth and competitive success of plants as has been demonstrated by Rai and Tripathi (1982). They observed that in Galinsoga parviflora, the ray-achenes were larger, heavier and contained more energy than disc-achenes. They produced seedlings which showed better survival and growth than those produced from the disc-achenes, and the plants produced from the former had greater competitive ability.

O. latifolia reproduces chiefly by vegetative means through the production of bulbs. The success of O. latifolia lies mainly in the ability of the plant to produce a large number of bulbs

during the growing season. The bulbs produced from a single clone show considerable variation in individual size and weight. Brown et al. (1985), observed strong correlations between ramet size and certain phenological traits in Clintonia borealis and Aster acuminatus. Since there is a strong relationship between propagule size and growth and development of plants, a study relating to the effect of bulb size on the growth of O. latifolia was undertaken.

MATERIALS AND METHODS

The experiment was conducted in a net house with polythene sheet roofing. Bulbs of three different sizes were selected taking care to ensure the uniformity in each category. The dry weight of large, medium and small categories of bulbs was determined and average values per bulb were 0.15 g, 0.1 g and 0.05 g respectively. Four bulbs of each size were planted in the experimental pots (21 cm diameter and 19 cm depth with a basal drainage hole) filled with equal quantity of garden soil on 1 August, 1987.




The six harvests were taken at 15, 30, 45, 60, 75 and 90 days from planting. At each harvest, bulb production, leaf area and dry matter yield were determined. For the determination of dry matter allocation to different plant parts, the latter were separated and oven-dried for 24 hours at 80°C. The dry matter yield per plant was computed from the yield data for different plant parts.

RESULTS

Plants raised from bulbs of different sizes showed differences in growth behaviour. Leaf area was maximum in plants raised from large bulbs although it showed a decreasing trend after the fourth harvest (Fig. 5B.1), whereas plants raised from small bulbs showed minimum leaf area. The production (number) of daughter bulbs increased with increasing bulb size and with time (Table 5B.1). Dry matter yield also followed a trend similar to daughter bulb production except that at the last harvest plants raised from larger bulbs showed a decrease in dry matter yield (Fig. 5B.2).

Greater biomass was allocated to belowground parts particularly to the bulbils or daughter bulbs. Allocation towards parent bulbs decreased with time, whereas the reverse was true in the case of daughter bulbs. Among the aboveground parts, maximum dry matter was allocated to leaf and minimum to the reproductive parts (Fig. 5B.3).

The plants raised from large bulbs showed maximum RGR (Table 5B.2) and NAR values (Table 5B.3). However, the leaf area ratio (LAR) was maximum in plants raised from small bulbs and minimum in plants from larger bulbs (Table 5B.4). Leaf weight ratio also followed similar trend as in the case of LAR (Table 5B.5).

Fig. 5B.1. Leaf area/plant of O. latifolia as affected by bulb size. Plants raised from small (), medium (), and large () bulbs.

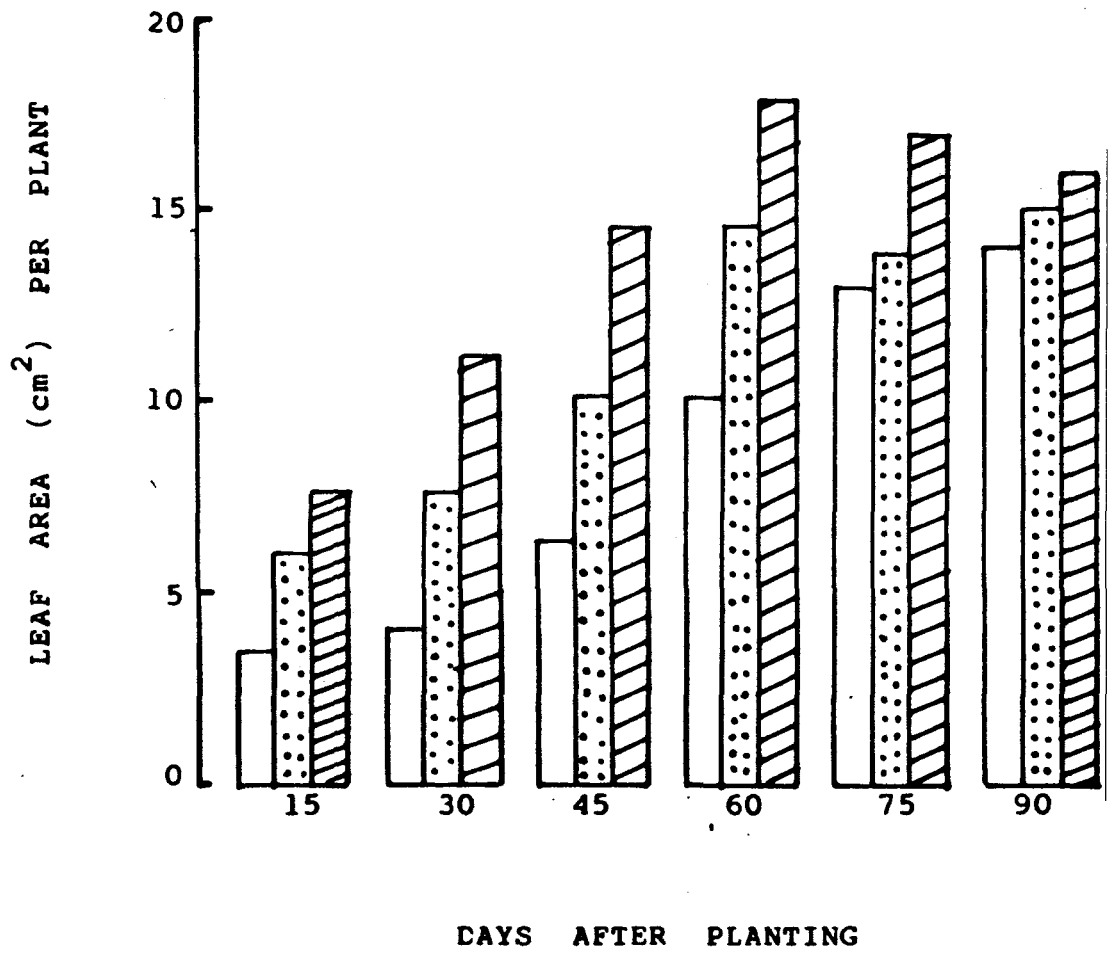


FIG.5B.1

TABLE 5B.1. DAUGHTER BULB PRODUCTION (NUMBER/PLANT) OF O. latifolia
 RAISED FROM BULBS OF THREE DIFFERENT SIZES AT 6 HARVESTS
 (H_1 TO H_6).

Bulb size from which plants were raised	No. of daughter bulbs/plant					
	H_1	H_2	H_3	H_4	H_5	H_6
Small	-	-	2	10	10	14
Medium	-	-	3	10	13	16
Large	-	1	6	14	15	18

(-) indicates absence of daughter bulb production.

Fig. 5B.2. Dry matter yield of O. latifolia plants raised from bulbs of three different sizes (●—● , small; ▲—▲ , medium; ■—■ , large).

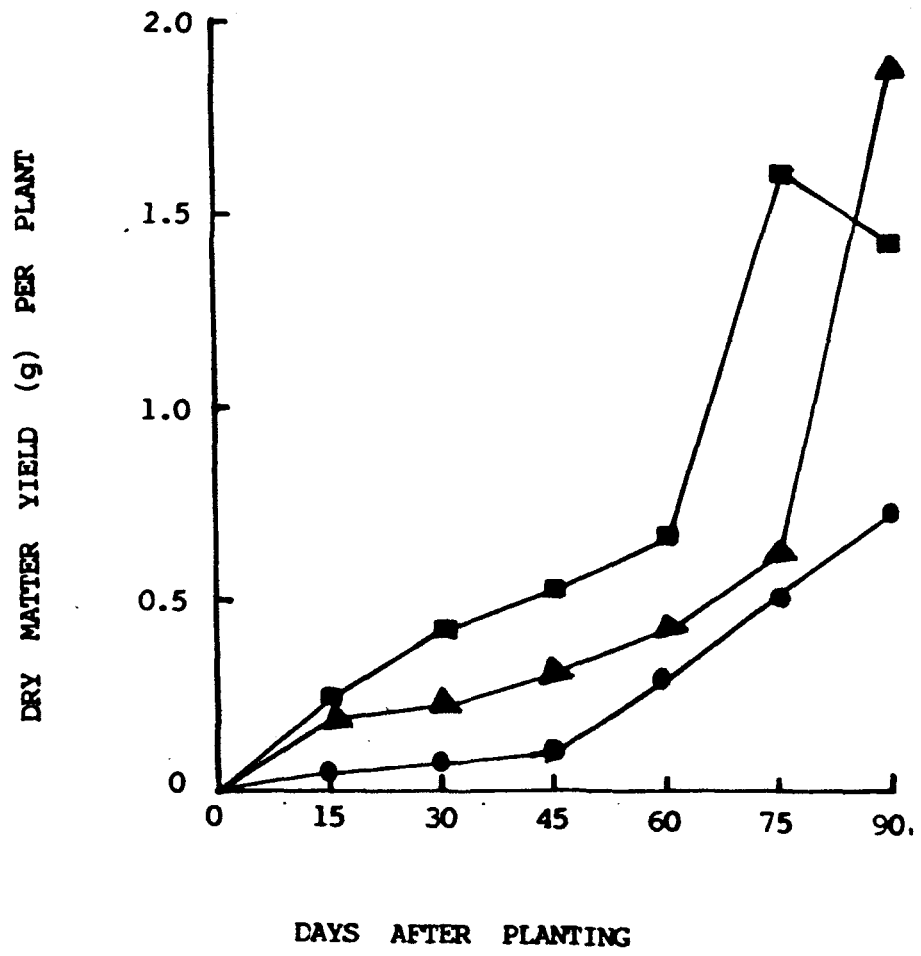








FIG. 5B.2

Fig. 5B.3. Percentage dry matter allocation towards roots (), parent bulb (), bulbils or daughter bulb (), petiole (), leaf (), and flowers () of O. latifolia as affected by bulb size.

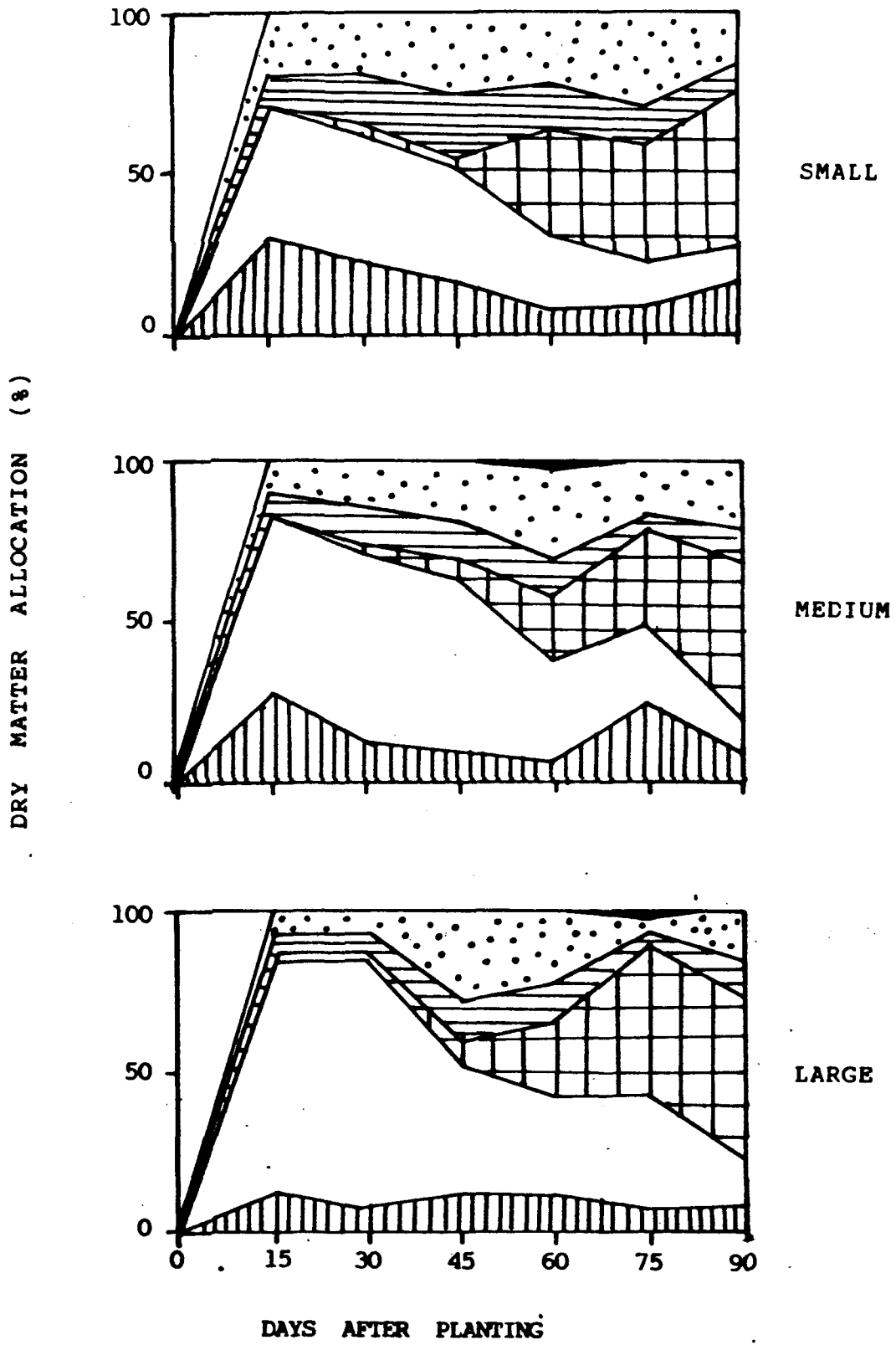


FIG. 5B.3

TABLE 5B.2. RELATIVE GROWTH RATE ($\text{mg mg}^{-1} \text{ day}^{-1}$) OF O. latifolia RAISED FROM BULBS OF THREE DIFFERENT SIZES (SMALL, MEDIUM AND LARGE).

Bulb size from which plants were raised	RGR between					
	0 - 15 days H_1	15 - 30 days H_2	30 - 45 days H_3	45 - 60 days H_4	60 - 75 days H_5	75 - 90 days H_6
Small	0.0045	0.0123	0.0090	0.0261	0.0378	0.0236
Medium	0.0060	-0.0148	0.0102	0.0360	0.0249	0.0441
Large	0.0146	0.0355	0.0155	0.0408	0.0611	0.0741

TABLE 5B.3. NET ASSIMILATION RATE ($\text{mg cm}^{-1} \text{day}^{-1}$) OF O. latifolia RAISED FROM BULBS OF THREE DIFFERENT SIZES.

Bulb size from which plants were raised	Days after planting					
	0 - 15	15 - 30	30 - 45	45 - 60	60 - 75	75 - 90
Small	0.20	0.23	0.14	0.47	0.22	0.12
Medium	0.15	-0.13	0.21	0.25	0.36	0.53
Large	0.32	0.35	0.25	0.23	0.51	0.64

TABLE 5B.4. LEAF AREA RATIO (cm²/g) OF O. latifolia RAISED FROM BULBS OF THREE DIFFERENT SIZES.

Bulb size from which bulbs were raised	Days after planting					
	15	30	45	60	75	90
Small	222.31	165.44	281.21	192.04	152.72	168.20
Medium	70.48	135.24	149.41	141.60	76.56	166.33
Large	59.63	59.52	97.70	179.45	51.61	89.54

TABLE 5B.5. LEAF WEIGHT RATIO (g/g) OF O. latifolia RAISED FROM BULBS OF THREE DIFFERENT SIZES.

Bulb size from which plants were raised	Days after planting					
	15	30	45	60	75	90
Small	0.231	0.210	0.238	0.229	0.284	0.180
Medium	0.087	0.152	0.212	0.298	0.115	0.130
Large	0.074	0.086	0.229	0.206	0.083	0.122

DISCUSSION

Bulbous plants have the potential to transfer substantial proportions of food reserves from one generation to the next. Consequently, plants from larger bulbs can perform better due to greater amount of food reserves in them. This seems to be true in case of O. latifolia where plant performance is correlated with bulb size. In another species of Oxalis (O. pes-caprae) also, plant size was found to be affected by bulb size (Lane 1984).

The increased daughter bulb production with increasing bulb size in O. latifolia is in agreement with the findings of Spencer (1986) and Eriksson (1988) who observed that tuber production in Potamogeton pectinatus and stolon production in Potentilla anserina respectively increased with increasing size of the propagules.

Plant dry weight is positively correlated with bulb size. However, the decreased dry weight of the plants raised from larger bulbs observed at the last harvest (Fig. 5B.2) may be attributed to increased leaf senescence in larger plants with advancing age.

In O. latifolia, the characteristic feature of biomass allocation pattern is that it devotes considerable amount of energy towards the belowground parts, particularly the bulbs. This is a characteristic attribute of bulbous plants (Bourdöt et al. 1985). The increased dry matter allocation to bulbils associated with a rapid decrease in dry weight of parent bulb throughout the experi-