1986

REPRODUCTİVE ALLOCATION IN FLOWERING PLANTS

WILSON, ANN MARGARET

REPRODUCTIVE ALLOCATION IN FLOWERING PLANTS

ANN MARGARET WILSON

PhD Thesis

submitted in partial fulfilment
of the requirements of the C.N.A.A. for a PhD
Plymouth Polytechnic, Dept. of Biological Sciences
in collaboration with the Unit
of Comparative Ecology -
University of Sheffield

October 1986

A M WILSON - REPRODUCTIVE ALLOCATION IN FLOWERING PLANTS

ABSTRACT

The proportion of resources which an organism devotes to reproduction has been assumed to be of great evolutionary and ecological significance. However, in previous studies of reproductive allocation (RA) in plants, there has been no consensus of precisely what is being measured nor how it should be measured. An attempt was made to determine the 'best' method of measuring RA and then apply this to a range of species with differing ecological strategies.

Under nutrient stress caused by a low N treatment Taraxacum officinale and Poa annua were found to maintain their RA despite up to 4 fold reductions in biomass. Under K and P deficient conditions there was a preferential allocation of these elements to reproductive structures in Taraxacum. Ruderal plants therefore, seem to maintain biomass RA and seed quality despite nutrient stress.

Although the nutrient RA in Taraxacum was found to be significantly different from biomass RA (KRA = 71% PRA = 66% BRA = 51.7%) the extent of the difference varied between treatments. There was therefore no obvious alternative currency to biomass.

The evolutionary consequences of reproduction may also be measured through a reproductive cost which may take the form of reduced future reproduction, survival or growth. Prevention of flowering in Digitalis purpurea resulted in an increase in the number of axillary buds produced. Similarly in Plantago lanceolata removal of flowers resulted in a 3 fold increase in production of buds. In both species realisation of a reproductive cost was prevented. The importance of individual variability was noted.

The importance of plant morphology was evident and was used to explain some of the anomalous RA values in the comparative experiment. RA values were collected for 40 species of Gramineae. RA was a useful ecological index which emphasised the ruderal element of a plant's strategy. When used in conjunction with other parameters particularly Rmax, RA produced a meaningful classification of species in terms of their ecological strategy.

C O N T E N T S

CHAPTER 1 - INTRODUCTION

The concept of resource allocation by organisms has been thought to be of evolutionary and ecological significance. The way in which an organism partitions finite resources between its various activities will determine the probability of its passing on its genes to succeeding generations. The 'principle of allocation' (Cody 1966) is that natural selection results in each organism optimising the partitioning of its resources to maximise fitness (see Ch. 4). This principle was originally developed to apply to birds but the constraints of a finite world where resources are limited and need to be subdivided, must also apply to plants.

Natural selection does not favour any particular pattern of allocation per se, but acts by optimising the genetic contribution of an individual to future generations, relative to the contribution of other individuals. Any allocation pattern that increases that contribution will be favoured. The proportion of resources allocated to reproduction will not necessarily be equivalent to fitness since finite resources devoted to reproduction must be obtained at the expense of other functions such as defence and growth. Nevertheless much attention has been focussed on the reproductive allocation or effort of species in relation to their ecological and evolutionary status.

The variability of plant size, number of inflorescences and reproductive capacity (the seed characteristics) of plants on fertile and infertile soils was first noted by Salisbury (1942). He drew attention to the broad correlations between the reproductive capacity of a species and its ecological status. However, as Harper and Ogden (1970) noted, reproductive capacity itself has not proved very successful as a criterion for making ecological comparisons and they

suggested that the proportion of total resources that a plant devotes to reproduction might be more useful.

Since their application of reproductive allocation or effort to plants there has been much controversy about what exactly constitutes reproduction and which method should be adopted in order to measure it. Some of the difficulties inherent in reproductive allocation studies are explored in Ch.2. Antonovics (1980) believes that much of the confusion in reproductive allocation studies arises from a confusion of perspective and purposes. Studies have differed in perspective in their interest in:

a. The mechanics of the generation of the allocation pattern in physiological terms.

b. The origin of the allocation pattern in an evolutionary sense (ie its adaptive significance).

c. The measurement of an allocation pattern as an approximation of the life-history of the organism.

A suitable method for measuring RA should be chosen dependent on the purpose of the study.

Harper and Ogden (1970) introduced the use of biomass allocation (the proportion of total biomass stored in each organ) as a way to study allocation patterns and this method has subsequently been used to approach a variety of questions (Gadgil and Solbrig 1972, Ogden 1974, Hickman 1975, 1977 Holler and Abrahamson 1977, Pitelka 1977). One of the most frequently posed questions in allocation studies is the effect

of stress on allocation patterns. In particular environments, certain patterns of resource allocation might confer greater fitness. Where a species has a plastic ability to adjust to environmental conditions the allocation pattern might be re-aligned to conform with changing environmental circumstances. An environmental stress might take many forms eg drought, shade or nutrient deficiency. The effect of one particular stress - nutrient deficiency - on reproductive allocation in two species is investigated in Ch.3.

The identification of biomass as the crucial limiting resource, however, has always been a critical assumption in many previous studies of RA. If the evolutionarily important allocation patterns are to be revealed then biomass itself should be the crucial limiting resource or alternatively it should follow the same allocation pattern as the limiting resource. It has been suggested (Lovett-Doust 1980a, Stewart and Thompson 1981) that mineral allocation might be a more appropriate currency by which to gauge RA. This suggestion is explored in Ch.4. through chemical analysis of the composition of plants obtained from the nutrient limitation experiment.

Although it might appear that it would be most adaptive for an organism to allocate as much of its resources to reproduction as possible (since this would seem to maximise its contribution to the next generation) this is often not the case. Within an individual, present growth and survival increase future survival and future reproduction. Present reproduction entails a reproductive cost in terms of future growth, reproduction and survival. Bell (1980) argues that measurement of this reproductive cost is more relevant to fitness than RA. It is this reproductive cost which has an evolutionary consequence. The

possibility of measuring reproductive cost in terms of future survival and growth (5.1) and future reproduction (5.2) is investigated in Ch.5. Once the most satisfactory method of measuring RA has been determined it can be applied in comparative experiments to determine the ecological and adaptive significance of various life history strategies. The value of comparative experiments has been noted by Grime (1984) and in Ch.6 the RA of various species of Gramineae of contrasting ecology is compared and discussed.

CHAPTER 2 - PROBLEMS INVOLVED IN MEASURING REPRODUCTIVE ALLOCATION

In many studies of reproductive allocation there has been no consensus of exactly what is being measured, nor how it should be measured. Consequently both conceptual and methodological difficulties arise.

2.1 Conceptual Problems

Much confusion occurs over the terminology used in RA studies and, to avoid further confusion, the rationale behind the terminology used in this work should be explained. The proportion of resources which a plant devotes to reproduction was originally termed the 'reproductive effort' (eg Harper and Ogden 1970). However, in an evolutionary context, this term does tend to imply thought and purposefulness on the part of the plant and could lead to misleading views and conclusions (Antonovics 1980). Moreover, the 'reproductive effort' as originally defined by Harper and Ogden (1970) only considered the energy or weight of the reproductive propagules (together with their protective tissues and dispersal aids where present). Stewart and Thompson (1981) and Waite and Hutchings (1981) have argued that this definition ignores the cost of producing any associated structures on which reproduction depends. In certain species eg scapigerous plants the investment in these structures can be considerable. "Reproductive Effort" has also been used as a term to cover this wider definition by some authors eg Gadgil and Solbrig (1972). However the term 'Reproductive Allocation' was used by Hickman 1975, 1977) to refer to this broader definition and this terminology was preferred by Waite and Hutchings (1981). Throughout this thesis 'RA' is used in the broader sense, meaning the total proportion of resources devoted to reproduction. Ideally this term should (for the reasons outlined in the following paragraph) refer to all the reproductive structures but some authors do not include all

reproductive structures in the definition.

Stewart and Thompson (1981) contend that RA or 'Total Reproductive Effort' as they term it, gives a more realistic estimate of the total resources devoted to reproduction than does seed output. The production of the floral apparatus and its associated structures is obviously part of the 'effort' involved in reproduction whereas seed output is the result of the interaction of this effort with a number of environmental variables such as pathogens, climate, predators, pollinators etc over which the plant has little or no control.

However, if this definition is accepted, it gives rise to a further conceptual problem. Some species eg scapigerous plants can be distinctly separated into vegetative and reproductive parts. In species with an erect leafy structure, the reproductive stem above the highest leaf may reasonably be counted as reproductive. However, difficulties arise when considering rosette plants where the flowering spike bears cauline leaves. These leaves may produce sufficient photosynthate to enable the production of the entire flowering structure. Indeed Bazzaz and Carlson (1979) have shown that flowers may bear a large proportion of the photosynthetic cost of their own production and undoubtedly the green scapes of scapigerous species must contribute much photosynthate to the production of the reproductive apparatus. Stewart and Thompson (1981) argue that if the concept of a limiting resource in the principle of allocation is to be meaningful then biomass or energy cannot be the appropriate currency by which RA should be gauged. They suggest that mineral allocation could be a plausible alternative and this possibility is investigated further in Ch.4.

An additional conceptual problem has been suggested by the work of Van Andel and Vera (1977). The reproductive strategy of a species may vary according to the level of stress in the environment. The level of mineral nutrient depletion which completely prevented the perennial Chamaenerion angustifolium from flowering, had no effect on the RA of an annual Senecio sylvaticus. This reflects a general problem inherent in comparing the RA of perennials and annuals. Moreover, in the case of Chamaenerion, which level of RA should be considered the norm; the RA under stress or without stress? Or should the range of possible RA levels within a species be measured? The problem of the variation in RA under conditions of stress (specifically nutrient stress) is considered in Ch.3 and the value of comparative experiments which investigate RA under uniform conditions is discussed in Ch.6.

It has also been postulated by Bell (1980) that RA may not be the quantity or factor which is of evolutionary importance to the plant. He suggests that it is the cost of reproducing which is of consequence in evolutionary terms. That is, the deleterious effect of a certain level of reproduction on future survival, growth and reproduction is of more significance than the quantitative level of that reproduction per se. This approach to measuring reproductive allocation is discussed in Ch.5.

All of these conceptual problems lead to methodological problems in the measurement of RA. These practical problems become evident when trying to design experiments on RA.

2.2 Methodological problems

If, as suggested in 2.1, allocation to all reproductive structures should be considered then the practical problem of exactly which

structures to include as reproductive material becomes app arent. Obviously, species can be chosen which have a structure that facilitates division into reproductive and vegetative parts, but when comparative experiments are desired (eg Ch.6) the problem becomes more acute. If all structures not possessed by the vegetative plant are counted as reproductive, then in annuals in which flowering invariably takes place eg Senecio vulgaris, RA should technically be regarded as 100%. A more conventional approach is to include either only the flowers or everything above the highest leaf as being reproductive. This latter definition seems preferable (and is usually adhered to throughout this thesis) since it includes the peduncles and those parts of the stem whose only function is the support of the flowers. However, it may underestimate RA in rosette plants with tall leafy flowering spikes such as Digitalis purpurea.

Related to the conceptual problem concerning the variation in RA under different environmental conditions is the problem of laboratory versus field experiments. Genetic and environmental influences on RA are not separable in the field. The problem is summarised by Gadgil and Solbrig (1972).

" ..... increased birth rate under conditions of DI mortality is not sufficient evidence for a r-strategy. .....The crucial evidence ..... is whether an organism is allocating a greater proportion of its resources to reproductive activities ..... under any and all DD and DI mortality conditions.

In some cases eg Raynal (1979) differences in RA between quarry and meadow populations, observable in the field, disappear when the plants are grown under controlled laboratory conditions. Environmentally cued

variations in RA tactics may occur in field experiments. Those investigators eg Gaines et al (1974), Newell and Tramer (1978) and Abrahamson (1979) who have only measured RA in the field have failed to eliminate any environmental effects on RA. The results of Harper and Ogden (1970) and Van Andel and Vera (1977) suggest that any given population of a species possesses a fixed maximum potential RA which is realised under ideal or optimum conditions.

Nevertheless, there are circumstances where conditions are presumed to be optimal and yet not all of the individuals in a population flower. The question then arises as to whether the true RA of the population is represented by the RA of the individuals which flowered or the RA of the population as a whole, including those individuals which did not flower and whose RA was consequently zero. This situation occurs in Ch.4 and Ch.7, although the solution adopted is different in each case. Perhaps this question can only be resolved in the context of each individual experiment and species under consideration.

A further practical difficulty concerns the timing of the measurement of RA. Since different parts of the reproductive apparatus attain their maximum size at different times it is possible that no single measurement can be entirely satisfactory. A possible solution to this problem would be to take serial harvests in order to determine the maximum development of each part and calculate RA by summing the maxima. This method could, however, over-estimate RA if (as seems likely) there is appreciable reallocation of resources between reproductive structures during the course of flowering. If the difference between serial estimates and single estimates is not great the single harvest method seems preferable because of the relative ease and simplicity of measurement.

In statistical analysis of RA data difficulties often occur because the figures under consideration are usually percentages or proportions. Although these figures can easily be transformed, it does make small variations in variables less easy to detect.

Consequently the area of RA research is fraught with various problems, both conceptual and methodological, which hinder the interpretation of existing research material. In the following chapters an attempt is made to resolve some of these problems, both by the re-examination of published data and by the presentation of the results of new experiments.

CHAPTER 3 - THE EFFECT OF NUTRIENT STRESS ON THE PLASTICITY OF REPRODUCTIVE ALLOCATION

3.1 Introduction

3.1.1 The advantages of a plastic allocation strategy

The partitioning of resources by organisms has been regarded as of great evolutionary and ecological significance. (see Chapter 1). The way in which an organism allocates limited amounts of resources to either growth, maintenance or reproduction will affect its fitness. In particular environments certain patterns of resource allocation might confer greater fitness. Thus, in organisms with plastic abilities to adjust to environmental circumstances, one might expect a re-alignment of the allocation pattern in different environments (Snell and Burch 1975). The modification of the basic genotypic programme or strategy may be expressed in a range of phenotypes representing varied tactics. The strategy itself determines the range of possible tactics (Bradshaw 1965) and the particular developmental pathway which is followed will depend on the environmental conditions to which the organism is exposed.

Genetically determined differences in allocation strategy may also be found in populations in different habitats (See chapter 6), Much of the available evidence pertaining to variations in RA does not distinguish between genetic and phenotypic variations and evidence which does not prove any observed variation in RA to be phenotypic has been omitted from this chapter.

3.1.2 Selection for phenotypic plasticity

The plant's strategy (or genotype) itself determines the possible range or breadth of possible tactics. Transplant experiments have shown that each genotype has its own genetically determined degree of modifiability or plasticity. Hiesey, Clausen and Keck (1942) found that plants of Achillea borealis from a large colony growing under favourable conditions produced very variable offspring and were apparently highly heterozygous. On the other hand, progeny from individuals growing in a small population on an exposed coastal bluff were much more nearly uniform indicating a much more severe action of selection in the latter locality. Bostock (1980) found that different populations of Tussilago farfara differed in the range of their plastic responses ie plants from certain areas exhibited more variation in their allocation patterns than others. Antonovics (1980) suggests that if the environment in which an individual is likely to find itself is unpredictable there may have been selection for phenotypic responses that allocate resources in such a way that life history is optimal for any particular environment. Similarly, Hickman (1975) argues that the developmentally plastic changes in reproductive strategy which he finds in Polygonum cascadense are the likely outcome of the short-term unpredictability of the environment in which the species grows. In extreme sites plants with a narrow range of responses may be selected whereas in less extreme and more variable sites plants with a wider spectrum of responses might be at a selective advantage (Briggs and Walters 1984).

3.1.3 The plasticity of reproductive allocation

Harper (1967) first raised the question of whether the proportion of a resource (in his case energy) which a plant allocated to seed production was fixed and characteristic of a species or group of

species, or whether it was plastic, being subject to change in response to environmental stress. It is known that plants display greater phenotypic plasticity than animals (Briggs and Walters 1984). Adaptive modifications may be initiated by a direct response to the environmental factor adapted to or may be triggered by other factors (Bradshaw 1965). Also, the plastic variations may be fixed early in development or may occur at any time as growth proceeds allowing a continuous adjustment to the environment. Species of indeterminate growth such as Vicia faba may respond to a stress such as density by altering the number of plant parts formed whereas species of determinate growth such as Helianthus annuus tend to respond by changes in the size of plant parts (Harper 1961).

Transplant experiments eg by Clausen, Keck and Hiesey (1940) have shown that the phenotype can be altered much more profoundly in some characteristics than in others. Stebbins (1950) argued that characters formed by long periods of meristematic activity eg total plant size will be more subject to environmental influences and are likely to be more plastic than characters formed relatively rapidly eg floral organs. Indeed, Silvertown (1982) notes that although total net assimilation and total seed production may be decreased drastically by stress or interference from other plants, RA is often less severely affected. Nevertheless, clear plasticity in RA is known to occur eg in iteroparous plants there may be years in which vegetative growth continues but no flowers are produced. Plastic differences in RA in response to environment have been found in annuals by Hickman (1975) for Polygonum cascadense and Snell and Burch (1975) for Chamaesyce hirta, and in perennials by Whigham (1973) for Uvularia perfoliata and by Ogden (1974) for Tussilago farfara.

3.1.4 The effect of environmental conditions on RA

In addition to studies which have studied the effect of nutrient availability on plastic variation in RA (see 3.1.5) there have been others which have considered the effect of other environmental influences on RA. Some authors have considered phenotypic variation in RA over environmental gradients in the field eg Hickman (1975, 1977) and Whigham (1973), while others have considered the specific effects of certain stresses such as density (Snell and Burch 1975, Waite and Hutchings 1982, Ogden 1974), light (Pitelka et al 1980, Lee and Cavers 1981) and water (Cunningham et al 1979). The results of this work have often been confusing since they frequently depend on the specific characteristics or strategy of the species studied eg whether they are annuals or perennials, have vegetative reproduction etc. In addition to this difficulty much of the available work which has observed species in field situations does not adequately distinguish between the effect of the different stresses which may operate at specific locations. De Ridder et al (1981) suggest that under different circumstances the effect of multiple stresses may counteract each other or work in the same direction eg water stress at an early stage in development may counteract the negative effect of nitrogen supply on the harvest index, whereas water stress at a later stage in development may increase the unfavourable effect. Grime (unpub) has found that plants of Poa annua react very differently in response to shortages of water, light or nutrients. The response of a plant may depend on whether the species has been regularly exposed to the particular stress during its evolutionary history. In this case it may have 'learnt' an appropriate response to the particular stress under consideration. Also the ratio of seed to total biomass is closely related to nutrient translocation processes from the vegetative to reproductive parts (Donald and Hamblin 1976) so that the stage in development at which

stresses occur is also important. Given these factors, it is crucially important that in work on RA the effects of different stresses are separated. Nevertheless, some generalisations about the range of possible phenotypic responses of RA to environmental variables can be made.

1. Constancy

The first possible response of RA to the environment is not to change at all ie to have an unplastic strategy. This type of response has been identified in several studies. The proportion of total biomass allocated to reproductive tissues in Senecio vulgaris (Harper and Ogden 1970), Senecio sylvaticus (Van Andel and Vera 1977), Taraxacum officinale (Gadgil and Solbrig 1972) and Veronica agrestis (Harris and Lovell 1980) was found to be constant over a range of artificial stresses such as reductions in pot size and nutrient concentrations. In many of these cases the stresses imposed caused great reductions in plant weights but nevertheless the proportional allocation to reproduction was maintained.

A possible variation on this type of strategy is to maintain a constant RA in those individuals which flower but to vary the proportion of flowering individuals. Many of the previous studies on RA have used population means in their analysis and thus variations in the numbers of plants which flower have been masked. This alternative reproductive strategy has been identified by Stewart and Thompson (1982).

The perennial Chamaenerion angustifolium showed no variation in individual RA with treatments of mineral fertilizer but at higher stress many plants failed to flower (Van Andel and Vera 1977).

Harper and Ogden (1970) found that at the highest stress level, flowering in Senecio vulgaris became very erratic. Similarly Pitelka et al (1980) found that light level affects size of Aster acuminatus. Only large plants produced flowers suggesting that light level affects sexual reproduction indirectly through plant size. Many plants need to attain a critical size or nutritional status before flowering can be initiated (Stewart and Thompson 1982) and thus environment may affect the population RA by limiting the size of plants and hence the resulting number of flowering plants.

ii. individual variation in RA

Variability in individual allocation to reproduction can be in 2 directions. An increase of RA in response to environmental harshness has been observed by Hickman (1975) for Polygonum cascadense. Plants allocated proportionately more of their biomass to reproduction in harsh, open, dry habitats. Populations of Andropogon scoparius behaved similarly (Roos and Quinn 1977). RA was phenotypically greater in early successional stages, probably because the date of first anthesis was later with increase age of field.

Alternatively, individual RA may decrease with increasing stress eg Chamaesyce hirta decreased the level of individual RA with increasing density (Snell and Burch 1975). The perennial Tussilago farfara decreased vegetative RA with increasing density but seed RA remained relatively constant (Ogden 1974).

iii. correlation of RA with plant size

A further possible mechanism of variation in RA has been identified by Reinartz (1984) and Waite and Hutchings (1982). In several populations of the biennial Verbascum thapsus there was a positive correlation between plant size and RA (Reinartz 1984). This type of strategy was also found in 3 populations of Plantago coronopus (Waite and Hutchings 1982) where RA increased as plant size increased. Waite and Hutchings (1982) suggest that the adaptive value of this strategy is related to the fact that the length of time before flowering in Plantago coronopus is flexible ie it has the option of completing an annual, biennial or perennial life cycle. Under these circumstances the costs of reproduction in terms of the subsequent probability of survival become particularly important. A plastic weight-related reproductive strategy can be considered an evolved adaptive trait which can be explained in terms of individual plant fitness.

3.1.5 The effect of nutrients on plastic variation in RA

The effect of nutrient availability on RA is not easily discernible. In many cases the relative biomass allocation to reproduction remains constant in spite of large effects on plant weight. This phenomenon was found for Senecio vulgaris by Harper and Ogden (1970) where despite a 7-fold decrease in plant weight as a result of decreased soil volume, the allocation to reproductive structures remained constant. Similarly Fenner (in press) found that RA in Senecio vulgaris remained fairly constant (30.9% - 32.6%) over a range of nutrient concentrations. Senecio sylvatica also showed a lack of response to the addition of mineral fertilizers (Van Andel and Vera 1977) as did Plantago coronopus (Waite and Hutchings 1982), Plantago major and Spergula arvensis (Trivedi and Tripathi 1982).

However in contrast to these studies, RA has been found to increase with addition of nutrients in 2 species of Asclepias (Willson and Price 1979), where the application of fertilizer increased the proportion of plant weight invested in pods, and for desert winter annuals (Williams and Bell 1981). Kawano and Hayashi (1977) found that the annual grass Coix ma-yuen generally responded to increased availability of nitrogen by increasing RA, while low nutrient levels reduced RA of Chamaescye hirta at all densities (Snell and Burch 1975). Similarly Lovett Doust (1980b) found that a low nutrient treatment had less than half the RA (biomass) of a control treatment in Smyrnium olusatrum. This effect was even more marked when the allocation of phosphorus was measured.

In some plants the effect of reduction in nutrients is to alter the proportion of plants which flower eg Chamaenerion angustifolium increased the proportion of flowering plants with increasing levels of fertilizer (Van Andel and Vera 1977). Suggestions of a similar effect have been found in Smyrnium olusatrum (Lovett-Doust 1980) and Senecio vulgaris (Harper and Ogden 1970).

Alternatively, De Ridder et al (1981) state that nitrogen application generally results in a decrease in the ratio of seed to total biomass in cereals. Williams and Bell (1981) suggest a possible explanation for this reaction. In some plants, under conditions of nitrogen deficiency, photosynthesis and growth are penalised in favour of reproduction, thus ensuring maximum seed production. However, when the deficiency is alleviated the competition between photosynthesis and seed production processes is reduced and the photosynthetic tissues benefit relatively more.

Despite the quantity of work on the general effect of nutrients on RA there is very little published work on the effect of individual nutrient elements on RA. Some of the work which assesses the effect of fertilizer applications on RA uses nitrogen fertilizer eg Kawano and Hayashi (1977) Williams and Bell (1981) and Trivedi and Tripathi (1982) but the observed response of RA to nitrogen varies. Interest in the effect of individual nutrient elements on RA has been stimulated by the controversy over the correct currency by which to measure RA (Lovett Doust 1980b, Thompson and Stewart 1981, Silvertown 1982). In Lovett Doust's (1980b) experiment on Smyrnium olusatrum the allocation of phosphorus is measured. However, there is no particular justification for phosphorus, rather than any other nutrient element, to be selected. Indeed, as Silvertown (1982) points out, the allocation of phosphorus and biomass to reproductive structures in the low nutrient treatment is very similar, suggesting that in fact phosphorus was not the limiting nutrient in impoverished soil. The limiting nutrient element could only have been determined by selective addition or limitation of various nutrient elements. Accordingly, the following experiment was designed, in order to:

i. determine the effect of selected nutrient deprivation on RA; and

ii. determine the most appropriate currency by which to measure RA.

3.2 Methods

3.2.1 Species

Species were selected using criteria which would enable efficient sampling and analysis. Taraxacum officinale and Poa annua were chosen because of their rapid growth rate and their facility in harvesting. In reproductive allocation studies it is important for a species to have relatively distinct vegetative and reproductive parts (see ch.2). It is also important that a species should not be pollinator limited, as occurs in certain species (Bierzychudek 1981), since this would affect the quantity of seed set. The presence or absence of pollination may also affect the weight of achenes produced in certain species (Van Leeuwen 1981).

Taraxacum officinale is a perennial species with a rosette growth form. The species is apomictic ie fruits ripen independently of fertilisation. Over 100 forms or clones have been recognised in the British Isles (Clapham, Tutin and Warburg 1962). It is usually found in waste places, waysides, meadows and grasslands and is generally considered to be adapted to a competitive grassland habitat (Bostock and Benton 1979). Bostock and Benton (1979) have also shown that Taraxacum officinale has a very low rate of vegetative reproduction and the absence of vegetative reproduction would simplify any subsequent analysis.

Seed had been collected from a single plant in the previous season and it was originally intended to use this seed. This would have reduced any genetic variability especially since the species is apomictic. Unfortunately, however, germination tests showed that hardly any of this seed was viable. Bostock (1978) has shown that Taraxacum

officinale seed stored in soil has a half life of approximately 3 months so the majority of seed does not survive to a subsequent growing season. Moreover Grime et al (1981) have shown that Taraxacum seed which has been dry stored for 3-6 months has a significantly lower germination rather than freshly collected seed. Consequently, seed had to be collected at the time (December) from whatever plants were available in local waste ground.

Seed from Poa annua - a ruderal grass - had been collected the previous season from a pasture site. Although often annual, biennial (or short-lived perennial) individuals of Poa annua are known (Law et al 1977). Individuals are generally inbreeding (Ellis 1974) so it was hoped that there would be little variation in seed collected from a homogeneous site. Poa annua is found in open habitats throughout the British Isles (Clapham, Tutin and Warburg 1962).

3.2.2 Nutrient Treatments

The seeds were germinated and grown in John Innes No 1 potting compost until they were large enough to be handled. The seedlings were then planted out in February 1981 into 5" pots containing perlite - a chemically expanded volcanic rock. This was considered to be a suitable neutral medium for plant growth. The pots were then placed in trays on raised benches in a greenhouse at Rumleigh experimental station. The greenhouse was kept at a temperature of minimum 15°C - maximum c. 23°C and additional light from mercury lights was available at the beginning of the season.

Control plants were watered with a standard nutrient solution obtained from tables in Hewitt (1966). The macro-nutrient composition was of the 4-salt type used by Shive and Robbins (1942) which has been

successfully used for a wide range of crops in sand and water cultures. The micro-nutrient composition was taken from complete nutrient solutions based on nitrate or ammonium nitrogen as used at Long Ashton (Hewitt 1966). This 4-salt nutrient solution was chosen in order to facilitate manipulation of the nitrogen, potassium and phosphorus content in any treatments.

The treatment plants were given nutrient solutions with ionically determined levels of deficiency of nitrogen, phosphorus and potassium. (See table 3.2.1 for exact composition of each treatment nutrient solution). These 3 nutrient elements were selected because they are mobile nutrients and are generally thought to influence plant growth and reproductive output (Chapin 1980). In total there were 7 different nutrient solutions: A, the control: B, 50% of the original N content: C, 20% of the original N content: D, 50% of the P content: E, 20% of the P content: F, 50%K : G, 20%K.

Very low or high pH can impair the absorption of certain minerals eg phosphorus and iron (Hewitt 1952). Since some of the compounds present in the original control nutrient solution had been replaced by others in the treatment nutrient solutions eg Na_2SO_4 for $NaNO_3$ it was decided to check the pH levels of the treatment nutrient solutions. The results are in table 3.2.2. Since there were no large discrepancies in pH level and Hewitt (1966) states that the influence of pH appears to be relatively unimportant between 5 and 7, (provided iron remains available) it was decided to proceed with the experiment.

Nutrient solutions were made up at 100x concentrations and diluted every week. 10ml of the diluted solution was added to each pot. Fresh iron citrate solution was made up weekly since this solution degrades in

TABLE 3.2.1 - COMPOSITION OF NUTRIENT SOLUTIONS
g/litre (after Shive and Robbins 1942)

MACRONUTRIENTS

	Salts	$NaNO_3$	$Mg\ SO_4 7H_2O$	$CaCl_2$	KH_2PO_4	$NaSO_4$	K_2SO_4
A	Control	0.34	0.514	1.1665	0.214	-	-
B	½N	0.17	"	"	0.214	0.142	-
C	1/5N	0.068	"	"	0.214	0.2272	-
D	½P	0.34	"	"	0.017	-	0.0683
E	1/5P	0.34	"	"	0.0428	-	0.10927
F	½K	0.34	"	"	0.107	-	$NaH2Po_4 2H_2O$ 0.12246
G	1/5K	0.34	"	"	0.0428	-	0.1959

MICRONUTRIENTS (PRESENT IN EACH SOLUTION)

	g/litre	Stock soln requirement
Fe Citrate $5H_2O$	0.0335	6.70 g
$MnSO_4\ 4H_2O$	0.00223	
$Zn\ SO_4\ 7H_2O$	0.00029	
$CuSO_4\ 5g_2O$	0.00025	
$H_3\ BO_3$	0.00031	
$Na_2M_oO_4\ 2HO$	0.00012	
NaCl	0.0058	
$C_oSO_4\ 7H_2O$	0.000056	

Each solution made up at 100 times concentrations from complete nutrient solutions used at Long Aston (Hewitt 1966)

AN EXAMPLE OF THE CALCULATION OF DEFICIENT NUTRIENT SOLUTIONS

	g/litre	Motor
$NaNO_3$	0.34	0.004

Na will be replaced by Na_2SO_4 for 50%N solution.

1m soln Na No_3 = 85g/litre

$0.34\text{g/litre} = \frac{0.34m}{85} = 0.004$

0.17g = ½ x 0.004

Mol wt Na_2SO_4 = 71

0.004 x ½ x 71 = 0.142g/litre

So for 50%N need 0.17g/litre $Na_2\ SO_4$
+0.142g/litre $Na_2\ SO_4$

TABLE 3.2.2 - PH OF NUTRIENT SOLUTIONS AT 10x CONCN

	A Control	B 50%N	C 20%N	D 50%P	E 20%P	F 50%K	G 20%K
PH	5.5	5.7	5.6	5.9	6.3	5.6	5.6

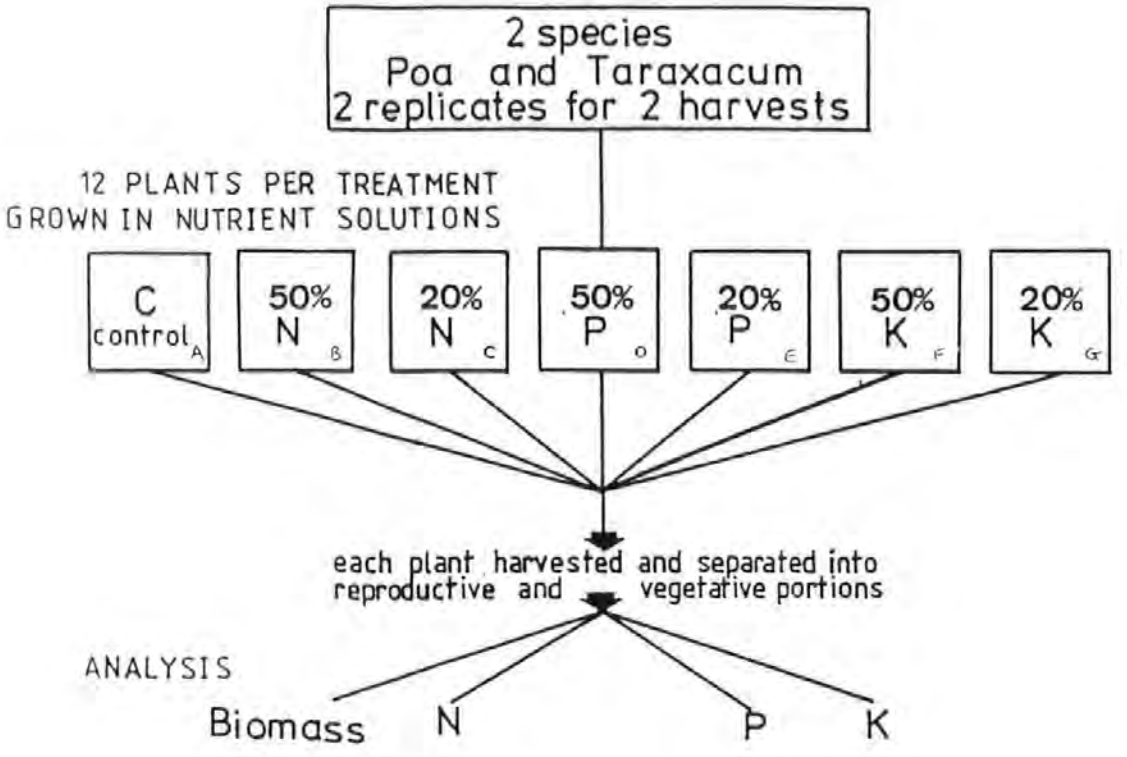


Fig 3.2.1 DESIGN OF EXPERIMENT

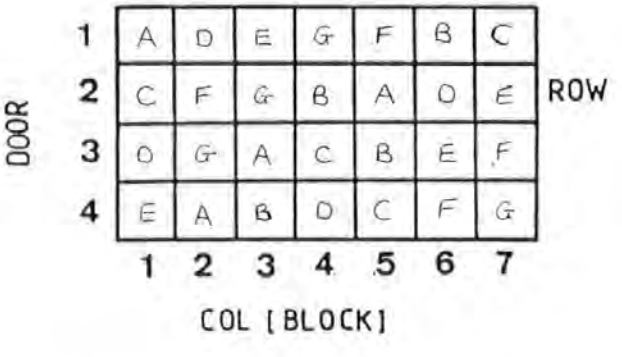


Fig 3.2.2 YOUDEN SQUARE DESIGN

light. As the plants might require additional water and watering from above might result in nutrient runoff, the plant pots were placed in trays with 6 pots in each tray.

Initially, it was hoped to take 2 harvests for each species, since RA might vary according to the flowering stage reached when the harvest was taken. Therefore an early harvest could be performed on one set of plants when the first inflorescences had matured. At this point the entire plant would be collected and separated into component parts. In addition a late harvest could be performed on another set of plants removing each individual inflorescence on maturity, followed by harvesting the entire plant at the end of the flowering season. This plan was carried out for Poa annua but it became obvious during harvesting that not all of the Poa would flower, thus reducing the sample size. It also seemed possible that not all of the Taraxacum would flower and, addition to this problem, Taraxacum characteristically develops only one flower at a time. Consequently, in order to maintain a reasonable sample size and because of the growth habit of Taraxacum, it was decided to perform only one harvest (late) on the entire group of Taraxacum plants. Plants were checked for mature inflorescences twice a week.

3.2.3 Experimental design

Altogether there were 168 plants per species - 7 treatments, 2 harvests and 12 plants per treatment (see fig 3.2.1). Each treatment was arranged in 4 trays of 6 pots. The physical width of the greenhouse bench only allowed a block 4 trays wide and 7 trays long, so an experimental design had to take this limitation into account.

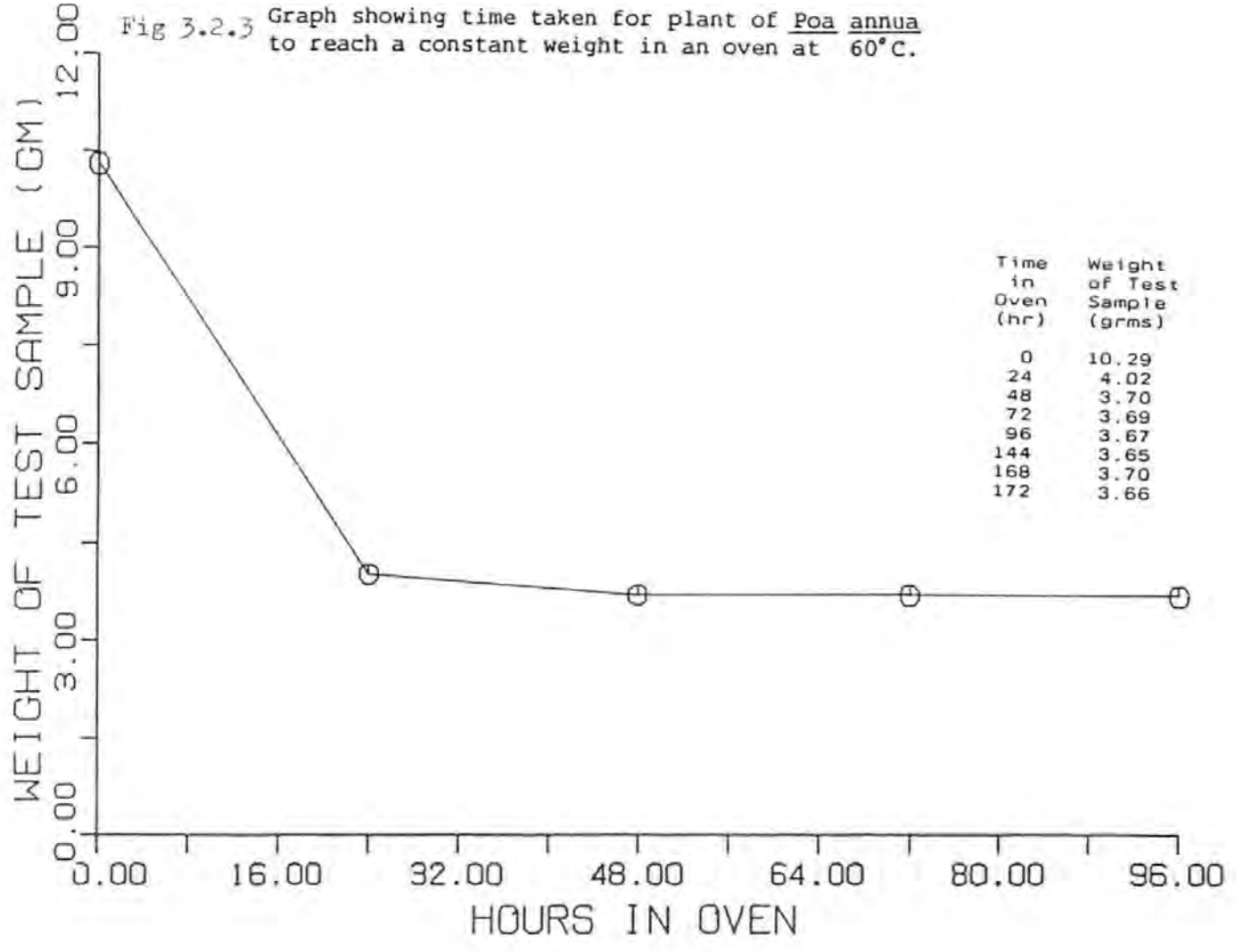
Normally, in the situation where there are 7 treatments, but the block size is only large enough for 4, an incomplete randomised block design would be used, allocating 4 of the treatments to each block in such a way that block effects can be eliminated. However, because it was possible to run 7 blocks (equal to the number of treatments) a more sensitive design - a Youden square could be adopted. The use of this design would also mean that any effects running along the blocks could be eliminated. The elimination of any possible environmental effects due to the location of the door, such as gradients of temperature, humidity etc would be important in the subsequent analysis of the results.
A Youden square design is essentially similar to a Latin square but with a number of rows missing (Johnson and Leone 1964). A 7x4 Youden square design was chosen from Fisher and Yates (1974) and the rows and columns randomised. The trays were then arranged on the greenhouse bench in this design (see fig 3.2.2).

3.2.4 Laboratory methods

After harvesting, reproductive parts were placed in manilla envelopes, labelled, and dried at 60°C until a constant weight was achieved (normally 48 hours see fig 3.2.3.) This temperature is not considered to be high enough to cause any significant loss of mineral nutrients (Allen 1974).

The vegetative parts of the early harvest *Poa* were collected when the first inflorescences matured. The vegetative parts of the late *Poa* were collected when the plants appeared to have stopped producing flowering initials. All the *Poa* had finished flowering by 5 August. Vegetative plant parts were similarly dried. It was hoped that the *Taraxacum* plants would display similar 'tailing off' of flowering but this was not the case. It was therefore decided to terminate the experiment on 26 October

Fig 3.2.3 Graph showing time taken for plant of Poa annua to reach a constant weight in an oven at 60°C.



Time in Oven (hr)	Weight of Test Sample (grms)
0	10.29
24	4.02
48	3.70
72	3.69
96	3.67
144	3.65
168	3.70
172	3.66

and all the Taraxacum plants were harvested. Initially, it was intended that roots should be collected and analysed but in practice it was impossible to separate the root material from the perlite by any method.

Once dried, plant parts were weighed on a Sartorius balance and stored in the envelopes to await further analysis. Air-dried plant material which has to be analysed for mineral content can be stored for long periods at room temperature in well-ventilated conditions (Allen 1974).

Plate 3.2.1 Taraxacum plants at Rumleigh

3.3 Results

3.3.1 Taraxacum

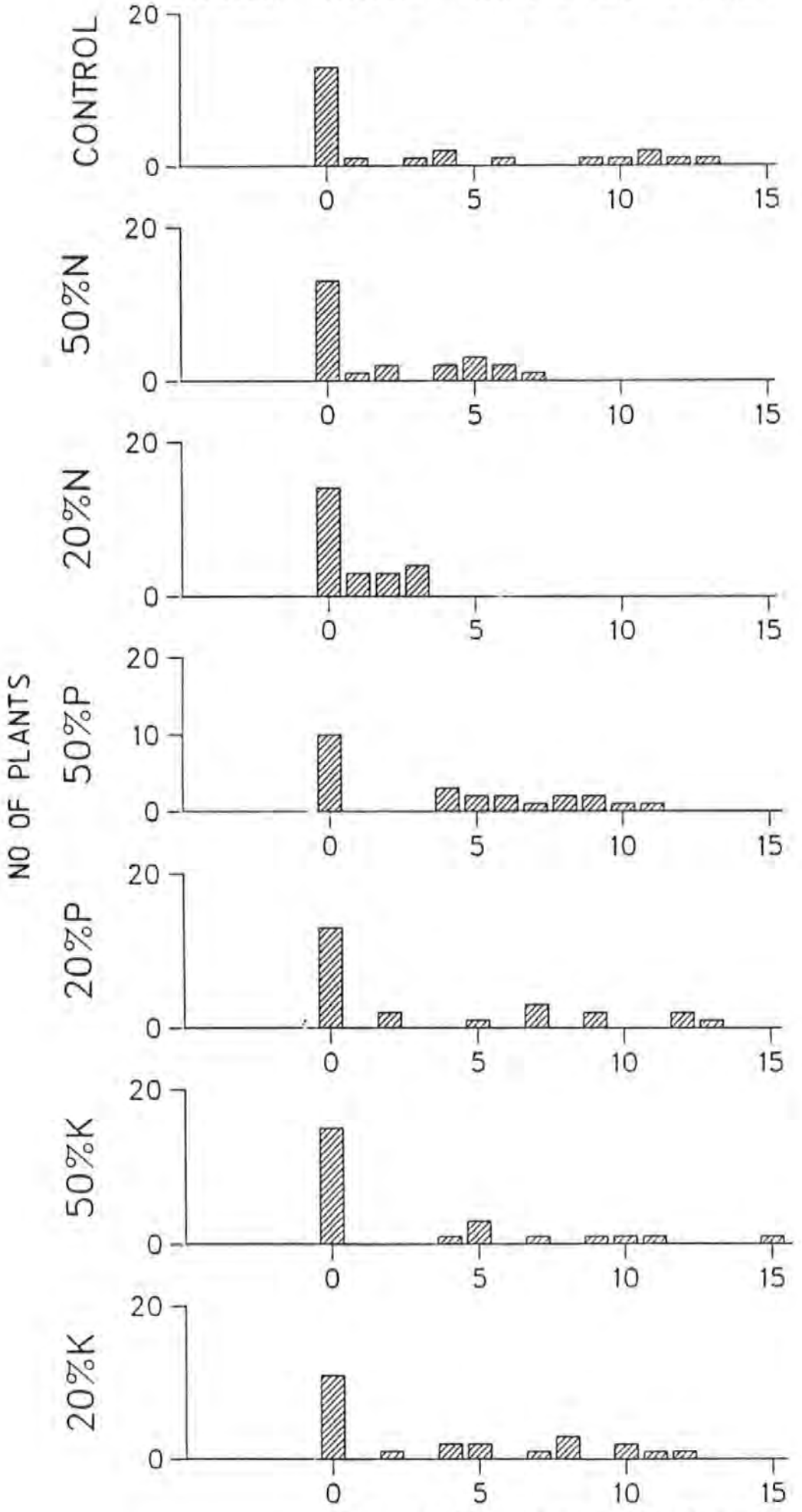
i. Data Analysis

The data obtained for the Taraxacum officinale plants were tested for normality using the normal probability plot correlation coefficient which measures the 'straightness' of a probability plot. This test statistic is essentially equivalent to the Shapiro-Wilk (1965) test (Ryan et al 1982) and compares favourably with 7 other normal test statistics (Filliben 1975). The values of the correlation coefficient obtained for the Taraxacum data were below the appropriate values in the tables of percentage points of the normal probability plot correlation coefficient. Consequently, the hypothesis of normality can be accepted.

It is obvious from fig 3.3.1 that there was no difference in the proportion of plants which flowered in each treatment. Approximately half the plants failed to flower in every nutrient treatment. It was possible that the plants which failed to flower were behaving as a separate and significantly different population. If this was the case, the inclusion of these plants in any statistical analysis might obscure any treatment effects.

T-tests comparing the vegetative dry weights for all the flowerers and non-flowerers (Table 3.3.1) show that the vegetative weight of the non-flowerers was significantly greater than the vegetative weights of the flowerers (excluding the weight of the reproductive parts). However the vegetative weight of the non-flowerers was consistently lower than the total weight of the flowering plants

Fig 3.3.1 TARAXACUM – FREQUENCY OF NUMBER OF FLOWERS



($P<0.001$). When the treatments are considered separately (Table 3.3.1 and Fig 3.3.3) it can be seen that the total weight of flowering plants was significantly higher in all cases. The weight of the non-flowering plants was significantly higher than the vegetative weight of the flowering plants in 6 out of 7 treatments. The exception was in treatment 3 - the 20%N treatment - where all the plants had very low weights (see later).

It was therefore decided to treat the flowering and non-flowering plants as two separate populations in the subsequent analysis. The number of plants which flowered in each treatment was not equal and a multivariate analysis of variance on samples with unequal sizes was not possible with the available statistical packages. In addition to this problem, the original experimental design had been based on trays rather than individual plants and theoretically the analysis ought to be performed on values per tray to conform with this design. To overcome these problems it was decided to perform multivariate analyses of variance on the data for mean tray weights. There were no significant differences between tray weights within each treatment.

Multivariate F-tests were computed by fitting a generalised linear model using 'GLIM' (Baker and Nelder 1978). In anova models the dependent variable y is considered to be the sum of a number of systematic components and a random component or residual having a normal distribution. Hence the model

$$y = \mu + CO\ RO + TR$$

was fitted where μ = generalised mean
CO = variance due to columns
RO = variance due to rows
TR = variance due to treatment

Fig 3.3.2 Mean Dry Weights under Different Treatments

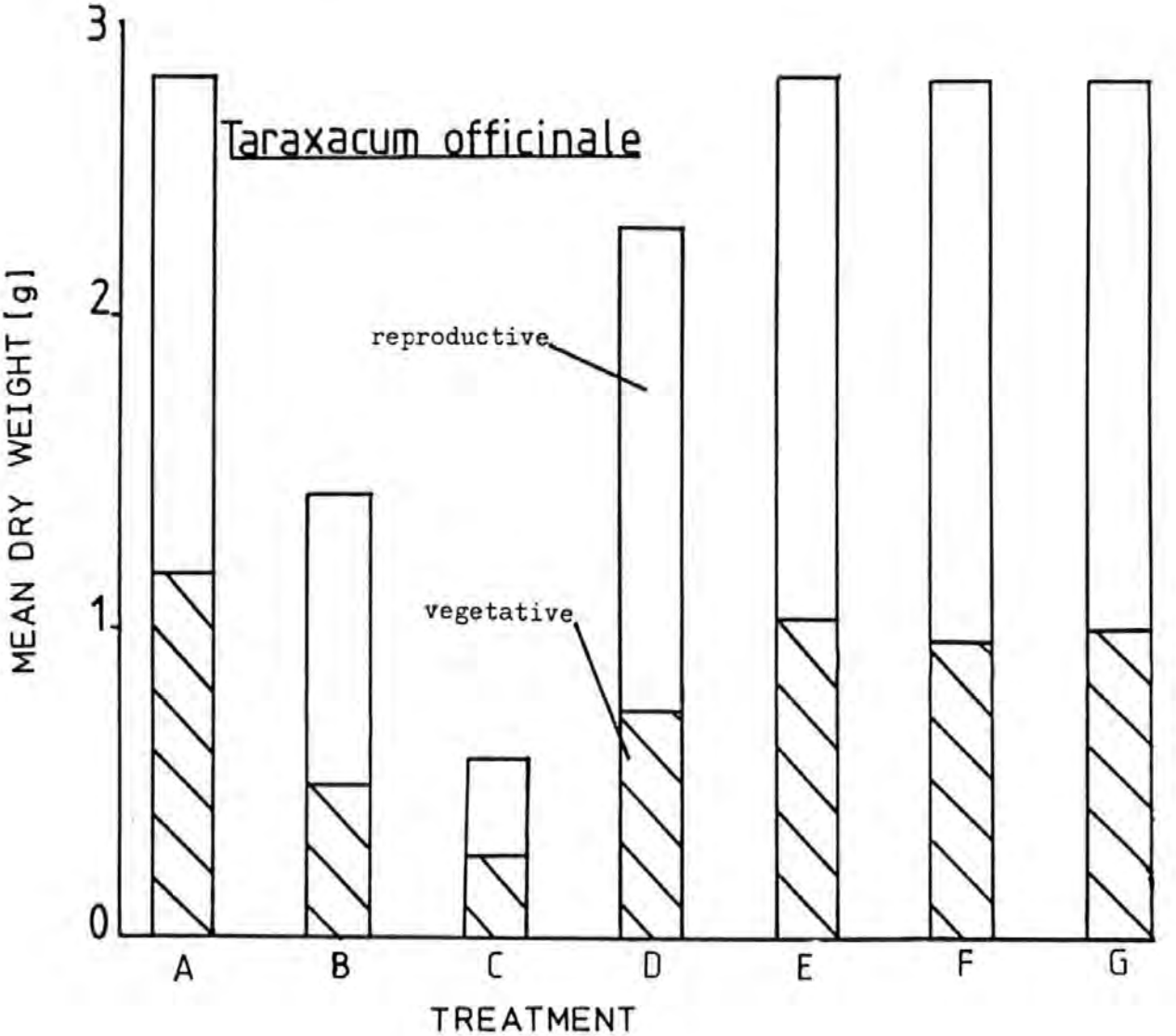


Table 3.3.1

RESULTS OF T-TESTS COMPARING DRY WT OF FLOWERERS AND NON-FLOWERERS

Treatment		A	B	C	D	E	F	G
Veg wt F's V Veg wt NF's	T	2.11	4.58	0.43	8.54	3.16	5.49	2.40
	DF	17.3	17.2	21.2	21.9	18.0	12.7	19.1
	P	0.050	0.000	0.67	0.000	0.0058	0.000	0.027
	Sig	<0.050	<0.001	NS	< 0.001	< 0.01	< 0.001	< 0.1
Veg wt NF's V Total wt F's	T	-5.69	-3.71	-4.47	-6.24	-4.37	-4.28	-4.76
	DF	12.9	21.8	14.3	15.2	12.5	8.9	19.7
	P	0.0000	0.0013	0.0000	0.0000	0.0009	0.0027	0.0000
	Sig	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.01	< 0.001

All data	Veg F v Veg NF	Veg F Total F	Tray	Means	Veg F v Veg NF	Veg NF v Total F
T	-5.6	-7.93			-4.02	-4.76
DF	164	117.7			48.8	45.4
P	0.0000	0.0000			0.0002	0.0000
Sig	0.001	0.001			0.001	0.001

F = flowering plants
NF = non flowering plants
T = t statistic
P = probability
DF = degrees of freedom
NS = not significant

Scattergrams, means, standard deviations, standard errors, t-tests, correlations and one way anovas were computed using 'Minitab' (Ryan, Joiner and Ryan 1976).

ii. Weights of components parts

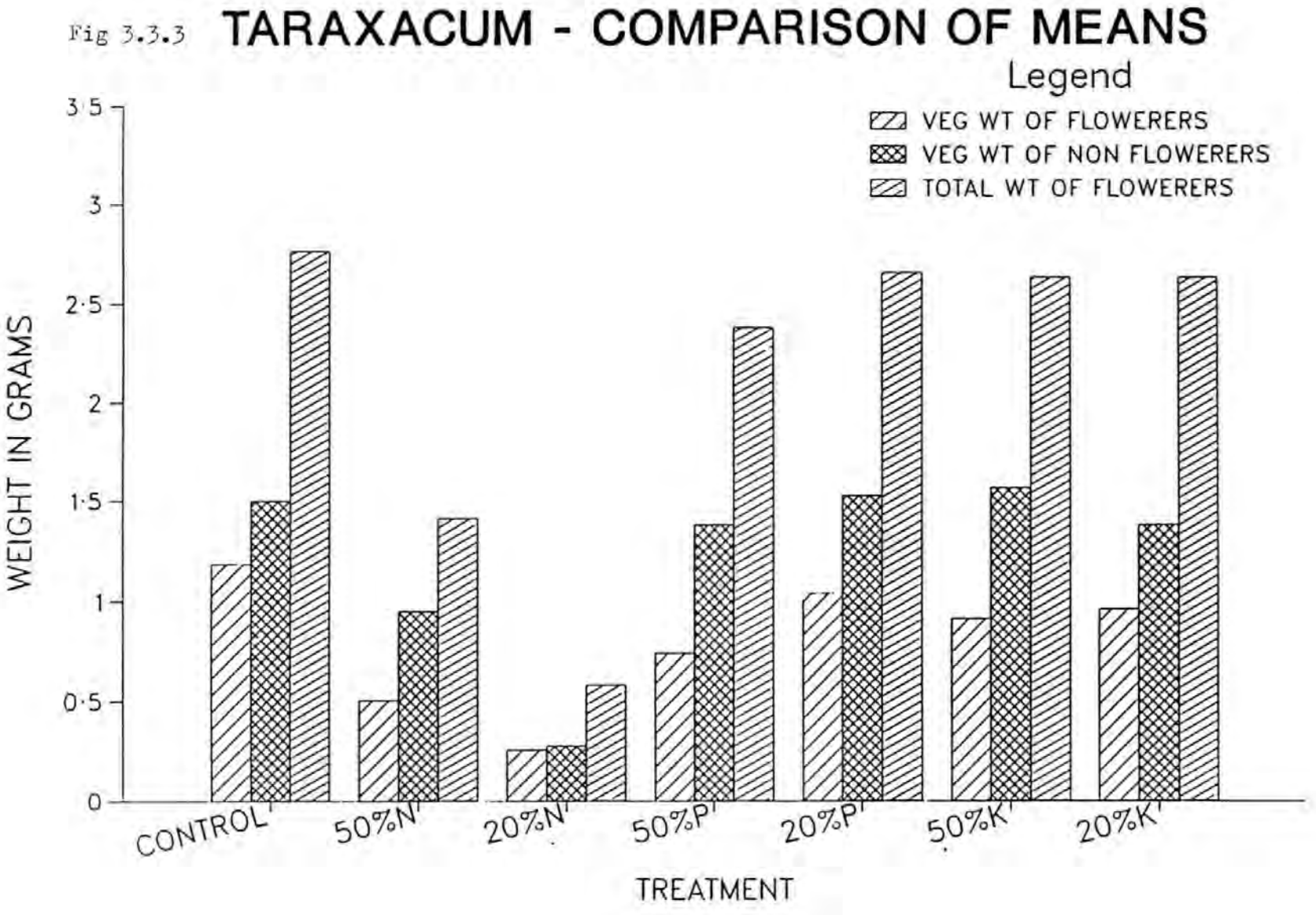
As noted above it was evident that the vegetative weight of the non-flowering plants was significantly higher than that of the flowering

plants (excluding reproductive parts). The total weight of both the non-flowering and flowering plants appears to have been affected by the treatments - in particular the 50%N and the 20%N treatments (see fig 3.3.2 and fig 3.3.3). The means for these figures are in Appendix 1. When this effect was tested using a multivariate anova, the effect of the treatments was found to be highly significant in all cases (Table 3.3.2). The vegetative weight of the non-flowerers was significantly affected ($P<0.001$) as was the the vegetative weight of the non-flowerers ($P<0.001$). This effect was more pronounced in the non-flowering plants. Reproductive weight in the flowering plants was significantly affected by treatment ($P < 0.01$) although less so than vegetative weight. Similarly the total weight of the flowering plants was affected by treatment ($P<0.01$).

The results of this multivariate analysis showed that the columns and rows had no significant effect on the data. Consequently it could be assumed that the position of the plants on the greenhouse bench had no effect on the results. In order to check the results of the F-tests on mean tray weights another one way anova was conducted on the data for individual plants (see table 3.3.3). The results show essentially the same pattern of significance.

To obtain an estimate of the specific treatments which were having an effect on the plant weights, the least significant difference was calculated for each of the significant anovas. By calculating the difference between the control mean and the treatment means and comparing this figure with the LSD it is possible to see which treatments are significantly different. It is evident that it was mainly the 50% and 20% N treatments which affected the plant dry weights. In the case of the total weights and non-flowering weights

Fig 3.3.3


TARAXACUM - COMPARISON OF MEANS
Legend
VEG WT OF FLOWERERS
VEG WT OF NON FLOWERERS
TOTAL WT OF FLOWERERS
WEIGHT IN GRAMS
3·5
3
2·5
2
1·5
1
0·5
0
CONTROL
50%N
20%N
50%P
20%P
50%K
20%K
TREATMENT

ANOVAS TARAXACUM – EFFECT OF TREATMENT Table 3.3.2

Vegetative wt/tray (Mean)

a. Flowerers

Source	df	SS	MS	F
Cols	6	0.855		
Rows	3	0.200		
Treats (Adj)	6	1.6367	0.2728	9.4722
Error	12	0.3463	0.0288	
				P<0.001
Total	27	3.038		

LSD = 0.261
Sig diffs = between Control and 50% N, 20% N, 50% P

b. Flowerers and Non-Flowerers

Source	df	SS	MS	F
Cols	6	0.0671		
Rows	3	0.016		
Treats	6	3.238	0.539	27.92
Error	12	0.2319	0.019	
				P<0.001
Total	27	4.158		

LSD = 0.212

c. Non-Flowerers

Source	df	SS	MS	F
Cols	6	1.071		
Rows	3	0.127		
Treats	6	4.3274	0.7212	20.258
Error	12	0.4276	0.0356	
				P<0.001
Total	27	5.953		

LSD = 0.290
Sig diffs = Control v 50% N + 20% N
Also 50% N v 20% N

Table 3.3.2

Reproductive wt/Tray (Mean)

d. Flowerers

Source	df	SS	MS	F
Cols	6	1.557		
Rows	3	0.259		
Treats	6	5.757	0.9595	5.956
Error	12	1.932	0.161	
				P<0.01
Total	27	9.505		

LSD = 0.616
Sig diffs = Control v 50% N, 20% N

Reproductive wt/Tray

e. Flowerers and Non-Flowerers

Source	df	SS	MS	F
Cols	6	2.385		
Rows	3	0.312		
Treats	6	1.5918	0.2653	3.72
Error	12	0.8552	0.07126	
				P<0.05
Total	27	5.144		

LSD = 0.41

Total wt/Tray (Mean)

f. Flowerers

Source	df	SS	MS	F
Cols	6	3.99		
Rows	3	0.66		
Treats	6	12.683	2.113	8.1614
Error	12	3.107	0.2589	
				P<0.01
Total	27	20.44		

LSD = 0.783
Sig diffs = Control v 50% N, 20% N
Also 50% N v 20% N

g. Flowerers and Non-Flowerers

Source	df	SS	MS	F
Cols	6	3.038		
Rows	3	0.346		
Treats	6	8.1036	1.3506	23.612
Error	12	0.6874	0.0572	
				P<0.001
Total	27			

LSD = 0.368

Number of Flowers per tray (Mean)

h. Flowerers

Source	df	SS	MS	F
Cols	6	68.00		
Rows	3	9.60		
Treats	6	81.28	13.546	3.548
Error	12	45.82	3.818	
				P<0.05
Total	27	204.7		

LSD = 3.01

Sig diffs = Control v 20% N

i. Flowerers and Non-Flowerers

Source	df	SS	MS	F
Cols	6	61.76		
Rows	3	7.44		
Treats	6	24.81	4.135	2.11292
Error	12	23.49	1.9575	
				P<0.1
Total	27			

Table 3.3.3

One way F-tests on all data - just flowerers

Source	df	SS	MS	F
Veg wt				
Treatment	6	6.6440	1.1073	11.49
Error	72	6.9365	0.0963	P<0.001
Total	78	13.5804		
Rep wt				
Treatment	6	17.817	2.969	8.87
Error	72	24.113	0.335	P<0.001
Total	78	41.929		
Number of flowers				
Treatment	6	310.74	51.79	5.48
Error	72	679.86	9.44	P<0.001
Total	78	990.61		
RA(propn)				
Treatment	6	0.1491	0.0248	1.11
Error	72	1.6144	0.0224	NS
Total	78	1.7634		
Total wt				
Treatment	6	43.365	7.227	18.14
Error	72	28.691	0.398	P<0.001
Total	78	72.056		
ASIN RA				
Treatment	6	561.8	93.6	1.09
Error	72	6198.0	86.1	NS
Total	78	6759.8		

the 20%N treatment was significantly different from the 50% N treatment. The 50% phosphorus treatment also seems to affect the vegetative dry weight but this effect disappears at the 20% P level.

Over the population of flowering plants as a whole, reproductive weight is correlated significantly with vegetative weight (see table 3.3.4).

ii. Numbers of flowers

From fig 3.3.1 it is obvious that the numbers of flowers produced by each plant was related to the treatments. The greatest number of flowers produced by a plant in the 50% and 20%N treatments was 7 and 3 respectively. However, 13 flowers were produced by one plant in the control treatment and 15 flowers were produced by one plant in the 50%K treatment. This is perhaps not surprising since the number of flowers produced by each plant was highly correlated with vegetative weight ($P<0.01$), reproductive weight ($P<0.001$) and total weight ($P<0.001$).

Analyses of variance on the numbers of flowers show that treatment had a significant effect ($P<0.05$). Calculation of the LSD (table 3.3.2) shows that this can mainly be attributed to the effects of the 20%N treatment on the number of flowers.

iv. Reproductive allocation

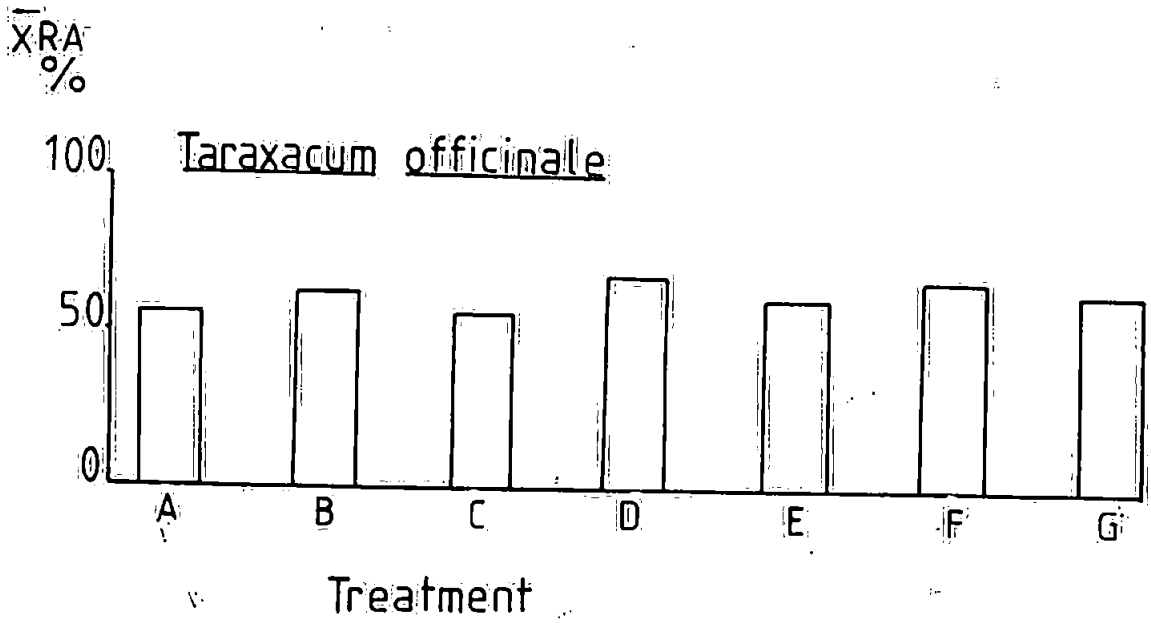
From consideration of fig 3.3.4 it is evident that there is no large variation between treatments in the proportion of dry weight allocated to reproduction. When an F-test was carried out on reproductive allocation the effect of the treatments was not significant ($P<.1$), see table 3.3.5. Similarly one way anovas on the data for individual plants are not significant (table 3.3.3).

Table 3.3.4

Taraxacum - Correlation Coefficients

	r	df	P
Vegetative weight v reproductive weight	0.347	78	$P < 0.01$
Vegetative weight v no of flowers	0.336	78	$P < 0.01$
Reproductive weight v no of flowers	0.892	78	$P < 0.001$
Total weight v no of flowers	0.826	78	$P < 0.001$
RA v No of flowers	0.531	78	$P < 0.001$
RA v reproductive wt	0.604	78	$P < 0.001$
RA v total wt	0.266	78	$P < 0.05$
RA v veg wt	-0.449	78	$P < 0.001$

Fig 3.3.4 REPRODUCTIVE ALLOCATION



Taraxacum - non flowerers included

Reproductive effort proportion

Source	DF	SS	MS	F
Blocks	6	0.3929		
Rows	3	0.0464		
Treats	6	0.0895	0.0149	1.568
Residual	12	0.1148	0.0095	NS
Total	27	0.6436		

Arcsin trans RA - Non-flowerers included

Blocks	6	.1729		
Rows	3	.0314		
Treats	6	.0552	92	1.4939
Resid	12	.0739	61.58	NS
Total	27	.3334		

RE - Non-flowerers omitted

Blocks	6	0.0467		
Rows	3	0.01316		
Treats	6	0.05611	0.00935	2.868
Resid	12	0.03913	0.00326	$P<.1$
Total	27	0.1551		

Arcsin trans RA - Non-flowerers omitted

Blocks	6	163.00		
Rows	3	46.5		
Treats	6	194.2	32.366	2.9006
Resid	12	133.9	11.158	$P<.1$
Total	27	537.6		

REAS effect of cols and rows - non-flowerers omitted

Columns

Source	DF	SS	MS	F
Treatment	6	233		
Rows	3	46.6		
Cols	6	124.1	20.6	1.8
Error	12	133.9	11.1	NS
Total	27	537.6		

Rows

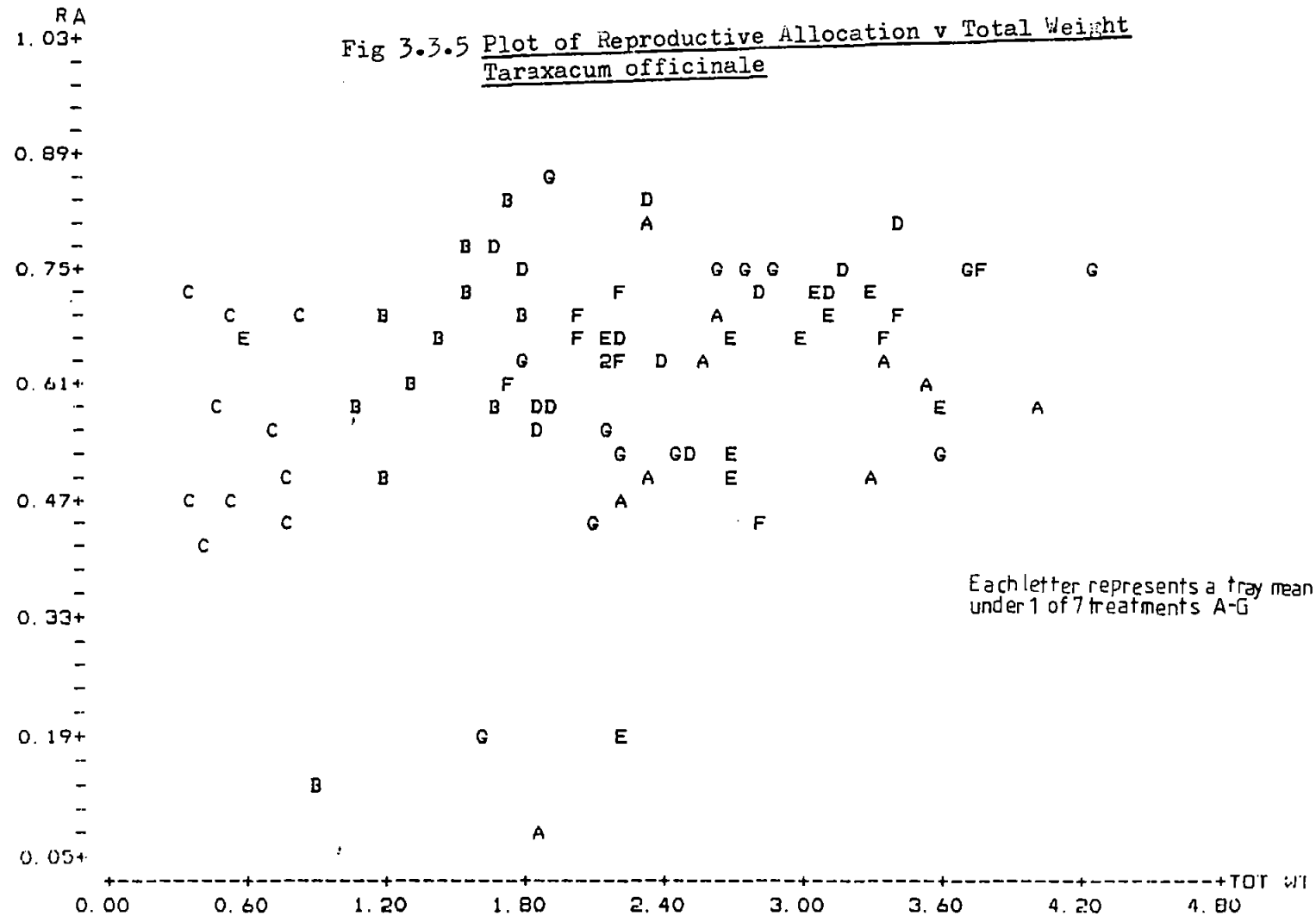
Treatment	6	233		
Cols	6	124.2		
Rows	3	46.5	15.1	1.3
Error	12	133.9	11.1	NS
Total	27	537.6		

Test on VW		Fit		DF	
			3.038	27	
		Fit + CO	2.183	21	0.855
0.2		+ RO	1.983	18	0.2
		TR	0.3463	12	1.6367

2.2859	Fit + TR =	0.7529	21	Fit + TR	0.7529	2.2859
0.199	+ RO =	0.5538	18	+ CO	0.5454	0.2075
2.075	+ CO	0.3463	12	+ RO	0.3463	0.1991

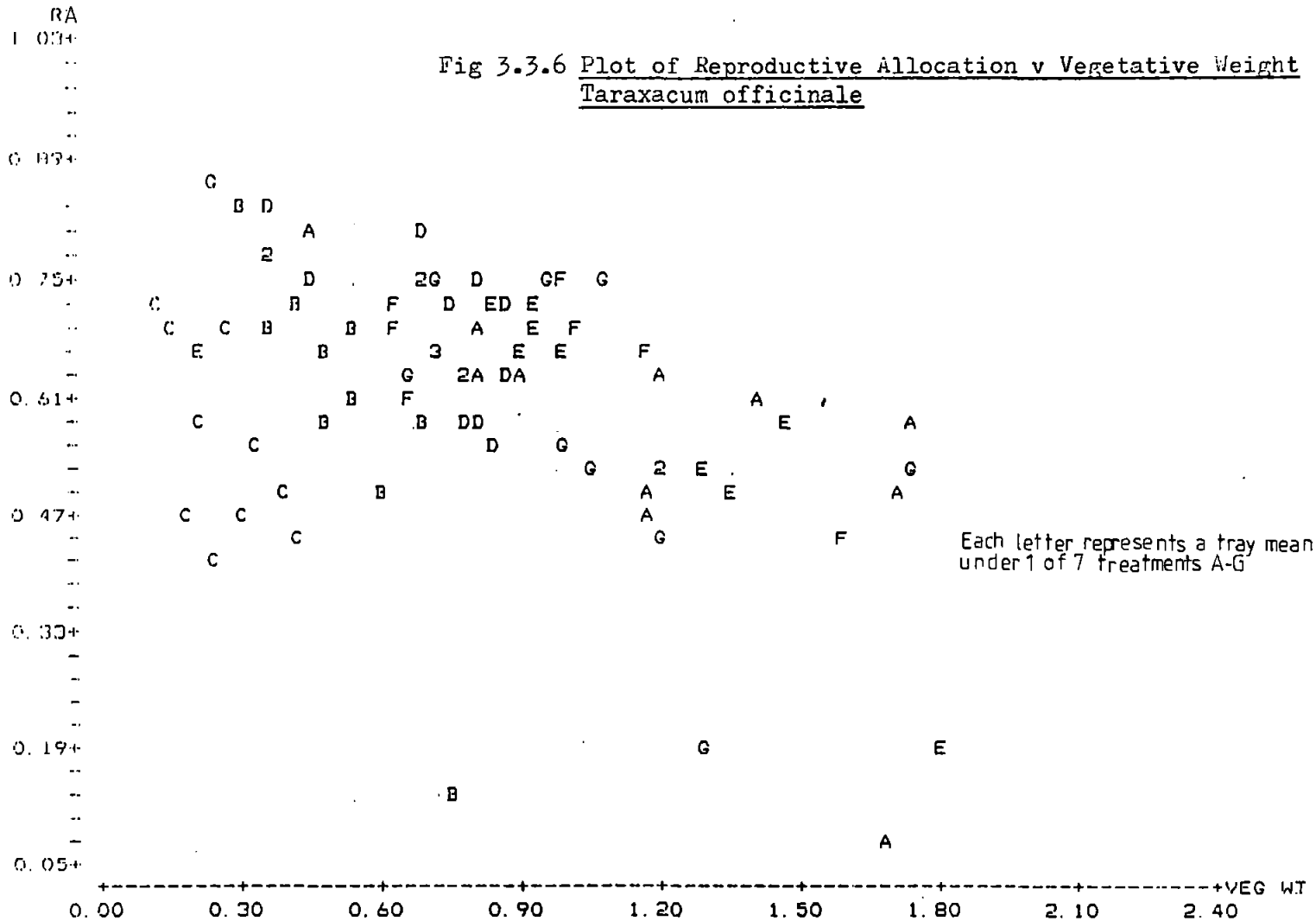
Reproductive allocation was significantly positively correlated with the total weight of the plants ($P<0.02$) although it is obvious from fig 3.3.5 that the proportion of variance in RA explained by total weight is small. RA was also significantly negatively correlated with vegetative weight ($P<0.001$) see fig 3.3.6.

Fig 3.3.5 Plot of Reproductive Allocation v Total Weight
Taraxacum officinale



CORRELATION OF RA AND TOT WT = 0.266

Fig 3.3.6 Plot of Reproductive Allocation v Vegetative Weight
Taraxacum officinale



CORRELATION OF RA AND VEG WT =-0.449

3.3 Results

3.3.2 Poa annua

1. Data analysis

The data obtained for Poa annua in both harvests were tested for normality using the normal probability plot correlation coefficient (Filliben 1975). The hypothesis of normality was accepted at the 5% level for all variables with the exception of vegetative weight in the first harvest. A log-transformation changed the value of the correlation coefficient from 0.870 to 0.988. The transformed values were used in any statistical analysis of the vegetative weight in the first harvest.

In each harvest 6 plants failed to flower and these plants appeared to differ in their morphology (see plate 3.3.1). The plants which failed to flower had a prostrate growth form with more vigorous tiller growth. This growth habit is typical of Poa annua ssp reptans (Hutchinson and Seymour 1982). When the mean vegetative weight of the non-flowering plants was compared with the mean weight of the flowering plants it was evident that the non-flowering plants were much larger (fig 3.3.1a). This difference was tested and was found to be highly signifcant ($P<0.001$) in both the first and second harvests (table 3.3.1a.).

The occurrence of non-flowering individuals also seemed to be random and bore no relation to the treatments.

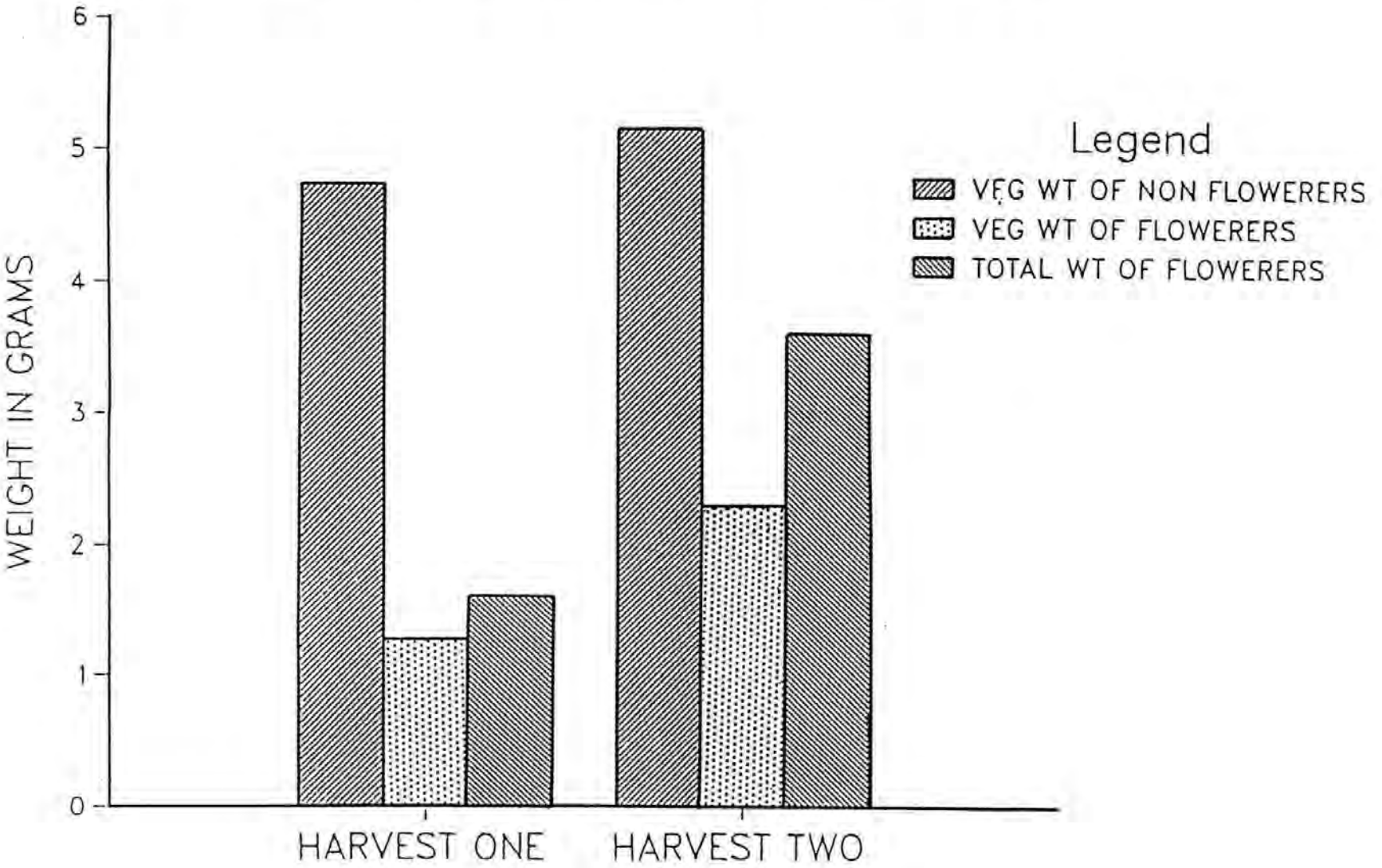
non-flowering plant

flowering plant

Plate 7.3.1 Two types of growth habit in Poa annua

Fig 3.3.1a

POA - COMPARISON OF MEANS



Results F-tests comparing veg wt of non-flowerers with veg wt and total wt of flowerers

Harv one	N	mean	st dev	SE mean
Veg wt non f's	6	4.740	0.978	0.40
Veg wt f's	78	1.273	0.815	0 092
			T = 8.46	
			DF = 5.5	
			P = 0.0004	
			P = <0.001	
Veg wt non f's	6	4.740	0.978	0.40
Total wt f's	78	1.614	0.869	0.098
			T = 7.60	
			P = 0.0006	
			DF = 5.6	
			P = 0.001	
Harv two				
Veg wt non f's	6	5.165	0.644	0.26
Veg wt f's	78	2.294	0.989	0.11
			T = 10.5	P = <0.0001
			DF = 7.0	P = <0.001
Veg wt non-f's	6	5.165	0.644	0.26
Total wt f's	78	3.62	1.39	0.16
			T = 5.04	DF = 9.2
			P = 0.0000	P = <0.001

Frequency of non-flowering plants

	Control	50%N	20%N	50%P	20%P	50%K	20%K
Harvest 1	2	1	0	1	1	1	0
Harvest 2	1	0	0	0	2	1	2

Consequently it was decided to treat the flowering and non-flowering plants as two separate populations and to exclude the non-flowering plants from any subsequent statistical analysis. To allow for the experimental design and to overcome the problems of unequal sample numbers, analyses of variance were carried out on the data for mean tray weights. There were no significant differences between mean tray dry weights within each treatment.

Multivariate F-tests were calculated using GLIM (Baker and Nelder 1978) and other statistical analyses, including one way anovas were calculated using Minitab (Ryan, Joiner and Ryan 1976).

ii. Weight of Component Parts

As noted above, the mean vegetative weight of the non-flowering plants was significantly greater than the mean total weight of the flowering plants. There were insufficient numbers of non-flowering plants to test whether treatment had a significant effect on their weight but it was obvious that treatment was not affecting the frequency of non-flowering individuals.

It is evident from Figs 3.3.2a and 3.3.3a that both the early and late harvests show the same pattern of response to the nutrient treatments. The treatment effect on vegetative weight was significant in both harvests (see tables 3.3.2a and 3.3.3a) and the higher F value in the later harvest shows that the effect was more pronounced when the plants had been growing longest. By calculation of the least significant differences and comparing the treatment mean weights in Appendix 1, it is possible to determine which treatments were significantly different from the control treatment. The 20%N treatment was signficantly lower than the control in both harvests and the 50%N treatment was significantly lower in the early harvest. However the 50%K vegetative weight was greater than the control weight in both harvests and the 50%P and 20%K treatments were greater than the control in the late harvest. The 50%N treatment was significantly greater than the 20%N treatment in both harvests. Since the rows and columns had no significant effect a one way analysis of variance was also conducted on the data for individual plants in table 3.3.4a and this shows similar results.

The reproductive weight of the plants was also significantly ($P<0.01$) affected by treatments in both harvests although the effect was less pronounced in the second harvest (tables 3.3.2a and

Fig 3.3.2a

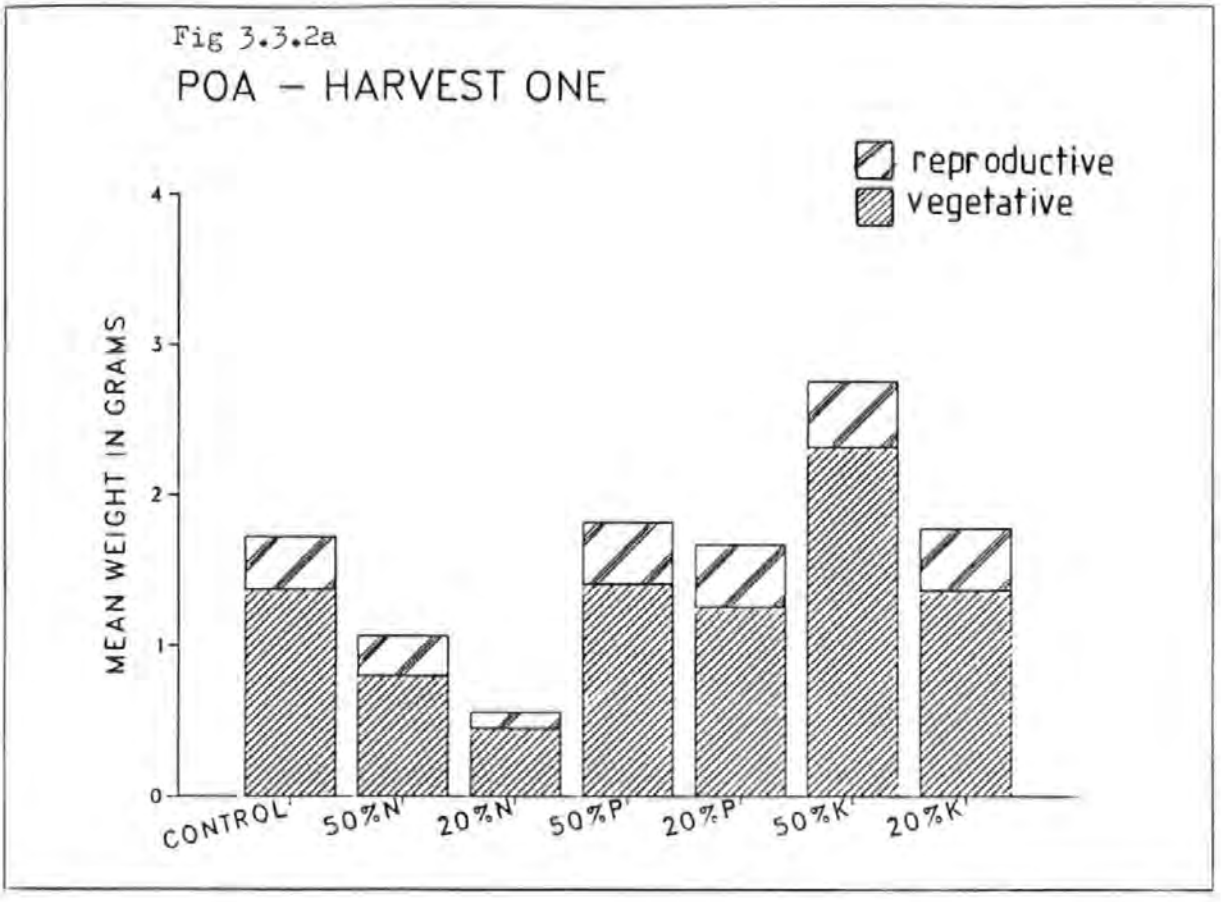
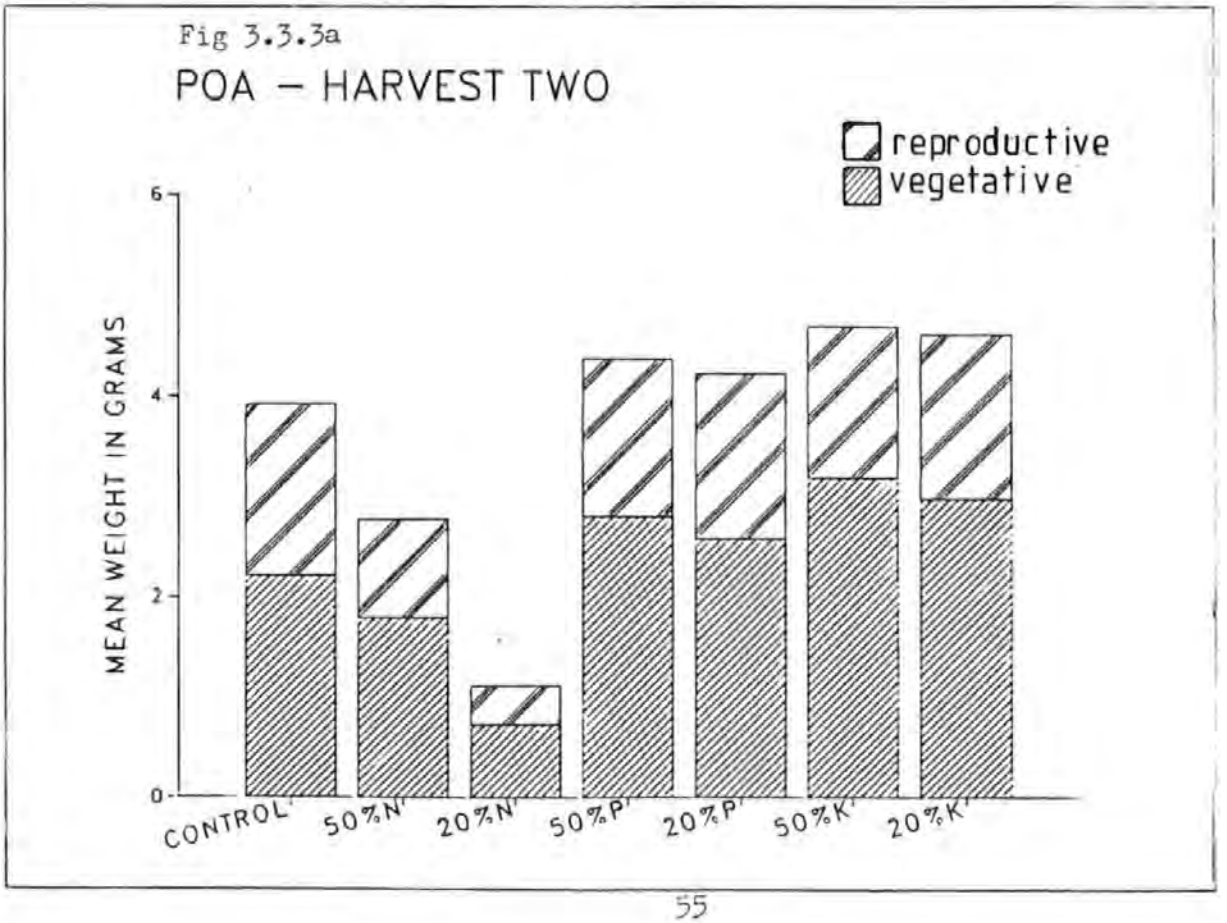


Fig 3.3.3a



Anovas poa harvest one

Vegetative wt - flowerers

Source	df	SS	MS	F
Cols	6	2.863		
Rows	3	0.63		
Treats	6	5.98	0.9966	6.442
Error	12	1.857	0.1547	
Total	27	11.33		P 0.01

LSD = 0.606 Sig Diffs = Control v 20%N. Also v 50%K (larger)

Log veg wt - flowerers

Source	df	SS	MS	F
Cols	6	1.956		
Rows	3	0.2		
Treats	6	4.3315	0.7219	11.315
Error	12	0.7665	0.0638	
Total	27	7.254		P<0.001

LSD = 0.389 Sig Diffs = Control v 50%N 20%N 50% K (larger)

Reprod wt - flowerers

Source	df	SS	MS	F
Cols	6	0.0478		
Rows	3	0.0161		
Treats	6	0.3173	0.05288	14.607
Error	12	0.04347	0.00362	P<0.001
Total	27	0.4247		

LSD = 0.092 Sig Diffs = Control v 20%N v 50%N (larger). Also 20%N v 50% N

Poa - harvest one anovas

Total weight - flowerers

Source	df	SS	MS	F
Cols	6	3.32		
Rows	3	0.6		
Treat	6	3.284	1.380	10.18
Error	12	1.626	0.1355	P<0.001
Total	27	13.83		

LSD = 0.5671 Sig Diffs = Control v 50%N, 20%N and 50%K (larger)

Anovas - harvest two

Vegetative weight - flowerers

Source	df	SS	MS	F
Cols	6	2.43		
Rows	3	0.09		
Treats	6	17.885	2.980	23.299
Error	12	1.535	0.1279	
Total	27	21.94		P<0.001

LSD = 0.5510 Sig Diggs = Control v 20%N (smaller). Also Control v 50%P, 50%K, 20%K 20%N v 50%N

Reproductive weight - flowerers

Source	df	SS	MS	F
Cols	6	0.867		
Rows	3	0.301		
Treat	6	5.563	0.927	5.178
Error	12	2.148	0.179	P<0.01
Total	27	8.879		

LSD = 0.6518 Sig Diffs = Control v 50%N, 20%N

Total weight - flowerers

Source	df	SS	MS	F
Cols	6	5.4		
Rows	3	0.15		
Treat	6	38.48	6.413	25.011
Error	12	3.077	0.2564	
Total	27	47.11		P<0.002

LSD = 0.779 Sig Diffs = Control v 20%N, 50%N (smaller) Control v 50%K 50%N v 20%N

One way anovas - poa harv one

Vegetative Weight

Source	df	SS	MS	F
Treatments	6	22.995	3.833	9.66
Error	71	28.179	0.397	
Total	77	51.174		P<0.001

LSD = 0.05.71 x $2\times\frac{0.397}{12}$ = 1.993 x .661 .2572
= .5126
Control v 50%N, v 20%N, 50%K larger

Reproductive Weight

Source	df	SS	MS	F
Treatments	6	0.9853	0.1642	12.60
Error	71	0.9253	0.130	P<0.001
Total	77	1.9107		

LSD = 0.293 50%P, 20%P, 50%K, 20%K v 20%N

LOGTEN vw

Source	df	SS	MS	F
Treatments	6	13.2053	0.5342	20.29
Error	71	1.8698	0.0263	P<0.001
Total	77	58.750		

Sig Diffs = Control v 50%N, 20%N, 50%Nv 20%N, 50%K larger

Total weight

Source	df	SS	MS	F
Treatments	6	31.926	5.321	14.43
Error	71	26.178	0.369	P<0.001
Total	77	58.104		

LSD = 0.494 Control v 50%N, 20%N, 50%K larger, 50%N v 20%N

Source	df	SS	MS	F
RA/Treatments	6	0.04125	0.00687	1.21
Prop Error	71	0.40246	0.00567	NS
Total	77	0.44371		

Source	df	SS	MS	F
Arcs in RA/ Treats	6	237.0	39.5	1.27
Error	71	2214.8	31.2	NS
Total	77	2451.9		

One way anovas - poa harv two

Vegetative wt

Source	df	SS	MS	F
Treats	6	49.404	8.234	22.51
Error	71	25.969	0.366	
Total	77	75.374		P<0.001

LSD = 0.571 = 1.993
= 0.4922 Control v 20%N, 50%P 50%K and 20%K larger
50%N v 20%N

Reproductive wt

Source	df	SS	MS	F
Treats	6	16.617	2.770	9.17
Error	71	21.436	0.302	
Total	77	38.053		P<0.001

LSD = 0.447 Control v 50%N, 20%N, 50%N, 20%N

Total wt

Source	df	SS	MS	F
Treats	6	117.228	19.538	43.64
Error	71	31.788	0.448	
Total	77	149.016		P<0.001

LSD = 0.544 Control v 50%N, 20%N 50% and 20%K larger

RA

Source	df	SS	MS	F
Treats	6	0.0956	0.0159	0.94
Error	71	1.2079	0.0170	NS
Total	77	1.3035		

Arcsin RA

Treat	6	437.1	72.9	0.94
Error	71	5527.5	77.9	NS
Total	77	5964.7		

3.3.3a). In the first harvest the 20%N treatment weight was significantly lower than the control whilst the 50%K treatment was significantly higher. In the second harvest both N treatments were significantly lower. The one way anovas show essentially the same pattern (table 3.3.4) although the N treatments were not significantly different from the control plants in the first harvest.

Similarly, the effect of treatments on total weight was significant in both harvests ($P<0.001$) although the F value was greater in the second harvest. The 50% and 20%N values were significantly lower than the control and the 50%K was significantly larger in both harvests.

Vegetative weight was significantly correlated with reproductive weight in both harvest one ($P<0.001$) and harvest two ($P<0.01$). See table 3.3.5a.

iii. Reproductive Allocations

The mean level of RA increased from 22.9% in the first harvest to 35.7% in the second harvest, but there was very little variation in the proportion of dry weight allocated to reproduction between treatments (Fig 3.3.4a). None of the analyses of variance was significant (table 3.3.4a and 3.4.6a).

RA was significantly correlated with vegetative weight in both harvests (see table 3.3.5a and figs 3.3.5a and 3.3.6a). RA was also significantly ($P<0.01$) negatively correlated with total weight in the first harvest (fig 3.3.7a) but this negative correlation was not apparent in the second harvest.

Table 3.3.5a

Correlations

Harvest one

	r	sig
Log veg wt v rep wt	0.502	P<0.001
veg wt v rep wt	0.254	P<0.05
RA v Total weight	-0.441	P<0.01
RA v rep wt	0.496	P<0.01
RA v log veg wt	-0.431	P<0.01
RA v veg wt	-0.565	P<0.01

Harvest two

Veg wt v rep wt	0.332	P<0.01
RA v total wt	0.197	NS
RA v rep wt	0.749	P<0.01
RA v veg wt	-0.256	P<0.02

Table 3.3.6a

Poa anovas on reproductive allocation

Harvest one - flowerers

RA Source	df	SS	MS	f
Cols	6	221		
Rows	3	75.5		
Treat	6	260.5	43.41	1.20
Error	12	431.2	35.93	NS
Total	27	988.2		

Arcsin RS

RA Source	df	SS	MS	f
Cols	6	103.9		
Rows	3	37.7		
Treat	6	137	22.83	1.340
Error	12	204.4	17.03	NS
Total	27	483.0		

Harvest two - flowerers

RA Source	df	SS	MS	f
Cols	6	186		
Rows	3	38		
Treat	6	585.6	97.6	1.3
Error	12	896.4	74.7	
Total	27	170.7		

Arcsin RA

RA Source	df	SS	MS	f
Cols	6	68.3		
Rows	3	13.6		
Treat	6	215.3	35.88	1.267
Error	12	339.8	28.31	
Total	27	637.0		

Fig 3.3.4a **REPRODUCTIVE ALLOCATION**

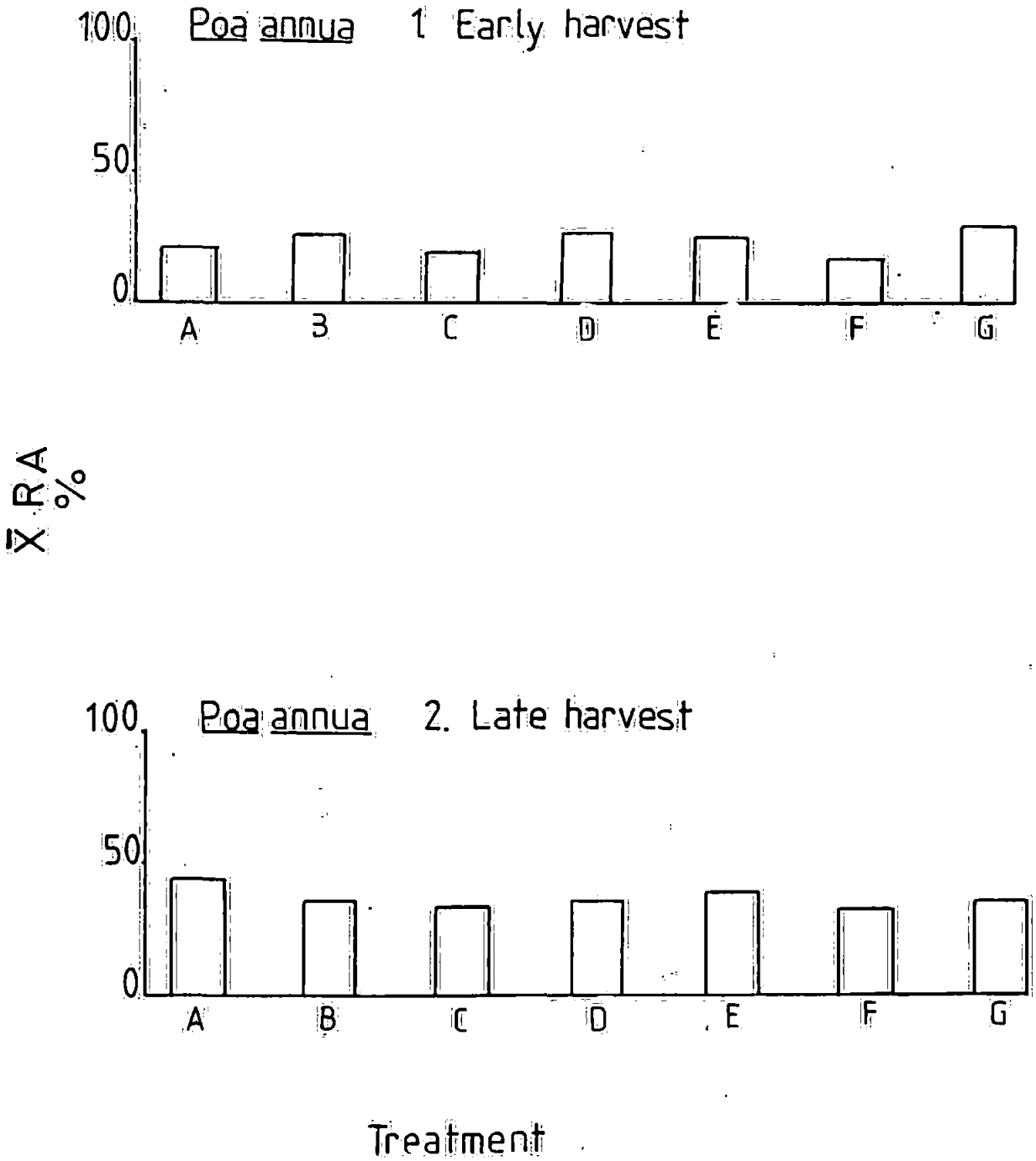
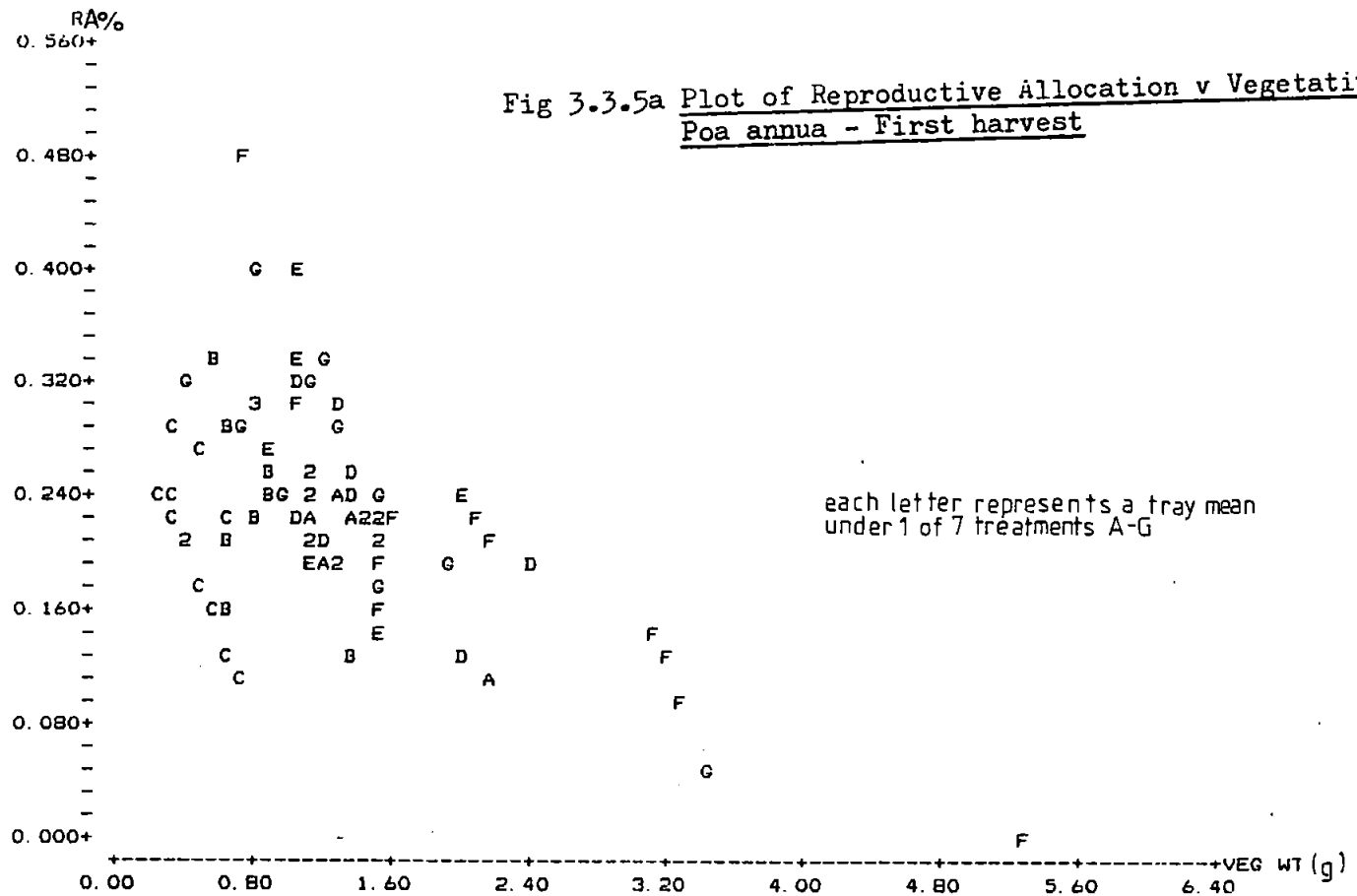


Fig 3.3.5a Plot of Reproductive Allocation v Vegetative Weight
Poa annua - First harvest



CORRELATION OF RA AND VEG WT =-0.565

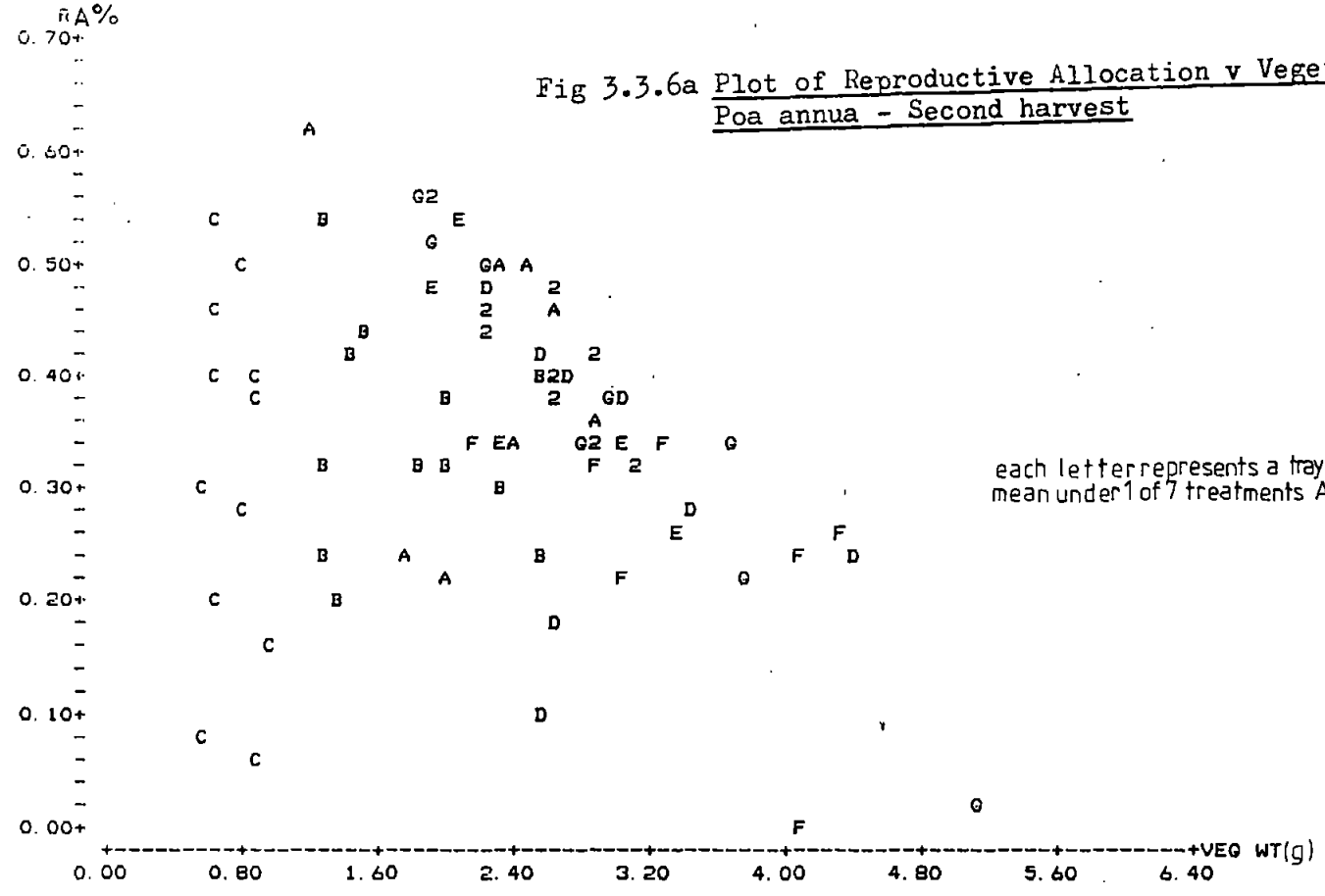
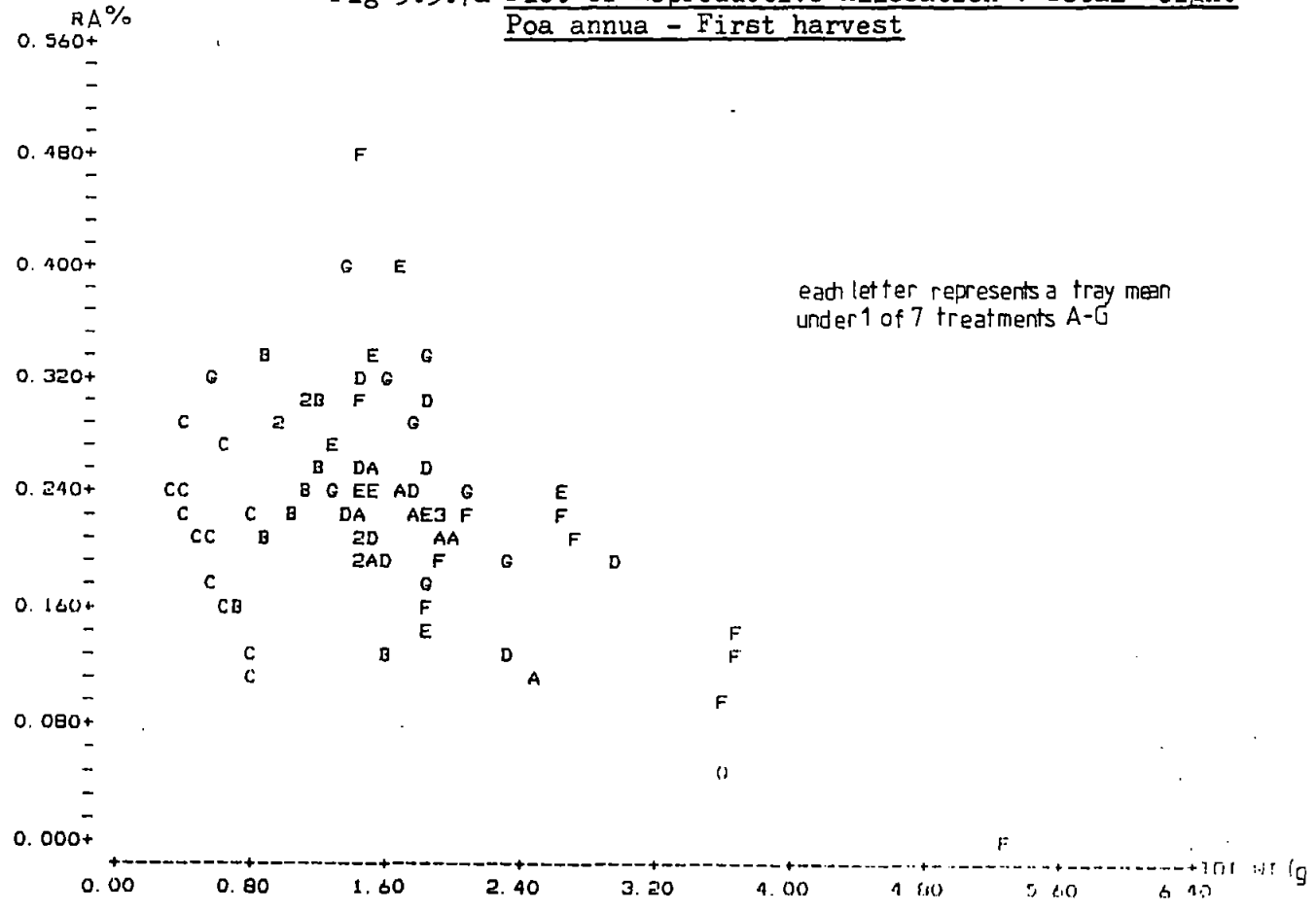


Fig 3.3.6a Plot of Reproductive Allocation v Vegetative Weight
Poa annua - Second harvest

CORRELATION OF RA AND VEG WT =-0. 256

Fig 3.3.7a Plot of Reproductive Allocation v Total Weight
Poa annua - First harvest



CORRELATION OF RA AND TOT WT =-0.441

3.4 Discussion

3.4.1 Plant weights

The most obvious effect of low nitrogen treatments was to cause a 3 and 4 fold reduction in total weight in *Poa annua* and *Taraxacum officinale* respectively. The mean weight of the plants decreased consistently with decreasing nitrogen supply. Slow and retarded growth is a characteristic sympton of nitrogen deficiency (Epstein 1972) and nitrate levels have been found to influence plant weights in *Spergula arvensis* and *Plantago major* (Trivedi and Tripathi 1982) and in *Phalsa* Sadhu et al (1975). Similarly Lovett Doust (1980), Waite and Hutchings (1982) and Fenner (in press) found that low concentrations of general nutrient solutions or fertilisers reduced plant weight.

Nevertheless, the potassium and phosphorus deficient treatments did not show a significant, consistent effect on plant weight nor any other parameter. It is possible that the concentration of K and P in the control nutrient solution were relatively much higher than the N concentration in terms of the specific requirements of these plants. Indeed Epstein (1972) suggests that the concentrations of P and K which are found in typical nutrient solutions are much higher than the concentrations found in typical soil solutions. Many plants do not require such high concentrations of P and K provided that adequate replenishment of nutrient levels is ensured eg Williams (1961) grew plants of *Hordeum vulgare* satisfactorily in culture solutions where the K concentration was kept at 0-01ppm. The concentration of K in the control treatment in this experiment was 117ppm (Hewitt 1966).

Despite the severe suppression of plant growth in the nitrogen deficient treatments, the probability of flowering was not altered in

either species. Similarly Lovett-Doust (1980) found that the effect of his most severe treatment (defoliation and deradication) of Smyrnium olusatrum which reduced the dry weight by 80%, only slightly affected the probability of flowering. This is in contrast to the behaviour of Chamaenerion angustifolium (Van Andel and Vera 1977) where a low mineral treatment reduced the proportion of plants which flowered.

In Poa annua the plants which did not flower were undoubtedly genetically dissimilar since their vegetative weight at the end of the experiment was greater than the mean total weight of the flowering plants. Therefore, these plants were not prevented from flowering by their inability to achieve a critical weight. However, in the case of the Taraxacum officinale plants, the mean weight of the non-flowering plants was consistently lower than the mean total weight of the flowerers. Nevertheless, a specific critical weight was not apparent since the mean weight of the non-flowerers in the control population was greater than the mean weight of the flowerers in the most deficient (20%N) Nitrogen treatment.

3.4.2 Reproductive Allocation

The mean value of RA obtained for all treatments was 51.7% for Taracaxum officinale and 28.7% (harvest one), 36.9% (harvest two) for Poa annua. These values are somewhat higher than the general values quoted by Harper (1977 after J Ogden). He cites values of RE for wild annuals of between 15-30% and for herbaceous perennials of between 0-25% but a review of the currently available literature (Table 3.4.1) indicates that several species have RAs outside these limits. The annual Polygonum kelloggii (Hickman 1977) has a reproductive allocation of 76% while the perennial palm Astrocaryum mexicanum allocates 32% of its biomass per year to reproduction (Sarukhan 1980). Alternatively,

REVIEW OF REPRODUCTIVE ALLOCATION LITERATURE

Guide to Strategy	Paper	Species	% RA	% SA	Information on RA method
Ruderal annuals	Harper and Ogden 1970	Senecio vulgaris		21.4	RC IR HS
				26.27	RB HI IR HS
				33.34	HI measured in cals IR HS
	Fenner (in press)	Senecio vulgaris	33	11	RB HO but seed collected daily
	Van Andel and Vera 1977	Senecio sylvaticus	21-24		RB IR HS RA
	Trivedi and Tripathi 1982	Spergula arvensis	20		RB IR HS CRE
	Hickman 1975	Polygonum cascadense	50		RB IR IO
	Hickman 1977	Polygonum cascadense	55	38-58	RB IR
	Snell and Burch 1975	Chamaesyce hirta	32		RB IR HS
	Pitelka 1977	Lupinus nanus	61	29	RC IR HS
	Hickman 1977	Polygonum douglasii	15		RB IR HO
	Hickman 1977	Polygonum kellogii	65		RB IR HO
	Hickman 1977	Polygonum minimum	10		RB IR HO
	Lee and Cavers 1981	Setaria glauca	18.7		RB HS
		Setaria verticillata	21.1		
		Setaria vindis	37.1		
	Kawano and Miyake 1983	Setaria viridis	49.5		RB IR
		Setaria glauca	27.5		
	Harris and Lovell 1980	Veronica persica	15.1		RB HO
		Veronica agrestis	25.0		
		Veronica hederifolia	13.3		
	McNamara and Quinn 1977	Amphicarpum purshii	29		RA IR HO above last node. Includes cleistogamous reproduction
	Gaines et al 1974	Helianthus annus	25		RB IR
	Jaksic and Montenegro 1979	Erodiur cicutarium	11		RB IR HO
	Cook 1975	Chenopodium rubrum	47-54		RB

Guide to Strategy	Paper	Species	% RA	% SA	Information on RA method
	Ogden 1974	Helianthus annuus	14		CRE
	Stern and Beech 1975	Senecio vulgaris	14-27		RB IR
		Calendula officinalis	27		
		Matricaria matrianioides	35		
		Carthamus tinctoris	13-23		
	Harper and Ogden 1970	Linum usitatissimum (linseed)	36		RB
		Linum usitatissimum (flax)	20		RB
		Avena fatua	34-61		RB
		Avena sativa (grain)	43-56		RB
		Avena sativa (forage)	29-47		
Desert winter annuals	Williams and Bell 1981	Chaenactis fremontii	39.1		RB IR HO
		Schismus arabicus	33.1		
		Baileya pleniradiata	40.9		
		Astralagus sabulorum	32.5		
		Crypthantha angustifolia	41.2		
		C. pterocaryo	30.8		
		Chaenactis caephoclinia	50.6		
		Plantago insularis	54.3		
	Bell et al 1979	Baileya pleniradiata	37		RB IR HO at time of max RA
		Astralagus sabulorum	34		
		Schismus arabicus	33		
		Oenothera deltoides	28		
		Chaenactis carphodinia	49		
		Plantago insularis	50		
		Phacelia crenulata	18		
		Camissonia brevipes	16		
Sahelian species	De ridder et al 1981	Eucaria boveana	38	4	RB HS
		Trigonella arabica	60	29	
		Medicago polymorpha	47	18	Reproductive ratio and seed ratio
		Plantago lagopus	40		
		Glaucium corniculatum	50	12	
		Schismus arabicus	48	31	
		Hordeum leporinum	26	11	
		Phalaris minor	35	16	
		Asphodelus tenuifolius	46	32	
		Stipa capensis	61	8	
		Astragalus cibarius	67	22	
		Astragalus utatensis	50	24	

Guide to Strategy	Paper	Species	% RA	% SA	Information on RA method
Biennial	Lovett-Doust 1980	Smyrnium olusatrum	25-39		RB IR HS
	Reinartz 1984	Verbascum thapsus	11-23		RB HO
	Caswell and Werner 1978	Dipsacus sylvestris	27		RB
	Abrahamson 1979	Daucus carota	39		RB IR HO
		Melilotus alba	11		
Ruderal grassland perennials	Harris and Lovell 1980	Veronica serpyllifolia		23.2	RB HO
	Tripathi and Harper 1973	Agropyron repens		0.1-0.9	RB IR HS
		Agropyron caninum		10.9-14.8	
	Lambert 1968	Dactylis glomerata		4.6	RB IR HO
	Gaines et al 1974	Helianthus grossseratus	6		RB IR
		Helianthus laetiflorus	16		
	Abrahamson 1979	Arisaema atrorubens	39		
		Hieracium floribundum	34		
	Abrahamson 1975	Rubusohispidus field	18.3		RB
		Rubusohispidus wood	9		Regression
	Bradbury and Hofstra 1976	Solidago candensis	9-12		RC IR HS
	Hawthorn and Cavers 1982	Plantago major	12-46		RB IR HO
	Linhart 1974	Veronica peregrina	38-43		RB
	Abrahamson and Gadgil 1973	Solidago nemoralis	49		RB HS
		Solidago speciosa	15-28		
		Solidago rugosa	4-10		
		Solidago canadensis	25		
Ruderal prennials +grassland perennials	Raynal 1979	Hieracium florentinum	7.9	4.5	RB IR HS
	Soule and Werner 1981	Potentilla recta	16.5 - 28.4		RB HS above ground
	Hawthorn and Cavers 1978	Plantago major	21		RB IR HO spike
	Trivedi and Tripathi 1982	Plantago major	12		IR HS
					RB IR HS CRE
	Waite and Hutchings 1982	Plantato coronopus	31-47	5-10	RB HO +HS RA?

Guide to Strategy	Paper	Species	% RA	% SA	Information on RA method
	Bostock and Benton 1979	Achillea millefolium	2.7		RA IR HS
		Artemisia vulgaris	2.3		Allocation of all reprod-
		Cirsium arvense	15.1		tive organs taken as %
		Taraxacum officinale	24.4		of total dry weight net
		Tussilago farfara	26.1		prodn. Achillea had figure of 21.5% if flowering plants alone used
	Ogden 1974	Tussilago farfara		4.7	RB HS
				5.9	RC HS
	Bostock 1980	Tussilago farfara	31	1	RB IR HO
	Stewart and Thompson 1982	Carex flacca	52		RB HS but chose peak
		Centaurea nigra	17		
		Leontodon hispidus	46		
		Plantago lanceolata	52.5		
		Plantago media	34.7		
		Poterium sanguisorba	17		
	Roos and Quinn 1977	Andropogon scoparius	24–42		RB HO reproductive tissue to lowest node
	Willson and Price 1980	Asclepias syrica	21	(3)	RB HO fruit RA
		Asclepias verticillata	23	(9.5)	Bracketed figs = flower RA
		Asclepias incarnata	10	(6)	
	Holler and Abrahamson 1977	Fragaria virginiana		5	RB HS harvest at peak
	Jurik 1983	Fragaria virginiana	13– 3		RMET + RB
			3–21		RB
		Fragaria vesca	3.1–4.7		RMET
			7.5–10.7		RB
Perennials	Van Andel and Vera 1977	Chamaenerion angustifolium			RB IR HS RA
	Lovett-Doust 1980(b)	Oenanthe crocata	8–9		RB IR HS
		Conopodium majus	7		
		Anthriscus sylvestris	19.2		
		Pastinaca sativa	12.4		
	Jolls 1984	Sedum lanceolatum	18.3–38.3		RB IR HO
			57.1–24.3		RB IR HO

Guide to Strategy	Paper	Species	% RA	% SA	Information on RA method
Stress tolerant perennials and shrubs	Kawano and Masuda 1980	Heloniopsis orientalis	10-25		RB IR HS evergreen varies with elevation
	Pitelka 1977	Lupinus arboreus	20	6	RC IR HS shrub
		Lupinus variicolor	18	15	RC IR HS herb
	Kawano et al 1982	Erythronium japonicum	10.9	5.0	RB IR HS forest herb
	Pitelka et al 1980	Aster acuminatus	3.48		RB IR HO forest herb
	Kawano and Nagai 1975	Allium victorialis ssp platyphyllum	2.6		RB HS CRE
	Cunningham et al 1975	Larrea tridentata			RB RA/time period Evergreen
	Sarukhan 1980	Astrocaryum mexicanum	37		RB IR HS Yearly budget of dry matter prodn over 120 years Iteroparous
	Gaines et al 1974	Helianthus hirsutus	2		RB IR

KEY

RA = Reproductive Allocation
RB = RA measured using biomass/weight
RC = RA measured using calories/energy

HO = one harvest taken
HS = sequential harvests taken

IR = include roots n estimations

CRE = crude reproductive effort as used by Harper and Ogden 1970

HI = Harvest index = $\frac{\text{seed weight}}{\text{Total weight at maturity}}$

RMET = metabolic costs of reproduction

the annuals Polygonum minimum and Erodium cicutarium may have RAs of less than 10% (Hickman 1977) and 11% (Jaksic and Montenegro 1979) respectively.

The high values obtained for Poa and especially Taraxacum are probably partly caused by the omission of any underground structures in calculation of the total biomass. Bostock and Benton (1979) obtain a value for Taraxacum officinale of 24.4% when underground biomass was included. It is evident from Table 3.4.1 that values of RA tend to be higher when underground biomass is omitted. In addition to this factor, many estimates of RA perform one harvest at the end of the season eg Pitelka et al (1980) or choose the highest value obtained for RA from a number of sequential harvests eg Bell et al (1979). Reproductive structures were collected over the whole season for both Taraxacum officinale and the second harvest of Poa annua. The discrepancy of 9% between the values for Poa annua in the first and second harvests demonstrates the need for caution when comparing RA values obtained by different methods.

Despite the 3 and 4 fold reductions in weight caused by the low nitrogen treatments, RA was not significantly different. There were wide variations in RA within the treatments eg the minimum and maximum values were:

Taraxacum	17.6 - 69.3%	Range = 51.7%
Poa 1st harvest	4.5 - 44.1%	= 39.6%
Poa 2nd harvest	5.2 52.4%	= 47.2%

but this demonstrates the variability of the populations and cannot be related to a treatment effect. Within species ranges of up to 36% have been quoted by Soule and Werner (1981).

This constancy of the relative biomass allocation to reproduction despite large reductions in plant weight is similar to the response found by Fenner (in press) for Senecio vulgaris under a range of nutrient concentrations. Harper and Ogden (1970) also found that Senecio vulgaris showed no significant difference in the proportion of energy allocated to seeds despite a 7-fold difference in plant weight. In this case stress was applied by reduction of the pot size. A similar homeostasis of allocation to sexual reproduction under different nutrient conditions occurred in Tussilago farfara (Ogden 1974). Spergula arvensis and Plantago major (Trivedi and Tripathi 1982), Senecio sylvaticus, and Plantago coronopus under greenhouse conditions (Waite and Hutchings 1982). All of this work (except Trivedi and Tripathi 1982) used a general combination of mineral nutrients and did not separate the effects of N, P and K. In the majority of these cases, where RA remains constant despite environmental stress the species under consideration is an annual or a ruderal from a typically unpredictable environment. In such species the postponement of reproduction to a later date when conditions may be more favourable is neither a possible (in the case of annuals) nor cost-effective (in the case of ruderals in an unpredictable environment) alternative. In these species the maintenance of a fixed proportion of biomass in reproduction despite environmental stress is a feasible strategy.

Alternatively Lovett Doust (1980) found that RA in the biennial Smyrnium olusatrum was significantly altered by a low nutrient treatment. Again, however the effect of the treatment on plant weight was much more significant. Similarly Snell and Burch (1975) found that an 8-fold decrease in nutrient levels diminished RA by 50% in the annual Chamaesyce hirta.

3.4.3 The relationship between RA and total biomass

RA in Taraxacum officinale was positively correlated with total weight ($P<0.05$) whereas in Poa annua, RA was negatively correlated with total weight in the first harvest ($P<0.01$) and there was no evidence of a relationship in the second harvest. A positive correlation of RA with plant weight was also found in field populations of Plantago coronopus (Waite and Hutchings 1982), Verbascum thapsus (Reinartz 1984), Plantago insularis and Phacelia crenulata (Bell et al 1979).

Hickman (1975) found that within different populations of Polygonum cascadense there was a positive correlation of RA with total weight but between populations there was a negative correlation, the smaller plants from the harsher habitats having higher RAs. A negative relationship between RA and total biomass was found in Erythronium japonicum (Kawano et al 1982) and Fenner (in press) implies that this negative correlation of RA with size may explain why many authors have discovered a negative relationship between RA and increasing successional maturity.

However, there is some evidence of no relationship between RA and total biomass (eg Kawano and Miyake (1983) for 5 congeners of the genus Setaria and Bell et al (1979) for 6 species of winter annuals. The species with a positive relationship between RA and total biomass eg

Plantago coronopus and Verbascum thapsus are much more similar in morphology to Taraxacum officinale than Poa annua with large inflorescences arising from a rosette of vegetative leaves. Bell et al (1979) suggest that the observed differences in RA between desert winter annuals are related to the morphology and possibly the physiology of the individual species. Taraxacum officinale can produce an indefinite number of flowers, (depending on the availability of resources) from the centre of the basal rosette with little change in the basic morphology or size of the rosette. However in Poa annua (as with other grasses such as Setaria spp each reproductive panicle is integrally linked to the vegetative leaves at the base of the culm. An increase in reproductive parts automatically entails a corresponding increase in vegetative parts so the relationship between the two remains constant irrespective of plant size. The importance of plant morphology has also been recognised by Armstrong (1982,1984) who proposes a theoretical approach to the study of reproductive strategies which is based on the constraints imposed by growth form and geometry rather than site-specific factors.

An alternative hypothesis to explain the presence or absence of a positive correlation of RA with plant weight in terms of strategy is proposed by Waite and Hutchings (1982). In plants with the option of having a high RA in favourable years or postponing reproduction until a later date if conditions are unfavourable, a weight-related plastic allocation strategy is advantageous. Reinartz (1984) suggests that the positive relationship between plant size and RA in Verbascum thapsus is caused by indeterminate reproductive growth after the leaf, caudex and root growth has ceased. The level of RA achieved is thus determined to some extent by environmental conditions.

As Taraxacum officinale is a perennial with the option to reproduce in a following season it would be advantageous to correlate its reproductive output with its size at a specific time. However for annuals such as Poa annua the maintenance of a high fixed RA regardless of environmental conditions (and the size of the plant) is favoured. It is possible that both the constraints of plant morphology and perennation strategy may determine the level of RA in a particular species.

4. THE APPROPRIATE CURRENCY

4.1 Introduction

4.1.1 The principle of allocation

In consideration of the genetical theory of natural selection, Fisher (1930) was one of the first to stress the significance of determining how natural selection adjusts the partitioning of the energy budgets of organisms. He drew attention to the division of resources between the gonads and soma. Subsequently, the 'principle of allocation' was proposed by Cody (1966) to explain variations in clutch size in birds. He suggested that the process of individual development represents a 'strategic' allocation of resources to competing demands or 'sinks'. The resources which Cody suggested were crucial for birds, were time and energy. Time and energy (which are in limited supply) were expended on the various sinks, such as defence, reproduction or maintenance of growth, in order to maximise an organism's fitness. Thus the 'principle of allocation' implies that under natural selection, organisms optimise the partitioning of the limited resource available in a way which maximises fitness.

Harper (1967) and Harper and Ogden (1970) implicitly accepted this principle as applicable to plants. It is assumed that the supply of the crucial resource is limited and that the different structures or activities are alternatives, so an increase in one means a decrease in another (Harper 1977). The proportion of resources which are devoted to reproduction as opposed to the development of a competitive growth form or defence against predators, has been seen as the character of greatest importance when considering plant life history strategy.

4.1.2 Which currency?

Early studies used energy or biomass as a currency by which to gauge reproductive allocation. Some studies have included calorimetric measurements eg Harper and Ogden (1970) and Ogden (1974). Abrahamson and Gadgil (1973) and Hickman and Pitelka (1975) consider that for plants, dry weight is an adequate measure of energy allocation and most subsequent studies have used dry weight allocation. Jolls (1984) found that allocation patterns based on kilojoules of energy and grams of biomass in Sedum lanceolatum were not highly correlated and warns against the danger of using biomass to represent energy in species that change morphologically or physiologically along an environmental gradient. Nevertheless, in principle biomass and energy are interchangeable if the calorific value of the material being sampled is known. However it has recently been suggested (Lovett-Doust 1980, Thompson and Stewart 1981, Abrahamson and Caswell 1982) that measurements of both biomass and energy may be inappropriate for several reasons.

The principle of allocation assumes a limited pool of resources which is not increased in size during the very process of allocation. Cody's hypothesis was based on the principle that reproductive parts make no energetic or material contribution to their own production. This is not the case for plants. There are now several studies showing that green fruit and accessory reproductive structures contribute carbohydrate to their own formation in native plants (Maun 1974, Bazzaz and Carlson 1979, Werk and Ehleringer 1983). Information about the partial carbon autonomy of fruits and flowersin agromomic varieties has been available for some time eg Flinn and Pate (1970).

In addition to this complication there is evidence that plants normally function at a level of photosynthetic activity below that of which they are capable (Harper 1977). The activity of the photosynthetic system appears to be determined by the demands made by various other organs such as meristems or storage structures rather than reproductive organs (Kahn and Sagar 1969) and photosynthesis may be limited by the availability of water or nutrients (Mooney and Gulman). Studies such as those by Lovett-Doust and Harper (1980) and Lovett-Doust (1980) indicate that under conditions where carbon is abundant other resources such as nitrogen or phosphorus appear to be limiting. Even Harper and Ogden (1970) whilst considering energy allocation suggest that under some circumstances mineral availability may be the limiting factor.

4.1.3 Arguments for the use of mineral allocation

Thompson and Stewart (1981) have suggested that since reproduction requires mineral nutrients but reproductive structures cannot contribute to the supply of mineral nutrients, mineral allocation may be more crucial than energy allocation. This is supported by evidence that plants are often nutrient limited (eg Rodin and Bazilevich 1967 and Chapin 1980) and that nutrient acquisition is linked to reproduction (eg Van Andel and Vera 1977 and Benzing and Davidson 1979). There are also dynamic movements of nutrients within the individual plant during its development (Williams 1955).

There is much physiological evidence that plants sacrifice photosynthesis and growth for the sake of reproduction. Developing fruits reduce or halt vegetative growth by monopolising supplies of mineral nutrients (Leopold and Kriedemann 1975). In forest trees 'mast' years of high seed production are followed by years with a poorer seed crop and lower growth rates (Harper 1977). This may be due to the depletion of mineral resources such as nitrogen and phosphorus.

Seeds of Fagus sylvatica contain 6 times as much mineral matter per gram dry weight as beech wood (Matthews 1963). In some plants reproduction is associated with the rapid senescence of leaves (eg cereal grains in Chapin 1980) and the appearance of symptoms usually associated with mineral deficiency. Wild plants in infertile habitats reduce their rates of turnover compared to plants in high nutrient environments even though this results in lower photosynthetic rates (Chapin 1980). In a polycarpic species, characteristic of infertile environments eg Eriophorum vaginatum (Goodman and Perkins 1959) it is possible for a maintainence nutrient budget to be continually recirculated from old to new tissues and (except for new growth) the mineral demand is only that for the seed crop. In monocarpic species growing in nutrient deficient habitats it is common to find that the plant has no remaining leaves when the inflorescence is formed eg in annual grasses on sand dunes (Harper 1977).

It may be that maximisation of photosynthetic rate is crucial at various points in a life cycle other than reproduction but since the focus of most allocation studies is on the partitioning of materials at reproduction it would seem that mineral allocation provides a plausible currency for gauging reproductive allocation.

4.1.4 Application of mineral allocation

Having suggested that minerals may be the limiting resource at the phase of reproduction in the majority of green plants, the problem arises of which particular minerals to measure. Different species may require the same qualitative resources (eg NPK) but differ in which particular resource limits their reproduction and for which the allocation patterns are crucial.

If total mineral allocation is taken it may mask any variation in proportional allocation eg Senecio sylvaticus allocated 56.7% P to reproductive structures but only 15.8% Ca and 35.5% biomass (Van Andel and Vera 1977). The mineral which provides the highest proportion of the total allocation to reproductive structures may vary in different conditions (Fenner 1985) eg when Senecio sylvaticus was grown under less fertile conditions, the element contributing the highest fraction of the total changed from P to N.

The small number of studies which have looked at mineral allocation do not seem to have reached any consensus on a crucial limiting mineral. Van Andel and Vera (1977) studying Senecio sylvaticus and Chamaenerion angustifolium found that no single nutrient paralleled the allocation of dry matter but if N, P and K were taken together a good approximation was obtained. Benzing and Davidson (1979) found that in Tillandsia circinnata patterns of N and P allocation did not follow carbon allocation.

Lovett-Doust (1980) chose to consider the allocation of P alone because of its crucial role as a storage element in seeds. The allocation patterns of P and biomass in Smyrnium olusatrum were found to be quite different and moreover, to be significantly altered by various treatments. Abrahamson and Caswell (1982) however, found that although the resource allocation patterns of biomass and various chemical elements were significantly different, the relative contributions of different elements were quite similar and they could not identify a best measure of allocation. All of these studies indicate a need for further research on the most appropriate currency and the response of this currency to nutrient limitation.

Consideration of mineral element allocation in plants however, should be treated with caution since some mineral elements are very mobile within the plant during different stages of development (Leopold and Kriedemann 1975) and concentrations of various elements in leaves are known to vary with the age of the plant. Uptake of certain minerals is also known to be affected by the presence or absence of other minerals.

4.1.5 Alternative currencies

In an attempt to account for the turnover of plant parts and to consider the total energy involved in producing and maintaining plant structures, Jurik (1983) developed a model to calculate the carbon dioxide costs of producing a biomass of given composition, determine the respiratory costs of maintaining that biomass and estimate photosynthetic carbon dioxide uptake. His measure of reproductive allocation is thus calculated to include the physiological costs of producing and maintaining the various reproductive and vegetative structures. Again however, in certain circumstances energy may not be the limiting factor.

An alternative approach to reproductive allocation which has been adopted recently is to measure the number of structures (Antonovics 1980) or modules (Tuomi et al 1982, Silvertown and Rabinowitz 1984) which are produced under various circumstances. Watson (1984) discusses the trade-off between reproduction and growth in a determinate plant Eichornia crassipes and concludes that reproductive allocation may be limited by meristem availability which is in turn limited by the developmental morphology of the ramets.

Many of the more recent studies of resource allocation have referred to the 'costs' of reproductive allocation (in whatever currency they may

be considering) eg Meagher and Antonovics 1982, Sohn and Policansky 1977, Lovett Doust and Cavers 1982). Bell (1980) argues that the measurement of reproductive effort (or allocation) in units of whatever currency is irrelevant to the evolution of life histories. He considers that the effort expended by an organism is only of evolutionary significance if it is transformed into units of fitness. This reproductive cost can be regarded as the effect of a given quantity of present reproduction on the expectation of future survival and/or future reproduction. The concept of reproductive cost is discussed in Ch 5.

The following experiment and subsequent analysis of nutrient concentration in the plant tissues was intended to determine whether mineral allocation provided a more suitable alternative, to dry weight allocation in RA studies.

4.2 Methods for Analysis of Nutrient Content

4.2.1 Selection of plants for analysis

The Taraxacum officinale plants grown in the experiment described in Ch3 were selected for analysis of nutrient content. Analysis of these plants would mean that the proportional allocation of the 3 nutrients (N P and K) in different parts of the plant could be determined. Moreover the effect of different levels and types of nutrient stress on this proportional allocation could be assessed.

The analysis was restricted to the T. officinale plants. Poa annua was excluded because it had been divided into early and late harvests and therefore there were insufficient replicates. In fact, even in Taraxacum the plant biomass was so small that individual plants were pooled to give a "tray" biomass to provide sufficient plant material for chemical analysis. Plants were pooled according to their treatment, tray number and flowering status. Thus there were 7 treatments x 4 trays x 3 flowering plants and reproductive parts of flowering plants). This pooling of plant parts was justified since statistical analysis of the data also considered tray values rather than individual plants.

4.2.2 Preparation of samples - grinding and digestion

Samples were ground in a hammer mill to pass a 5 mm sieve and stored in acid-washed plastic vials. Samples stored in this way can be kept for several years without a significant change in their mineral composition (Ulrich and Hills 1973). An oxidation process is necessary for the destruction of organic matter, involving combustion or acid oxidation, before a complete elemental analysis can be carried out. Acid digestion procedures are generally preferable because there is no

volatilisation of elements (eg phosphorus), they are fairly rapid, and more than one nutrient element can be determined from one digest solution (Allen 1974). As a consequence of the limited amount of plant material available and in an effort to reduce processing time it was decided to carry out one acid digest which could be used for all 3 analyses (ie N, P and K).

After consideration of the various types of digest which were possible it was decided to perform a traditional Kjeldahl digestion. This digestion procedure is considered to be the best for nitrogen determination since wet oxidation systems containing nitric and/or perchloric acid are unsuitable and result in low recovery rates (Allen 1974). The use of this digestion method also avoided any danger of explosion through the use of strong oxidising agents such as perchloric acid or hydrogen peroxide. However, the use of this digestion procedure means that perhaps not all of the total phosphorus present in the samples would be recovered. Since the object of the experiment was to determine proportional allocation rather than quantitative total amounts this was not considered to be a great problem. The results could be considered as amounts of phosphorus recoverable using a Kjeldahl digestion.

4.2.3 Digestion - principle

The Kjeldahl method for determining total nitrogen is based on the conversion of organic nitrogen to ammonia through digestion and its subsequent estimation by distillation and titration. Each aspect of the process has been studied by Bradstreet (1965). In the digestion procedure the sample is heated with concentrated sulphuric acid in a long necked digestion flask. The reaction rate is accelerated by adding sodium or potassium sulphate to raise the boiling point and a

catalyst containing usually copper, mercury or selenium. The process oxidises the nitrogen to ammonium sulphate and this is estimated by distillation (Pearson 1970) see 4.2.5.

4.2.4 Digestion - method

The method employed to digest the samples was based on that used by Avery and Bascombe (1974).

0.5g of sample was placed in a Tecator digestion tube then 1 salt mixture Kjeldahl tablet (Fisons) was added. Each tablet contains 1g Na_2SO_4 and 0.5g Selenium. 10ml of concentrated Sulphuric acid (H_2SO_4) was pipetted into the flask and the flask was swirled so that no particles adhered to the bottom of the tube. The samples were then heated overnight using the Tecator 1016 acid digestor with the autostep controller set to the following programme.

1 hour	at	50	°C	with	a	15	min	ramp
1 "	"	100C	"	"	"	10	"	"
1 "	"	150	"	"	"	10	"	"
1 "	"	200	"	"	"	10	"	"
1 "	"	250	"	"	"	10	"	"
1 "	"	300	"	"	"	10	"	"
3 hours	"	350	"	"	"	10	"	"

The Tecator 1016 acid digestor allows up to 40 samples to be boiled while any fumes produced are drawn off by an exhaust system. The heating block was controlled by a programmable autostep controller which allows the block to be brought up to the required temperature in stages. The use of heating blocks is described by Faithfull (1969).

The following morning the digested samples were made up to 100 ml with distilled water in a volumetric flask. The samples were then stored in acid washed and Decon 90-soaked screw top, glass bottles in a fridge. 3 sets of 40 digestions (including blanks) were carried out.

4.2.5 Nitrogen - principle

The Kjeldahl digestion converts organic nitrogen to ammonium nitrogen, which after dilution is in an approximately 5% acid solution. The classical method for estimating ammonium nitrogen is by distillation. There are some colorimetric methods available but they are not considered to be as accurate as distillation (Allen 1974). Use of an ammonia electrode was considered (Powers, Van Gent and Townsend 1981) but rejected on the grounds that several distillations would have to be performed to calibrate the electrode anyway and that the electrode which was available was unreliable.

During the distillation process free ammonia is liberated from the diluted digest by steam distillation in the presence of excess alkali (sodium hydroxide). The distillate is collected in a receiver containing excess boric acid combined with an indicator solution. The ammonia is then titrated with standard hydrochloric acid up to a pH of 4.5. The standard apparatus used for the distillation is a Hoskins apparatus shown in fig 4.2.1 (Hoskins 1944).

4.2.6 Nitrogen - method

The Hoskins apparatus was prepared by passing steam through the system for several minutes. 8 mls of extract and 12 mls of distilled water (ie as if the original digest had been made up to 250 ml) were added to the inner chamber of the apparatus via the tap funnel (A). The tap funnel was rinsed with distilled water. A boric acid/indicator mixture

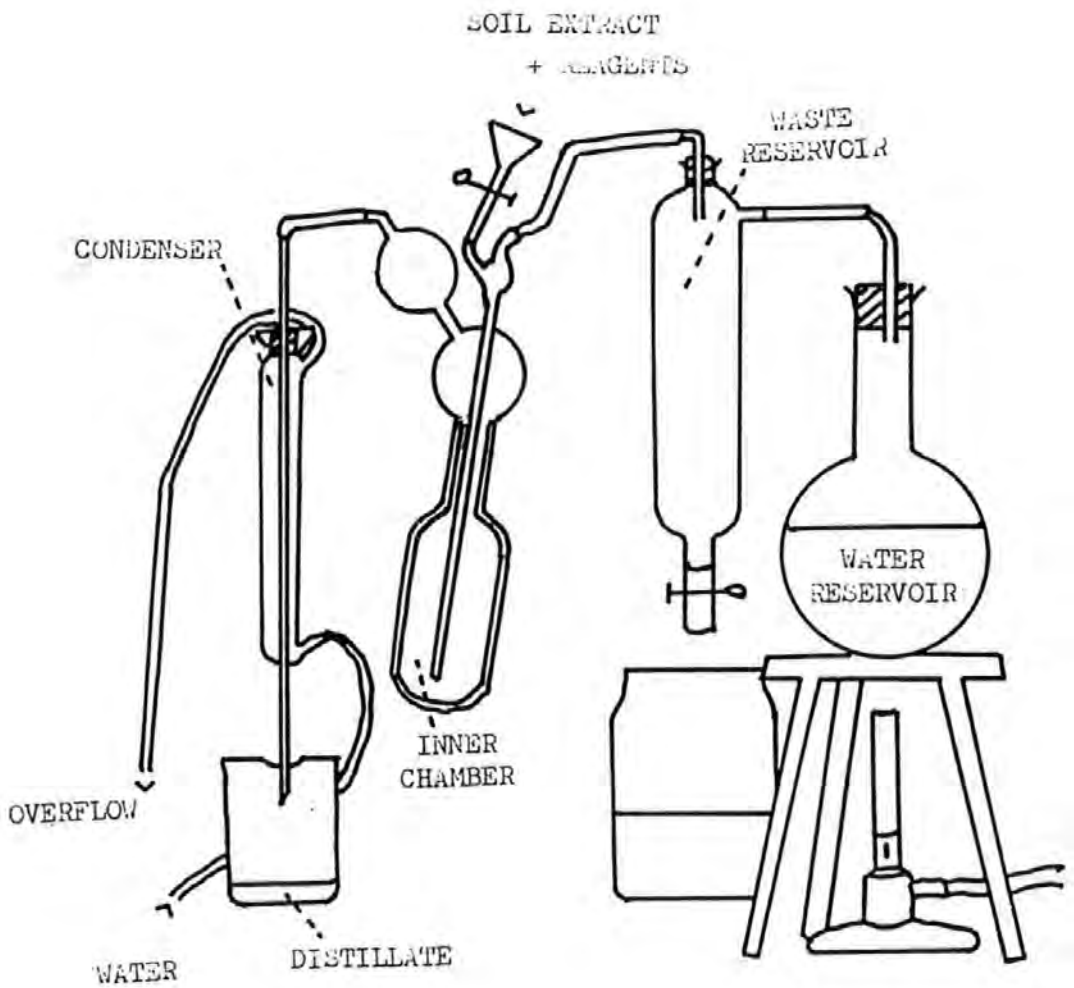


Fig 4.2.1 HOSKINS APPARATUS

was prepared by adding 25 ml of mixed indicator to 1 litre of 2% H_3BO_3. The mixed indicator was prepared by combining 0.1g methyl red and 0.2g bromo-cresol green and dissolving in 250 ml ethanol. This was adjusted to a greyish mid-colour with dilute NaOH or HCl (Ma and Zuazaga 1942).

5 ml of boric acid/indicator solution was added to a 50ml flask and placed in position to receive distillate, with the tip of the condenser just below the liquid surface. 5ml of 10_N NaOH was added to the tap funnel and gently let into the chamber followed by a rinsing with distilled water. A small amount of liquid was left in the funnel to act as an air lock. 10ml of distillate was collected and titrated against 0.01N HCl, the colour changing from green through colourless to a pink end point. The inner chamber was emptied and rinsed after each sample. Blanks were carried out using 20ml of distilled water.

$$\%N = \frac{(\text{ml HCl for sample} - \text{ml for blank}) \times 0.175}{\text{sample mass (g)}}$$

4.2.7 Phosphorus - principle

Although titration and gravimetric methods are available, colorimetry is almost always used for determination of phosphorus. Two chromogenic systems are favoured, molybdenum blue and the yellow vanadomolybdate method. The molybdenum blue method is the most sensitive (Allen 1974).

In a suitably acidified solution phosphate reacts with molybdate to form molybdo-phosphoric acid which is then reduced to the intensely coloured molybdenum blue complex and determined spectrophotometrically. The details of the chemical reaction are described in Jackson (1958). Many reducing agents have been recommended but in this case ascorbic acid was used.

The spectrophotometer measures the concentration of an element within a sample by measuring the transmittance or absorbance of light through the sample. The intensity of the colour which develops in the presence of the specific element indicates the amount of that element which is present. This is compared to a calibration curve which is drawn from known standards.

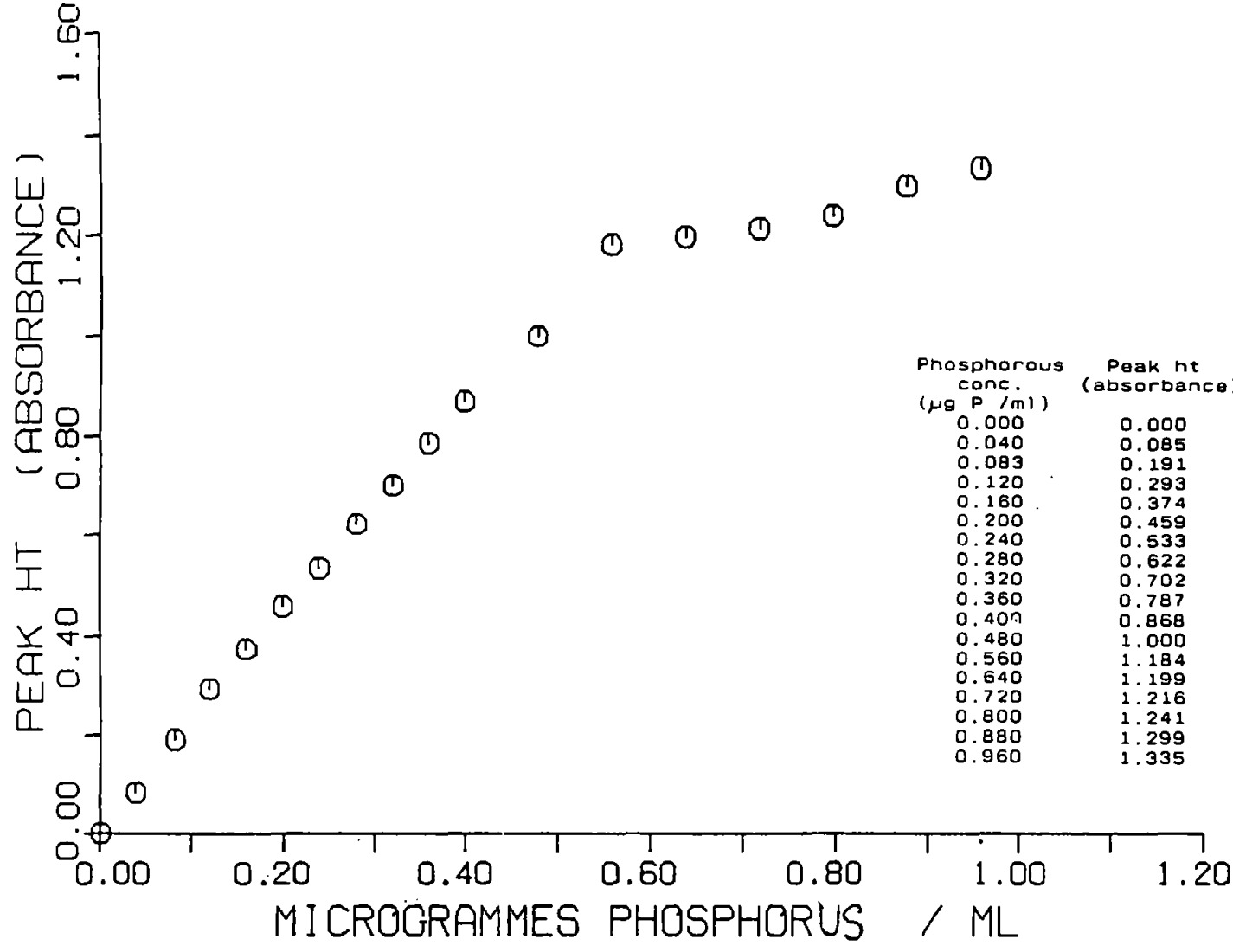
When light is passed through a solution the ions become excited and a particular wavelength is emitted. The peak of an element's scan is usually peculiar to that element eg for phosphorus the peak is at 880 nm. A small amount of sample is placed in a glass cell or cuvette alongside a cell containing distilled water. A beam of light is passed through both cells and the absorbance or transmittance compared, then registered on a scale.

4.2.8 Phosphorus - method

The method which was used on the samples is taken from Mackereth, Heron and Talling (1978) which was based on a modified Murphy and Riley (1962) method.

All glassware was acid washed and soaked in Decon 90 before use. A standard solution was prepared by dissolving a 4.390g of potassium dihydrogen phosphate (KH_2PO_4) in distilled water and making up to 1 litre. 1 ml of this solution contained 1mg PO_4-P. A working standard solution was prepared daily by diluting this solution x 100 so that 1ml contained 1µg P. From this solution a rough calibration was obtained. At the end of the analysis, when the range of concentrations present in the sample was known, a more accurate calibration (Fig 4.2.2) was determined.

Fig 4.2.2 PHOSPHORUS CALIBRATION CURVE



Phosphorous conc. (µg P /ml)	Peak ht (absorbance)
0.000	0.000
0.040	0.085
0.083	0.191
0.120	0.293
0.160	0.374
0.200	0.459
0.240	0.533
0.280	0.622
0.320	0.702
0.360	0.787
0.400	0.868
0.480	1.000
0.560	1.184
0.640	1.199
0.720	1.216
0.800	1.241
0.880	1.299
0.960	1.335

5ml of sample was pipetted into a 250 ml flask and 0.5ml of phenolphthalein indicator, was added. 2N Sodium hydroxide solution was added until a pink colour appeared, then this colour was discharged with 1% sulphuric acid solution. 0.5N sodium hydroxide solution was carefully added until the pink colour was just restored. This neutralisation step ensured that the pH of the solution was not too low to interfere with the subsequent colour development. The acidity in this method must be carefully controlled since at low acidity, the molybdate itself will give a colour in the absence of phosphate (Allen 1974).

8mls of working reagent was added to each flask using an automatic dispenser. The working reagent consisted of 5 parts 14% sulphuric acid (a), 2 parts of ammonium molybdate solution (b) (30g in 800 ml water), 2 parts of ascorbic acid solution (c) (5.4g in 100 ml water) and 1 part potassium antimonyl tartrate solution (d) (0.68g in 200 ml water). a and b were mixed first, then c was added and mixed, followed by d. This reagent was mixed daily since the absorbic acid deteriorates in the presence of light. The solution was made up to 250ml with distilled water and left for exactly 10 minutes for the colour to develop. The absorbance of the solution at 800 nm was measured in a 4cm cell against a blank prepared from distilled water. The instrument used was a Pye SP 8-100 ultra violet spectrophotometer. Absorbance readings were compared to the calibration graph which was prepared using dilutions of the standard solution. Blanks were subtracted where necessary.

$$\text{Concn of sample} = \frac{(C \times 100)}{\text{wt of sample in g}} \quad g^{-1}$$

Where C= mg of P obtained from graph

4.2.9 Potassium - principle

The intense emission line given by potassium in a flame enables very low concentrations to be determined by flame photometry - the arc line for potassium being 766 nm. Residual acids occasionally have a slight effect and for this reason, blanks which had been digested in a similar way to samples were used.

The flame photometer operates by taking up a small amount of sample into the system by means of a vacuum pump. This minute amount of sample is vapourised and burned in a natural gas flame within the instrument. The light emitted from the flame passes through a specific filter (appropriate for potassium) and onto a photoelectric cell. Depending on the intensity of the colour a reading can be taken from the scale. As with the spectrophotometer a calibration must be carried out using known standards.

4.2.10 Potassium - method

A stock solution of 1000 ppm was prepared by dissolving 1.9068g dry KCl in water and making up to 1 litre. Working standards were diluted to produce a range between 100 ppm K-0 ppm K. Where samples were over this range the sample solution was diluted. The K filter was selected on the Corning 400 flame photometer and the gas pressure and slit width were adjusted.

A calibration curve was prepared from the range of standards by setting the top standard to a suitable large scale deflection and the 0 ppm standard to zero. The sample solutions were aspirated into the flame and the atomiser and burner were flushed with distilled water in between samples. Blank determinations were subtracted where necessary.

$$\%K = \frac{(C\ ppm) \times soln\ vol\ (ml)}{104 \times sample\ wt}$$

If C = ppm K obtained from graph

4.3 Results

4.3.1 Data analysis

The normality of the data on nutrient concentrations was tested using the normal probability plot correlation coefficient (Ryan et al 1982). The values of r which were obtained all lay within the $P<0.05$ limits except the values for nitrogen concentration in the reproductive parts of the flowerers. A log transformation was applied and the transformed data were used in any subsequent analysis of variance. Analyses of variance were carried out using GENSTAT (Alvey, Galwey and Lane 1982) which could take account of the Youden square design. All other statistical analysis was carried out using Minitab (Ryan et al 1976).

4.3.2 The effect of plant material on nutrient concentrations

The concentrations of N, P and K in the Taraxacum plants were very different (Table 4.3.1). When the concentrations in the 3 types of plant material were averaged potassium had the highest mean concentration of 18.6 mg/g, followed by nitrogen at 12 mg/g and lastly phosphorus 0.079 mg/g. The mean concentrations of nutrients in the 3 types of plant material (1. non-flowering plants - NFs; 2. vegetative parts of flowering plants - VF's; and 3. reproductive parts of flowerers - RFs) under the 7 different treatments are shown in fig 4.3.1. The mean concentrations of N present in the 3 types of plant material were not significantly different (Table 4.3.1). However both P and K were present in higher concentrations in the RFs than in the VFs. Moreover the concentration of P and K in the reproductive tissue was significantly higher than in the tissue of the non-flowering plants.

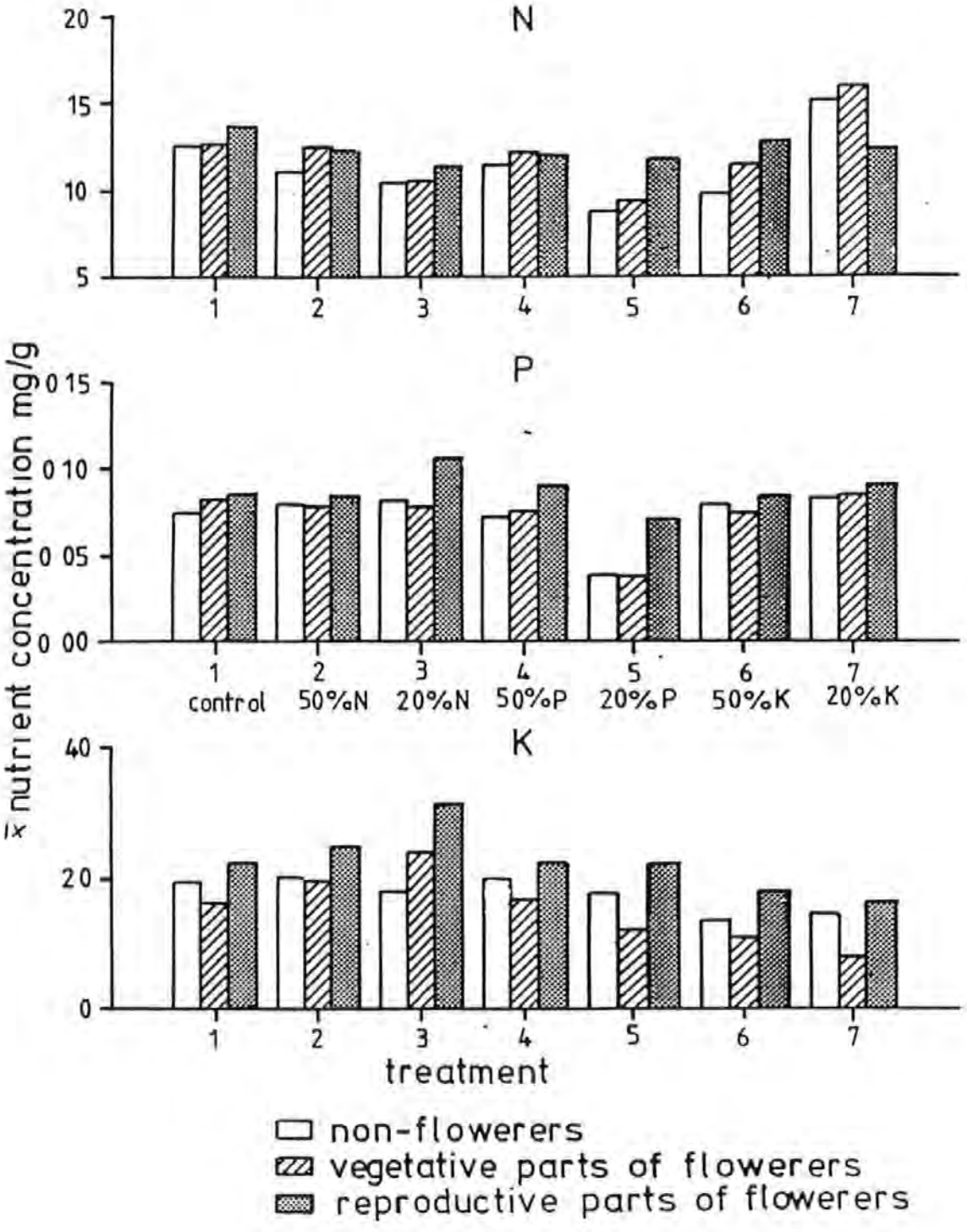
Mean concentrations of N, P and K and 1-tests comparing non-flowerers and vegetative+reproductive parts of flowerers

	mean concn mg/g			seed enrichment ratio
Nitrogen				
Non-flowerers	11.32	- T = 1.14 NS x	T = 1.70 NS x	1.01
Veg flowerers	12.29	- T = 0.21 NS x		
Rep flowerers	12.44			
Phosphorus				
Non-flowerers	0.073	- T = 0.42 NS	T = -3.49 P = 0.0010 ***	1.183
Veg flowerers	0.07504	T = -2.92 P = 0.0052 **		
Rep flowerers	0.08878			
Potassium				
Non flowerers	17.68	T = 1.56 NS x	T = 4.34 P = 0.0001	1.45
Veg flowerers	15.56	T = 4.67 P = 0.0000 ***		
Rep flowerers	22.68			

SD ** $P < 0.01$ *** $P < 0.001$

x = sig using anova

Fig 4.3.1 Nutrient Concentrations in Taraxacum



A two-way anova which took account of both the effect of treatment and the effect of type of plant material confirmed that the type of plant material which had been analysed had a significant effect on the concentrations of nutrients. This effect was least pronounced for N *(VR = 3.94) and most pronounced K (VR = 77.46). For both N and P the concentrations in the NFs were on average lower than the concentrations in the VFs but for K the mean concentration in the non-flowerers was higher than in the VFs.

The mean concentration of all 3 nutrients was higher in the reproductive tissue. This higher concentration can be expressed as the 'seed enrichment ratio' (Benzing and Davidson 1979) or the ratio of the concentration in the reproductive parts to the concentration in the vegetative parts (Table 4.3.1).

4.3.3 Nutrient concentration - the effect of treatment

The two-way anovas in Table 4.3.2 show that treatment had a significant effect on P and especially K concentration, but it is evident from Fig 4.3.1 that the effect of treatment was not consistent. There was also a significant interaction between treatment and the type of plant material which was analysed in the case of K concentration. To explore these relationships further, separate one way analyses of variance were carried out on each type of plant material. The variance ratios are in Table 4.3.3 and the anova tables with standard error of differences in Appendix 2. The means obtained from the two-way anova were plotted graphically (figs 4.3.2-4.3.4) and where significant ($P<0.05$)

* VR = variance ratio

Two-way anovas on concentration and type of plant material

Nitrogen

Source	VR	df	Prob
Treatment	0.780	6/12	NS
Type of material	3.945	2/40	0.05
Treat type	1.815	12/40	NS

Phosphorus

Source	VR	df	Prob
Treatment	6.649	6/12	0.001
Type	16.734	2/40	0.001
Treat type	1.527	12/40	NS

Potassium

Source	VR	df	Prob
Treat	12.372	6/12	0.001
Type	77.458	2/40	0.001
Treat type	4.427	12/40	0.001

Table 4.3.3

Summary of variance ratios for nutrient analysis

Effect of treatment on:		VR	DF	PROB
Non-flowering N concn		2.822	6/11 (1)	NS
Non-flowering P concn		28.269	6/11 (1)	P<0.001
Non-flowering K concn		2.66	6/11 (1)	NS
Flowering veg parts	N concn	1.51	6/11 (1)	NS
" " "	P "	5.083	6/11 (1)	P<0.01
" " "	K "	8.974	6/11 (1)	P<0.01
Flowering rep parts	N concn	0.385	6/11 (1)	NS
" " "	P "	1.435	6/11 (1)	NS
" " "	K "	21.789	6/11 (1)	P<0.001
Total non-flowering	N	6.771	6/12	P<0.01
" "	P	32.306	6/12	P<0.001
" "	K	14.684	6/12	P<0.001
Total flowering veg	N	12.692	6/11 (1)	P<0.001
" "	P	7.863	6/11 (1)	P<0.01
" "	K	4.168	6/11 (1)	P<0.05
Total flowering rep	N	4.864	6/11 (1)	P<0.05
" "	P	3.679	6/11 (1)	P<0.05
	K	5.444	6/11 (1)	P<0.01
Total plant	N	9.887	6/11 (1)	P<0.001
	P	5.418	6/11 (1)	P<0.01
	K	9.119	6/11 (1)	P<0.001
RA in terms of	N	1.143	6/11 (1)	NS
untransformed	P	1.854	6/11 (1)	NS
	K	2.755	6/11 (1)	NS
	Biomass	2.868	6/12	NS
RA in terms of	N	1.154	6/11 (1)	NS
Asin trans	P	1.908	6/11 (1)	NS
	K	2.82	6/11 (1)	NS just
	Biomass	2.9	6/12	NS just (3.00 P<0.05
Two way RA treat v RE method				
	Treat	2.117	6/12	NS
	RE method	36.375	3/60	P<0.001
Treat	RE method	2.874	18/60	P<0.001

Table 4.3.4

Correlation coefficients of different methods of measuring RA

	B	K	P
K	0.842		
P	0.644	0.664	
N	0.762	0.753	0.769

All values P<0.001

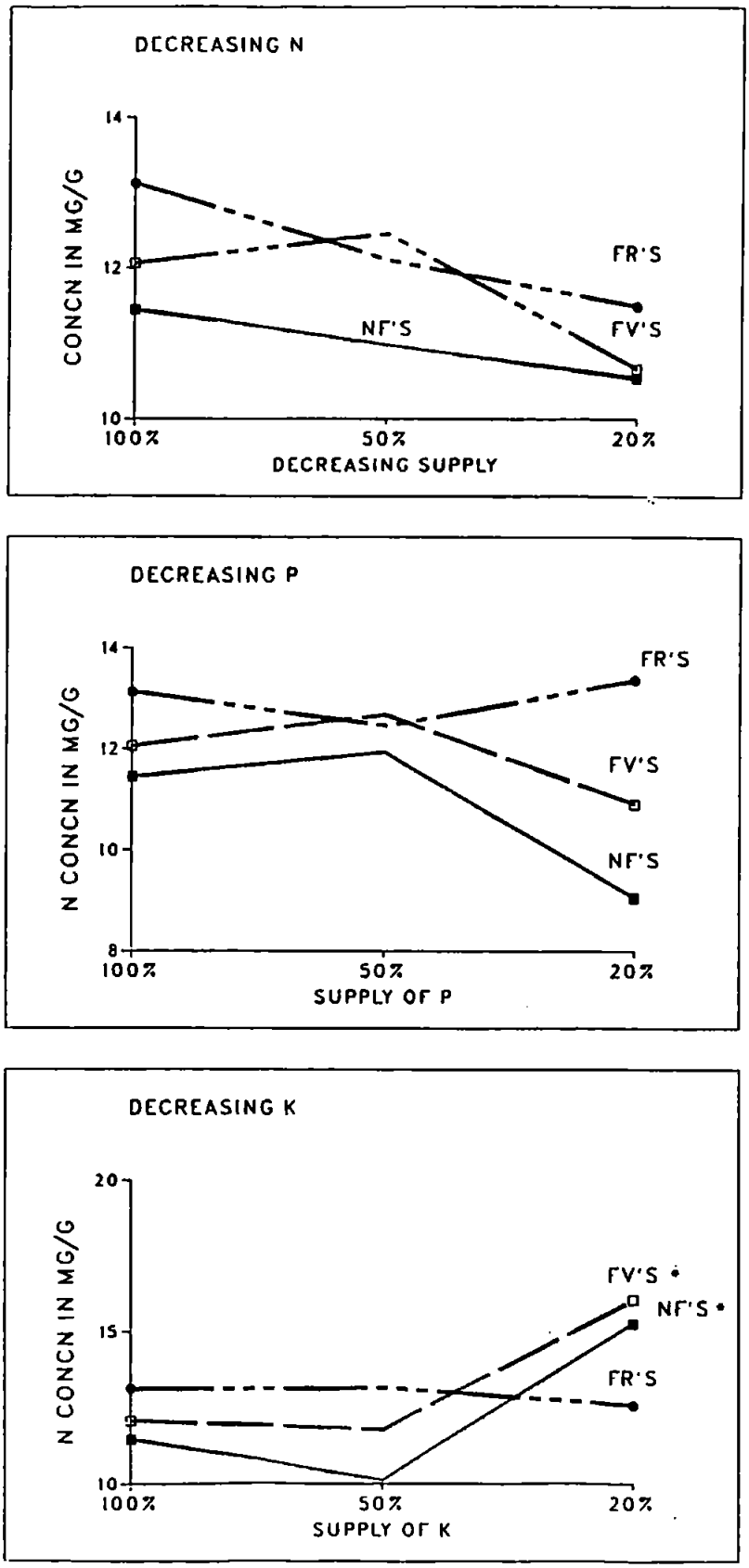
differences between the nutrient deficient means and the complete nutrient solution mean occurredit is indicated on the graphs.

The way in which the concentration of N varies with decreasing nutrient supply is shown in fig 4.3.2. The anovas show that there was no significant treatment effect on N concentration but nevertheless some general trends can be observed from the graphs. Tissue N concentration generally declined with decreasing supply of both N and P but this effect was not statistically significant. In contrast, the concentration of N in the NFs and VFs increased sharply in the 20%k treatment. The concentration of N in the reproductive tissue was generally more constant than in the vegetative tissue.

There was a highly significant effect of treatment on P concentration ($P<0.001$) which is most marked in the NFs ($P<0.001$) and the VFs ($P<0.01$) see fig 4.3.3. Decreasing N and K supply caused the concentrations of P in the non-flowerers to increase significantly, whereas a reduction in the P supply resulted in a significant drop in P concentration in both the NFs and VFs. The concentration of P in the reproductive tissues was again much less variable although there was an indication of a slight increase in concentration at the lowest level of N supply.

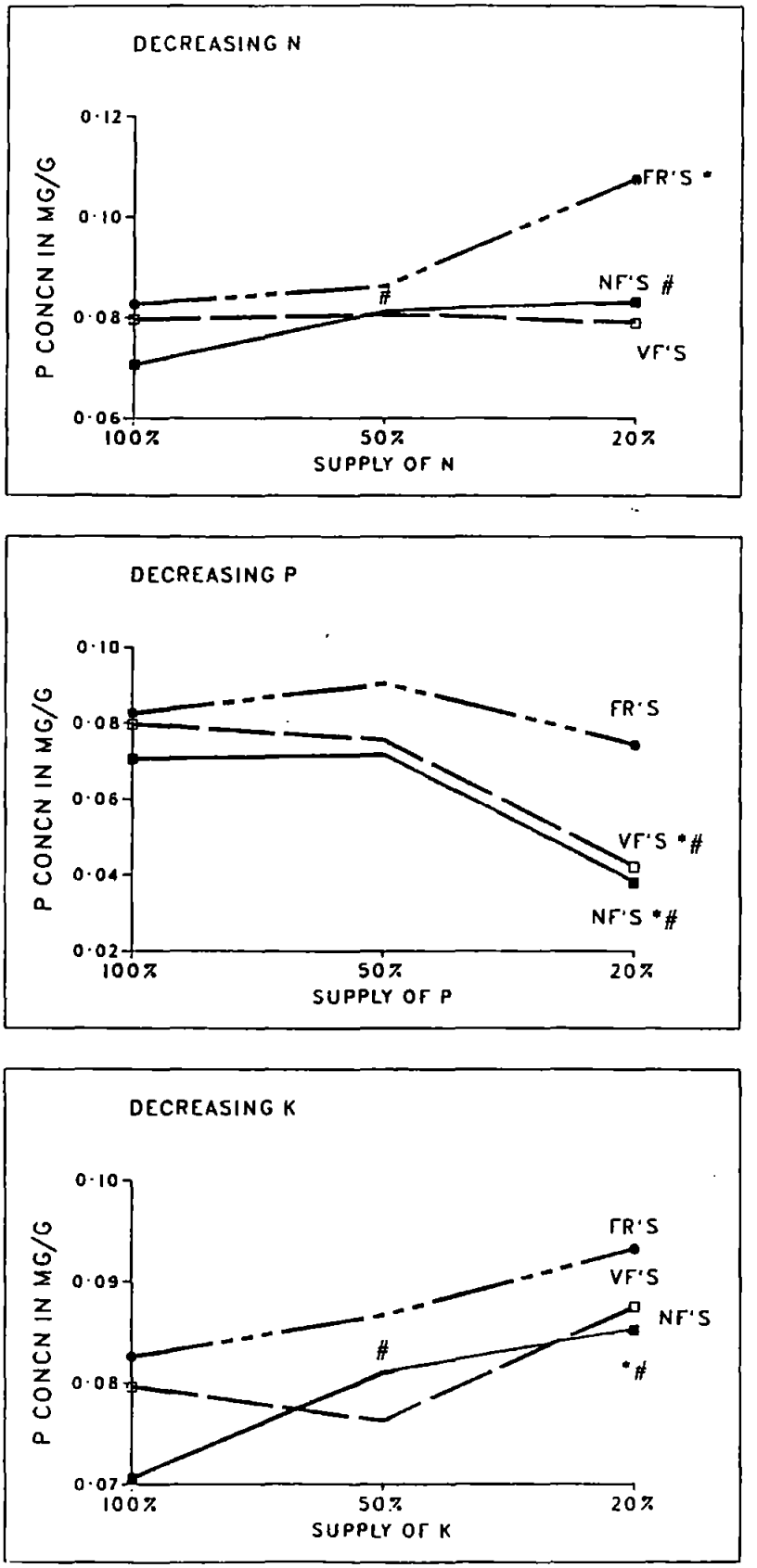
The concentration of K in the Taraxacum plants showed the most marked and consistent response to treatment (Fig 4.3.4). This effect was most marked in the FRs ($P<0.001$) and the FVs ($P<001$). K concentration in all 3 types of plant material, declined with decreasing supply of K. However K concentration in the RFs and VFs rose significantly with decreasing N supply. P supply had no obvious effect on K concentration.

Fig 4.3.2 THE EFFECT OF DECREASING NUTRIENT SUPPLY ON N CONCENTRATION IN THE NON-FLOWERERS (NF'S), VEGETATIVE PARTS (VF'S) AND REPRODUCTIVE PARTS (RF'S) OF THE FLOWERERS



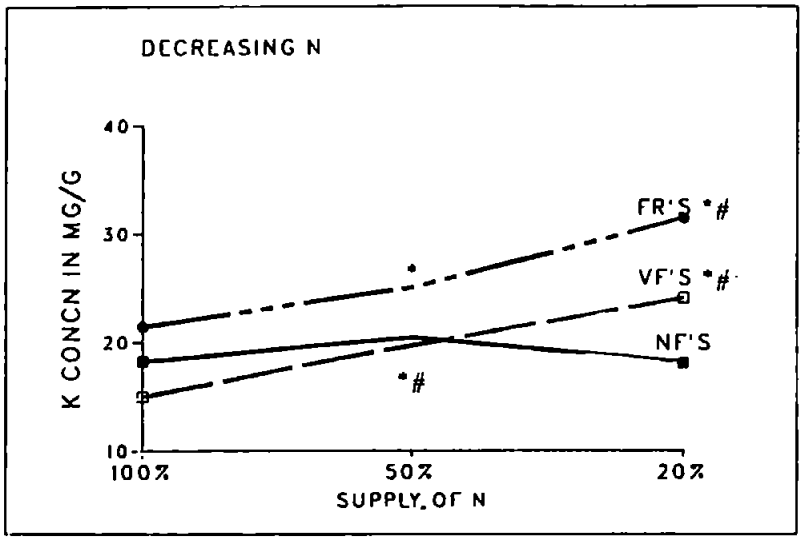
* = p 0.05 of sig diff from 100% value (twoway)

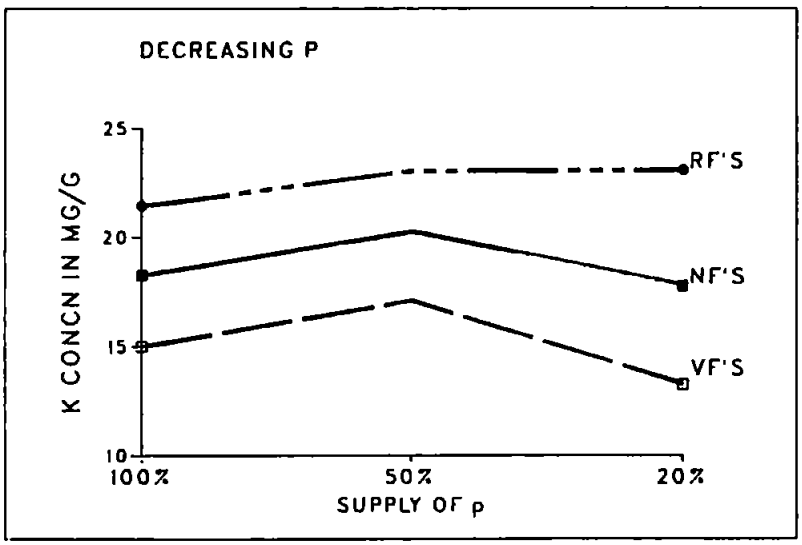
Fig 4.3.3 THE EFFECT OF DECREASING NUTRIENT SUPPLY ON P CONCENTRATION IN THE NON-FLOWERERS (NF'S), VEGETATIVE PARTS (VF'S) AND REPRODUCTIVE PARTS (RF'S) OF THE FLOWERERS

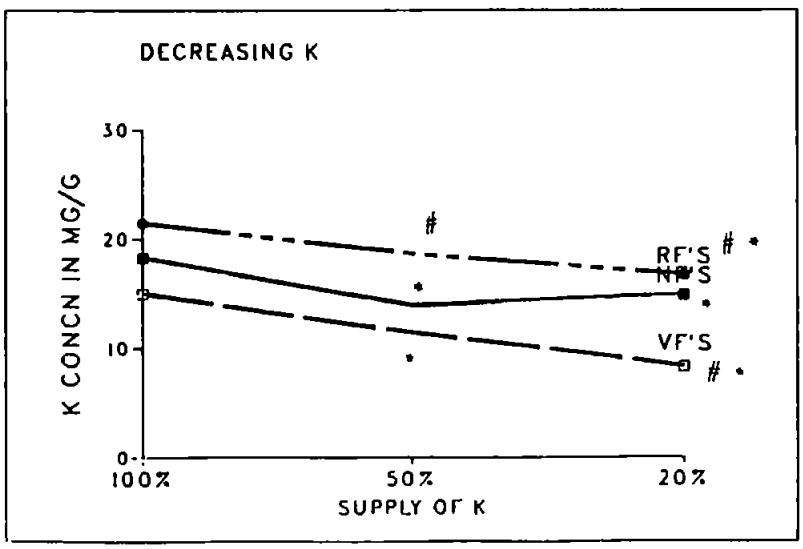


* = p 0.05 of sig diff from 100% value (twoway)
# = P 0.05 of sig diff from 100% value (oneway)

Fig 4.3.4 THE EFFECT OF DECREASING NUTRIENT SUPPLY ON K CONCENTRATION IN THE NON-FLOWERERS (NF'S), VEGETATIVE PARTS (VF'S) AND REPRODUCTIVE PARTS (RF'S) OF THE FLOWERERS







* = P 0.05 OF SIG DIFF FROM 100% VALUE (TWOWAY)
# = P 0.05 OF SIG DIFF FROM 100% VALUE (ONEWAY)

4.3.4 The total amount of NPK

The total amount of NPK per tray was determined by multiplying the mean dry weight per tray and the mean nutrient concentration per tray. Consequently the pattern of total nutrient content (Fig 4.3.5) was very similar to the pattern of biomass allocation seen in Ch 3.3. One way anovas showed that treatment had a significant effect on the total amount of N, P and K in each type of plant material (Table 4.3.2). Using the standard error of the differences of the means it was possible to calculate which treatments had significantly different means from the control and these are indicated on Fig 4.3.5.

The low levels of all total nutrients in the 50% and 20%N treatments reflect the low plant weights achieved under these treatments. Significantly lower P amounts were found in the low P treatments and significantly lower K amounts were found in the low K treatment. Low total amounts of N were found in the vegetative parts of the flowerers in the low phosphorus treatments. The total amount of each nutrient in the reproductive structures was always significantly lower in the 20%N treatment (reflecting low plant weight) but only affected under the 50%N treatment in the case of N allocation. Total allocation of nutrients in reproductive structures was not significantly affected by any other treatments.

4.3.5 Reproduction allocation

Four different methods of measuring reproductive allocation were assessed - 1. Biomass allocation, 2. N allocation, 3. P allocation and 4. K allocation. Fig 4.3.6 shows the mean values for each different method under each treatment. The standard error of the difference of the overall means (regardless of treatment) of each method were obtained from the two way anova in Table 4.3.2 and this enabled

Fig 4.3.5 TOTAL AMOUNT OF NPK IN TARAXACUM PLANTS

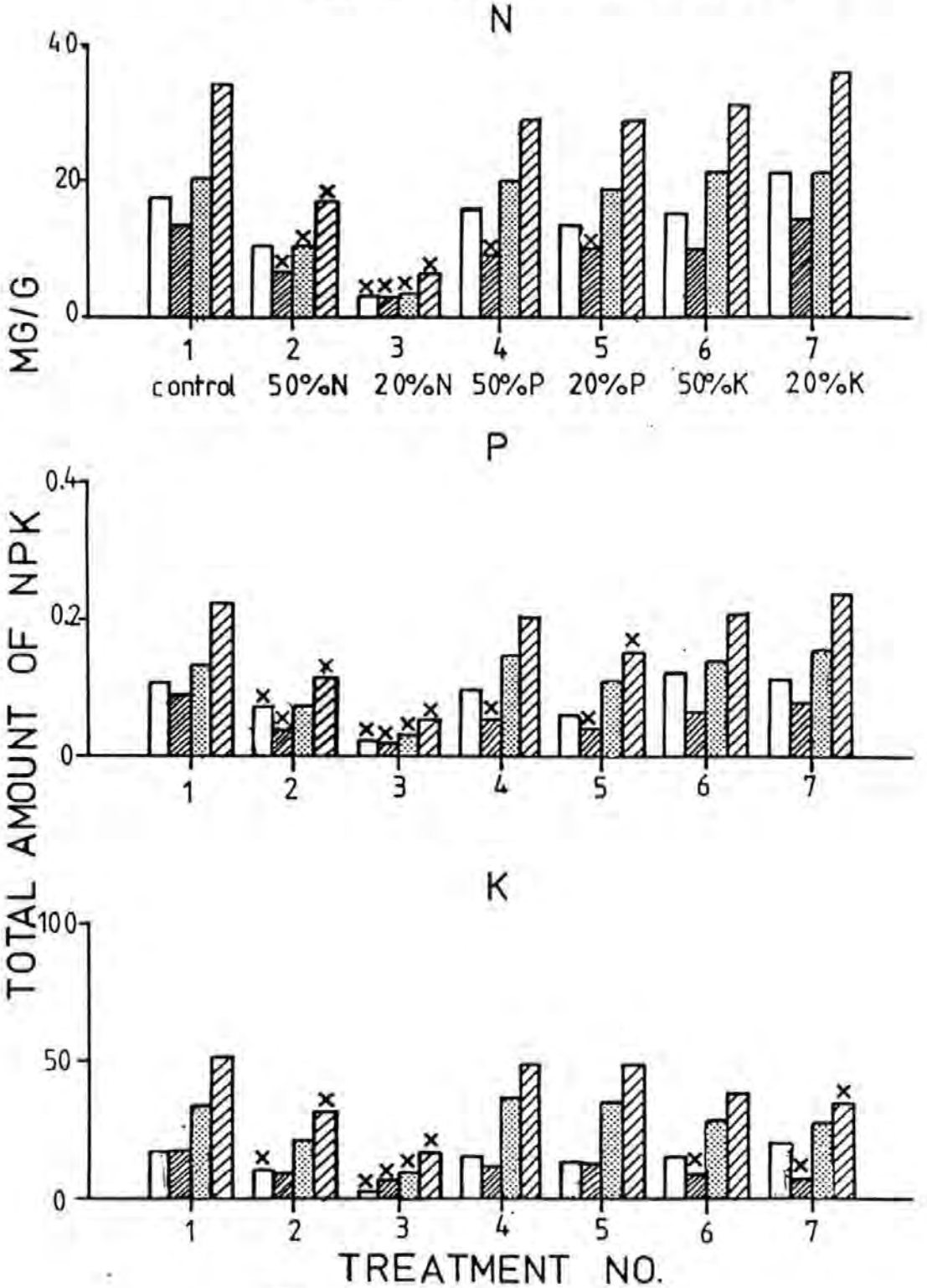
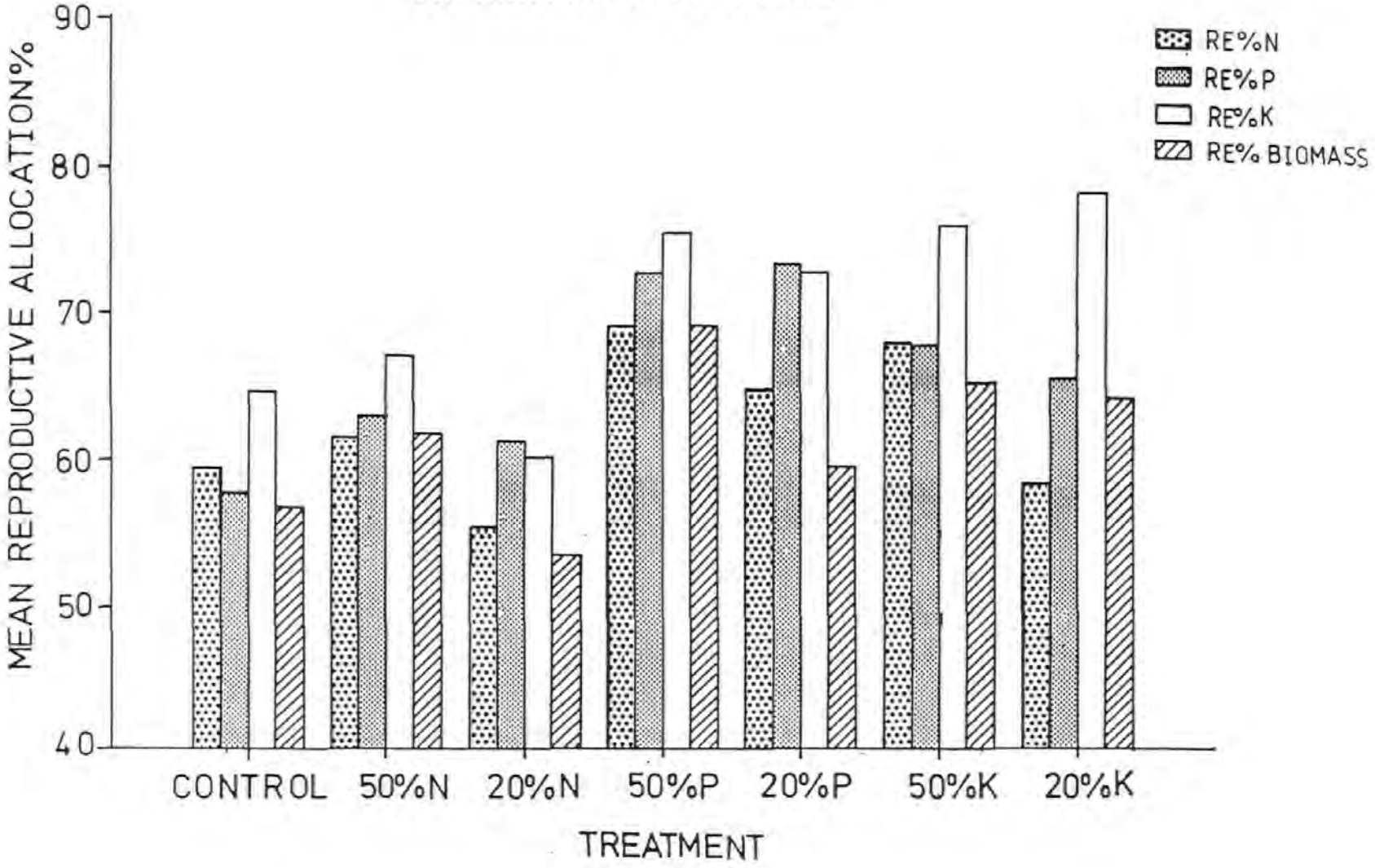


Fig 4.3.6 DIFFERENT TYPES OF REPRODUCTIVE ALLOCATION
TARAXACUM OFFICINALE



comparison of each method. K RA (71%) and P RA (66%) were significantly higher than Biomass RA (61%) and N RA (62%). Moreover K RA was significantly higher than P RA. The different methods were highly correlated with each other (Table 4.3.4).

Both one way anovas on each separate method and a two way anova on all methods showed that treatment had no significant effect on any of the ways of measuring RA. Nevertheless it is obvious from fig 4.3.6 and fig 4.3.7 that there seems to be a trend towards higher K allocation in the low K treatments and a higher P allocation in the lower P treatments. Nevertheless there were insufficient replicates to enable the null hypothesis to be rejected.

The two way anova showed that the methods of measuring RA were significantly different with a high variance ratio of 36.37. There was a significant interaction between method of measuring RA and treatment which was probably attributable to the slightly increasing K and P RA with decreasing K and P supply. To test the amount of variability between methods of measuring RA within each treatment one way anovas were carried out on separate treatments (see Table 4.3.5).

It is evident from this table that whereas in some conditions the methods of measuring RA did not differ significantly (eg the 100% nutrient solution). In others there was a significant effect (eg the 20%K treatment).

Fig 4.3.7 DIFFERENT METHODS OF MEASURING RA

THE EFFECT OF DECREASING NUTRIENT SUPPLY

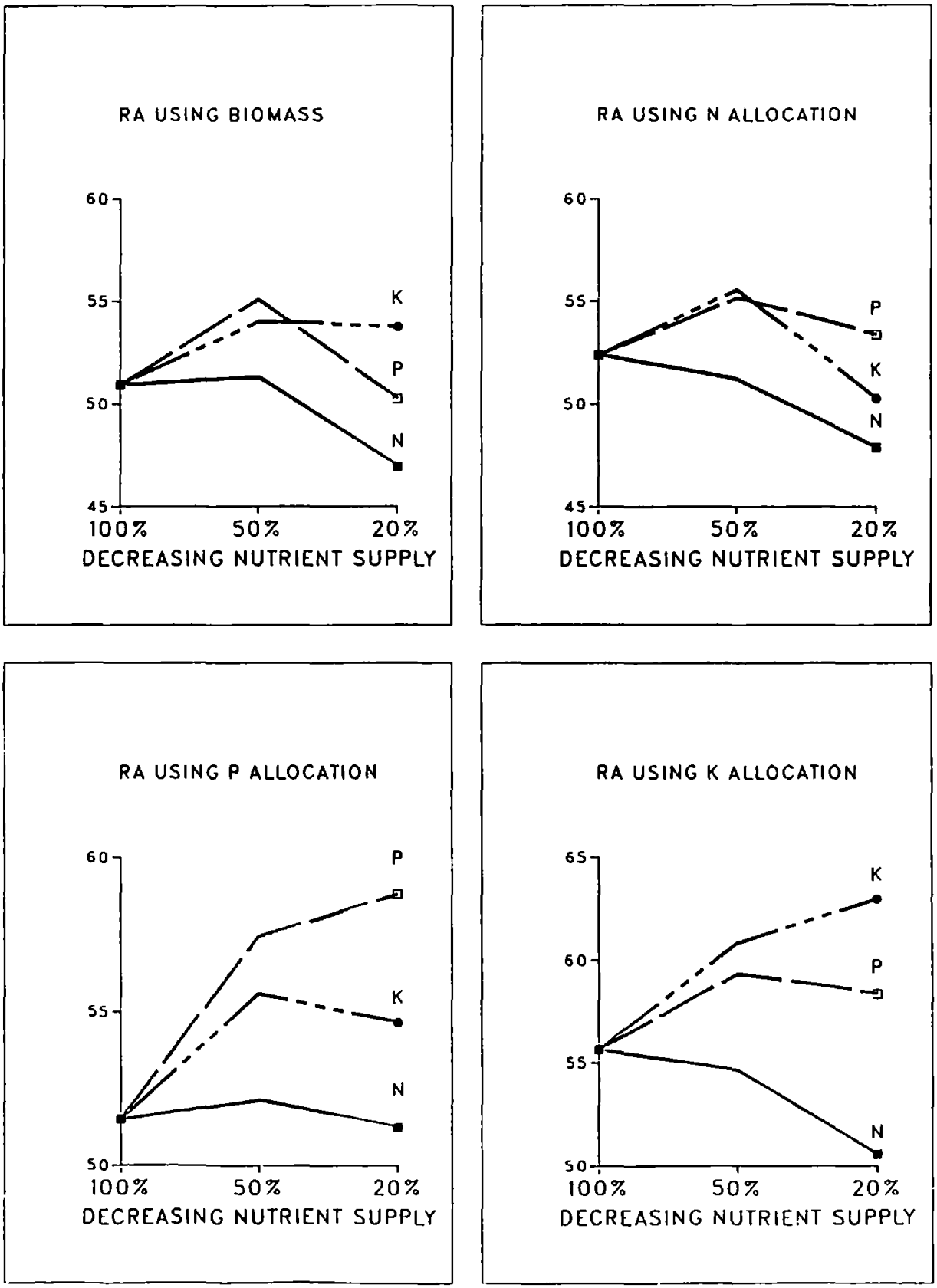


Table 4.3.5

The effect of different RA methods within each treatment

	VR	df	Prob
100% N P K	3.138	3/9	NS
50% N	4.118	3/9	P<0.05
20% N	3.143	3/9	NS
50% P	2.717	3/9	NS
20% P	8.625	3/9	P<0.01
50% K	5.153	3/9	P<0.05
20% K	38.891	3/9	P<0.001

4.4 Discussion

4.4.1 Concentrations

The mean concentrations of K (18.6 mg/g) and N (12 mg/g) in the tissue of the Taraxacum plants fall well within the ranges quoted in Epstein (1972). Ranges of 8.7-20.0 mg/g for N and 5.2 - 47.4 mg/g for K are given for 13 species from various environments. The concentration of P however (0.08 mg/g) is lower than the given range - 0.9 - 3.7 mg/g. A P concentration of 0.02 - 0.05 mg/g was found in the heartwood of Pinus rigida trees (Woodwell et al 1975) but the flowers contained 2.4 mg/g. A perchloric acid digestion is normally recommended for P determination (Allen 1974) and the use of the Kjeldahl digestion on the plant material may have resulted in low P recovery rates. Absolute concentrations however are not necessary when considering the proportional allocation of P. A higher concentration of K to N seems to be quite common in certain species eg Aster macrophyllus, Coreopsis palamata, Sanguinaria canadensis (Gerloff et al 1966), Aster acuminatus, Solidago macrophylla (Siccama et al 1970).

Numerous studies have found higher concentrations of N, P and K in the reproductive structures of a variety of mesophytic herbs and arid region shrubs eg Pate and Flinn 1973, Van Andel and Vera 1977, Benzing and Davidson 1979. Lovett-Doust 1980, Williams and Bell 1981, Ernst 1983, Fenner 1985. One of the easiest ways of comparing these values is to look at the seed enrichment ratios. (Table 4.4.1)

The SER values obtained for Taraxacum are much lower than those obtained by Fenner (1985) and Benzing and Davidson (1979). This difference must be partly attributable to the analysis of all reproductive structures in Taraxacum whereas Benzing and Davidson (1979) and Fenner (1985) analysed seeds for mineral content.

Table 4.4.1

Seed Enrichment Ratios

	N	P	K
Taraxacum	1.01	1.183	1.45
Senecio sylvaticus Seeds no roots (Fenner 1985)	2.7	5.74	0.35
T. circinnata Seeds includes roots (Benzing and Davidson (1979)	2.53-3.23	1.98-2.68	1.09-1.7
Lupinus albus (fruits)	3.89	4.1	2.68
L. angustifolius includes roots (Hocking and Pate 1978)	2.29	2.1	1.4
Erodium glutinosum	0.993	2.127	0.542
Phleum arenarium includes fruits and leaves on soil (Ernst 1981, 1983)	2.155	0.622	0.252
Reproductive structures			
Plantago insularis	2.53		
(including root)	4.02		
Eschscholtzia glyptosperma	1.47		
includes roots	2.27		
(Williams and Bell 1981?			

The values obtained by Williams and Bell (1981) for N concentration which considered all reproductive structures are more comparable. Moreover it is evident from the Williams and Bell (1981) figures that the inclusion of root biomass as part of the 'vegetative' fraction tended to increase the SER. Both Benzing and Davidson (1979) and Hocking and Pate (1978) included root biomass in their estimates. The wide range of SERs for N, P and K in Table 4.4.1 indicate that there is much interspecific variation in the reproductive concentration of nutrients.

The high SER of K in Taraxacum is also probably due to the inclusion of the scape and pappus in the reproductive fraction. Ernst (1983) found that N and P were concentrated in the caryopses of Phleum arenarium whereas K was concentrated in the associated reproductive organs such as the spikelets and fruit stalks. In Senecio sylvaticus grown on unamended soil (Van Andel and Vera 1977) 35.7% of the total K allocation was found in the receptacles and bracts, 5.5% in the pappus and 11% in the fruits. In Chamaenerion angustifolium the flowers and capsules contained 21% of the total K, the pappus 0.6% and the seeds 0.7%. In contrast, the allocation of N was more constant - 3.6% - 4.7% for each part. A possible explanation for the high concentration of K in the scape of the Taraxacum plants is that K has an important role as an osmotic regulator (Sutcliffe and Baker 1974). High K concentrations seem to result in higher osmotic pressure in the seive tubes which improved the flow rates and hence turgor pressure (Mengel and Haeder 1977). This is likely to be particularly important in Taraxacum officinale where the scape is hollow and fleshy with abundant, milky latex.

The mean concentration of N and P in non-flowering plants generally remained lower than the concentration in the vegetative parts of the flowering plants. This would suggest that insufficient quantities of these elements had been accumulated to enable flowering to proceed. In contrast however the concentration of K in the non-flowering plants was always significantly higher than in the vegetative parts of the flowering plants. Hocking and Pate (1978) found that the concentration of K in plants of Lupinus albus just before fruiting (8.8 mg/g) was more than twice that in the non-reproductive parts at plant maturity (4.4 mg/g) whereas the concentration in the reproductive parts (11.8 mg/g) at plant maturity was higher. Similarly Lovett-Doust (1980) found that plants of Smyrnium olusatrum which persisted in a vegetative condition and failed to flower maintained higher concentrations in the vegetative organs.

It seems that certain plants can internally transfer mineral nutrients from one location (eg the above ground vegetative) parts to another (eg the reproductive parts) depending on the sites of greatest meristematic activity. This property of efficient internal translocation is not only related to mineral deficient habitats (Harper 1977) but is also a physiological feature of many ruderal species (Chapin 1980).

4.4.2 The effect of mineral deficiency on mineral concentrations

A reduction in supply of a specific nutrient was always accompanied by a decrease in that nutrient's concentration in the vegetative tissue of both flowerers and non-flowerers. This was also the case in the reproductive tissue for K concentration. A similar trend was observed in the reproductive tissue for N and P concentration but it was not significant.

This correlation of nutrient supply with nutrient concentration has been well documented for crop plants eg Williams 1955, 1961, Sadhu et al 1975 a + b, Chapin 1980 and tissue analysis is used as an indicator of deficiencies in crop plants (Ulrich and Hills 1967). In crop plants reduced nutrient availability usually result in an increased root: shoot ratio (Chapin 1980). However, the results of the increased root: shoot ratio and increased root absorption capacity usually don't fully compensate for the reduced nutrient availability. Consequently the concentration and total quantity of nutrients absorbed generally decrease with decreasing availability (Ulrich and Hills 1967). In general these changes in concentration tend to be greater in the leaves than other organs (Goodall and Gregory 1947). This response may be less evident in wild plants (Chapin 1980) because of their greater variation in growth rate, less growth response to nutrient availability and smaller range in tissue nutrient concentrations.

Changes in the vegetative concentration of N in response to N supply have been noted in Tundra species (Shaver and Chapin 1980), Desert Winter Annuals (Williams and Bell 1981), Senecio vulgaris (Fenner 1985), Tillandsia circinnata Benzing and Davidson (1979) Dactylis glomerata (competition experiment) Lambert (1968) and Van Andel and Vera 1977. Similar responses to phosphorous supply were found for Tundra species (Shaver and Chapin 1980), Eriophorum vaginatum (Tamm 1954), Fenner (1985), Benzing and Davidson (1979), Van Andel and Vera (1977), Lovett Doust (1980) and Ernst (1981) and K supply by Fenner (1985), Van Andel and Vera (1977), Goodman and Perkins (1968), Benzing and Davidson (1979). However many of these studies use general NPK fertilizers eg Fenner (1985) Lovett Doust (1980) or compare plants grown in various dilutions of natural soil eg Ernst 1981, Van Andel and Vera (1977) or in natural conditions eg Benzing and Davidson (1979) so

it is difficult to assess whether the observed changes in concentration in specific nutrients are responses to that specific nutrients' availability or responses to availability of several nutrients.

The changes in concentration of nuitrients in the seed were much less marked. This maintenance of more stable nutrient concentrations in seed regardless of external nutrient supply has been noted by Fenner (1985) Lovett Doust (1980) and Benzing and Davidson (1979). However Fenner (1985) and Ernst (1981) did find a positive correlation between K supply and its concentration in seeds as is indicated in Taraxacum. Seed concentration has been shown to be affected by external nutrient supply in the case of N by Williams and Bell (1981), Ernst 1983 and Schweizer and Reis (1969) and in the case of P by Austin (1966). Benzing and Davidson (1979) did find some specimens of Tillandsia circinnata from very impoverished situations with low concentrations of N P and K.

The response of nutrient concentrations in Taraxacum to the availability of other nutrients was quite varied. One of the most significant changes in concentration associated with nutrient supply was an increase in K content in the flowering plants (both vegetative and reproductive) with decreasing N supply. This rise in concentration with decreasing N was also evident to a lesser degree in the case of P concentration. It is obvious (see Ch.3) that the supply of N restricted plant growth in both the 50% and 20%N treatments. The concentration of N in these plants was therefore below the level giving optimal growth or the 'critical concentration'. Under these circumstances the reduced growth caused by the N deficiency would enable an accumulation of all other nutrients in the plant tissue (Ulrich and Hills 1967). This effect may also have been exacerbated by

an antagonistic interaction between K+ and NH_4 + ions (Robson and Pitman 1983) and NO_3 and PO_4 (Bouma 1983). This may also explain the rise in N concentration at low levels of K supply and rise in P concentration in the non-flowerers at low K supplies. It has been known for some time that when more of a particular element is provided, its concentration in the plant increases whilst levels of other elements may fall eg P decreased from 3200 ppm to 1612 ppm in the ash of a grassland sward when an NPK fertiliser was used rather than just NP (Sutcliffe and Baker 1974). It is obvious therefore that the results of studies which look at nutrient allocation in response to general fertilisers should be treated with caution.

4.4.3 Total amounts of nutrients

The total quantity of a particular nutrient was strongly influenced by the quantity of biomass produced. There was a strong treatment effect on total quantities of nutrients which was largely attributable to the depression of biomass by the low N treatments. This effect was only overcome when treatment had had a marked effect on concentrations. Low P and K concentrations caused by low P and K availabilities resulted in significantly lower total quantities of P and K in the plants in these treatments. This effect of biomass on total nutrient contents was also noted by Twyford and Walmsley (1974) who found that the total nutrient contents in the organs of banana was related to the size of the plant organs. Lovett Doust (1980) argued that since the total amounts of P present in the different organs reflected in part the allocation of biomass, a more accurate picture of the processes involved during fruit formation could be obtained from consideration of nutrient concentrations.

Total nutrient content in reproductive parts was again much more constant (see also Fenner 1985) and Benzing and Davidson (1979) and only showed significant reductions under the 20% N treatment. The only exception to this was for N concentration which showed significantly lower total amounts in the seeds in both the 20% and 50%N treatments (see later discussion of RA).

4.4.4 Reproductive allocations

The proportions of N, P and K allocated to reproductive structures in Taraxacum are higher than most of the values reported in the available literature. See Table 4.4.2. However, many of these values included root biomass and only considered seed allocation in their estimation. Had this been undertaken for Taraxacum the values would have been lower. The mean N RA of 61% for all reproductive structures is most similar to values obtained by Williams and Bell (1981) for winter desert annuals. Smyrnium olusatrum (Lovett Doust 1980) had a P RA of 68-74% so 66% for Taraxacum is not excessively high. However the K RA of 71% is much higher than most values in Table 4.4.2 although 52.2% was recorded by Van Andel and Vera (1977) for all reproductive structures in Senecio sylvaticus. It is probable that the majority of the K RA in Taraxacum is attributable to large quantities of K in the scape as suggested earlier.

The different methods of measuring RA gave significantly different results. KRA and PRA were significantly higher than BRA and NRA. This concurs with the results of Abrahamson and Caswell (1982) who found that the patterns of allocation of biomass and nutrients in populations of Verbascum thapsus were different. They concluded that biomass allocation does not reflect nutrient allocation. Similarly Lovett-Doust (1980) and Van Andel and Vera (1977) found that the allocation patterns of P and N + P respectively were different from those of biomass.

RA (in whichever currency) was not significantly affected by treatment despite an apparent trend towards higher P and K allocation in deficient supplies of P and K. Van Andel and Vera's (1977) results comparing nutrient allocation in Senecio sylvaticus under different nutrient availabilities were similarly inconclusive.

However, Lovett-Doust (1980) found that allocation of P to reproductive structures was reduced in a low nutrient treatment and a higher fraction was found in the tuberous root system of Smyrnium olusatrum. In contrast Fenner (in press) found that with increasing nutrient stress a higher proportion of the total quantity of N P and K was allocated to seeds. Williams and Bell (1981) found that the reaction to nutrient additions in desert winter annuals was species-specific. Species which were relatively nitrogen rich under natural conditions allocated any additionally available N to reproductive tissues whereas species which were nitrogen-deficient under natural conditions allocated any additional N to photosynthetic tissues. This suggested that under deficient conditions species which were N-poor allocated N to reproduction at the expense of the vegetative organs. Spratt and Gasser (1970) found that wheat incorporates a higher fraction of its

The Effect of Nutrient Stress on Different Types of Reproductive Allocation

Table 4.4.2

Reference	Biomass RA $\bar{X}$	Biomass RA Increasing supply of mins			N RA $\bar{X}$	N RA			P RA $\bar{X}$	P RA			K RA $\bar{X}$	K RA		
Wilson 1985																
Taraxacum																
N	61	53.6	61.8	56.89	62	55. 5	61.5	59.4	66	61.3	63.1	57.8	71	60.1	67.1	64.8
Increasing P		59.5	69.06	56.89		64.84	69.0	59.4		73.3	72.7	57.8		72.7	75.5	64.8
Increasing K		64.26	65.31	56.89		58.3	67.9	59.4		65.6	67.7	57.8		78.2	76.0	64.8
Fenner 1985																
Seeds	11.72	12.4	12.7	11.9 10.4 11.2	26.3	32.3	30.2	26.6 21.1 21.1		51.8	50.1	42.5 38.0 37.6		4.97	4.95	4.75 3.68 3.95
All reprod Structures	32.9	32.0	32.2	33.9 33.1 33.4												
VA Vera 1977																
Senecio sylvaticus	22.7	21.2	24.3	22.6	42	44.7	48.1	33.3	44.6	34.6	56.7	42.6	38.1	30.0	52.2	32.0
C.angustifolium	11.15		3.7 (11.1)	11.2	16.6		15.9	17.3	16.3		18.0	14.7	21.1		22.3	20.0
Williams 1948 Avena									65.7	72	82	43				
Ernst 1983																
P.arenarium	23.2	23.9	28.0	17.8					40	55	45	20	Similar trend			
Lovett Doust 1980																
S.olusatrum									68–74							
Benzing and Davidson 1979																
T.Circinnata					14.9–33.3				12.6–28.7				9.1–16.2			
Williams and Bell 1981																
Winter desert anns	31–54				46–76											
Twyford and Walmsley 1974																
Banana					20.23				24–30				21–37			

total N pool into grain when N is limiting and Ernst (1983) found that Phleum arenarium allocated more P and K to the caryopses with increasing nutrient stress.

The general trend observed in Taraxacum, of increasing the relative P and K allocation to reproductive structures with decreasing nutrient availability, therefore seems to be a widespread phenomenon. This trend is probably partially a consequence of preferential reallocation of nutrients within the plant at the time of fruiting. Gregory (1953) has shown that in the developing cereal plant over 90% of P and N is accumulated before the plant has made 25% growth in dry weight and it was earlier noted that there appeared to be some retranslocation, particularly of K in Taraxacum. Retranslocation at the reproductive stage can involve losses of N, P and K of c.74% from leaves of Lupinus albus grown in mineral sufficient conditions (Hocking and Pate 1974). In conditions of low mineral supply this translocation 'pull' by the reproductive parts would be even stronger. Moreover more nutrients would be needed to increase the root:shoot ratio. The fact that nutrient RA in Taraxacum does not decline and even shows a tendency to increase strengthens Grime's (1977) hypothesis that ruderal plants react to stress by growth responses which maximise seed production at the expense of a rapid curtailment of vegetative development.

Nevertheless even under extreme deficiencies there must be a critical minimum level of vegetative development in order to maintain the photosynthetic apparatus. This may explain why nutrient RA often declines in the most extreme (20%) treatments (Table 4.4.2). This is particularly true when nitrogen is limited and maintenance of nitrogen levels in the leaves may be particularly important for photosynthesis. It was noted earlier that total allocation of N was exceptionally lower

in the reproductive parts in both the 50% and 20% N deficiency treatments. A peak of nutrient RA at moderate levels of nutrient stress but a fall under extreme conditions is also evident in the data of Van Andel and Vera (1977) on Senecio sylvaticus. Similarly Williams (1948) found that when Avena was grown at low, medium and high levels of P availability it allocated 72, 82 and 43% of its internal P to RA. He surmised that plants grown with excessive P supply derived 93% of their inflorescence P supply from other plant parts whereas P deficient plants only derived 30% from these sources. In the plants with excessive P supply a more accessible form of P was obtained from the senescent breakdown of other plant parts whilst in the deficient plants P was more readily derived from the growth medium. There is known to be a close correlation between concentration and retranslocation rate from older leaves (Hill et al 1978) and some nutrients are less easily reallocated under deficient conditions. The fall in RA under extreme nutrient limitation may be a consequence of lower levels of reallocation from other plant parts and also the need to maintain the critical minimum level of nutrients in the leaves necessary for photosynthesis.

Although the methods of measuring RA were significantly different it was obvious from the results that the extent of this difference varied from treatment to treatment. Within the control treatment, the 20%N treatment and 50%P treatments the difference between methods was not significant but within the 20%K and 20%P treatments the difference in methods was highly significant. This reflected the higher allocation of K and P under these treatments.

This result has obvious implications for studies of nutrient RA of species in different environmental conditions. Abrahamson and Caswell

(1982) also found that there were significant nutrient x population interactions in Verbascum thapsus and inferred that between population trends in biomass allocation did not reflect qualitative trends in mineral element allocation. They concluded that it was not safe to assume that the allocation of biomass accurately measured the allocation of nutrients but could not identify a more appropriate currency. Allocation of K to reproductive structures is consistently higher than N P and B allocation in Taraxacum but under nutrient sufficient conditions this difference is not significant. When grown in natural soil Senecio sylvaticus (Van Andel and Vera 1977) had greatest RAs with regard to P but in less fertile conditions N was the greatest contributor.

Mineral nutrient RA is to a certain extent a function of biomass allocation since it is the product of nutrient concentration and dry weight. In Taraxacum N P and K RA were highly correlated with biomass RA and Abrahamson and Caswell (1982) indicated that although the nutrient RA differed in the various populations the relative contributions of the different elements were quite similar. Obviously nutrient RA does vary under different environmental conditions and the variations are element and species-specific. In comparative experiments where conditions are optimal biomass seems to be a reasonable currency since it is to some extent an integration of a number of physiological processes and is undoubtedly easier to measure.

CHAPTER 5 REPRODUCTIVE COST

5.1 Introduction

5.1.1 Why consider reproductive cost

The concept of a 'cost' associated with reproduction is implicit in many allocation studies and has been a basic tenet of life history strategy models. Bell (1980) suggested that in consideration of life history strategies it is the 'reproductive cost' to the individual which is of evolutionary importance rather than the reproductive effort or allocation during one specified time period. He argues that measuring reproductive allocation in units of whatever currency is irrelevant since these units are only of evolutionary significance if they are transformed into units of fitness. Only when this transformation is performed is the reproductive cost, 'the generally deleterious effect of present reproduction on future survival or fecundity or both', being measured.

This argument was also propounded by Sohn and Policansky (1977) when considering the relative importance of sexual and asexual reproduction in the mayapple, Podophyllum peltatum. They conclude that it is necessary to understand how changes in reproductive strategy can alter the extinction rates of various genotypes. An estimate of the allocation to various plant parts is meaningless.

The traditional measures of allocation (particularly when applied to perennial plants) fail to take account of the trade-offs between current reproduction and the residual reproductive value (or chances of future survival and reproduction), (Antonovics 1980). Moreover the physiological costs of reproduction may themselves be time specific. A

single fruit can incur a different cost to a plant depending on the stage in the life cycle at which it is produced (Lovett Doust and Eaton 1982). To facilitate this understanding of the evolutionary process one needs an estimate of reproductive cost or the effect of a given quantity of present reproduction on the expectation of future survival or reproduction.

5.1.2 The theory of reproductive cost

Life histories can be regarded as 'sets of age-specific rates of reproduction and risks of death' (Law 1979a). Fisher (1930) established the basis for the modern demographic theory of life histories which has been developed into complex and varied models (see Stearns 1976 for review). Such models consider how particular life histories will maximise an organism's fitness given that the environment imposes certain mortality constraints (eg Bell 1976) or causes shifts in mortality and fecundity patterns (eg Schaffer 1974). That is, they assume that there is a cost inherent in reproduction.

Organisms in these models are assumed to achieve an optimal 'fitness' in their life histories. Fitness can be defined as the rate of increase which is attributable to the reproduction occurring during a lifetime of variable duration (Bell 1980). It must be remembered that fitness is a relative term and can only have meaning in comparison to other organisms (Harper 1977). Calow (1978) suggests that the definition of fitness in terms of replicative capacity can only hold where resources are unlimited. A more subtle definition of fitness is in terms of the extent to which a particular trait comes to monopolise the resources available to it in a given habitat (Lotka 1922). Nevertheless, the majority of life history models assume fitness can be regarded as rate of increase.

Fisher (1930) proposed that the genetic fitness of a class of organisms would be given by the Malthusian parameter r which can be calculated from the demographic function

$$Vo = \sum_{x=1}^{\infty} lx\ mx\ e^{-rx}$$

Where lx = probability of living to age x

mx = fecundity of age x

r = rate of population increase

e = base of natural logs

v = reproductive value

(Antonovics 1980)

The contribution of any particular age class x to future generations is

$$Vx = \sum_{t=x}^{\infty} \frac{lt\ mt\ ^{-}e^{\ rt}}{lx^{-}lx}$$

or the 'reproductive value' at age x. Schaffer (1974, 1979, 1983) and others suggest that the optimal phenotype will be that which, by proper choice of reproductive allocation or effort at each age x, maximises the reproductive value.

The reproductive value can be partitioned into 2 components (Williams 1966) ie present progeny and future progeny.

$$Vx = mx + \frac{\sum_{t=x+1}^{\infty} (tmte^{-rt}}{lx\ e^{-rx}}$$

where mx = present progeny or present fecundity and the rest is the future progeny or residual reproductive value.

If there is indeed a trade-off between resources allocated to present reproduction and those allocated to future reproduction or growth and survival we would expect to observe a negative relationship between present reproduction and residual reproductive value in practice. Unfortunately, the theory of life history models has surpassed the data available for testing the assumptions and predictions ofthe models, perhaps because of the difficulty of collecting data. The large amount of information necessary for evaluating the models has limited their application to qualitative questions such as predicting the occurrence of iteroparousvs semelparous reproduction (Schaffer and Gadgil 1975, Schaffer and Schaffer 1977, Law 1979a). The deficiency of appropriate data has been pointed out by Law (1979b) and is particularly true for data on plant life histories where perhaps the time constraint is the limiting factor. This lack of appropriate quantitative data is possibly why studies of life history strategies have focussed on allocation patterns. However some evidence does exist which indicates that there is a relationship between present reproduction and future survival, reproduction and growth.

5.1.3 Evidence for the existence of a reproductive cost

When a plant initiates reproduction an investment of considerable magnitude has begun. Reproductive structures require an outlay of materials and metabolic energy and the diversion of resources to reproduction can affect growth and future reproduction. Flowering and fruiting are accompanied by decreased growth in many species (Willson 1983) and because total clutch size commonly increases with size of parent, decreased growth means that size-related increases in fecundity

are likely to be diminished. Current photosynthate is used in seed production of many species such as Hydrophyllum appendiculatum (Morgan 1971) but stored materials may be used in others (Mooney and Hays 1973). Reproductive cost therefore may be discernible as an increase in mortality, decrease in future reproduction and decrease in subsequent size or growth.

i. Mortality

In a monocarpic plant the cost of reproduction is death. There is some evidence that death in annual plants can be postponed indefinitely if reproduction is prevented (Calow 1978). Harper (1977) quotes an example where an annual Reseda odorata was maintained for several years as a vigorous perennial by removal of the flowering primordia. As soon as it was allowed to flower and set seed it died.

The evidence of a link between reproduction and the risks of mortality in polycarpic plants is more tenuous. There are several cases where high rates of reproduction are associated with short lives eg Bocher and Larsen (1958), Langer (1956) and Langer et al (1964). The act of reproducing might increase the plant's susceptibility to agents of mortality. For several species the probability of death is greatest during periods of active growth eg 3 species of Ranunculus (Sarukhan 1974, and Sarukhan and Harper 1983). In the grass Phleum pratense Langer (1956), flowering tillers had higher mortality rates than non-flowering tillers. Oka (1976) found that annual forms of wild and cultivated rice (Oryza perennis and Oryza sativa) had a higher juvenile mortality than perennial forms.

Law (1979b) in a comprehensive study of the costs of reproduction in Poa annua found that there was a tendency for reproduction early in life to increase the risks of subsequent mortality although this tendency disappeared when total reproduction over the whole season was considered. Sohn and Policansky (1977) produced a model based on data for Podophyllum peltatum which indicated that a decrease in future survival was associated with the successful bearing of fruit.

Data for animals are more comprehensive (see Stearns 1976 for review). Murdoch (1966) found that the survival of adult female Carabidae from near the end of one breeding season to the start of the next was negatively dependent on their breeding success in the first season. Similarly the survival rate of individual rotifers Asplancha in a clone was negatively related to their average fecundity (Snell and King 1977).

ii. Future reproduction

Negative correlations of plant fecundity with residual reproductive value have been found in Podophyllum peltatum (Sohn and Policansky 1977) and Poa annua (Law 1979b). The probability that the mayapple would be sexual in the future decreases if it successfully bears fruit in the current season. This is because the reduction in the length of new internodes associated with the production of fruit decreases the probability that the next season's shoots will be sexual. Families of Poa annua with large numbers of inflorescences in the first year have low numbers of inflorescences in the second year.

A characteristic age-associated decrease in reproductive output has been reported for many grass species eg Poa pratensis (Evans and

Canode (1971) and Holcus lanatus (Bocher and Larsen 1958). Stark et al (1949) found that the seed yield of Bromus marginatus declined from 1243 kg per hectare to 467, 380 and 319 kg per hectare in successive years.

In years when mango plants, (Mangifera indica) produce a heavy crop the tree makes few new vegetative shoots (Harper 1977). Since inflorescences are borne on new shoots the tree loses the potential for reproduction in the year following a large seed crop. This link between reproduction and growth/size and hence subsequent reproduction is also found for Chamaelirion luteum by Meagher and Antonovics (1982). Flowering in a particular year resulted in a reduction in size in the following year and size was correlated with inflorescence size, flowering schedules and mortality rates in juveniles. The reduction in size was greater in female plants implying that the costs of reproduction were greater in female plants. It would seem that reproduction has a cost in terms of growth and in many species this may be linked with subsequent reproduction and risks of mortality.

iii. Growth/size

It has been shown in many plant species eg Werner (1975), Sohn and Policansky (1977) and Bierzychudek (1982) that size plays an important role in determining the physiological fate of an individual. If, as previously suggested, size affects the probability of future reproduction, then the effect of present reproduction on future growth must be critical.

There is ample qualitative evidence of the existence of trade-offs between reproductive and non-reproductive functions eg Leonard

1962), which is mainly based on evidence from crop plants such as tomatoes. The early quantitative evidence derives from negative correlations of annual variation in crop size with annual growth increments in trees. Eis et al (1965) found the width of annual rings in some conifers was depressed only during the years of cone production. Holmsgaard (1956) found that the annual ring width of Fagus sylvatica in good mast years (every 6 or 7 years) may be only half the average ring width in unaffected years. (For other examples see Harper 1977).

In wild plants the most detailed information is from Law (1979b) and Sohn and Policansky (1977). Families of Poa annua which produced large numbers of inflorescences in their first year were smaller in size in the second year than families which had produced fewer inflorescences. In the mayapple the production of fruit was approximately equivalent to the production of one new internode. Shoots which produced fruit were found to have shorter rhizomes than those with flower or fruit failure. In studies on 2 winter annuals, Catapodium rigidum and Catapodium marinum Clark (1980) found that leaf life expectancy late in the life cycle was significantly negatively correlated with caryopsis weight. Early in the life cycle, leaf numbers were negatively correlated with caryopsis weight. An uncommonly large seed crop in Betula allegheniensis and Betula papyrifera resulted in dwarfed foliage, failure to develop terminal buds, die back of branches, a reduced growth in height and diameter, followed, not surprisingly, by very low levels of flowering in subsequent years (Gross 1972).

The available evidence therefore, does seem to indicate that there is a cost associated with reproduction. This cost is often realised

by a decrease in growth and subsequent reproduction and an increase in risks of mortality.

5.1.4 Approaches to measuring reproductive cost

Antonovics (1980) suggests that a possible approach to approximating the trade-offs between present and future reproduction, growth and mortality is by field measurements using size rather than age-dependent data. This method is particularly relevant in studies of species where life histories are determined by size rather than age. Individuals are marked in natural populations over successive years and their initial size is related to their size and survival the following year as a function of their flower and seed production. Antonovics (1980) applied this idea to Plantago lanceolata and found that in the population under consideration, flowering had little effect on subsequent size or mortality, probably because flowering was not initiated until the plant had grown to a size where the mortality rate was low. The idea was also applied to Chamaelirion luteum (Meagher and Antonovics 1982) where size was correlated with inflorescence size, flowering schedules and mortality rates in juveniles.

Experimental manipulations whereby reproductive structures are removed at an early stage of development are another possible approach to defining reproductive cost. In effect, this method was used in early studies of the correlation between vegetative and reproductive growth (Leonard 1962); exscision of flowers to improve vegetative growth, seed set or prolong flowering periods is a well known horticultural technique.

Antonovics (1980), using data by Caisse (unpub), describes an experiment where day length was manipulated to control flowering in

genetically identical, cloned individuals of Plantago lanceolata. In one set of cloned genotypes flowering was induced and in another identical set it was not. In the flowering plants a slight increase in leaf growth was followed by a slower production of leaves. An estimate that one inflorescence was equivalent to 2.76 leaves was obtained. In order to extend this value to a life history, knowledge of the contribution of leaves to future survival and growth would be required.

This approach is also proposed by Silvertown and Rabinowitz (unpub ms) who suggest a method of measuring reproductive cost in indeterminate plants like the cucumber. Cost is measured in numbers of metamers (in this case internodes) produced when flower buds (male, female and both) are excised. Salisbury (1942) noted an inverse relationship of fruiting and stolon formation in Galeobdolon luteum and of flowering and bulbil formation in Allium carinatum. In these two cases costs may be assessed in terms of alternat forms of reproduction.

5.1.5 Difficulties

The impact of flowering on an individual's future life history in the field is confounded by the effects of the environment (Antonovics 1980). In field studies genetical influences on reproductive allocation are not readily separated from environmental influences. In order to distinguish the genetic component in the conflict between present reproduction and the residual reproductive value it is necessary to perform experiments over several seasons on genetically identifiable populations. Few experiments of this nature have been performed (but see Law, Bradshaw and Putwain 1977), presumably because of the difficulty of obtaining and maintaining the requisite plant populations.

A further possible difficulty concerned with the entire concept of reproductive cost has been identified by Watson (1984) and Antonovics (1980). In some species where photosynthesis and growth is 'sink' rather than 'source' limited reproduction may have little cost since photosynthesis and or translocation may be limited by the availability of sinks (eg reproductive structures or meristems) into which photosynthate can be transported. Watson (1984) finds that reproduction in Eichornia crassipes is limited by the availability of meristems. Examples of 'sink' limited systems have been given by Wareing and Patrick (1975). These systems may have evolved where there are advantages in limiting plant size so that the plant may not require excessive resources such as in seasonally unpredictable or 'stressful' habitats. Tuomi et al (1982) suggest that their inability to find a reproductive cost in dwarf shoots of Betula pendula may be because plants only use excess resources in reproduction. Nevertheless the concept of reproductive cost is a useful one, particularly in the case of indeterminate plants.

5.2 Method - Foxglove

The aim of the experiment was to determine whether there was a 'cost' associated with reproduction in a particular species. The 'cost' of reproduction in one year could manifest itself in one of several ways in the second year. There might be reduced survival, growth or subsequent reproduction which would be proportional to the level of reproduction in the first year. It would also be possible to determine whether there was any relationship between sexual reproduction and vegetative expansion.

Digitalis purpurea is usually thought to behave as a biennial (Clapham, Tutin and Warburg 1959), reproducing in its second year and then dying. However under certain circumstances eg when the inflorescence is damaged (Harper 1977) it may behave as an iteroparous perennial reproducing over several years (Van Baalen and Prins 1983). The growth form of this plant with its basal rosette of leaves and flowers arranged in a long erect raceme facilited manual excision of a certain proportion of flowers. The experiment was designed to show whether the level of reproduction in the first year affected the plant's subsequent survival or growth.

At the time of the initation of the experiment (December 1982), there was no Digitalis purpurea seed available from wild populations. Therefore some 'native' seed was procured from a commercial seed firm (The Seed Exchange, Helen McEwen, 44 Albion Road, Sutton, Surrey). Since biennial plants usually need to attain a minimum size before flowering is initiated (Werner 1975) it was necessary to encourage plant growth in the early stages of the experiment. Therefore seeds were germinated in seed trays of John Innes compost in a heated

greenhouse at Skardon Place at the end of December. They were then taken to Rumleigh experimental station on the 24 January and repotted in larger polythene pots and left in an unheated greenhouse until they were large enough to be potted out. The plants were left outside for a few nights prior to being planted out in case there was a vernalisation requirement for this particular population (Van Baalen and Prins 1983). The plants were planted out in a 4m x 20m rectangular plot on the 13 March.

The experimental design (fig 5.2.1) was chosen to minimise any effects which might run along or across the rectangular plot. Lengthwise environmental effects were particularly important since the plot ran down a slope. 80 plants were planted approximately 1m apart in 5, 4 x 4 Latin squares with 4 treatments. The Latin square designs were obtained from Fisher and Yates (1963). Hence there were 20 plants in each of 4 treatments and each Latin square contained 16 plants. Colour coded and numbered canes were placed beside each plant to identify each treatment (fig 5.2.1).

In treatment A the control, the plants were left to flower normally with no removal of flower buds whilst in treatment D all of the flower buds were manually excised. The intermediate treatments B and C were determined by counting the number of flower initials on several immature flower spikes. There were approximately 100 flowers on each spike so it was decided to leave c. 50 flowers on treatment B plants and c. 20 flowers on treatment C plants.

Removal of flower buds from the base of the racemes started on June 9 and was completed on July 11. After this date any mature seed capsules from plants in treatments A, B and C were collected, dried at 60^{o}C for

Fig 5.2.1

DESIGN FOR FOXGLOVE EXPERIMENT

SLOPE OF HILL→

4 m

D_1	C_2	A_3	B_4	C_5	A_6	B_7	D_8	C_9	B_{10}	D_{11}	A_{12}	D_{13}	B_{14}	A_{15}	C_{16}	C_{17}	A_{18}	B_{19}	D_{20}
A_1	B_2	C_3	D_4	B_5	D_6	C_7	A_8	D_9	C_{10}	A_{11}	B_{12}	C_{13}	D_{14}	B_{15}	A_{16}	A_{17}	D_{18}	C_{19}	B_{20}
C_1	D_2	B_3	A_4	D_5	B_6	A_7	C_8	B_9	A_{10}	C_{11}	D_{12}	B_{13}	A_{14}	C_{15}	D_{16}	D_{17}	B_{18}	A_{19}	C_{20}
B_1	A_2	D_3	C_4	A_5	C_6	D_7	B_8	A_9	D_{10}	B_{11}	C_{12}	A_{13}	C_{14}	D_{15}	B_{16}	B_{17}	C_{18}	D_{19}	A_{20}

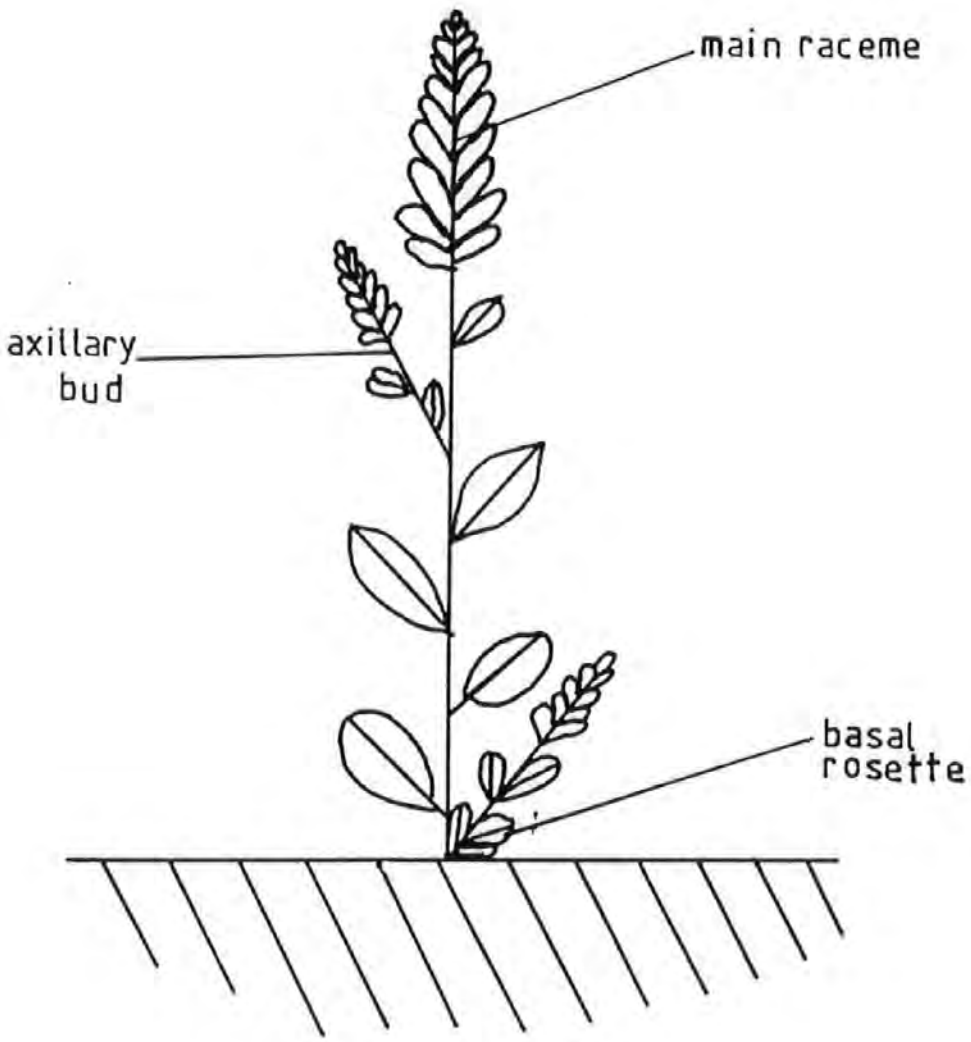
20 m

A = no flowers removed - uncoloured cane
B = 1/2 flowers removed - blue cane
C = 4/5 flowers removed - red/blue cane
D = all flowers removed - red cane

24 hours and stored in manilla envelopes. Capsules were removed at least twice a week to prevent any loss of seed through capsule dehiscence. During the course of the experiment it became obvious that some plants were producing basal rosettes and some were producing axillary buds on the flowering spike (See fig 5.2.2). Basal rosettes were included as part of the primary plant's reproduction and any flowering spikes produced from these rosettes were treated in the same way as the primary spike. However any axillary buds were removed as they were produced and a note was made of the number of buds that each plant produced.

By September 8 1983 all the mature capsules had been collected and by October 27 the last axillary buds were removed. The plants were then left over the winter. The diameter of each rosette was measured in March 1984 and the remaining above-ground vegetative parts of each plant were collected in April 1984. The vegetative parts were dried at 60°C for 48 hours in an oven and then weighed on a Oertling TP40 balance. Seed was extracted from the seed capsules of each plant using wire sieves and the weight of the seed and capsules and the number of capsules per plant noted. The weight of 20 seeds for 10 plants from treatments A and C was also measured on a Sartorius 1201 MP2 balance.

Fig 5.2.2



Diagrammatic Representation of Digitalis Plant

Plate 5.2.1 i Experimental Design at Rumleigh
ii Production of a Basal Rosette - Digitalis

5.3 Results - Foxgloves

At the end of the experimental period nine plants had died. Four of these plants were in the control population (c. 100 seed capsules), four were in treatment in B (c. 50 seed capsules) and one was in treatment C (c. 20 seed capsules). The death of these plants appeared to be caused by a fungal infection, some of the affected plants showing signs of infection before the end of the flowering season. Botrytis cinerea was identified as causing up to 32% mortality in dense stands of Digitalis by Van Baalen and Prins (1983) whilst at lower densities pre-flowering mortalities were 5-20% per year.

A summary of the results (ie the means for each treatment for the number of capsules, dryweight of capsules, dry weight of seeds, number of axillary buds, diameter of rosette in second year, weight of leaves and weight of root in second year) are shown in Table 5.3.1. The normal probability plot correlation coefficients (table 5.3.1a) show that the majority of variables fell within the 5% probability level for the normal distribution, the exceptions being the number of axillary buds that each plant produced and the root weight. These two variables had slightly positively skewed distributions. A square root transformation was applied to the data on number of axillary buds, and a log transformation was applied to the root weight data prior to any application of analysis of variance methods.

The relationships between the variables can be seen in the correlation matrix in table 5.3.2. It is evident from this table that there are some interesting associations between the various parameters. The number of capsules produced by each plant can be regarded as a measure of the treatment since the maximum number of capsules were produced in

Characteristics of Foxglove Data

Variable	Dry wt caps (g)		Dry wt (g) Seed	No of Axillary Buds	Diam (cm)	Wt lves (g)	wt rt (g)	$\bar{x}$ caps (g)	$\bar{x}$ seed (g)
All Data.									
N	80		80	80	75	77	77	50	50
X	3.29		5.22	34.3	69.75	116.6	54.1	0.0763	0.078
SD	2.68		4.53	32.8	8.21	51.3	34.6	0.0020	0.0039
SE	0.30		0.51	3.7	0.95	5.9	3.9	0.1062	0.1775
Treatment A	No. of Caps	Dry wt Caps (g)							
N	20	20	20	20	18	19	19	20	20
$\bar{X}$	100.4	6.70	11.08	9.40	72.06	124.7	55.8	0.066	0.1114
SD	19.5	1.66	3.06	9.21	7.52	38.8	37.6	0.114	0.0277
SE	4.4	0.37	0.68	2.06	1.77	8.9	8.9	0.006	0.0062
Treatment B									
N	20	20	20	20	18	18	18	20	20
$\bar{X}$	56.65	4.348	6.77	28.3	69.1	116.7	58.8	0.776	0.120
SD	7.31	0.746	1.78	24.3	11.6	58.3	45.0	0.015	0.0311
SE	1.64	0.167	0.40	5.4	2.7	13.7	10.6	0.0033	0.01775
Treatment C	20	20	20	20	20	20	20	20	20
N	25.5	2.118	3.029	27.0	69.45	124.2	44.0	0.0844	0.122
$\bar{X}$	7.27	0.540	0.786	23.0	6.33	47.4	14.0	0.0161	0.0318
SD	1.67	0.121	0.176	5.1	1.42	10.0	3.1	0.00036	0.0071
SE									
Treatment D									
N	20	20	20	20	19	20	20	20	20
$\bar{X}$	0	0	0	72.4	68.53	101.1	58.1	0	0
SD	0	0	0	31.4	6.76	58.7	36.0	0	0
SE	0	0	0	7.0	1.55	13.1	8.1	0	0

Table 5.3.1a

Probability plot correlation coefficients

$P < 0.05$ for $n = 80 = 0.984$

Dry wt caps	0.997
Dry wt seeds	0.993
No of axillary buds	0.937
Sq rt no of axillary buds	0.995
Logten 1+x no of ax buds	0.978
Diameter	0.991
Wt lves	0.995
Wt root	0.811
Logten wt root	0.966
Sq rt rt wt	0.966
Mean wt of caps	0.987
Mean wt of seed	0.985

Table 5.3.2

Correlation Matrix

	No of capsules	wt of capsules	Wt of seed	No of axillary	Diam	Wt of lvs	Wt of root	$\bar{\bar{X}}$ wt caps
Wt of capsules	0.962**							
Wt seed	0.936**	0.964**						
No of buds	-0.574**	0.557**	-0.516					
Diam	0.166	0.134	0.157	-0.121				
Wt lvs	0.117	0.112	0.089-	-0.341**	0.558**			
Wt root	0.085	0.075	0.056	-0.012	0.526*	0.355**		
$\bar{\bar{X}}$ wt caps	-0.485**	-0.173	-0.211	-0.258*	-0.145	-0.026	-0.023	
$\bar{\bar{X}}$ wt seed	-0.216	0.010	0.215	0.324**	0.048	-0.024	0.003	0.646*

** = P<0.01 (0.302)
* = P<0.5 (0.232)

treatment A (the control), whereas no capsules were produced in treatment D. Treatments B and C had intermediate numbers of capsules. As would be expected, the number of capsules was highly correlated with total weight of capsules and total weight of seed but it was also significantly negatively correlated with the number of axillary buds produced and the mean weight of each capsule (that is the total weight of capsules produced/number of capsules per plant). Similarly the total weight of capsules and seed produced per plant was negatively correlated with the number of axillary buds. The number of axillary buds produced per plant was positively correlated with the mean weight of each capsule and the mean weight of seed in that capsule.

The diameter of the rosette in the second year was positively correlated with leaf and root weight in the second year and leaf and root weight were correlated with each other. The number of axillary buds produced was negatively correlated with the weight of leaves.

To take account of the experimental design and test the effect of treatment more rigorously, analyses of variance were carried out using GENSTAT (table 5.3.3). These analyses show that the effect of treatment is highly significant in the case of number of axillary buds produced and the mean weight of capsules. The number of axillary buds produced increases from a mean of 9.4 in the control treatment where plants were allowed to flower normally, to a mean of 72.4 in the treatment where all of the flowers were removed. (The intermediate treatments both have mean numbers of c. 28). Concurrently, the mean weight of each seed capsule increases from 0.0668g in treatment A to 0.0844g in treatment C. There is a similar trend in mean seed weight but it is not statistically significant.

Foxglove Anovas Effect of Treatment

1. No of axillary buds

Source	DF	SS	SS%	MS	VR
Block	4	1004.2	1.23	251.1	
Col	3	2954.7	3.63	984.9	
Block.Row	15	1154.1	14.20	770.3	
Block.Col	12	7451.7	9.16	621.0	
Block.Row.Col					
Treat	3	46143.5	56.71	15381.2	30.62
Residual	37(5)	18581.7	22.83	502.2	P<0.01
Total	40	64725.2	79.54	1618.1	
Grand Total	74	87690.0	107.76		

2. Sq rt trans of no of axillary buds

Block	4	6.069	1.03	1.517	
Col	3	19.510	3.30	6.503	
Block.Row	15	89.007	15.06	5.934	
Block.Col	12	52.264	8.84	4.355	
Block.Row.Col					
Treat	3	337.573	57.12	1112.524	33.525
Residual	37(5)	124.189	21.01	3.356	
Total	40	461.761	78.13	11.544	P<0.01
Grand Total	74	628.611	106.37		

3. Diameter

Blocks	4	362.98	7.28	90.74	
Cols	3	64.00	1.28	21.33	
Block.Row	15	908.45	18.23	60.56	
Block.Col	12	855.79	17.17	71.32	
Block.Row.Col					
Treat	3	161.76	3.25	53.92	0.743
Resid	37(5)	2685.62	53.88	72.58	NS
Total	40	2847.38	57.13	71.18	
Grand Total	74	5038.54	101.09		

4. Mean weight of capsules = wt caps/no of caps

Block	4	0.00071251	4.83	0.00017813	
Col	3	0.00090038	6.10	0.00030013	
Block.Row	15	0.00537724	36.44	0.00035848	
Block.Col	12	0.00727886	49.33	0.00060657	
Block.Row.Col					
Treat	2(1)	0.00315827	21.40	0.00157914	16.486
Resid	23(19)	0.00220315	14.93	0.00009579	
Total	25	0.00536143	36.33	0.00021446	P<0.01
Grand Total	59	0.01963041	133.03		

4. Mean wt of seed/capsule = wt of seed/no of capsules

Source	DF	SS	SS%	MS	VR
Block	4	0.0037066	6.93	0.0009267	
Col	3	0.0072031	13.47	0.0024010	
Block.Row	15	0.0345325	64.59	0.0023022	
Block.Col	12	0.0169112	31.63	0.0014093	
Block.Row.Col					
Treat	2(1)	0.0013152	2.46	0.0000576	2.037
Resid	23(19)	0.0074244	13.89	0.0003228	
Total	25	0.0087396	16.35	0.0003496	NS
Grand Total	59	0.0710930	132.98		

5. Weight of root

Block	4	4915	5.51	1229	
Col	3	3477	3.90	1159	
Block.Row	15	15149	16.98	1010	
Block.Col	12	14920	16.73	1243	
Block.Row.Col					
Treat	3	3017	3.38	1006	0.768
Residual	37(5)	48448	54.32	1309	NS
Total	40	51466	57.70	1287	
Grand Total	74	89926	100.82		

6. Log weight of root

Block	4	0.20103	7.29	0.05026	
Col	3	0.11178	4.05	0.03726	
Block.Row	15	0.35779	12.97	0.02385	
Block.Col	12	0.42298	15.34	0.03525	
Block.Row.Col					
Treat	3	0.11777	4.27	0.03926	0.920
Resid	37(5)	1.57250	57.01	0.04250	NS
Total	40	1.69028	61.28	0.04226	
Grand Total	74	2.78386	100.93		

To test whether this trend in seed weight per capsule could be attributed to an increase in numbers of seeds or an increase in individual seed weight, samples of seed were taken from the A and C treatments and weighed in the laboratory. Samples of 20 seeds from 10 plants were collected and weighed on a Sartorious 1201 MP2 balance. The means were then tested using a t-test in MINITAB.

	N	mean	SD	SE
Treatment a	10	0.00167	0.000267	0.000084
c	10	0.00191	0.000367	0.00012

t = 1.67 p = 0.11 df = 16.4 not significant

Again, although there is a trend towards a higher mean weight in the treatment where flowering is partially prevented, it is not statistically significant.

A regression analysis of the number of axillary buds on the number of capsules was also carried out using GENSTAT. The relationship between the two variables was significant and the percentage variance accounted for 32.1%.

YVAR = Axillary buds

Regression Coefficients

	Estimate	SE	T	
Constant	56.19	4.65	12.09	
ncaps	-0.4797	0.0774	-6.19	p<0.01

y = 56.19 - 0.4797x

5.4 Discussion - Foxgloves

Manual removal of the flowers in Digitalis purpurea resulted in an increase in the number of axillary buds, and this increase was proportional to the number of flowers removed. The mean weight of any remaining seed capsules also increased proportionally with the number of flowers removed. There was also a tendency for the mean weight of seed produced per capsule to increase with decreasing number of flowers and perhaps a slight tendency for plants with greater numbers of flowers to be more susceptible to disease and mortality.

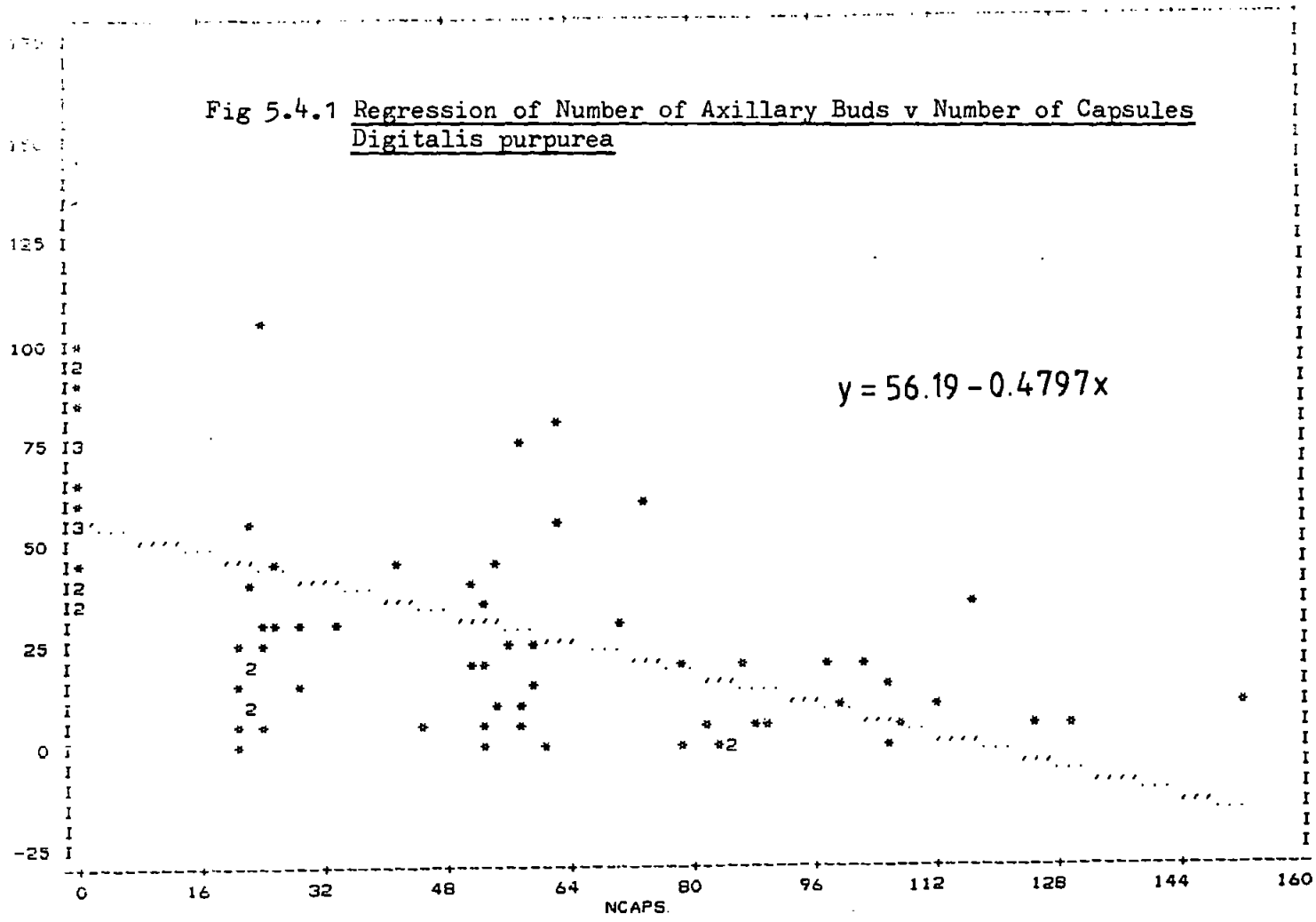
Although there was a tendency for the plants with larger reproductive allocations to be more susceptible to disease, the majority of plants survived the winter following flowering. This behaviour can be attributed to the production of secondary basal rosettes in the year of flowering. The production of these secondary rosettes which allows repeated flowering in Digitalis is more common in early successional sites where intra and inter-specific competition is low (Van Baalen and Prins 1983). The experimental layout at Rumleigh experimental station, where plants were situated at least 1m apart, probably simulated an early successional site. Under these circumstances Digitalis can be regarded as a 'short-lived perennial' (Salisbury 1942). This formation of secondary rosettes and repeated flowering is not found in most other 'biennial' and monocarpic species like Dipsacus sylvestris (Werner 1977) and Daucus carota (Holt 1972). The Digitalis plants may have obtained sufficient resources from their immediate environment to allow secondary rosette information which enabled the majority of plants to survive another season. A reproductive cost may have been more evident if plants had been subject to the competition present in a late successional environment.

Nevertheless, there was an observed tendency towards greater susceptibility to disease in the plants with greater reproductive allocations and this can be considered to be an indication of a reproductive cost. The probability of death has been related to reproduction in several species eg Reseda odorata (Harper 1977), Holcus lanatus (Bocher and Larsen 1977), Phleum pratense and Festuca pratensis (Langer et al 1964) and Poa annua (Law 1979b). Although it has been noted that the act of reproducing might increase the susceptibility of a plant to the physical and biotic agents of death (Willson 1983), mortality as a result of disease has not been distinguished as a specific factor.

The most significant effect of artificially reducing reproductive allocation was an associated increase in the number of axillary buds produced by each Digitalis plant. There is a highly significant negative correlation between the number of seed capsules produced and the number of axillary buds initiated. Although there is much evidence of a trade-off between reproductive and non-reproductive functions (see 5.1), it is questionable whether the production of axillary buds in Digitalis should be regarded as a non-reproductive function. If the buds had been allowed to develop each would have produced a small flower-spike with approximately 10 flowers on it. It can be seen from fig 5.4.1 that the production of one axillary bud is roughly equivalent to the removal of 2 flowers. Had the axillary buds been allowed to develop further the equivalent number of flowers might have been greater.

Perhaps an alternative approach might be to regard these excised buds as new metamers (Silvertown and Rabinowitz unpub MS) where each new metamer that a plant produces is also, potentially the point of origin for a

Fig 5.4.1 Regression of Number of Axillary Buds v Number of Capsules Digitalis purpurea



set of reproductive organs. Silvertown and Rabinowitz (MS) suggest that reproductive effort in indeterminate plants might be measured by comparing the number of flowering nodes or metamers produced in plants in which all the flowers have been removed with plants in which no flowers have been removed. Plants in which all the flowers have been removed are considered to reach the total potential vegetative size. Digitalis purpurea is not an indeterminate plant but the numbers of axillary buds can be regarded as numbers of new metamers.

In Silvertown and Rabinowitz's measure of RE

$$RE = (N3 - N4)/N3$$

Where N3 = the number of nodes produced when all reproductive organs are removed and N4 = the number of flowering nodes produced by the control. If this equation is applied to the data for axillary buds a ratio of 0.87 is obtained. A RA of 87% seems rather high even for a ruderal annual using conventional methods of RA estimation but there are no comparable data by which to gauge the validity of the results.

The fact that the mean weight of individual capsules increased with a reduction in the total number of capsules per plant seems to indicate that there was a preferential allocation of resources to any remaining seed capsules. There was a similar trend in seed weight per individual capsule although this difference was not large enough to be significant. A test of the individual seed weight in each plant showed that there was no significant difference in seed weight between treatments. Maun and Cavers (1971) found that the mean weight per seed in Rumex crispus was progressively higher as a greater proportion of flower whorls were removed. However, one possible explanation of the

larger capsule and seed per capsule weights was their location on the flower spike. In treated plants it was the flowers near to the base of the flower spike which were allowed to remain intact (see plate 5.4.1). In a normal foxglove raceme, the flowers tend to decline in size as the top of the spike is approached. The seed capsules in the lower positions on the control plants might also have been larger but the inclusion of small seed capsules from the tip of the flower spike would make the overall mean capsule weight lower than in treated plants. Maun and Cavers (1971) also found that in Rumex crispus the heaviest seeds were found on the lowest branches of the panicle.

The original intention of the experiment was to test whether there was a reproductive cost in Digitalis purpurea which was expressed in terms of increased subsequent mortality or decreased subsequent growth. Despite the fact that there was some slight evidence of increased susceptibility to disease, the numbers involved were very small. The capacity of Digitalis purpurea to produce secondary basal rosettes under certain circumstances which survive the winter, meant that reproductive cost in terms of mortality could not be adequately assessed. Moreover, the prevention of flowering on the main flowering spike in Digitalis resulted in diversion of resources to the production of axillary buds (which would have produced flowers themselves) rather than to the basal rosette or root. Consequently the specific reaction of this particular species confounded the aims of the experiment. A more appropriate species might have been Verbascum thapsus which does not produce secondary basal rosettes although axillary bud production might still prove a problem.

Nevertheless, it was evident that the level of reproductive allocation was directly related to the number of axillary buds that were produced.

The removal of approximately 2 flowers resulted in the production of one axillary bud. Had the axillary buds been allowed to mature they would have produced approximately 10 flowers. However it may be that adverse environmental factors such as the lower position of axillary buds on the stem, smaller size of flowers and their inherent later date of anthesis would result in a lower seed output of flowers on axillary buds. The eventual seed output of one axillary bud might be equivalent to that produced by 2 seed capsules on the main flowering spike but this could only be tested by further experimental work.

In theory reproductive cost is a more crucial measure that RA of what is important to a plant in evolutionary terms. However, it can be expressed in many ways in numerous different species and may therefore prove as, or even more difficult than, RA to measure and evaluate.

Plate 5.4.1 i Position of Removed flowers - Digitalis
ii Experimental Design at Skardon Place
(see Section II)

5.5 Plantago lanceolata and Taraxacum officinale

5.5.1 Introduction

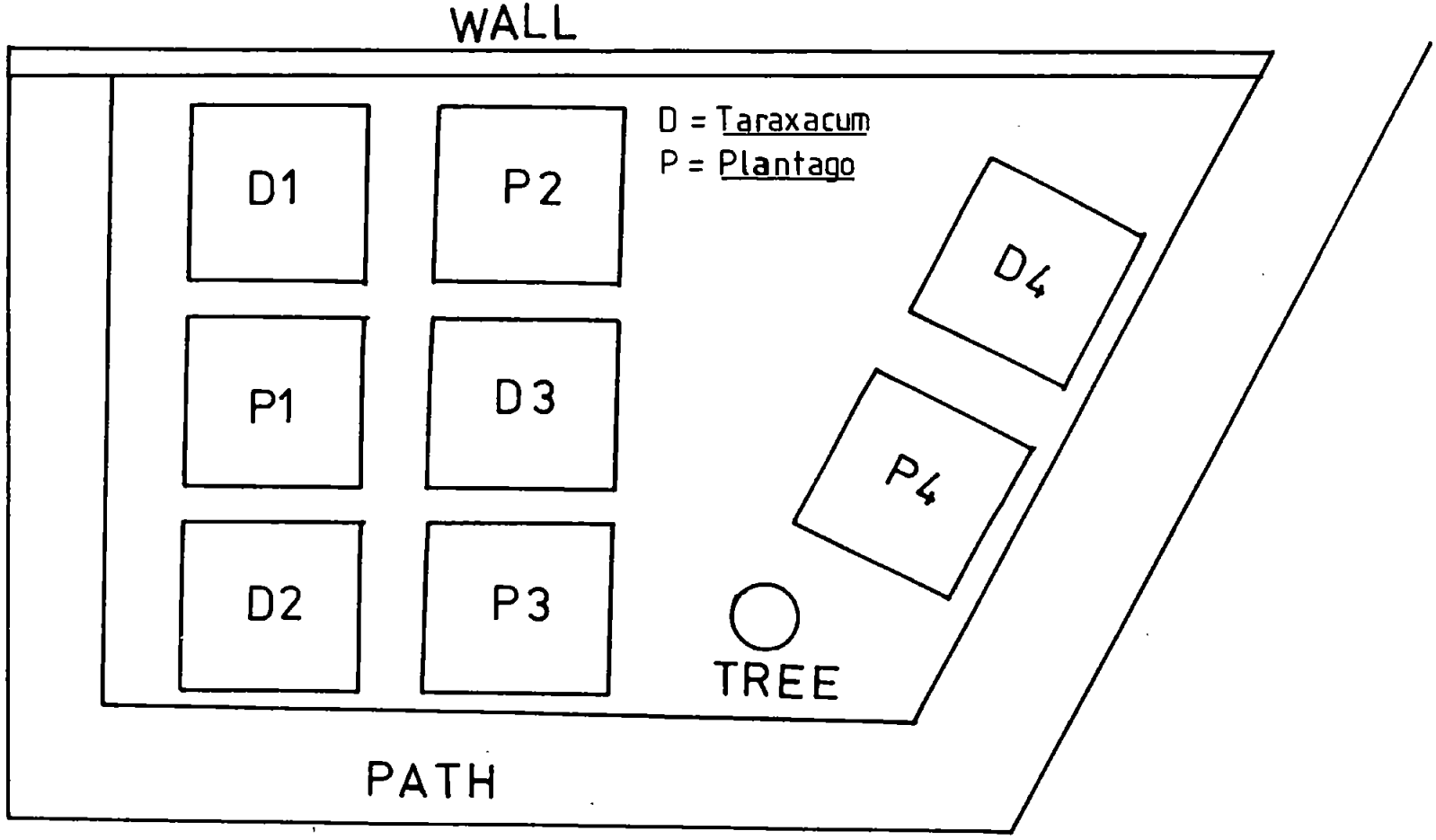
In addition to increased mortality, a cost associated with reproduction might be realised in the form of reduced subsequent reproduction ie there might be a decline in the residual reproductive value associated with the level of past reproduction. An experiment was therefore designed to assess whether current level of reproduction has an effect on subsequent reproduction. Current reproduction was artificially manipulated by removal of a certain proportion of flowers as in the Digitalis experiment in Section 5.1. The effect of this manipulation on subsequent reproduction was assessed by noting the level of reproduction in the year following treatment.

5.5.2 Method

Plantago lanceolata and Taraxacum officinale were selected as two perennial species with an appropriate growth form. Both have a basal rosette of leaves and are scapigerous, which facilitates the removal of flowers and the separation of biomass into vegetative and reproductive fractions.

Seed was collected from wild plants in Autumn 1980 and germinated in trays of John Innes compost in April 1981. The seedlings were planted out when they were large enough to handle on 1 May 1981 at Skardon Place near Plymouth Polytechnic. The plot which had been allocated to the experiment was cleared and plants were planted in 4, 4x4 Latin squares with plants placed 30 cm apart. (See fig 5.5.1 for location of the plots).

Fig 5.5.1



Diagrammatic Representation of Location of Plantago[P] and Taraxacum[D] Plots

From previous observations of Plantago plants in the field (Wilson 1980) it was decided that approximately 12 scapes could be expected per plant. Taraxacum officinale was thought to produce a roughly similar number of scapes per year so identical treatments were applied to each species. In treatment A (the control) plants were allowed to flower normally. In treatments B and C, 6 and 2 flowers were allowed to mature, respectively. Any spikes which were produced over and above this number were removed manually by excision of the flower initials as they became visible. In treatment D flowering was completely prevented by manual excision of the flower initials. Removal of the flower initials took place twice a week and commenced in the case of the Plantago plants on 26 June. One plot (P4) did not commence flowering until 21 July and thereafter grew very slowly since it was located under the shade of a tree. In this case it was decided that the treatment should be continued throughout the summer of 1982 and the results assessed in 1983. Similarly the Taraxacum plants did not commence flowering until 13 August 1981 so in all ofthe Taraxacum plants treatment was also continued through the summer of 1982. A note was made of the number of heads that were removed per plant. Plots were regularly weeded to keep them free of weeds and slug pellets and 'Pepper dust' were applied as required.

Plantago plants in plots P1, P2 and P3 were left over the winter and allowed to flower normally in 1982. These plants were then harvested and separated into reproductive, vegetative and root fraction in September 1982. These fractions were dried and weighed on an Oertling TP40 balance. The number of mature seed heads produced per plant was also noted.

Treatment commenced again on the remaining Plantago plot on 17 March 1982 and on all the Taraxacum plots on 30 March. The diameter of each Taraxacum rosette was noted at this time. All of these plants were allowed to flower normally in the summer of 1983. However, because Taraxacum produces such dispersive seeds, spikes had to be removed as soon as they were mature. It was decided that an estimate of reproductive weight in this species would be very time consuming but a record of total numbers of flowers produced was made. Numbers of spikes in scapigerous species is often highly correlated with reproductive weight (Wilson 1980). At the end of the Taraxacum season in July 1983 plants were harvested and similarly dried and weighed. The remaining Plantago plot was harvested in August 1983.

5.5.3 Results

i. Plantago lanceolata

A summary of the data for Plantago lanceolata is given in table 5.5.1. All of the variables which were later tested using analysis of variance fell within the 0.05 probability limits of the normal probability plot correlation coefficient. The correlation coefficients in table 5.5.2 show the general relationships between the variables. Vegetative, root, reproductive and total weight are highly correlated with each other and the number of flowers produced in the second year is again highly correlated with these parameters. The total numbers of spikes initiated in the first year was significantly negatively correlated with the number of spikes allowed to remain intact on the plant. Reproductive allocation was significantly positively correlated with total weight, root weight, reproductive weight and the number of spikes produced in the second year.

Table 5.5.1

Summary of Plantago Data

A	Veg wt (g)	Rt wt (g)	Rep wt (g)	Total wt (g)	RE%	No of Fs in YR1	No of Fs in YR2	No of Fs removed
n	15	15	15	15	15	15	15	15
X	6.72	10.31	42.1	59.2	61.5	47.4	46.2	47.4
Med	5.69	11.10	33.4	58.0	65.9	50.0	26.0	50.0
SD	4.58	5.61	34.6	39.9	21.5	16.8	38.7	16.8
SE	1.18	1.29	8.9	10.3	5.6	4.3	10.0	4.3
B								
n	16	16	16	16	16	16	16	16
X	5.08	12.7	56.3	74.1	64.5	6.0	66.7	104.4
Med	4.70	14.4	22.6	41.3	66.3	6.0	32.5	102.5
SD	4.17	10.1	60.7	72.5	22.6	0.00	71.9	36.5
SE	1.04	2.5	15.2	18.1	5.6	0.00	18.1	9.1
C								
n	16	16	16	16	16	16	16	16
X	3.28	10.92	42.2	56.4	67.1	2.0	54.0	123.5
Med	1.75	8.65	46.1	58.3	74.8	2.0	44.0	113.0
SD	4.83	8.39	32.2	41.4	20.7	0.0	50.2	50.0
SE	1.21	2.10	8.0	10.4	5.2	0.0	12.5	12.5
D								
n	14	16	16	14	14	16	16	16
X	5.71	12.36	55.1	77.1	64.1	0	65.2	133.4
Med	6.09	11.82	54.4	77.3	73.4	0	56.5	124.5
SD	2.81	7.47	42.2	51.6	22.4	0	48.2	45.0
SE	0.75	1.87	10.6	13.8	6.0	0	12.1	11.2
Total								
n	61	63	63	61	61	63	63	63
X	5.16	11.60	49.0	66.5	64.4	13.3	58.2	103.0
Med	4.81	10.62	40.1	58.2	73.7	2.01	41.0	105.0
SD	4.29	7.86	43.5	52.7	21.3	20.9	53.2	50.7
SE	0.55	0.99	5.5	6.7	2.7	2.6	6.7	6.4

Table 5.5.2

Correlations - Plantago

	Veg wt	Rt wt	Rep wt	NFs Yr 1	NFs Yr 2	NFs removed
Total wt						
Rt wt	0.587**					
Rep wt	0.412**	0.805**				
NFs x 2	0.513**	0.832**	0.926**			
NFs x 1	0.199	-0.050	-0.004	-0.058		
NFs rem	-0.185	0.016	0.008	0.119	0.530**	
Total wt	0.514**	0.875**	0.990**	0.947**	-0.004	-0.004
RE	0.030	0.367**	0.653**	0.557**	0.052	-0.107
0.603**						

For 60 df 0.05 prob = 0.25*
0.01 " = 0.325**

Analyses of variance which took account of any environmental effects eg the shade of the wall and tree, were computed using GENSTAT. The effect of treatment did not have a significant effect on any of the variables except the number of spikes initiated in the first year (table 5.5.3). The mean number of spikes initiated (and allowed to flower) in the control treatment was 47.4 whilst the number of spikes initiated and removed in treatments B, C and D were 104.4, 123.5 and 133.4 respectively. This effect was highly significant ($P<0.01$).

One factor which may account for the lack of treatment effect may be the high variability of the Plantago population. This variability is often at its lowest in the control population and increases in the treated populations eg the standard deviation of numbers of spikes in year 2 in treatment A is 38.7 but in treatments B, C and D is 71.9, 50.2 and 48.2 respectively.

ii. Taraxacum officinale

A summary of the Taraxacum data is given in table 5.5.4 and the correlation coefficients in table 5.5.5. Again, leaf weight, root weight and total weight are highly correlated with each other. The diameter of the plant rosette at the beginning of the second year is correlated with root weight ($P<0.05$) at the end of the second year. The number of spikes produced in the second year is correlated ($P<0.05$) with leaf weight in the second year and also with the number of spikes initiated in the first year. The number of spikes initiated in the first year was positively correlated with the number of spikes in the second year and leaf, root and total weight in the second year.

Table 5.5.3

Plantago - Anovas

Variance ratios for the effect of treatment
n = 3/30 (3)

1.	Vegetative weight	VR = 1.931 NS
2.	Weight of root	VR = 0.863 NS
3.	Weight of reproductive matter	VR = 1.035 NS
4.	No of spikes in second year	VR = 1.032 NS
5.	No of spikes produced	VR = 11.156 P<0.01
6.	RA	VR = 1.107 NS

Effect of treatment on no of spikes produced and removed in the first year

Source	DF	SS	SS%	MS	VR
Block	3	9829	6.17	3276	
Col	3	1581	0.99	527	
Block.Row	12	17424	10.93	1452	
Block.Row	9	4810	3.02	534	
Block.Row.Col					
Treat	3	66543	41.76	22181	11.156
Residual	30(3)	59645	37.43	1988	
Total	33	126188	79.18	3824	
Grand Total	60	159832	100.30		

Table 5.5.4

Summary of Taraxacum Data

Treatment A	NFs yr1	NFs yr2	Leaf wt (g)	Root wt (g)	Total wt (g)	Diameter (cm)	NFs remaining
n	16	16	16	16	16	16	16
X	60.6	49.2	15.3	34.5	49.8	37.94	60.6
Med	59.5	41.5	12.9	33.9	44.7	38.50	59.5
SD	20.6	30.3	12.3	20.6	30.4	5.62	20.6
SE	5.2	7.6	3.1	5.2	7.6	1.40	5.2
B							
n	16	16	16	15	15	16	16
X	6.0	38.6	18.3	39.5	58.5	39.25	45.2
Med	6.0	27.5	11.2	39.8	56.8	40.50	41.0
SD	0.0	23.9	18.6	24.2	36.7	5.09	18.5
SE	0.0	6.0	4.6	6.2	9.5	1.27	4.6
C							
n	16	16	16	16	16	16	16
X	2.0	38.9	16.3	36.1	52.4	37.19	54.4
Med	2.0	32.5	13.5	33.2	54.2	38.50	40.5
SD	0.0	31.9	10.8	15.2	21.7	7.88	35.9
SE	0.0	8.0	2.7	3.8	5.4	1.97	9.0
D	16	16	15	16	15	16	16
n	0						
X	0	60.1	20.7	36.5	56.6	40.62	69.9
Med	0	61.0	14.6	33.4	44.0	41.00	54.0
SD	0	34.5	16.8	13.9	28.9	5.51	39.5
SE	0	8.6	4.3	3.5	7.5	1.38	9.9
Total							
n	64	64	63	63	62	64	64
X	17.2	46.7	17.6	36.6	54.2	38.75	57.6
Med	4.0	38.0	13.9	36.1	51.2	40.00	50.0
SD	27.3	31.0	14.7	18.5	29.3	6.12	30.7
SE	3.4	3.9	1.9	2.3	3.7	0.76	3.8

Table 5.5.5

Taraxacum - Correlation Coefficients

	No of flows yr1	No of flows yr2	Leaf wt (g)	Rt wt (g)	Diameter (cm)	No of F's rem
No of fs yr2	0.087					
Leaf wt	0.035	0.264*				
Rt wt	0.073	-0.223	0.533**			
Diam	-0.023	0.081	0.128	0.352**		
No of fs rem	0.153	0.394**	0.661**	0.363**	-0.039	
Tot wt	0.065	-0.005	0.844**	0.904**	0.295*	0.571**

For n = 60 0.05 prob = 0.25*
0.01 prob = 0.325**

A more rigorous test of the effect of treatment was carried out using ANOVAs on GENSTAT. Environmental effects could be eliminated in this test. The data on vegetative weight were markedly skewed so a log transformation was applied to this data before the analysis. Table 5.5.6 shows that none of the effects of treatment were significant. This is possibly because of the high variability inherent in the population eg see standard deviations in table 5.5.4. Two parameters, the number of spikes initiated in the first year and the number of spikes produced in the second year are almost significant. The means show that the largest mean number of spikes initiated in the first year is in the treatment where all spikes were removed but that this trend was not consistent between treatments and, because of the high variability of the population, was not large enough to be significant. Similarly, the mean number of spikes produced in the second year was highest in the treatment where all spikes were removed but again the trend was not consistent and the high variability of the population made any statistical inferences difficult.

5.5.4 Discussion

Reproductive allocation in Plantago lanceolata was 64%. This is somewhat higher than the estimate of 20% for Plantago major obtained by Hawthorn and Cavers (1978). However estimates of 31-47% have been obtained for Plantago coronopus (Waite and Hutchings 1982) and 34.7% for Plantago media (Stewart and Thompson 1982).

It was evident from the means of numbers of spikes produced in the second year (c.47 in Taraxacum and 58 in Plantago) that the assumption that plants in an experimental situation would behave similarly to plants in the field was an erroneous one. The conditions in the

Taraxacum – anovas

Effect on treatment on

1.	Weight of veg matter	VR = 0.683 NS
2.	Log wt veg matter	VR = 1.446 NS
3.	Wt of root	VR = 0.682 NS
4.	Diameter	VR = 1.721 NS
5.	No of spikes initiated in year	VR = 2.371 NS (just)
6.	No of spikes produced in second year	VR = 2.164 NS (just)

n = 3/31 (2)

(2.9) significance level.

experimental plot allowed the plants to reach much greater sizes than had been anticipated, thus perhaps greater numbers of flowers should have been allowed to set seed in the intermediate B and C treatments. Moreover plants should have been planted further apart to avoid any intraspecific competition in their second year of growth. The diameter of Taraxacum officinale plants was c. 40 cm at the beginning of the second year and with plants only spaced 30 cm apart intraspecific competition was probably a complicating factor by the end of the second flowering season.

The data on Plantago lanceolata show that the greater the number of flowers that were removed in the first year the greater the number of flowers that were initiated. Thus there was a compensatory mechanism in Plantago (similar to the production of axillary buds in Digitalis) which prevented any assessment of subsequent reproductive cost. Any resources which might have been diverted to reproduction in the second year were used in a 3 fold increase in current reproductive effort (measured in terms of numbers of flowers initiated). The mean number of flowers initiated in the first year in the control population was 47 whereas in the treatment where flowering was completely prevented it was 133.

This compensatory mechanism is not so evident in the Taraxacum population. There is a tendency for the plants in the treatment where flowering was prevented to have greater mean numbers of flowering initials in the first year, numbers of flowers in the second year, leaf weights and diameters but the variability in the population is so great that the difference between treatment means is not significant.

In Taraxacum the numbers of flowers initiated in the first year is highly correlated with the number of flowers in the second year, leaf weight, root weight and total weight in the second year. This correlation suggests that large, productive plants in the first year remained large, productive plants in the second year. The importance of individual differences within plant populations has been pointed out by Begon (1984). Slight genetic variations in size of relative growth rate which are present at the beginning of a growth period are exacerbated by density, so that over a period of time the size or weight distribution of the population becomes skewed with a few large plants and many small plants. Thus plants with an initial slight advantage in size become even larger relative to the rest of the population. During the second year of the experiment plants of both species began to overlap each other and intra-specific competition became a possible complicating factor in the experiment. This process may partly explain why the variation in both populations is so large.

This experiment therefore has further emphasised the different expressions of reproductive cost that may be present in various species and the difficulty of measuring reproductive cost in the field. Moreover it has also illustrated the possible importance of individual variation in evolutionary ecology which may have been overlooked in previous work which has placed its emphasis on the mean rather than the variation present within a population.

CHAPTER 6 COMPARATIVE REPRODUCTIVE ALLOCATION IN GRASSES

6.1 Introduction

6.1.1 Strategies and tactics

An organism's basic life history strategy is determined by its genotype. Within that strategy or genotype there are a range of possible developmental patterns or tactics which may be adopted under different circumstances (Harper and Ogden 1970, Harper 1977). The tactic or phenotype to be adopted under specific conditions is selected in response to environmental cues (Bradshaw 1965, Harper and Ogden 1970, Stearns 1976) and where these tactical changes in allocation occur it is possible that the phenotypes themselves are adaptive (Harper 1977). Bateson (1963) proposed that genetic control might prevail when patterns of variation in the environment are predictable but phenotypic flexibility should be favoured when unpredictability is the rule.

It is important to realise therefore that variations in reproductive allocation may be as a result of variations in strategy and hence genetically based, or alternatively as a result of variations in tactics which are phenotypic responses to environmental cues. In some studies differences in reproductive allocation may be the result of both genotypic and phenotypic responses. Phenotypic variations in reproductive allocation have been discussed in Ch.3. The present chapter is confined to discussion of comparative differences in strategic reproductive allocation ie the genetic response. A single species may display variations in strategy eg Gadgil and Solbrig (1972) identify 4 different 'biotypes' of Taraxacum officinale. Linseed and Flax, which are different forms of Linum usitatissimum, have been

selected for seed and straw production respectively. In Linseed allocation of dry matter to seed is c.36% while in Flax it is c.20% (Harper and Ogden 1970).

The value of comparative experiments where environmental effects can be removed or controlled has been stressed by Grime (1965). Unfortunately many of the published studies on comparative reproductive allocation do not adequately separate the respective effects of strategy and tactics on reproductive allocation. Consequently many of the results have to be viewed with caution.

6.1.2 Theory

Naively, it might appear that the most adaptive allocation pattern is one which puts most resources into reproduction since this would seem to maximise the contribution to the next generation (Antonovics 1980). However, as we have already seen in Ch.5, there is a trade-off between present reproduction and future reproduction and survival. In practice there is a wide variation in the amounts of resources allocated to reproduction and the way in which various organisms adopt different reproductive allocation strategies in different environments has been the subject of much theoretical debate and practical research.

The most generally accepted theory concerning life history strategies is the concept of r- and K- selection which was initially developed by MacArthur and Wilson (1967). Originally r- selection meant selection for high population growth in uncrowded populations and K- selection referred to selection for competitive ability in crowded populations. The original meaning of r- and K- selection has been expanded by various authors including Pianka (1970), (1972), Gadgil and Solbrig (1972) and Southwood (1977). The expanded concept may suggest that

r-selection occurs in habitats where density independent mortality is prevalent, ephemeral habitats, and in cases where species allocate a large proportion of resources to reproduction whilst K- selection occurs in habitats where density dependent mortality is prevalent, stable habitats, and in cases where species show low reproductive allocation (Parry 1981). Gadgil and Solbrig (1972) suggested that r-selected genotypes may have a greater reproductive allocation, higher birth rate and shorter lifespan than K- selected genotype. Harper (1967) suggested the possibility that colonising species of plants would have higher reproductive allocations than plants of mature habitats, while Hirshfield and Tinkle (1975) extended this argument to predict that semelparous species should show higher reproductive efforts than related iteroparous species. In summary, the extended concept of r- and K- selection predicts an association of life-history traits into 2 groups (Stearns 1977):

1. r- selection - early age of maturity, large number of young, semelparity, no parental care, a large reproductive effort.

2. K- selection - delayed reproduction, small number of young, iteroparity, parental care and a smaller reproductive effort.

Consequently many of the comparative studies on reproductive allocation have tried to relate observed differences in the level of reproductive allocation to r- and K- selection.

Despite the ubiquity of the theory of r- and K- selection, reservations about its general validity have been raised by various authors. Stearns (1976) points out that the theory of r- and K- selection assumes a deterministic environment. He suggests that in a fluctuating

environment with a population near equilibrium, the environment may cause high juvenile mortality. In these circumstances populations should evolve a smaller reproductive effort and greater longevity. This theory has been termed the stochastic model of life history evolution as opposed to the deterministic model of r- and K- selection (Solbrig 1981).

Wilbur et al (1974) and Wilbur (1976) maintain that the concept of r- and K- selection is an oversimplification and that other factors will affect life history strategies such as size, dispersal, predation and environmental uncertainty. Gadgil and Solbrig (1972) may have implied this indirectly when they suggested that r- and K- selection only really operates in the context of closely related taxa. The differences between species or higher taxa are likely to involve many adaptive changes (but see later). Wilbur (1976) confined the use of r- and K- selection to the original definition based on crowding or competition and advocated the concept of a multidimensional selection regime. One dimension was envisaged as the continuum from r- to K- selection and other dimensions could include environmental uncertainty, predation etc.

A further criticism of r- and K- selection, particularly as applied to plants has been pointed out by Grubb (1976). In many habitats growth rate and reproductive rate are much less important than the ability to survive natural stresses. Grime (1977) proposed that stress and disturbance may interact to select for patterns of allocation. He suggests that to some extent many of the inconsistencies related to the extended theory of r- and K- selection can be resolved by recognising the distinction between the juvenile and mature phases of life cycles (Grime 1979). A 3 strategy model is proposed which can be reconciled

with the concept of r- and K- selection (see fig 6.1.1).

The 3 basic strategies which are recognised are 'ruderal' 'competitive' and 'stress tolerant' which can be located on a triangular model depicting the relative importance of competition, stress and disturbance (see fig 6.1.2). Ruderal plants would be expected to have a large proportion of annual production devoted to seeds whilst competitive and stress tolerant plants would have smaller proportions devoted to seeds. Flowering in stress tolerant plants would tend to be delayed and intermittent (Grime 1979). This theory of plant strategies has been adopted by some researchers to explain patterns of allocation eg Trivedi and Tripathi (1981) but as yet there have been no comprehensive studies relating allocation patterns to c- s- and r- selection.

6.1.3 Reproductive allocation in different habitats

There have been numerous and varied studies of reproductive allocation in various habitats and many of the conclusions have been conflicting. The majority of the published work can be divided into 3 categories:

i. studies which look at reproductive allocation of entire communities in different habitats;

ii. studies which consider closely related species and relate the observed differences in RA to their habitats;

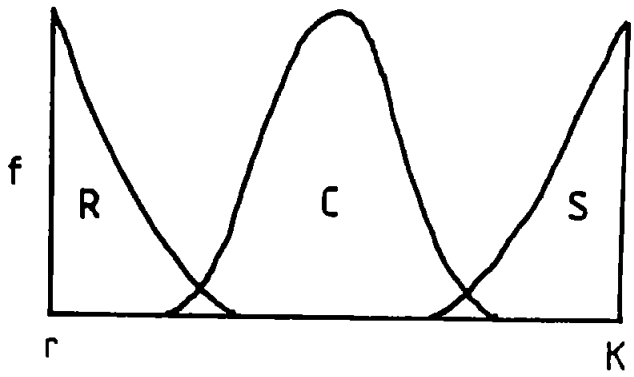


Fig 6.1.1 Diagram describing the frequency (f) of ruderal (R), competitive (C), and stress-tolerant (S) strategies along the r-K continuum.
(after Grime 1977)

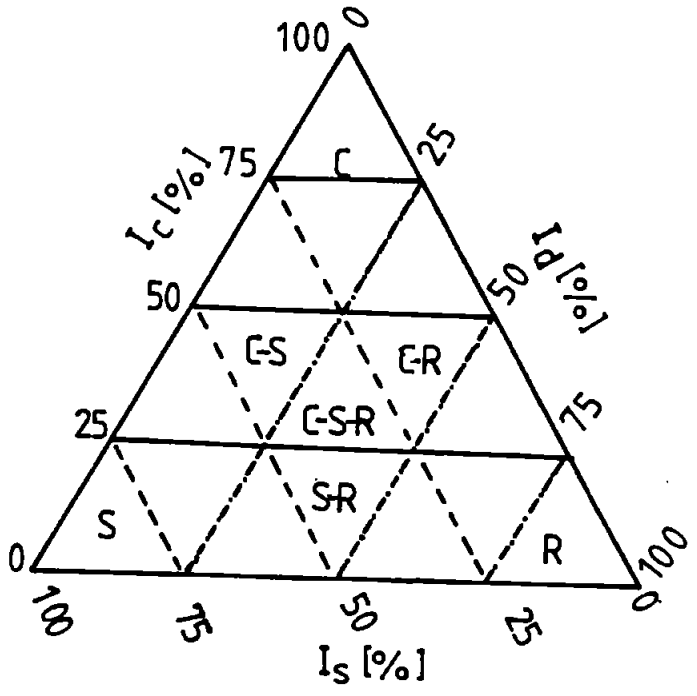


Fig 6.1.2 Model describing the various equilibria between competition, stress, and disturbance in vegetation and the location of primary and secondary strategies. I_C, relative importance of competition (——); I_S, relative importance of stress (– – –); I_d, relative importance of disturbance (——).
(after Grime 1977)

iii. studies which consider populations of a single species in different habitats.

6.1.3.i Community reproductive allocation

As would be expected from the observed trade-offs between present reproduction and future survival and reproduction, community reproductive allocation is typically higher in semelparous plants than in iteroparous plants. In a community of field species, Abrahamson (1979) found the average floral and fruiting RA of annuals (20%) to be significantly greater than perennials (12%). Introduced annuals had higher RA's than native annuals. Similarly Struik (1965) found that the average RA of annuals was higher than perennials in forest (25>9%) and in open habitats (28>10%). Primack (1977) found that for 40 species of Plantago reproductive allocation was on average higher in annuals (2.3 mg seed per $10cm^2$ leaf) than perennials (1.6mg seed per $10cm^2$ leaf). An annual Lupinus species was found to have a greater RA than 2 perennials (Pitelka 1977).

However, despite this apparent trend in community RA, Willson (1983) notes several examples of individual species RA being 'high' in perennials eg 26% in Lupinus arboreus (Pitelka 1977), 35% in Solidago speciosa (Abrahamson and Gadgil 1973) and 'low' in annuals eg 10% in Polygonum minimum (Hickman 1977) and 5% in Impatiens capensis (Abrahamson and Hershey 1977). Some biennials have a high RE eg 27% in Dipsacus sylvestris (Caswell and Werner 1978) and 25-35% in Smyrnium olusatrum (Lovett-Doust 1980) but in Pastinaca sativa the level of RA recorded is 12% (Lovett-Doust 1980b). These individual examples may of course be exceptions to the general community 'rule'.

In many of these cases the situation may be complicated by the presence of various modes of vegetative reproduction in perennials (see 6.1.4). In addition to this factor, most existing estimates of RA are based on the biomass of the reproductive parts as a proportion of the whole plant (or sometimes total above ground biomass). Perennials maintain at least some of their biomass from year to year. Jurik (1983) has suggested that if RA is measured including the metabolic costs of production then the absolute differences in the RA of annuals and perennials may often be less than has been measured using conventional methods. The metabolic costs of production comprise the total energy required to produce and maintain plant structures and Jurik (1983) estimates these using a predictive model. For perennials then the relevant index of RA which should be made on an annual basis, is the allocation to reproductive parts as a proportion of the annual increment in total biomass (Willson 1983). However, in practice very few studies use this measure. It can be seen, therefore, that as yet the disparity of RA in semelparous and iteroparous species is not clearly defined.

Given that annuals, at least on the community level, tend to have a higher level of RA than perennials, it is perhaps not surprising that RA seems to decline from open habitats (which often contain more annual species) to closed habitats such as forests (which often contain more perennial species). This pattern was found by Struik (1965), Gadgil and Solbrig (1972), Newell and Tramer (1977) and Abrahamson (1979). Abrahamson (1979) found that the average RA of perennials in an open field (12%) was greater than that in the forest (8%). In fact there were no annuals present in the forest community. Comparing a 1 year field, a 10 year field and a forest, Newell and Tramer (1978) found that RA in an early successional field (24%) exceeded that in both the

other habitats (5% each). Stewart and Thompson (1982) found a decrease in RA from an open quarry to grassland but found an intermediate level of RA in woodland. They attributed this apparent anomaly to interspecific competition, as did Luftensteiner (1980) who found a higher RA in the ground flora species of a woodland than in a nearby meadow. In general therefore, studies of RA in communities over successional seres tend to confirm the predictions of r- and k-selection ie average RA in communities of early successional stages tends to be higher than average RA of communities in late successional stages.

6.1.3 ii. Reproductive allocation of related species in different environments

Many of the studies of RA which have been used to support the theory of r- and k- selection have looked at several closely related species in their native habitats. Any observed differences in RA are then related to differences in their specific strategies. Some of the earlier studies looked at RA in related species over a successional sequence. Abrahamson and Gadgil (1973) looked at 4 species of Solidago at a dry site, wet site and hardwood site and found that the species found in the dry (early successional) site had higher RAs than the species found in the hardwood site (late successional). The wet meadow site had intermediate values. Two species were found at more than one site and in these cases the same general pattern was displayed. RA in S.nemoralis (dry) > S.speciosa (dry) > S.canadensis (wet) > S.speciosa (wood) > S.rugosa (wet) > S.rugosa (wood). Similarly Gaines et al (1974) found that Helianthus annuus, a species of sunflower characteristic of old field sites, had a greater RA than H.grosserratus (roadside ditch) H.laetiflorus (prairie) H.hirsutus (forest).

In contrast with these studies Bradbury and Hofstra (1976) working on Solidago canadensis and Werner and Platt (1976) working on other Solidago species found no clear gradient of RA across a soil moisture gradient. Nevertheless Werner and Platt (1976) did find the total weight of seeds per stem was less in the prairie population than in the old field population and that seeds were fewer but larger in the prairie.

Latitudinal variations in RA in related species have been investigated by McNaughton (1975) in 3 species of Typha. He suggested that populations from short growing season locations should be more subjected to r- selection and in fact the northern climate specialist, T. angustifolia, did have a higher biomass investment in fruit production. Perhaps the most comprehensive study of this type was conducted by Primack (1979) on 40 species of Plantago. Annual species were found to have higher RAs than perennial species and perennial 'weed' species had higher RAs than perennial 'nonweeds'. Rare species had lower RAs and spring annuals had higher RAs than summer annuals. However, since the specimens were collected either from field populations or herbarium collections it is not certain that there were no phenotypic environmental factors in the data.

Other studies which indicate that there is a discernible variation in RA between closely related species which can be interpreted as a strategic adaptation to habitat are Pitelka (1977) for 3 Lupinus species, Wilbur (1976) for milkweeds, Asclepias species, Lee and Cavers (1981) for 2 Rumex species, Hawthorn and Cavers (1978) for 2 Plantago species and Benzing and Davidson (1979) for 2 Tillandsia species. Solbrig (1981) found that of the several species of Viola studied the species with the highest RA is a ubiquitous colonising species and he interprets this as evidence of an r- strategy.

However, Hickman (1977) found that species of Polygonum did not vary RA uniformly along a moisture gradient and warns against incautious application of r- and k- selection theory. Similarly Bell et al (1979) found that differences in RA of 8 desert winter annuals were species specific not site specific.

6.1.3.iii Reproductive allocation of single species populations in different environments

Genetic habitat-based variation in RA within a single species was first identified by Gadgil and Solbrig (1972) for Taraxacum officinale. They discovered a greater frequency of a biotype with a high RA in a population from an environment subject to high density independent mortality. Similarly, Grace and Wetzel (1981) found that biotypes of Typha latifolia found in habitats exposed to high levels of disturbance had a higher level of allocation to sexual reproduction. Genetically based differences in RA among populations of a single species over an environmental gradient have also been found by Abrahamson and Gadgil (1973) for Solidago speciosa and S rugosa and by Bostock (1980) for Tussilago farfara. Douglas (1981) found that RA increased with altitude for Mimulus primuloides and that this difference was genetically based. Roos and Quinn (1977) also found some evidence of genetic differences in RA in Andropogon scoparius which first increased then decreased sexual RA with increasing age of field. Both genetic and environmental factors have been found to effect RA in populations of Plantago lanceolata growing in central North Carolina (Antonovics 1980).

Changes in RA in different environments have also been reported by Abrahamson (1975), Whigham (1973), and Kawano and Masuda (1980) but it is not known whether these differences are genetically based. In many

species a phenotypic, tactical variation in RA in different environments has been noted but this variation has disappeared when plants have been grown in a homogeneous environment eg Hickman (1975), Holler and Abrahamson (1977), Abrahamson and Hershey (1977), Raynal (1981), and Reinartz (1984). The reproductive effort of a population may also vary over time. Soule and Werner (1981) found differences in RA of populations from 3 different habitats in one year but not the next and Jaksic and Montenegro (1979) found that resource allocation patterns changed from year to year in populations of herbaceous species in the Chilean matorral.

Perhaps it is not surprising that field studies on single species at several sites do not necessarily agree with theoretical predictions since as Soule and Werner (1981) point out, resource allocation patterns in a single species can be extremely variable both in time and space. This variability can be both genetic and phenotypic (see Ch.3). The theory is based on the optimal adaptive characteristics in a population (Hickman 1975, Hirshfield and Tinkle 1975, Werner 1976).

6.1.4 Changes in vegetative reproductive allocation with habitat

Previously, only changes in sexual reproductive allocation have been considered. In some species, vegetative RA may be an alternative to sexual RA and thus complicate any observed patterns. Allocation to vegetative RA can be very high eg 48% in Podophyllum peltatum (Sohn and Policansky 1977), 26% in Achillea millefolium (Bostock and Benton 1979) and 23% in Tussilago farfara (Ogden 1974). Williams (1975) predicted an emphasis on sexual reproduction and long distance dispersal of populations at high density and greater vegetative reproduction at low density.

In species with both sexual and vegetative reproduction Bradbury and Hofstra (1976) and Werner and Platt (1976) found no recognisable shifts in RA (of both kinds) over an environmental gradient. However sexual RA decreases while vegetative RA remains relatively constant as the environment becomes shadier for some herbaceous species. (Struik 1965, Abrahamson 1975, Pitelka et al 1980). Similarly Jurik (1983) found sexual RA of Fragaria virginiana and F. vesca decreased in shade but the vegetative RA did not show a tendency to vary between sites. Contrary to Williams' (1975) predictions, allocation to vegetative propagation in Mimulus primuloides changed little with increasing environmental harshness (elevation) (Douglas 1981). Also, Bostock (1980) found that Tussilago farfara plants from the most severe habitat studied had a higher vegetative and a lower seed RA.

Pitelka et al (1980) suggest that in Aster acuminatus resources are only devoted to sexual reproduction rather than vegetative reproduction when extra resources are available. This is similar to the effect found in Amphicarpum purshii by McNamara and Quinn (1977) and Gymnarrhena micrantha (Zeide 1978) where only larger plants produce aerial sexual fruits as opposed to underground asexual fruits which are always present. Bostock and Benton (1979) suggest that selection need not act in the same direction on seed and vegetative reproduction. In their study of 5 perennial composites they suggest that seed and vegetative reproduction should be summed to give an estimate of r-ness or K-ness. When this was done Tussilago farfara is the most r-strategic and Achillea millefolium the most K- strategic. Because this distinction corresponds to the likely degrees of disturbance in each species' typical habitat they contend that it accords with the predictions of r- and K- selection.

6.1.5 Validity of comparisons

Because of the wide variety of methods used to determine reproductive allocation (see Ch.2) the absolute values of RA obtained for different species are difficult to compare. Many studies have used the Harper and Ogden (1970) definition of reproductive effort which considers only the weight of the propagules themselves. Others have included the weight of associated structures eg Hickman 1975. Some have included below ground biomass and others have excluded it.

In the majority of studies no account is taken of the different morphologies of the plants which are compared (see Ch.2). The problem of differences in morphology of plants can be illustrated by reference to some of the data of Stewart and Thompson (1982). They include all the component parts necessary to reproduction in their definition of RA. Therefore in scapigerous species such as Carex flacca the stem is included in the estimate. However, in order to exclude any photosynthetic tissue, in the case of species with leaf-bearing stems such as Centaurea nigra RA only includes structures above the highest leaf. Consequently Carex flacca is estimated as having an RA of c.51% whereas Centaurea nigra has an RA of c.17%. This would seem to be an anomaly since the majority of the biomass of Centaurea nigra is composed of stems which support the reproductive structures. The apparent anomaly is in fact an inevitable consequence of arriving at a definition of RA applicable to plants of widely varying morphology.

A further problem, already briefly alluded to, is that in many field studies the differential genetic and environmental effects are not separated. Even if a shift in RA is demonstrated the direction of the shift may vary with the position of the plant relative to its optimal environmental conditions (Soule and Werner 1981). The inadequacy of

field data obtained under controlled conditions was first suggested by Gadgil and Solbrig (1972) and is emphasised by Thompson and Stewart (1981). Measurements made under identical, close to ideal conditions are more likely to illustrate the genetically programmed reproductive strategies. The results of Harper and Ogden (1970) and Van Andel and Vera (1977) indicate that any given population of a species possesses a fixed maximum potential RA which is realised under optimal or close to optimal conditions. This optimal potential RA is likely to be more useful as a predictive, comparative measure. The lack of appropriate data means that many of the generalisations forwarded by Harper and Ogden (1970) and Harper (1977) have not been proved or disproved conclusively.

6.2 Method

6.2.1 Introduction

The aim of this experiment was to determine the optimal potential reproductive allocation for a range of grass species of contrasting ecology. As yet there has been no comprehensive study relating reproductive allocation to C-, S- and R- strategies. Grime (1974) suggested that the ruderal axis in his strategic model might be related to reproductive allocation. This hypothesis could be examined by comparing the reproductive allocations of species from C-, S- and R- environments. The case for comparative experiments has been argued by Grime (1965, 1984) and Grime and Hunt (1974). They emphasise the need for broadly based research which can put the selection forces and design constraints which have interacted to determine the current ecology of plants into general perspective. Moreover, comparative, laboratory based experiments may allow much economy of effort in research designed to recognise the general functional characteristics of large numbers of species.

It was decided that species from different environments should be selected from within the Gramineae. The comparison of species within one family allows greater flexibility in terms of possible range of habitats than if the comparison is restricted to plants within one genus. A comparison of species from different families might lead to difficulties in comparing reproductive allocation because of differences in plant structure (see Ch.2). Species in the Gramineae are relatively similar with respect to their morphology so problems of this type are diminished. This family is one of the most prominent contributors to the contemporary British flora in terms of both numbers of species and biomass (Grime 1984). The Gramineae also exhibits a

wide-ranging distribution in terms of habitat although it occurs most frequently (relative to other species) in grassland and wasteland habitats (Grime, Hodgson and Hunt 1985). A further practical reason for choosing the Gramineae as the family for reproductive allocation comparison is that a high proportion of annual and perennial grasses are capable of germinating immediately after collection, with few pre-germination requirements (Grime et al 1981).

6.2.2 Species

In the summer of 1981 as many different species of Gramineae as possible were collected from various habitats in Devon and SE Cornwall (see map 6.2.1 and table 6.2.1). There is a deficiency of calcareous habitats in Devon and in order to broaden the range of possible species, additional species were obtained from collections of seed at the Unit of Comparative Ecology (NERC), University of Sheffield. These species were Briza media, Avenula pratensis and Koeleria macrantha. To obtain an estimate of the ecological amplitude of one particular species, seed of Holcus lanatus was collected from 4 different habitats ie rough grassland in Plymouth, a hedgerow at Bere Alston, topsoil on waste ground near the Polytechnic and moorland on Dartmoor. Seeds were stored in manilla envelopes at room temperature until February 1982.

Unfortunately, lack of greenhouse space meant that not all of the collected species could be cultivated. Species selection was carried out on the basis of under or over-representation of the habitat, germinability and the availability of data for Rmax and morphology index (Grime 1979) which would facilitate comparison of the species eg Melica uniflora was excluded because of lack of data whereas Elymus repens was excluded because it showed very low germinability. Grime et al (1981) also found that Elymus repens displayed low germination

Map 6.2.1

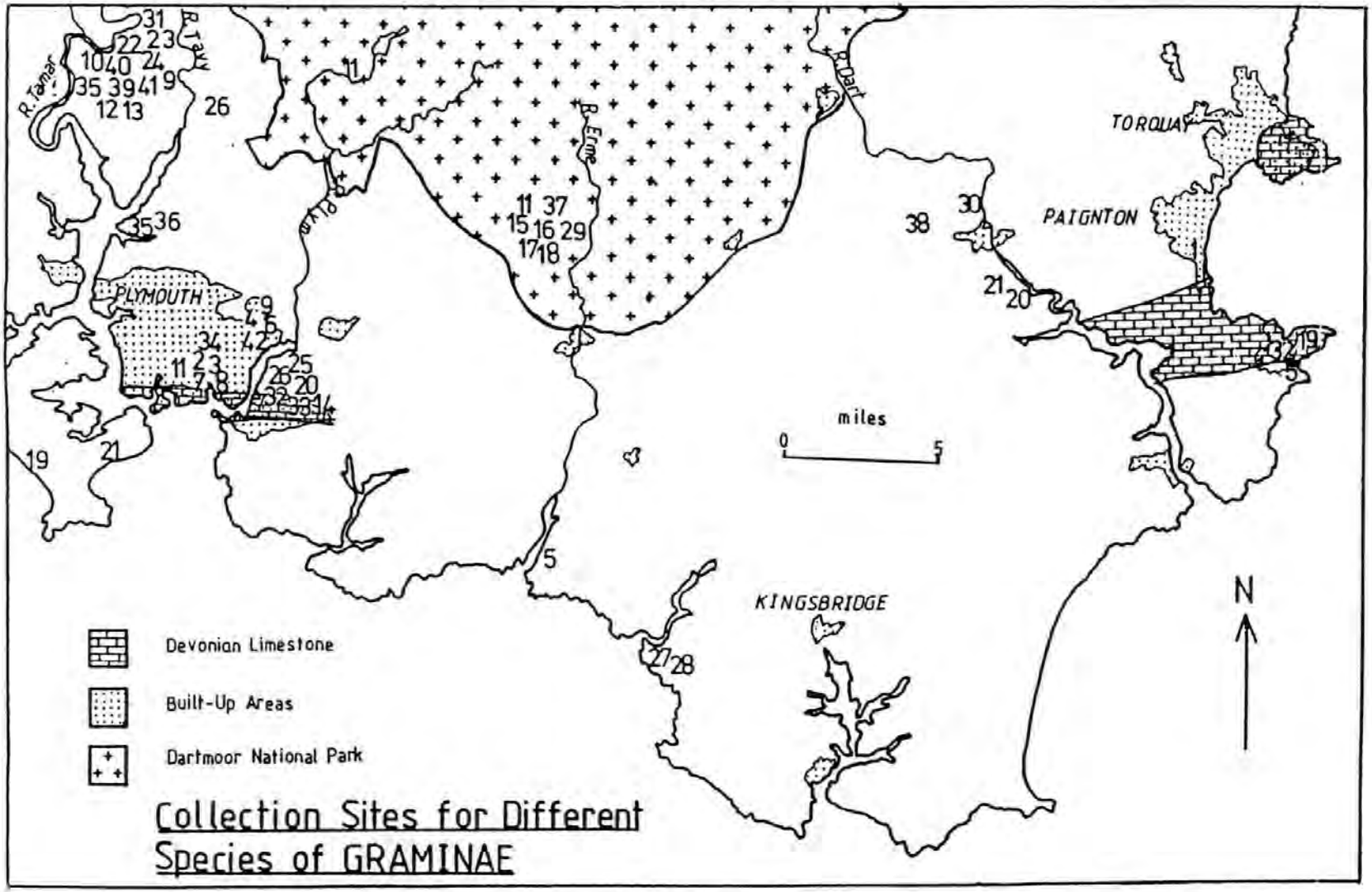

R. Tamar
R. Tavy
R. Plym
R. Erme
R. Dart
PLYMOUTH
TORQUAY
PAIGNTON
KINGSBRIDGE
miles
0
5
N
Devonian Limestone
Built-Up Areas
Dartmoor National Park
Collection Sites for Different Species of GRAMINAE

Table 6.2.1

KEY TO MAP No on Map	Species	Grid Reference OSGB sheet 202 (1936) and 201		Date
	Wasteland and rough grassland			
1	Bromus sterilis	289800mE	60100mN	26.7.81
2	Hordeum murinum	248300mE	55300mN	4.8.81
3	Lolium perenne	248300mE	55300mN	4.7.81
4	Arrhenatherum elatius	247800mE	55400mN	4.7.81
5	Bromus hordaceous	251400mE	54000mN	6.7.81
		261700mE	47200mN	27.7.81
6	Dactylis glomerata	249000mE	55700mN	26.7.81
7	Festuca arundinacea	248500mE	55600mN	4.8.81
8	Poa trivialis	248500mE	54800mN	27.7.81
9	Poa annua	244200mE	68000mN	24.8.81
10	Elymus repens	244100mE	67100mN	26.10.81
11	Holcus lanatus (rough grass)	249000mE	54000mN	29.9.81
11	Holcuslanatus (waste)	248100mE	67400mN	4.8.81
12	Agrostis capillaris	250700mE	55400mN	18.8.81
13	Agrostis stolonifera	244200mE	67000mN	29.9.81
14	Phalaris canariensis	250600mE	54500mN	18.8.81
	Moorland			
15	Molinia caerulea	262500mE	61500mN	24.9.81
16	Nardus stricta	262600mE	61500mN	18.8.81
17	Danthonia decumbens	262600mE	61500mN	19.8.81
18	Festuca ovina	262600mE	61500mN	21.7.81
19	Festuca rubra	294300mE	56500mN	8.81
11	Holcus lanatus	262500mE	61500mN	9.9.81
	Woodland and Hedgerow			
20	Festuca gigantea	251200mE	54400mN	18.8.81
		276800mE	61400mN	8.81
21	Brachypodium sylvaticum	244000mE	51000mN	25.6.81
		276800mE	61400mN	8.81
22	Bromus ramosus	244500mE	67000mN	29.9.81
23	Elymus caninus	244400mE	67800mN	29.9.81
24	Melica uniflora	244500mE	67000mN	3.8.81
25	Milium effusum	251500mE	55700mN	18.8.81
26	Holcus mollis	251500mE	55700mN	18.8.81
		248800mE	66100mN	25.10.81
		244400mE	67000mN	29.9.81
11	Holcus lanatus (hedgerow)	244200mE	68000mN	24.8.81
	Sand dunes			
27	Elymus farctus	266200mE	43700mN	8.81
28	Vulpia bromoides	266200mE	43800mN	8.81

No on Map	Species	Grid Reference OSGB sheet 202 (1936) and 201		Date
	Freshwater			
29	Deschampsia caespitosa	262500mE	61500mN	18.8.81
30	Glyceria fluitans	279500mE	61700mN	8.81
31	Phalaris arundinacea	244200mE	68000mN	19.8.81
	Dry calcareous			
32	Trisetum flavescens	250700mE	55000mN	18.8.81
		251400mE	54000mN	18.8.81
33	Poa compressa	251400mE	54000mN	27.7.81
34	Desmazeria rigida	248300mE	55700mN	21.7.81
	Dry acidic			
35	Aira caryophyllea	244500mE	61100mN	29.7.81
		244000mE	67400mN	6.81
36	Aira praecox	244500mE	61100mN	29.7.81
37	Deschampsia flexuosa	262400mE	61100mN	18.8.81
	Pasture			
38	Alopecurus pratensis	277500mE	61750mN	4.8.81
39	Anthoxanthum odoratum	244500mE	67100mN	25.6.81
40	Phleum pratense	245100mE	68000mN	24.8.81
41	Poa pratensis	243800mE	67700mN	7.81
42	Cynosurus cristatus	248300mE	55300mN	28.9.81
	Additional species	(not on map)		
43	Briza media	Sheffield		1979
44	Koeleria macrantha	Sheffield		1979
45	Avenula pratensis	Sheffield		1979

rates for up to 6 months after collection. The selected species are listed in table 6.2.2.

6.2.3 Cultivation

Seeds were germinated on moistened filter paper in petri dishes and transferred to 5" pots containing John Innes potting compost when they were large enough to handle. Ten seedlings of each species were potted out in March 1982 (although not all of the 10 plants survived - see results). Those species which had a chilling requirement ie Bromus ramosus, Molinia caerulea and Nardus stricta (Grime et al 1981) were placed in moist sand in petri dishes in a refrigerator for 3 weeks at a temperature of c. 5^{o}C before germination.

The pots containing the plants were then placed on wooden slats on a Dexion framework in an unheated greenhouse at Scardon Place near the Polytechnic. The pots were arranged in a randomised block design and were re-randomised every 2 weeks. The design could therefore be regarded as completely random in any subsequent analysis. The plants were watered as required - in the summer twice every day. At the height of the summer when growth was at its maximum, a general liquid fertilizer was applied. It was noted however, that some plants (eg specimens of Deschampsia flexuosa) died after this treatment. Small amounts of rust appeared on some species eg Holcus lanatus at the beginning of the 1983 season and this was treated by applying a Benlate fungicide.

Species which were known to attain a large size eg Deschampsia caespitosa and Brachypodium sylvaticum were initially p otted up in 7" pots whilst species which appeared to outgrow their 5" pots were transferred to 7" pots as necessary (see table 6.2.2). Thus the

Selected Species

		7" pot
1.	Aira praecox	
2.	Aira caryophyllea	
3.	Anthoxanthum odoratum	
4.	Elymus caninus	
5.	Arrhenatherum elatius	
6.	Elymus farctus	
7.	Alopecurus pratensis	
8.	Agrostis capillaris	
9.	Brachypodium sylvaticum	
10.	Bromus ramosus	
11.	Bromus hordaceous	
12.	Bromus sterilis	
13.	Briza media	
14.	Desmazeria rigida	
15.	Cynosurus cristatus	
16.	Dactylis glomerata	
17.	Deschampsia caespitosa	
18.	Deschampsia flexuosa	
19.	Festuca arundinacea	
20.	Festuca gigantea	
21.	Festuca ovina	
22.	Festuca rubra	
23.	Glyceria fluitans	
24.	Avenula pratensis	
25.	Hordeum murinum	
26.	Holcus mollis	
27.	Koeleria macrantha	
28.	Lolium perenne	
29.	Milium effusum	
30.	Molinia caerulea	
31.	Phleum pratense	
32.	Phalaris arundinacea	
33.	Poa annua	
34.	Poa pratensis	
35.	Poa trivialis	
36.	Danthonia decumbens	
37.	Trisetum flavescens	
38.	Vulpia bromoides	
39.	Agrostis stolonifera	
40.	Holcus lanatus (grass)	
41.	Holcus lanatus (Hedgerow)	
42.	Holcus lanatus (topsoil)	
43.	Holcus lanatus (moorland)	

intention was to obtain an estimate of reproductive allocation for species which had been grown in optimum conditions.

6.2.4 Harvesting

For all species, the panicle and stem were collected above the highest leaf on the culm. In immature panicles this was taken to be at the first node. In some species, particularly the annuals, flowering occurred in a simultaneous flush eg *Aira caryophyllea*. In these cases harvesting of all the panicles was carried out when the majority were mature. The remaining vegetative parts were cut off at ground level.

Ideally, root biomass should also have been collected. However it was found that separation of the grass roots from the compost was extremely difficult and resulted in much loss of root material. The harvested plant parts were then placed in manilla envelopes and dried in an oven at $60^{o}C$ for 48 hours. In the case of other species eg *Holcus lanatus* or *Dactylis glomerata*, panicles matured individually. If one of these plants had flowered by the end of the first season the vegetative parts were harvested then ie October 1982. However, if a plant had not flowered in the first season it was left until the end of the second season ie October 1983 before harvesting of the vegetative parts took place. In some species no flowering had occurred at the end of this period eg *Avenula pratensis*, whereas in others eg *Briza media* only a certain proportion of the original 10 plants had flowered. Once dried, plant parts were placed in a large polystyrene tray and weighed on a Oertling TP40 balance.

Plate 6.2.4 Grasses at Skardon Place

6.3 Results

6.3.1 General characteristics of data

The flowering behaviour of the different species of Gramineae is shown in Table 6.3.1. Twenty plants out of a total 430 did not survive and of the remaining plants 4 species failed to flower in the time available (Avenula pratensis, Elymus farctus, Festuca rubra and Phalaris arundinacea). Eight of the 22 species which flowered and were harvested in the first year were annuals (see table 6.3.1). Species which showed very low numbers of flowering plants (<35%) were Briza media, Deschampsia caespitosa, Milium effusum, Molinia caerulea and Agrostis stolonifera.

The means and standard errors for vegetative weight, reproductive weight and reproductive allocation for each species are shown in table 6.3.2. The means for reproductive weight include values of 0 for those plants which did not flower. For those species where the flowering rate was less than 100%, the mean reproductive weights for the flowering plants alone are given in table 6.3.3. Reproductive allocations are based on the values for reproductive weight in table 6.3.2. The vegetative weights range from a maximum mean of 127.9g in Deschampsia caespitosa to a minimum mean of 3.4g in Aira praecox. Reproductive weights range from 27.3g in Bromus sterilis to 0.01g in Milium effusum and Molinia caerulea. Reproductive allocation expressed as the percentage dry weight allocated to reproductive structures ranges from 66.3% in Desmazeria rigida to 0.23% in Molinia caerulea and 0.02% in Milium effusum. Zero values of RA were given to species which did not flower.

Flowering Behaviour of species

Table 6.3.1

Species	No Flowering	Harv Yr 1	Harv Yr 2
1. Aira praecox	10/10	✓ a	
2. Aira caryophyllea	10/10	✓ a	
3. Anthoxanthum odoratum	10/10	✓	
4. Elymus caninus	10/10	✓	
5. Arrhenathenaum elatius	10/10	✓	
6. Elymus farctus	0/10		✓
7. Alopecurus pratensis	7/10		✓
8. Agrostis capillaris	10/10	✓	
9. Brachypodium sylvaticum	10/10	✓	
10. Bromus ramosus	8/8	✓	
11. Bromus hordaceous	10/10	✓ a	
12. Bromus sterilis	10/10	✓ a	
13. Briza media	3/10		✓
14. Desmazeria rigida	10/10	✓ a	
15. Cynosurus cristatus	10/10	✓	
16. Dactylis glomerata	10/10	✓	
17. Deschampsia caespitosa	2/10		✓
18. Deschampsia flexuosa	6/8		✓
19. Festuca arundinacea	8/8	✓	
20. Festuca gigantea	9/10	✓	
21. Festuca ovina	9/10		✓
22. Festuca rubra	0/10		✓
23. Glyceria fluitaris	6/10		✓
24. Avenula pratensis	0/9		✓
25. Hordeum murinum	10/10	✓ a	
26. Holcus mollis	6/9		✓
27. Koeleria macrantha	7/10		✓
28. Lolium perenne	10/10	✓	
29. Milium effusum	1/10		✓
30. Molinia caerulea	1/5		✓
31. Phleum pratense	10/10	✓	
32. Phalaris arundinacea	0/7		✓
33. Poa annua	10/10	✓ a	
34. Poa pratensis	8/10		✓
35. Poa trivialis	10/10	✓	
36. Danthonia decumbens	5/8		✓
37. Trisetum flavescens	10/10	✓	
38. Vulpia bromoides	10/10	✓ a	
39. Agrostis stolonifera	3/10		✓
40. Holcus lanatus - grass	10/10		✓
41. - hedgerow	8/9		✓
- waste	3/9		✓
- moorland	8/10		✓

a = annual

Summary of data for each species

Species	No	Mean veg wt (g)	SE veg wt (g)	Mean Rep wt (g)	SE Rep wt (g)	Mean RA%	SE RA%	Mean Total wt(g)	SE Total wt(g)	RMAX
A praecox	1	3.43	0.24	4.24	0.37	54.94	1.42	7.66	0.57	0.87
A caryphollea	2	3.89	0.27	5.07	0.54	55.55	2.03	8.97	0.78	-
A odoratum	3	11.6	1.58	1.92	0.50	14.12	2.90	13.52	1.87	0.94
E caninus	4	51.22	17.86	17.26	1.11	25.14	1.08	68.47	2.5	-
A elatius	5	44.6	8.6	5.75	1.37	11.40	1.18	50.3	9.5	1.30
E farctus	6	87.4	17.1	0	0	0	0	8.74	17.1	-
A pratensis	7	18.81	1.46	0.566	0.15	3.00	0.82	19.38	1.47	1.29
A capillaris	8	27.2	4.5	1.94	0.34	8.24	1.62	29.2	4.5	1.36
B sylvaticum	9	44.13	3.01	15.81	2.00	25.64	1.86	59.9	4.6	1.35
B ramosus	10	41.7	5.00	8.02	1.99	16.22	3.34	49.7	5.8	-
B ramollis	11	19.34	1.43	19.60	1.79	50.18	1.51	38.94	3.02	-
B sterilis	12	35.10	1.16	27.20	5.0	40.90	4.4	62.3	4.8	-
B media	13	18.82	2.71	0.12	0.06	0.56	0.29	18.94	2.72	1.11
D rigida	14	3.73	0.32	7.25	0.53	66.28	1.32	10.98	0.81	1.60
C cristatus	15	10.10	1.55	3.93	0.49	30.5	3.4	14.03	1.87	1.54
D glomerata	16	91.1	8.7	13.89	1.99	13.94	2.00	105.0	8.3	1.31
D caespitosa	17	127.9	24.6	0.368	0.29	1.08	0.98	128.93	77.36	1.45
D flexuosa	18	10.5	4.7	1.14	0.63	13.6	8.0	11.6	4.7	0.81
F arundinacea	19	77.4	4.0	6.69	1.41	7.55	1.11	84.1	5.3	-
F gigantea	20	25.9	3.6	5.46	1.28	17.0	3.2	31.4	4.1	1.44
F ovina	21	29.5	6.3	1.46	0.48	6.23	2.49	31.0	6.3	1.00
F rubra	22	55.4	6.3	0	0	0	0	55.4	6.3	1.18
G fluitans	23	15.84	2.55	0.161	0.083	1.33	0.79	16.0	2.52	1.33
Av pratense	24	22.6	3.00	0	0	0	0	22.6	3.00	0.75
H murinum	25	28.58	1.05	26.06	2.12	47.11	1.99	54.64	2.73	1.76
H mollis	26	16.37	3.02	1.24	0.54	6.15	2.12	17.6	3.5	1.44
K macrantha	27	15.6	3.2	0.92	0.42	8.3	4.2	16.56	2.99	0.94
L perenne	28	17.29	2.06	3.95	0.69	18.67	2.59	21.24	2.37	1.30
M effusum	29	34.5	4.6	0.01	0.01	0.02	0.02	34.5	4.6	1.11
M caerulea	30	3.45	0.63	0.01	0.01	0.23	0.23	3.46	0.65	-
P pratense	31	26.4	3.5	2.148	0.22	8.70	1.29	28.5	3.5	-
P arundinacea	32	31.2	9.6	0	0	0	0	31.2	9.6	-
P annua	33	7.35	1.20	9.13	1.23	57.5	5.3	16.48	2.02	2.70
P pratensis	34	22.63	3.07	0.782	0.25	3.61	1.21	23.41	3.16	1.26
P trivialis	35	15.17	1.69	4.33	0.51	23.43	3.07	19.49	1.81	1.401
S decumbens	36	3.48	0.47	0.266	0.17	5.20	2.63	3.74	0.59	0.60
T flavescens	37	12.27	1.29	4.07	0.60	25.25	2.41	16.35	1.69	-
V bromoides	38	5.61	0.64	8.07	0.81	58.97	2.65	13.67	7.31	-
A stolonifera	39	25.7	4.8	0.29	0.238	0.86	0.54	26.0	4.9	1.48
H lanatus-grass	40	39.0	6.6	1.84	0.38	6.37	1.8	40.9	6.5	2.01
H lanatus-hedgerow	41	43.7	11.4	1.484	0.294	4.92	0.97	45.2	11.2	2.01
H lanatus-waste	42	59.4	20.2	0.238	0.156	0.61	0.38	59.7	20.2	2.01
H lanatus-moorland	43	46.9	12.2	1.29	0.38	4.16	1.41	4.81	1.21	2.01

Flowering behaviour of species

Means and SD's of species with less than 100% flowering

Species	N flowering out of 10	$\bar{x}$ veg wt (g) (flowering plants only)	SE	$\bar{x}$ rep wt (g) (flowering plants only)	SE	Discrepancy between two reproductive weights	RA% (flowering plants only)*
A pratensis	7	19·62	1·98	0.806	0.122	0.24	3·76
B media	3	21·56	0·44	0.4100	0.208	0.29	1·87
D caespitosa	2	54·85	28·47	1.84	1.06	1.47	5·42
D flexuosa	6	12·03	6·22	1.52	0.79	0.38	18·1
F gigantea	9	27·27	3·77	6.07	1.26	0.61	18·9
F ovina	9	30·39	6·98	1.62	0.51	0.16	6·92
G fluitans	6	15·42	2·67	0.268	0.123	0.11	2·21
H mollis	6	18·71	4·23	1.86	0.68	0.62	9·22
K macrantha	7	13·84	2·40	1.32	0.54	0.40	11·8
M caerulea	1	4·35	—	0.05	0.00	0.04	1·14
P pratensis	8	22·34	3·34	0.977	0.274	0.19	4·51
D decumbens	5	4·04	0·62	0.426	0.265	0.16	8·32
A stolonifera	3	27·01	10·58	0.97	0.72	0.68	2·88
H lan hedge	8	33·93	6·65	1.67	0.259	0.19	6·23
H lan waste	3	36·55	3·01	0.713	0.348	0.475	1·84
H lan moor	8	38·72	6·13	1.61	0.41	0.32	5·20
M effusum	1	54·10	—	0.10	0.00	0.09	0·18

* These values used in Figs 6.4.2 - 6.4.9.

Overall the data had probability plot correlation coefficients of 0.849 for vegetative weight and 0.866 for reproductive weight. With 410 individuals under consideration the data are positively skewed, showing a greater occurrence of small values and few occurrences of large reproductive and vegetative weights. However, at the individual species level this skewness is not apparent eg for Aira praecox r = 0.997 which for an n of 10 falls within the 5% probability level for the normal probability plot correlation coefficient.

6.3.2 Reproductive and vegetative weights

Mean vegetative weight has been plotted against mean reproductive weight for each species in fig 6.3.1. The species located at the periphery of each axis had the greatest reproductive and vegetative weights eg Dactylis glomerata, Elymus caninus, Bromus sterilis and Hordeum murinum. Species near the origin eg Molinia caerulea and Sieglingia decumbens had low vegetative and reproductive weights. Species in which not all of the individuals flowered would have had higher reproductive allocations if just the flowering plants had been considered. These species are replotted in fig 6.3.2 showing the difference between the two means. The value of this difference is listed in table 6.3.3. The general pattern of the species distribution is almost unaltered by the use of a 'just flowering plants' mean (the maximum difference between means is 1.47g) but it is obvious that some species show a greater discrepancy between the two means than others. The species where this difference was most pronounced were Deschampsia caespitosa, Agrostis stolonifera, Holcus mollis, Festuca gigantea and Holcus lanatus (topsoil waste near Poly). All these differences were greater than 0.45g.

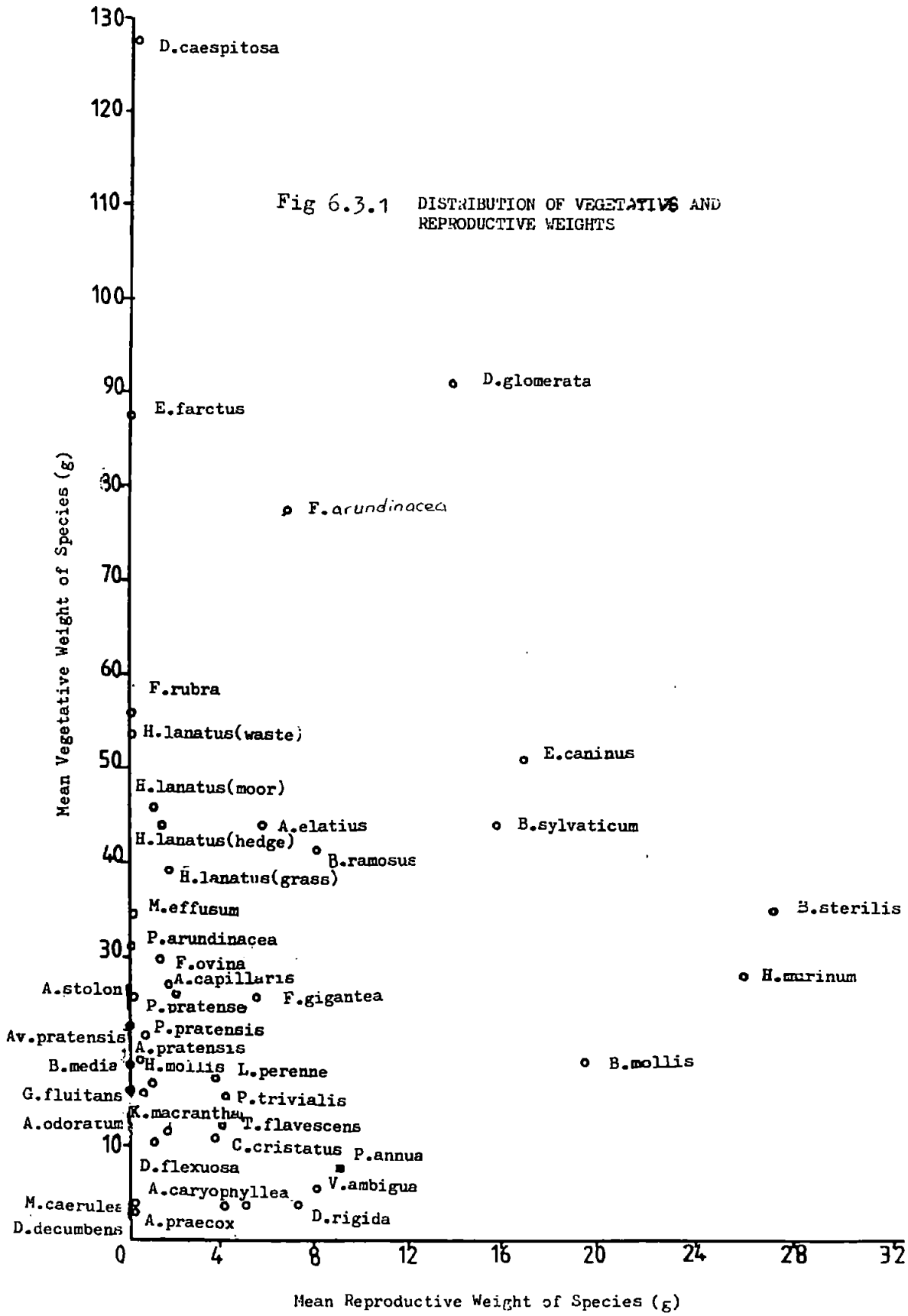


Fig 6.3.1 DISTRIBUTION OF VEGETATIVE AND REPRODUCTIVE WEIGHTS

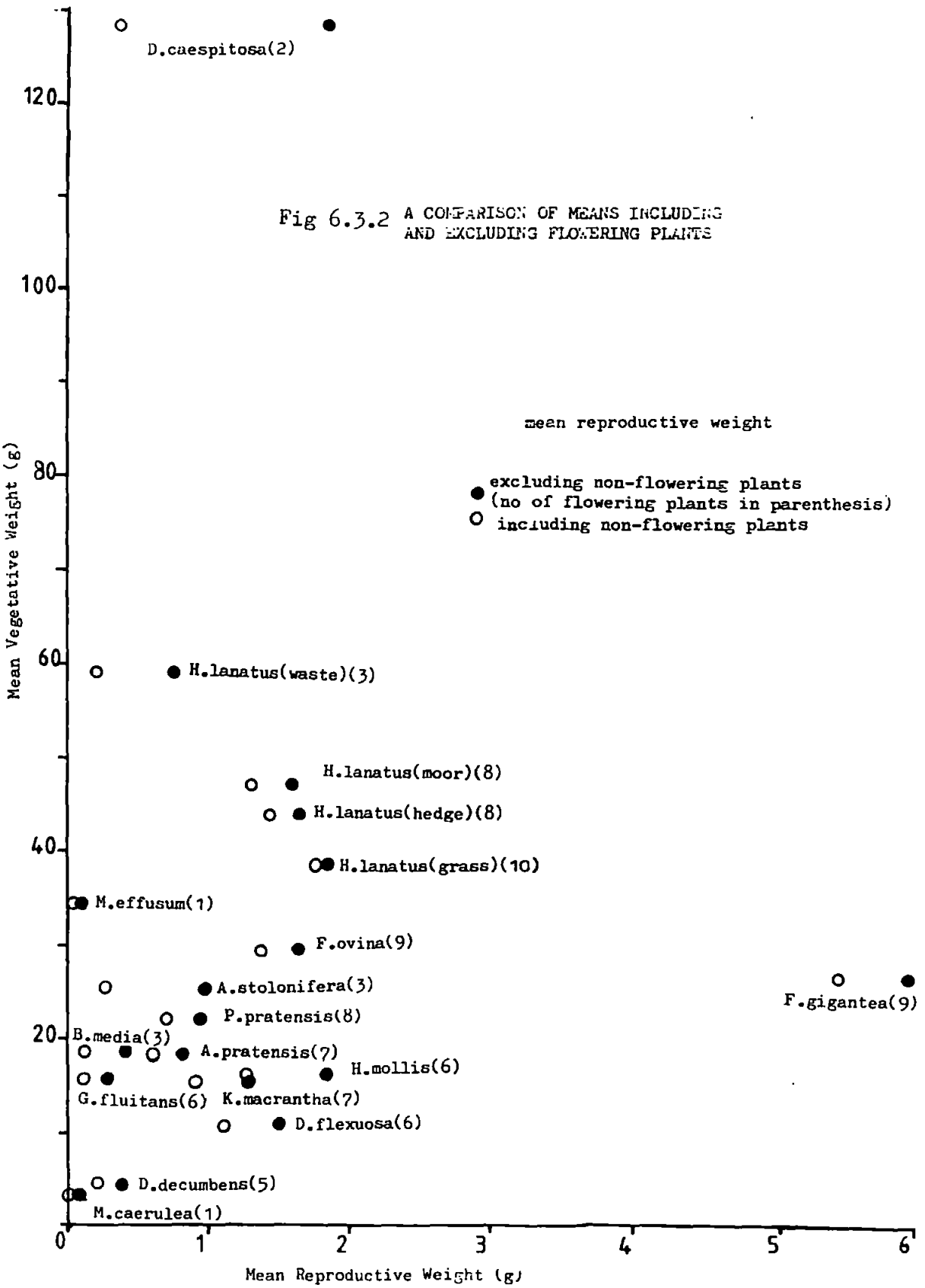


Fig 6.3.2 A COMPARISON OF MEANS INCLUDING AND EXCLUDING FLOWERING PLANTS

When vegetative weight is plotted against reproductive weight for individual plants of each species some characteristic patterns of distribution are evident (see fig 6.3.3). The species can roughly be divided into 9 groups according to their pattern of distribution of vegetative and reproductive weights. Table 6.3.4 includes the key to the groups in fig 6.3.3.

Group 1 consists of those species in which there is an obvious positive correlation between vegetative weight and reproductive weight. A typical example of the pattern shown by this group is displayed by Arrhenatherum elatius (fig 6.3.4). Species in group 2 show a similar correlation between vegetative and reproductive weights but in these species a threshold critical vegetative weight seems to be necessary before flowering can occur ie there are no very low vegetative weights. The slope of the relationship tends to be less steep. A typical representative of this group is Festuca arundinacea where the lowest vegetative weight is c. 60g (fig 6.3.5).

Species in group 3 eg Cynosurus cristatus (fig 6.3.6) show no evidence of any relationship between reproductive and vegetative weight but are scattered around a central point. Similarly Danthonia decumbens (fig 6.3.7) and Molinia caerulea in group 4 show this sort of pattern but with much lower weights, whilst members of group 5 eg Dactylis glomerata (fig 6.3.8) have much greater weights.

Species in groups 6 and 7 displayed much more variability in their reproductive weight than was evident in the other groups. Group 6 eg Bromus sterilis (fig 6.3.9) includes species with relatively high vegetative weights and very variable reproductive weights. Group 7 eg Desmazeria rigida (fig 6.3.10) contains species with variability in reprodutive weights but with much lower vegetative weights.

Table 6.3.4

Key to Groups in Figure 6.3.3

Group 1
Arrhenatherum elatius
Holcus mollis
Anthoxanthum odoratum

Group 2
Festuca arundinacea
Elymus caninus
Bractypodium sylvaticum

Group 3
Cynosurus cristatus
Lolium perenne
Poa trivialis

Group 4
Danthonia decumbens
Molinia caerulea

Group 5
Dactylis glomerata
Bromus ramosus
Festuca gigantea

Group 6
Bromus sterilis
Bromus hordaceous
Hordeum murinum

Group 7
Desmazeria rigida
Vulpia ciliata
Poa annua
Aira caryophyllea
Aira praecox

Group 8
Agrostis capillaris
Festuca ovina
Briza media
Alopecurus pratensis
Phleum pratense
Poa pratensis
Agrostis stolonifera
Koeleria macrantha
Deschampsia Flexuosa
Holcus lanatus (grassland)
Holcus lanatus (moorland)
Holcus lanatus (hedgerow)

Group 9
Deschampsia caespitosa
Elymus farctus
Phalaris arundinacea
Milium effsum
Glyceria fluitans
Avenula pratensis
Festuca nibra
Holcus lanatus (waste)

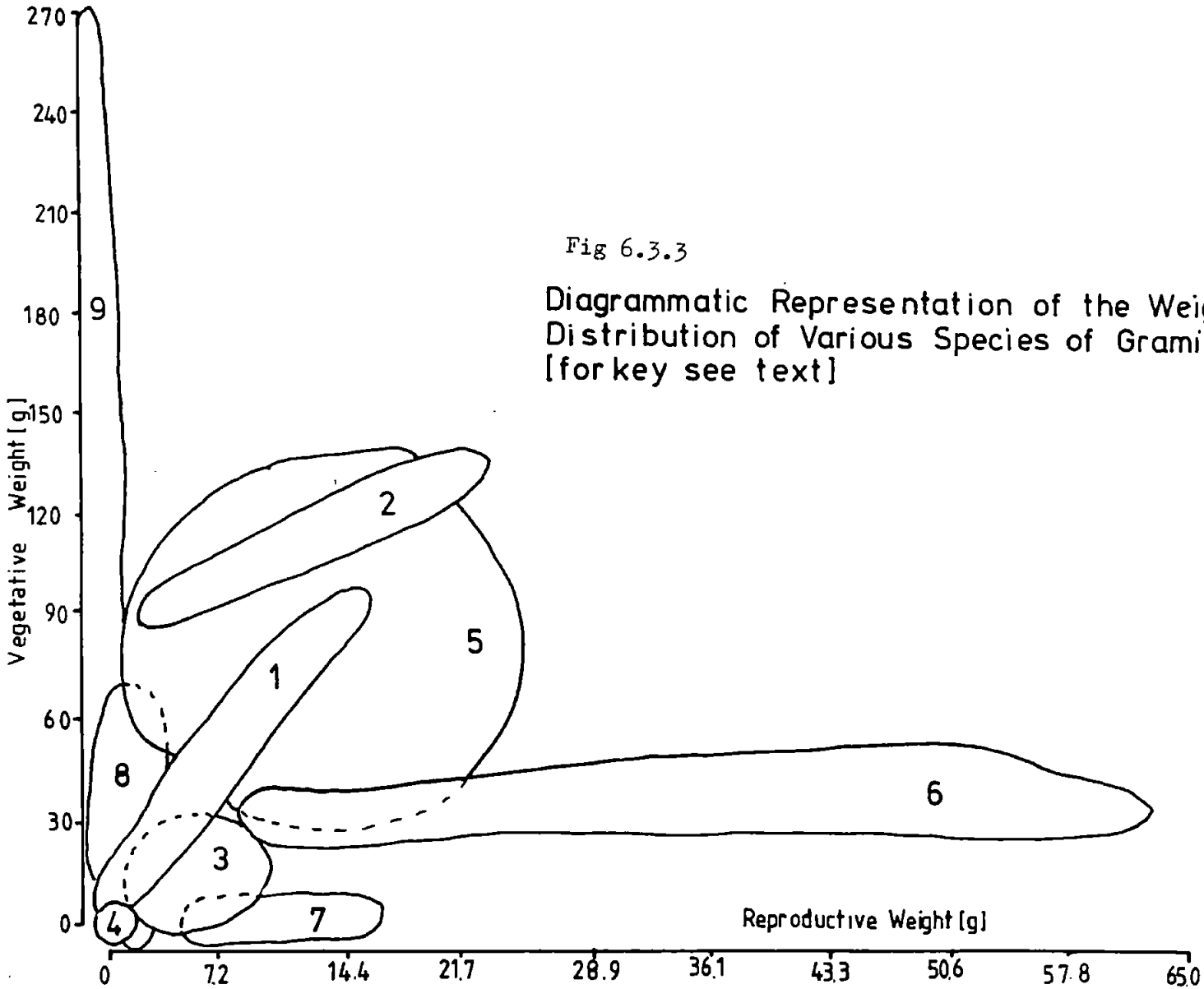


Fig 6.3.3

Diagrammatic Representation of the Weight Distribution of Various Species of Gramineae [for key see text]

Groups 8 and 9 contain species with a wide range of vegetative weights and a very low range of reproductive weights. Agrostis capillaris (fig 6.3.11) is a typical representative of group 8. Reproductive weights are much less variable than vegetative weights. In group 9 eg Deschampsia caespitosa (fig 6.3.12) vegetative weights can have an extremely wide range but often many plants do not flower. If they do flower then the reproductive weights attained are very small.

The fact that one of the populations of Holcus lanatus (Poly waste topsoil) was assigned to a different group reflects its different behaviour. Only 3 out of the 9 individuals from this population flowered and those which did flower had much lower RAs. There is a significant ($P<0.05$) difference between the RA of the 3 flowering Holcus lanatus plants from the Poly waste topsoil (mean 1.8%) and the Lipson grassland plants (mean 6.4%) and the Bere Alston hedgerow plants (mean 4.9%). This would seem to indicate that reproductive allocation strategy within a species may vary from one habitat to another.

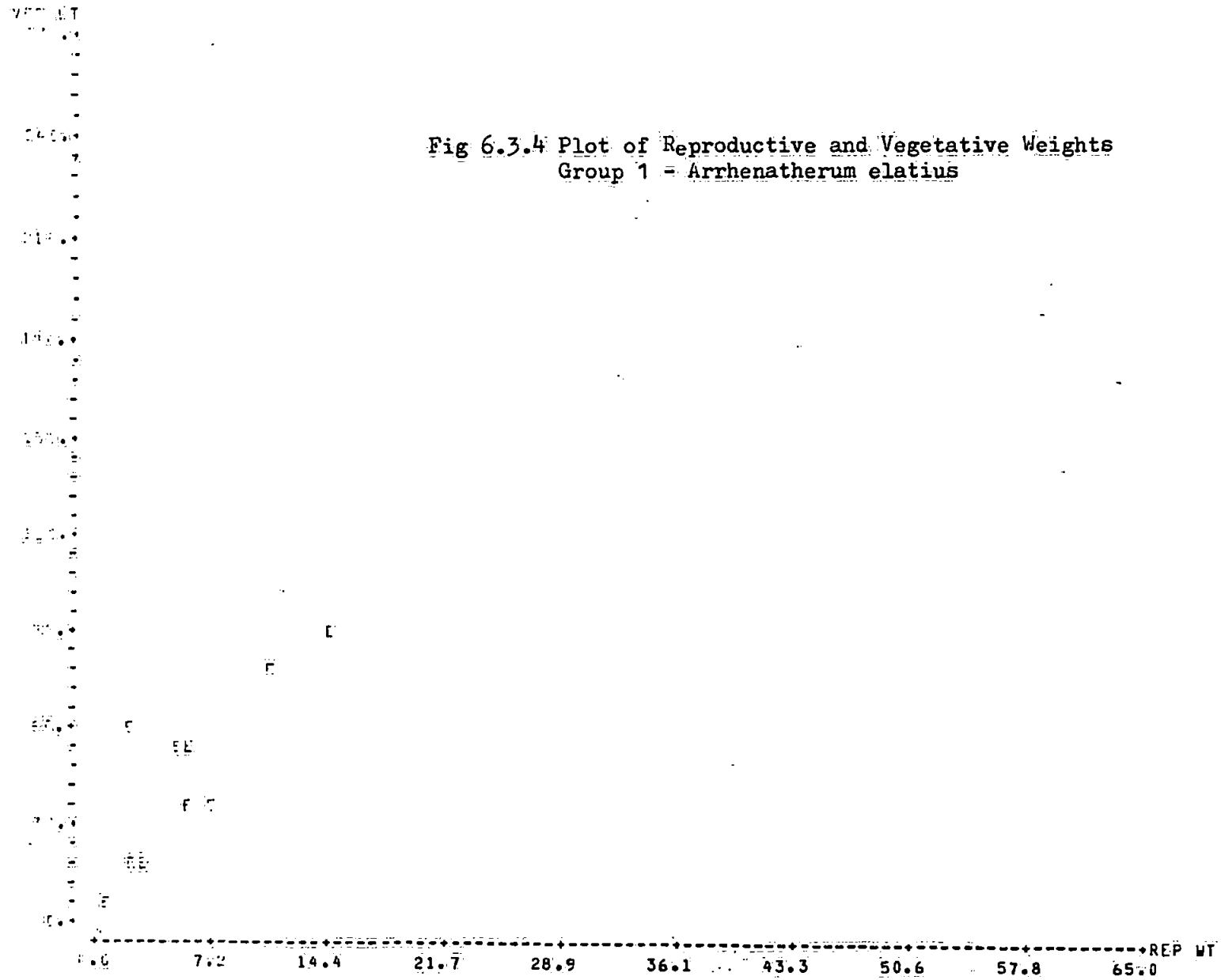


Fig 6.3.4 Plot of Reproductive and Vegetative Weights
Group 1 = Arrhenatherum elatius

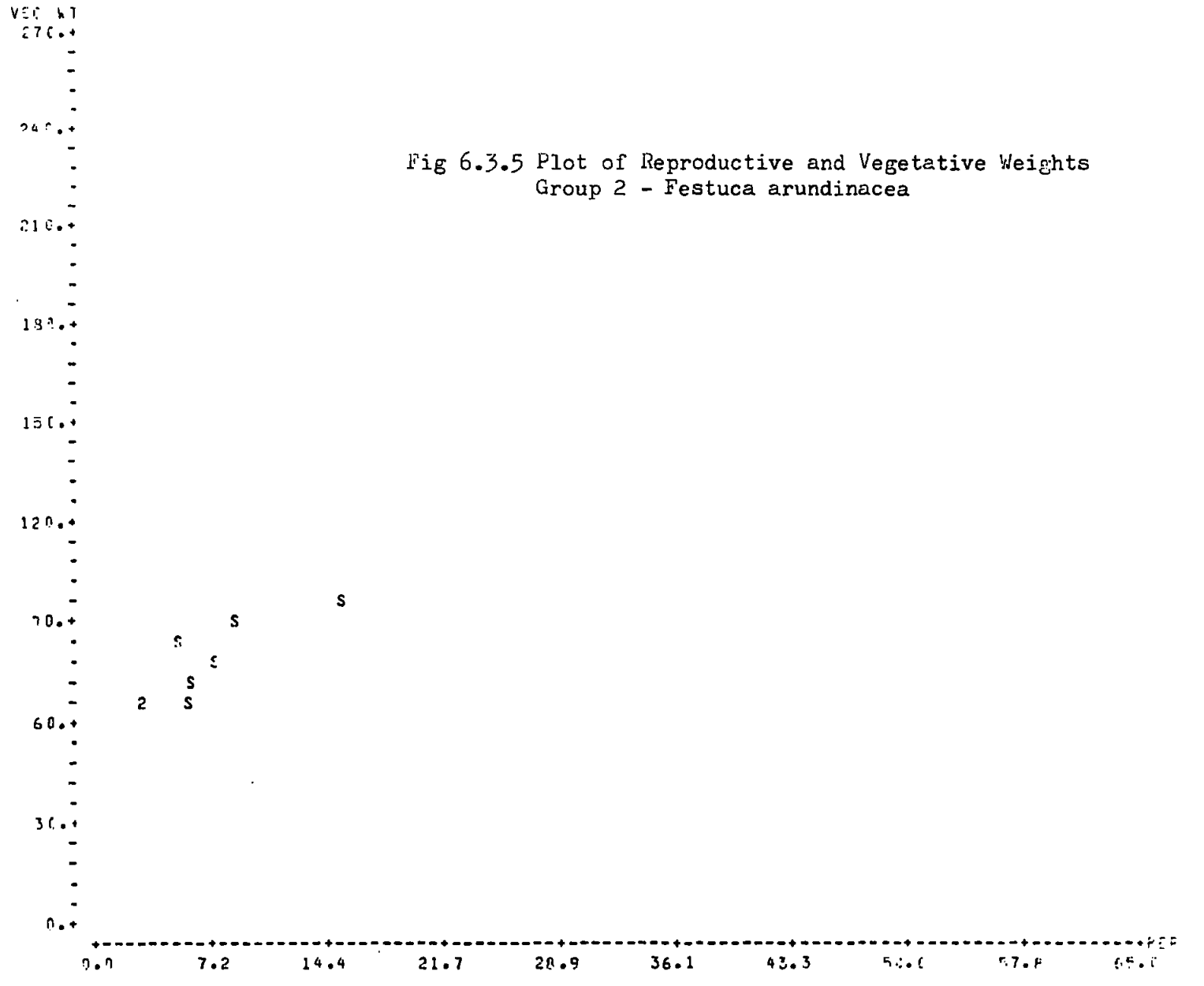


Fig 6.3.5 Plot of Reproductive and Vegetative Weights
Group 2 - Festuca arundinacea

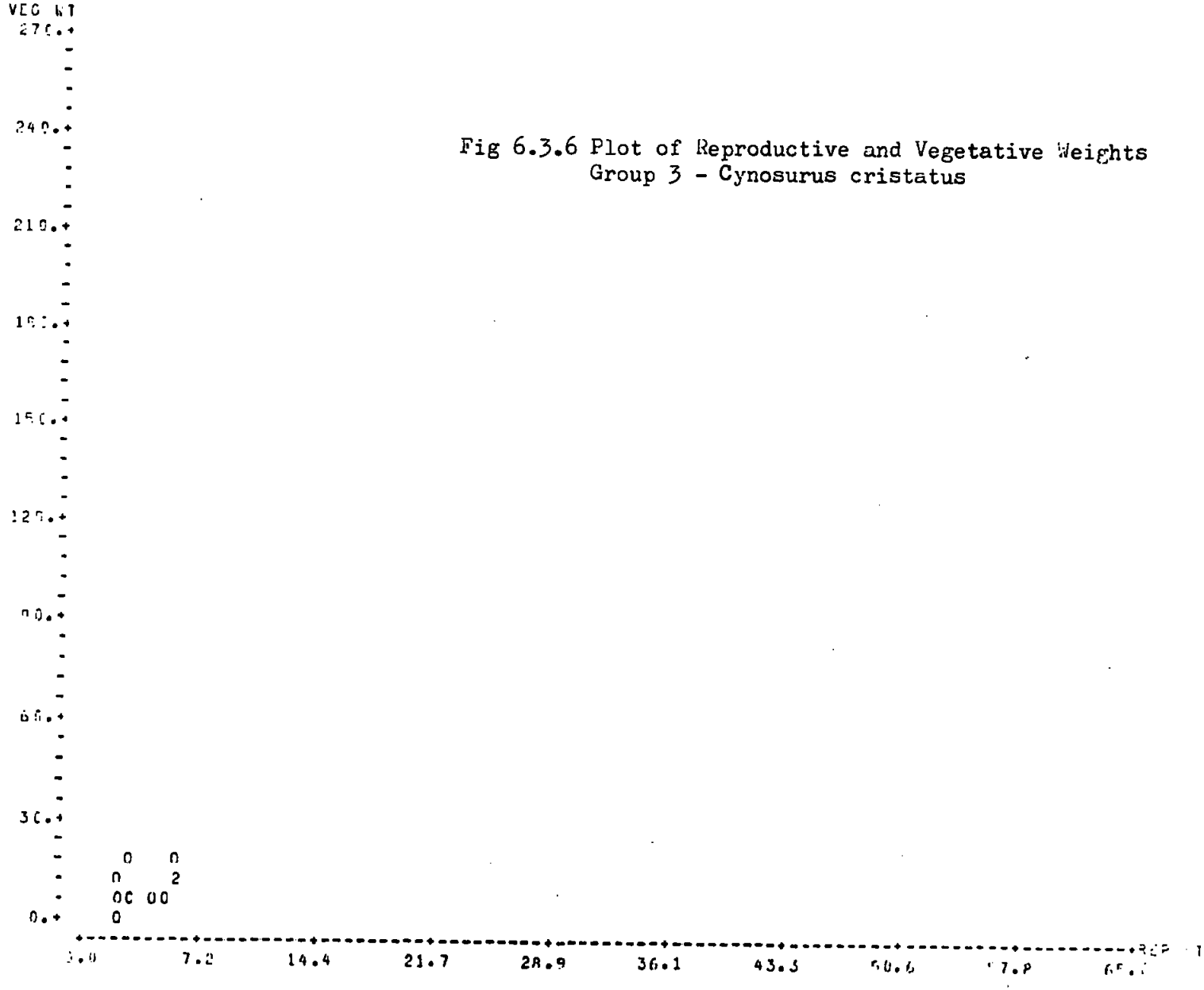


Fig 6.3.6 Plot of Reproductive and Vegetative Weights
Group 3 - Cynosurus cristatus

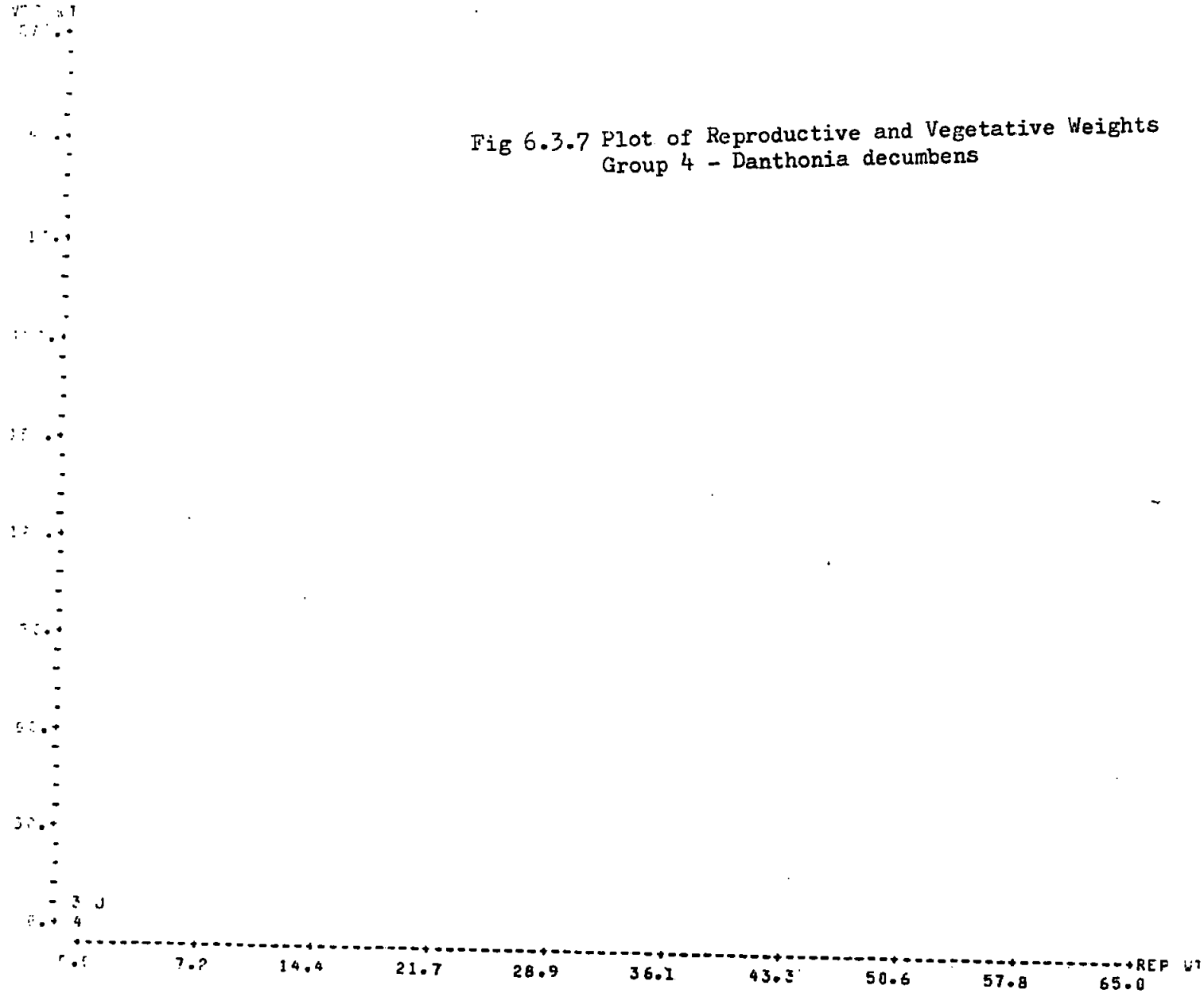


Fig 6.3.7 Plot of Reproductive and Vegetative Weights
Group 4 - Danthonia decumbens

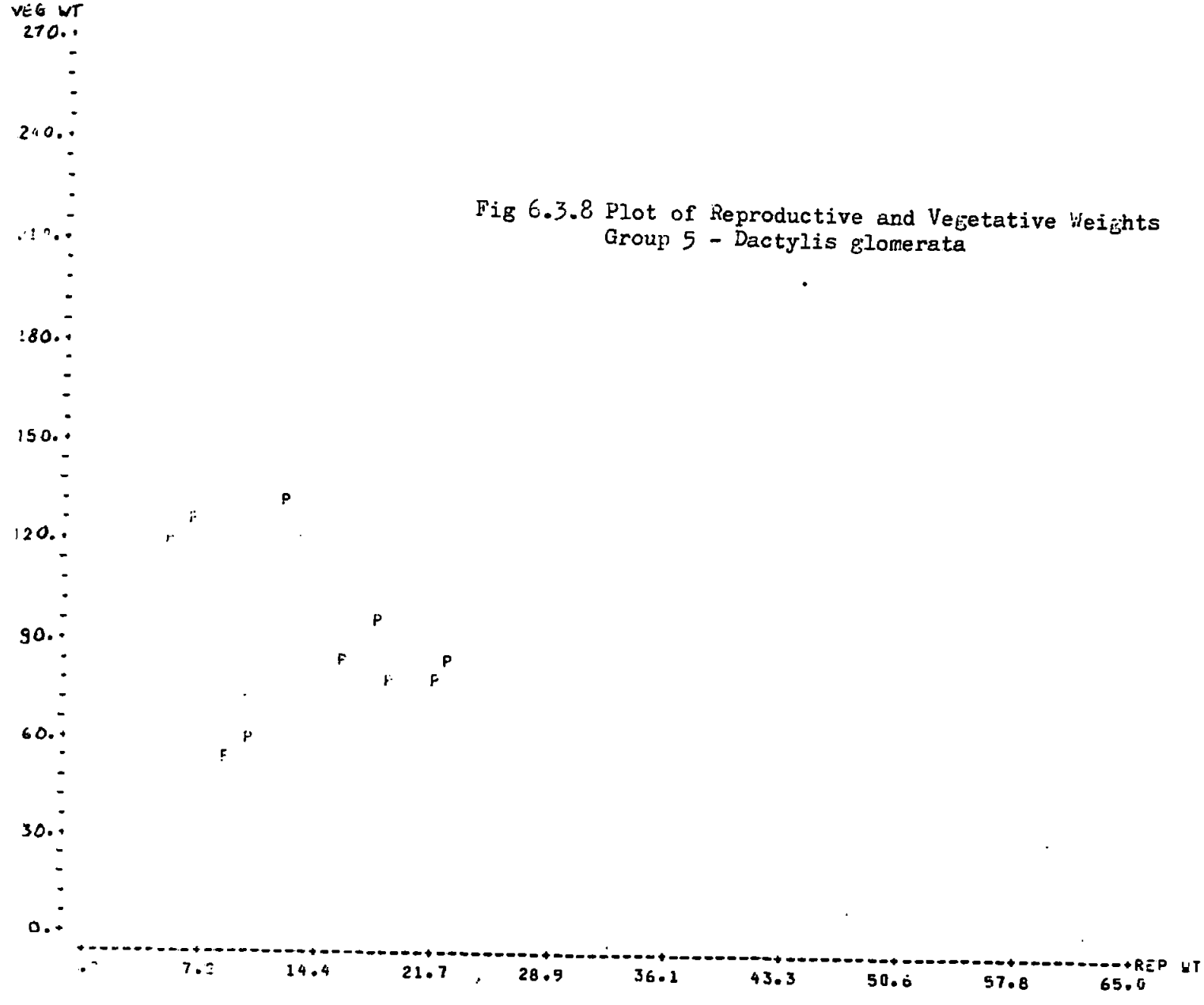


Fig 6.3.8 Plot of Reproductive and Vegetative Weights
Group 5 - Dactylis glomerata

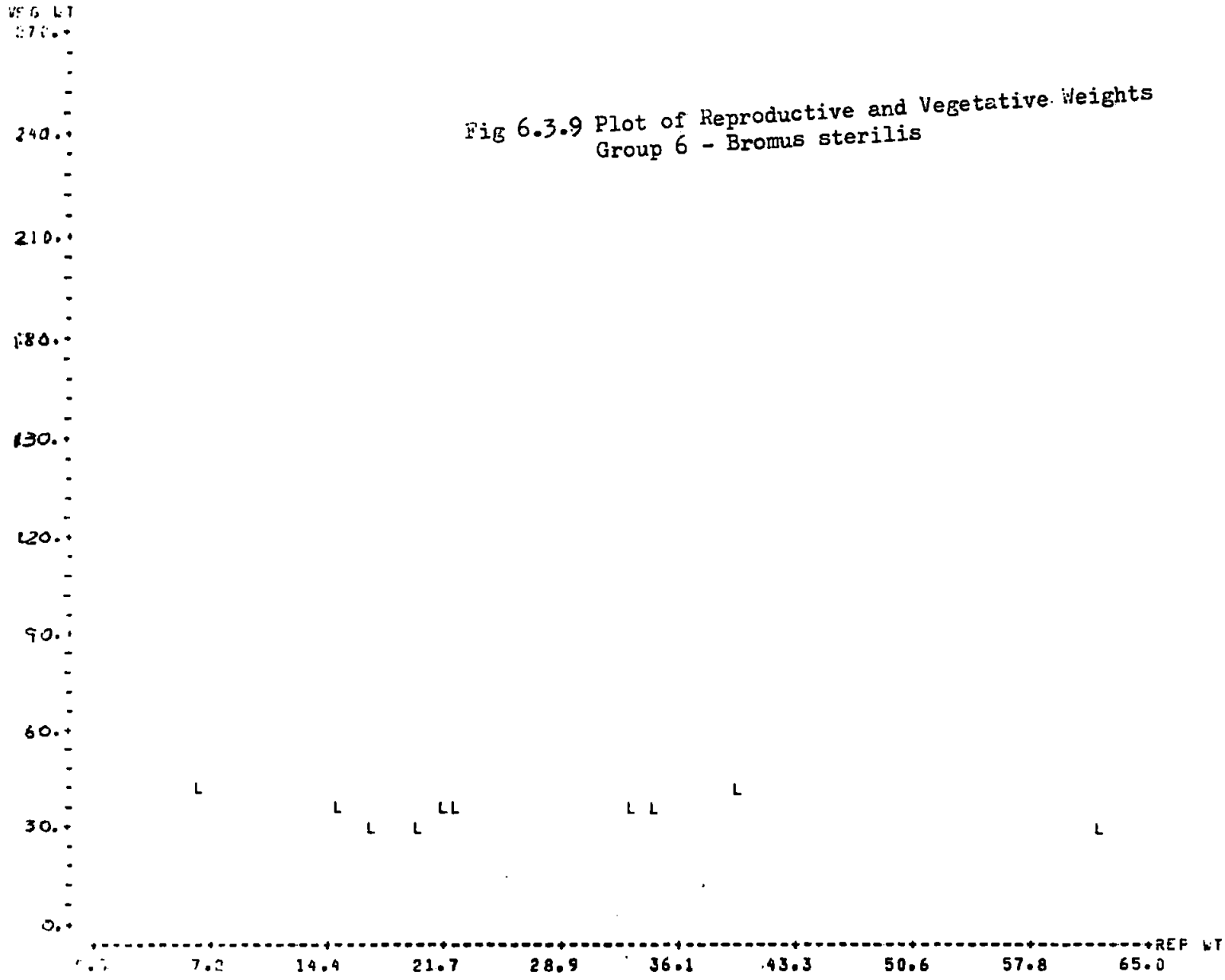


Fig 6.3.9 Plot of Reproductive and Vegetative Weights
Group 6 - Bromus sterilis

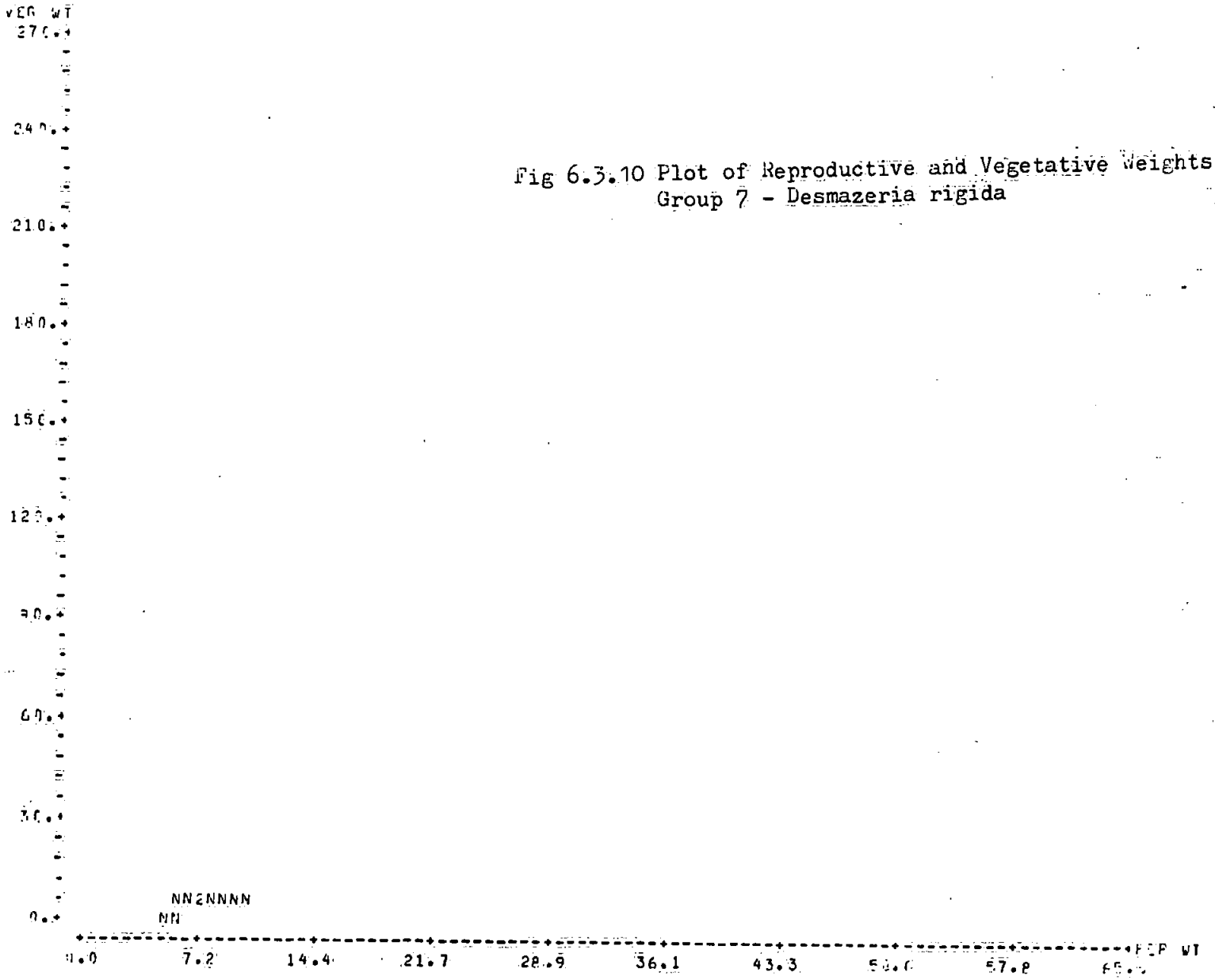


Fig 6.3.10 Plot of Reproductive and Vegetative Weights
Group 7 - Desmazeria rigida

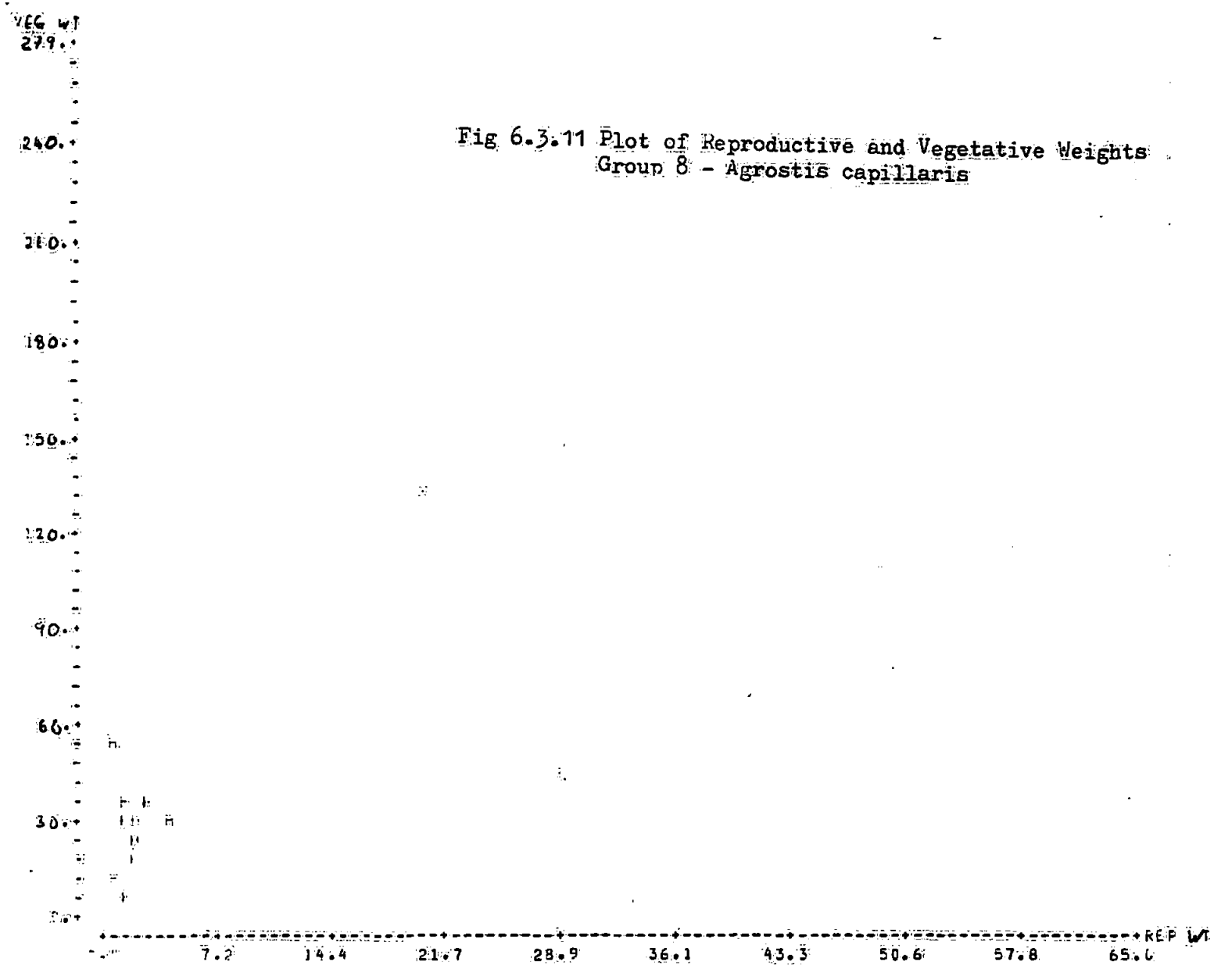


Fig 6.3.11 Plot of Reproductive and Vegetative Weights
Group 8 - Agrostis capillaris

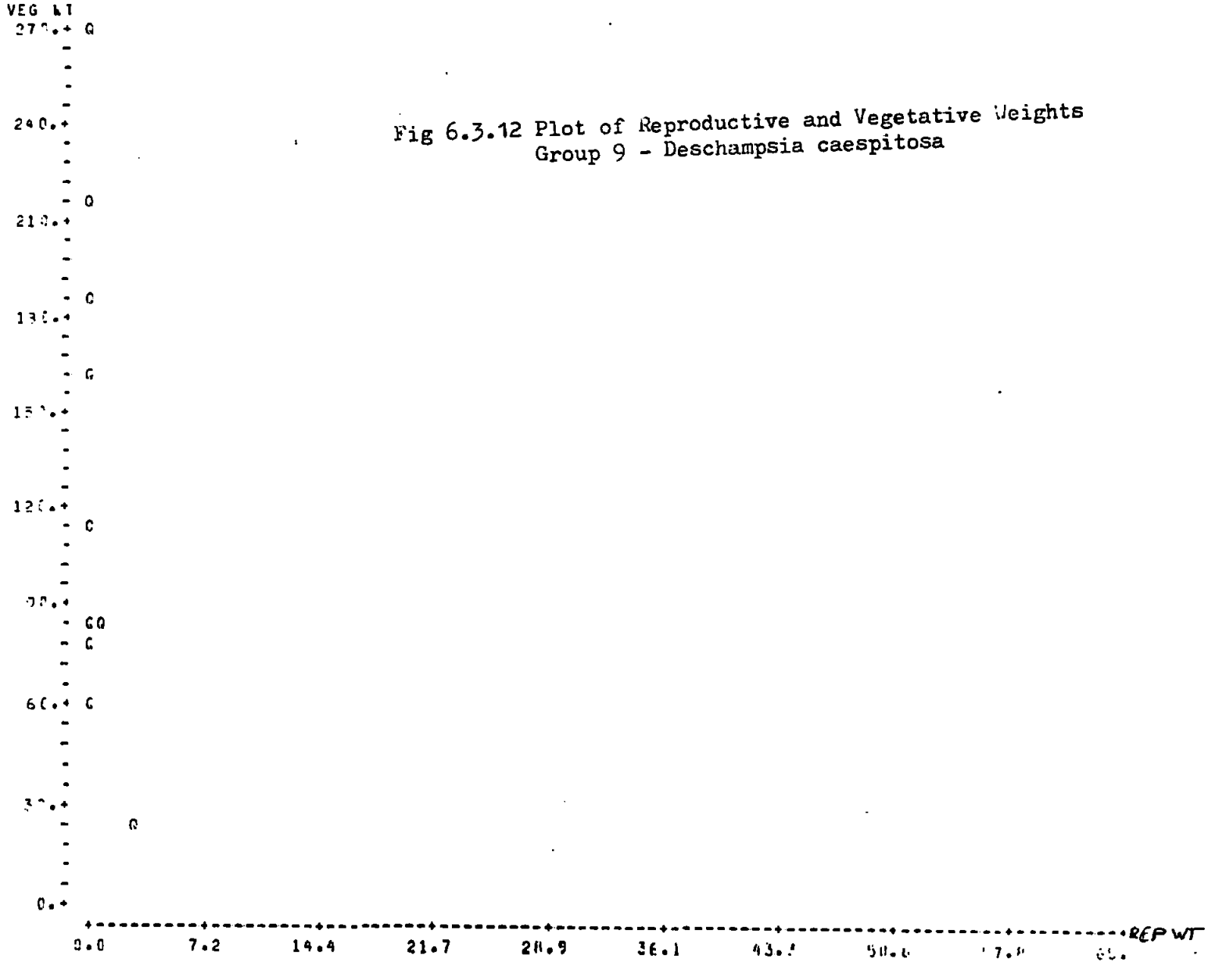


Fig 6.3.12 Plot of Reproductive and Vegetative Weights
Group 9 - Deschampsia caespitosa

6.4 Discussion

In general the reproductive behaviour of the various species of Gramineae is consistent with that proposed for ruderal, stress-tolerant and competitive strategies (Grime 1977). Comparable data on reproductive allocation in grasses from other sources are sparse but some generalisations can be made.

The ruderal annuals have a very large proportion of their annual production devoted to reproduction (66.3% in *Desmazeria rigida* - 40.9% in *Bromus sterilis*). All the annual species flowered in the first season and in every species every individual flowered. Similar high values for reproductive allocation in annual ruderals have been reported for *Phleum arenarium* - 37-44% (Ernst 1981), *Setaria viridis* 49-42% and *Setaria glauca* 27-53% (Kawano and Miyake 1983) and *Avena fatua* 56-61% (Harper and Ogden 1970). *Amphicarpum purshii*, an annual pioneer species has a reproductive allocation of 29% (McNamara and Quinn 1977).

Stress-tolerant species eg *Danthonia decumbens*, *Briza media* and *Milium effusum* showed low levels of reproductive allocation (5.2%, 0.5% and 0.02% respectively) and often not all of the individuals had flowered by the end of the second season. Amongst those species in which a proportion failed to flower, *Elymus farctus*, *Avenula pratensis* and *Festuca rubra* can be regarded as stress-tolerant. *Phalaris arundinacea* is generally regarded as competitive (Grime 1979). However it may only be capable of being competitive in its own specialised wet and nutrient-rich habitat. The conditions provided for this species in the experiment may not have been suitable and this would provide an explanation for its poor performance.

The competitive species generally had an intermediate to low reproductive allocation eg Arrhenatherum elatius 11.4%, Dactylis glomerata 13.9% and Lolium perenne 18.7% reflecting their high investment in vegetative biomass. The flowering behaviour of the competitive species was also more consistent. In all the aforementioned species every individual flowered. Lambert (1968) found a RA of 4-6% in Dactylis glomerata but this value included roots. Root biomass was not included in estimates of reproductive allocation in this experiment. Low levels of RA in dominant grasses were usual in those species characteristic of environments of low to moderate productivity eg Molinia caerulea 0.2% and Deschampsia caespitosa 1.1%. Tripathi and Harper (1973) found a low RA of 0.1 - 0.9% in a rhizomatous competitive ruderal Elymus repens, where Elymus caninus, a tussock grass, had a value of 10.9 - 14.8% (including roots). In this experiment Elymus caninus had a RA of 25.1% but again this did not include root biomass. The perennial caespitose grass Andropogon scoparius attained RA values of 24-42% (Roos and Quinn 1977).

From the evidence above it seems that although reproductive allocation can be used as an indication of an extreme ruderal strategy or an extreme stress-tolerant strategy, there is a large intermediate region between these two poles containing species of widely varying ecology. Further information on species characteristics is needed to assess plant strategy in this intermediate area. The problem is illustrated by reference to Tripathi and Harper's (1973) data on Elymus caninus and Elymus repens. The rhizomatous competitive ruderal has a much lower RA than Elymus caninus, a tussock grass typically found in shady environments. They suggest that this difference is a consequence of their different patterns of growth. Elymus repens, has a much greater capacity for clonal expansion and Harper (1977)

proposes that clonal growth and reproduction by seed may be alternative processes.

Further evidence of the tendency of growth form to influence reproductive allocation values can be gained by considering many of the species of Gramineae with intermediate RA values. Brachypodium sylvaticum, Bromus ramosus and Festuca gigantea are all species characteristic of shaded woodland or hedgerow habitats. In such a stressed habitat relatively low RAs would be anticipated. However the observed RA values of these tufted perennial species were 25.6%, 16.2% and 17.0% respectively. In contrast Holcus mollis, a rhizomatous grass also typically found in shaded habitats had a RA value of 6.1%. Similarly competitive ruderals with a tufted growth form such as Cynosurus cristatus (30.5%), Lolium perenne (18.7%) and Poa trivialis (23.4%) had much higher RA values than Rhizomatous or highly stoloniferous species like Poa pratensis (3.6%) and Agrostis stolonifera (0.8%).

The plots of reproductive weight against vegetative weight for the different species of Gramineae in this experiment show that these two parameters may be related to each other in different ways in different species, perhaps dependent on plant morphology and structure. The mean reproductive allocation for a particular species provides a useful general indication of the relationship between vegetative and reproductive biomass but within the species there may be further tactics which are not evident from consideration of the mean alone.

Differences in plant morphology and growth rate were taken into account by Grime (1974) when he produced a classification of plant strategies using Rmax (the maximum potential relative growth rate) as a stress

axis and CI (competitive index) as a competitive axis. He also proposed that RA might provide an additional 'ruderal' axis, although the importance of reproductive allocation (or effort) in assessing plant strategy was first recognised by Harper and Ogden (1970). One of the aims of this study was to determine the value of RA as a criterion as opposed to (and in conjunction with) Rmax and CI. With this intention an alternative third axis was constructed on the third side of Grime's (1974) triangular model (fig 6.4.1). Species were then ordinated on this triangle using pairs of this 3 parameters (Rmax, CI and RA) and the results compared. Values for Rmax and CI were obtained from the Unit of Comparative Plant Ecology (NERC), University of Sheffield. Unfortunately values for all 3 parameters were not available for all of the species of Gramineae, but complete data for 30 species were available. (Each population of Holcus lanatus is treated as a separate species). Data on RA and CI were available for 41 species and these species have been plotted on the appropriate ordination. The values of RA used in the diagrams and the following analyses were those obtained for the flowering plants only since there was a possibility that the numbers of non-flowering plants in the small sample might not be representative.

Fig 6.4.2 shows the conventional triangular model where Rmax is plotted against the competitive index. Fig 6.4.3 shows Rmax plotted against RA and Fig 6.4.4 shows CI plotted against RA. Both of the ordinations involving RA tend to show an agglomeration of species near the edge of the axis due to the large number of species with low or zero RA values. Although these graphs give a general indication of the value of each parameter it is difficult to judge them objectively. Moreover none of the diagrams combine the effect of all 3 criteria. A mathematical classification of the species according to various combinations of the

Fig 6.4.1 KEY TO TRIANGULAR PLOTS

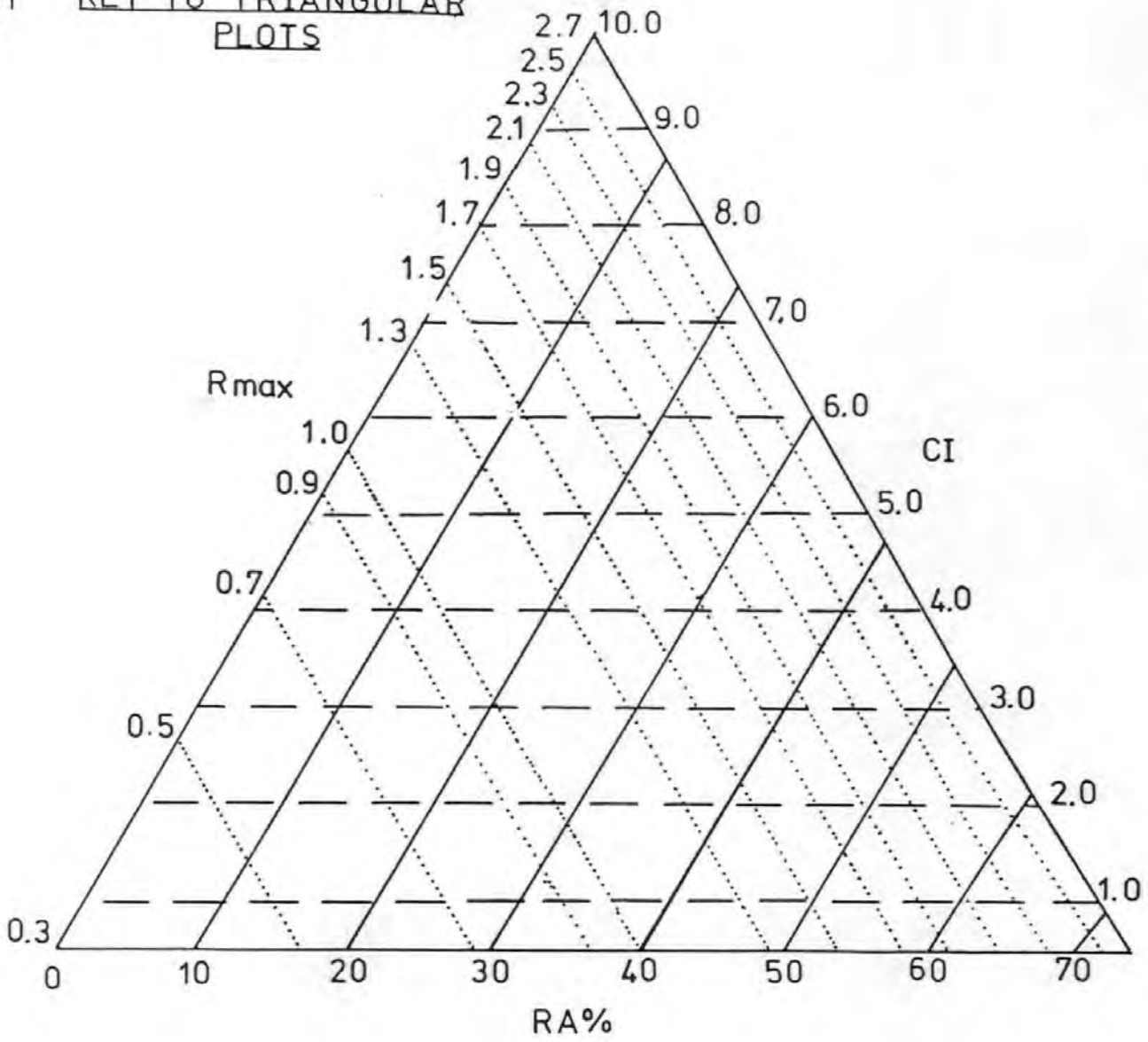


Fig 6.4.2 Rmax v CI

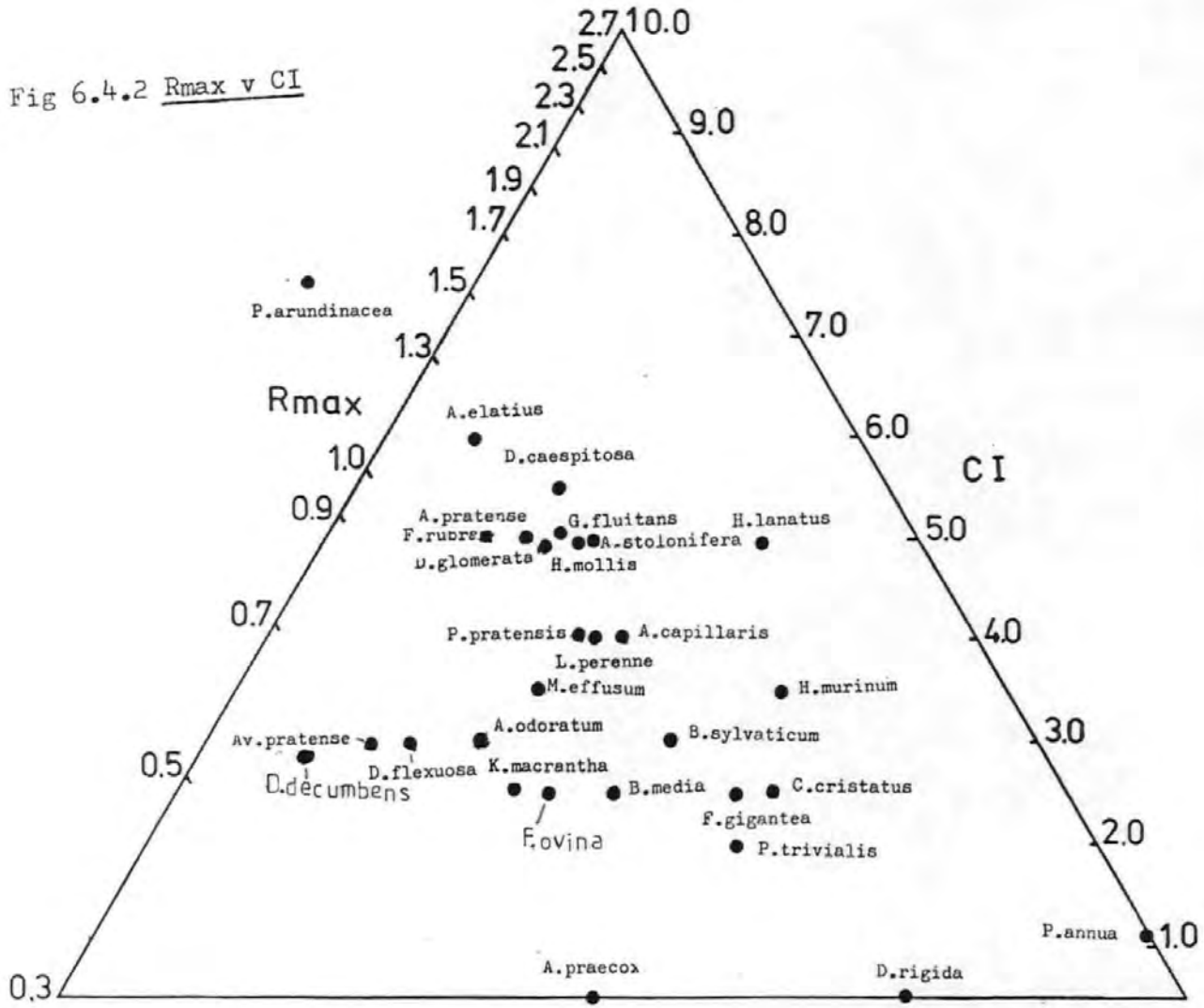


Fig 6.4.3 Rmax v RA

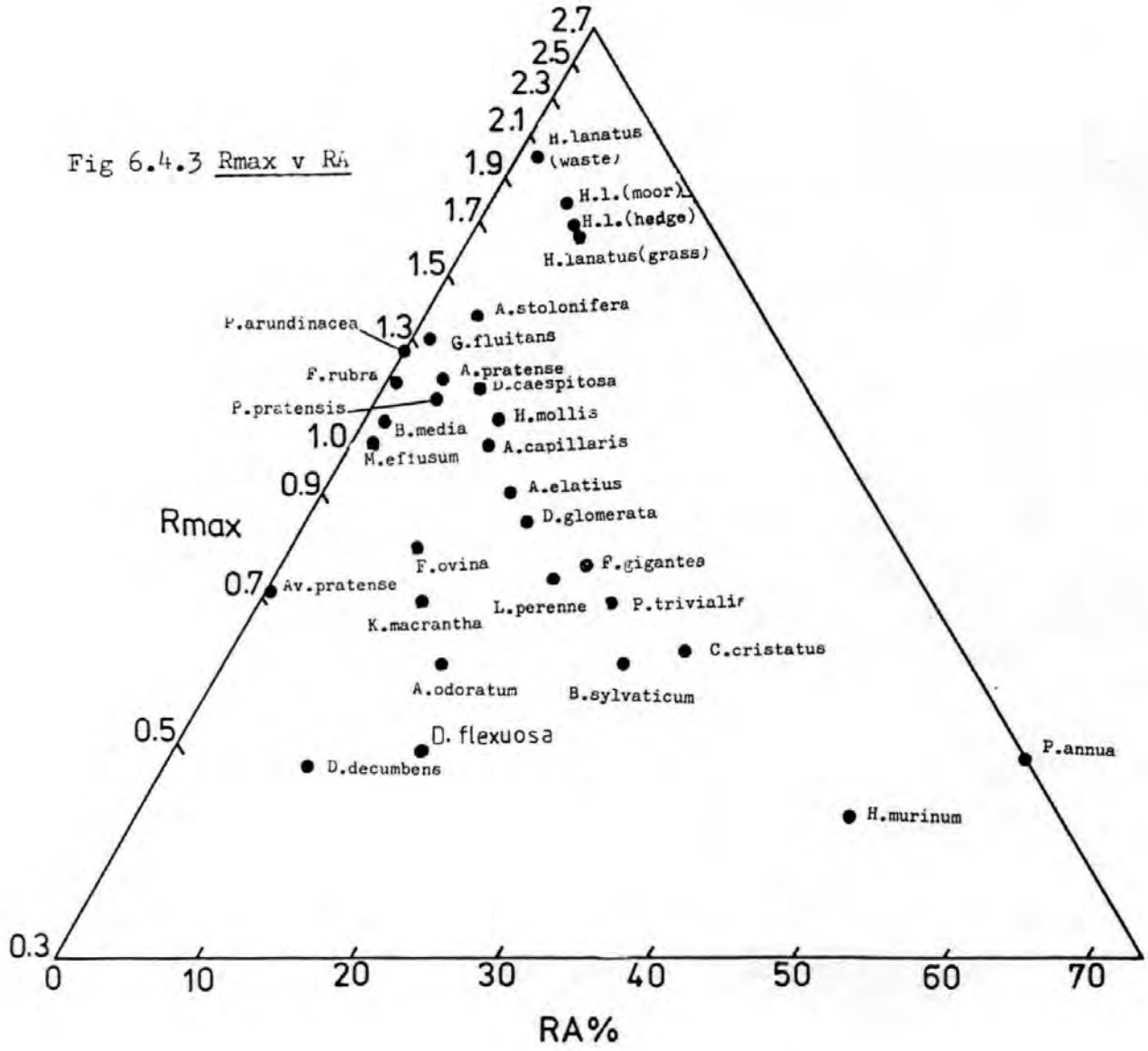
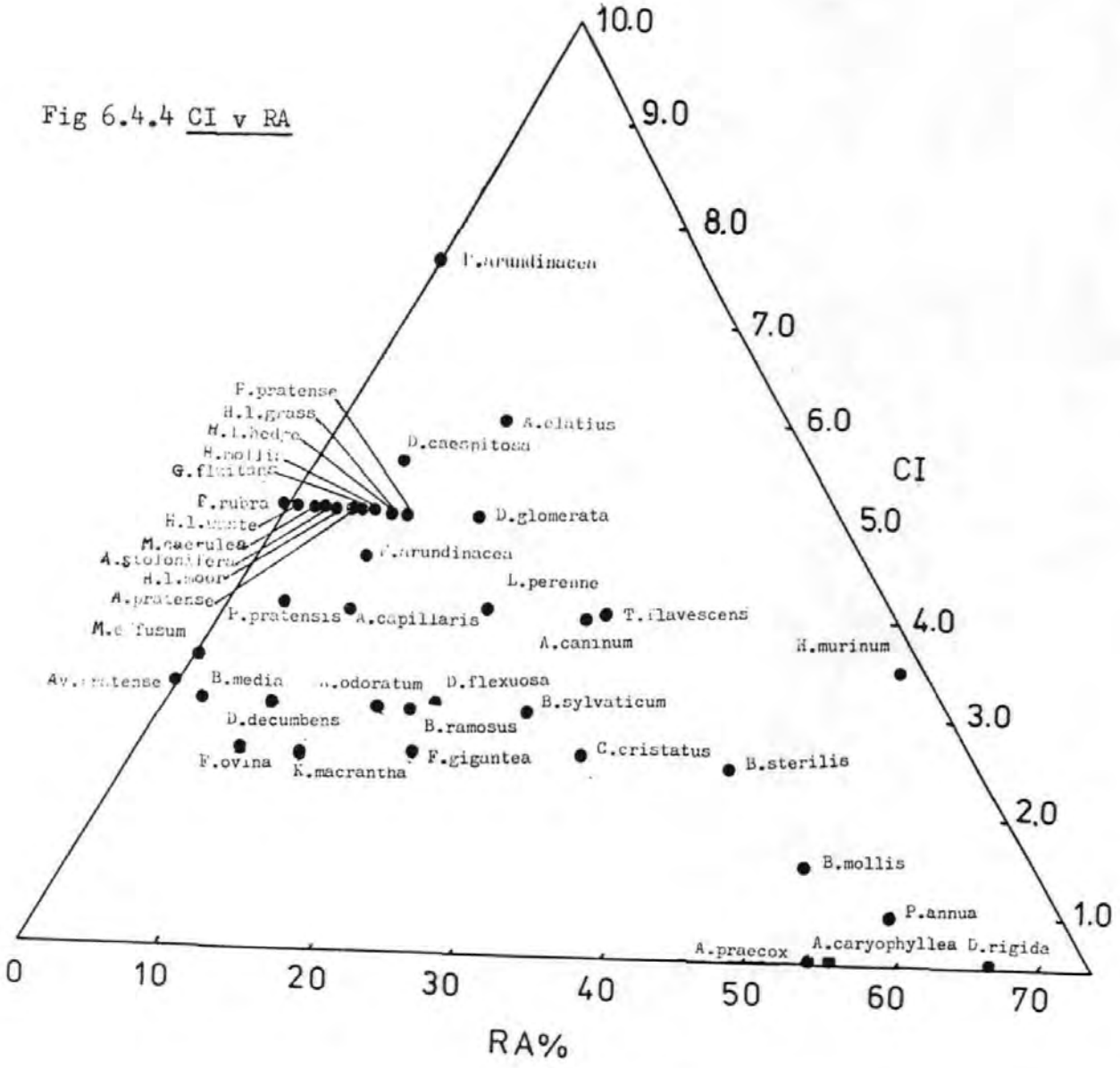


Fig 6.4.4 CI v RA

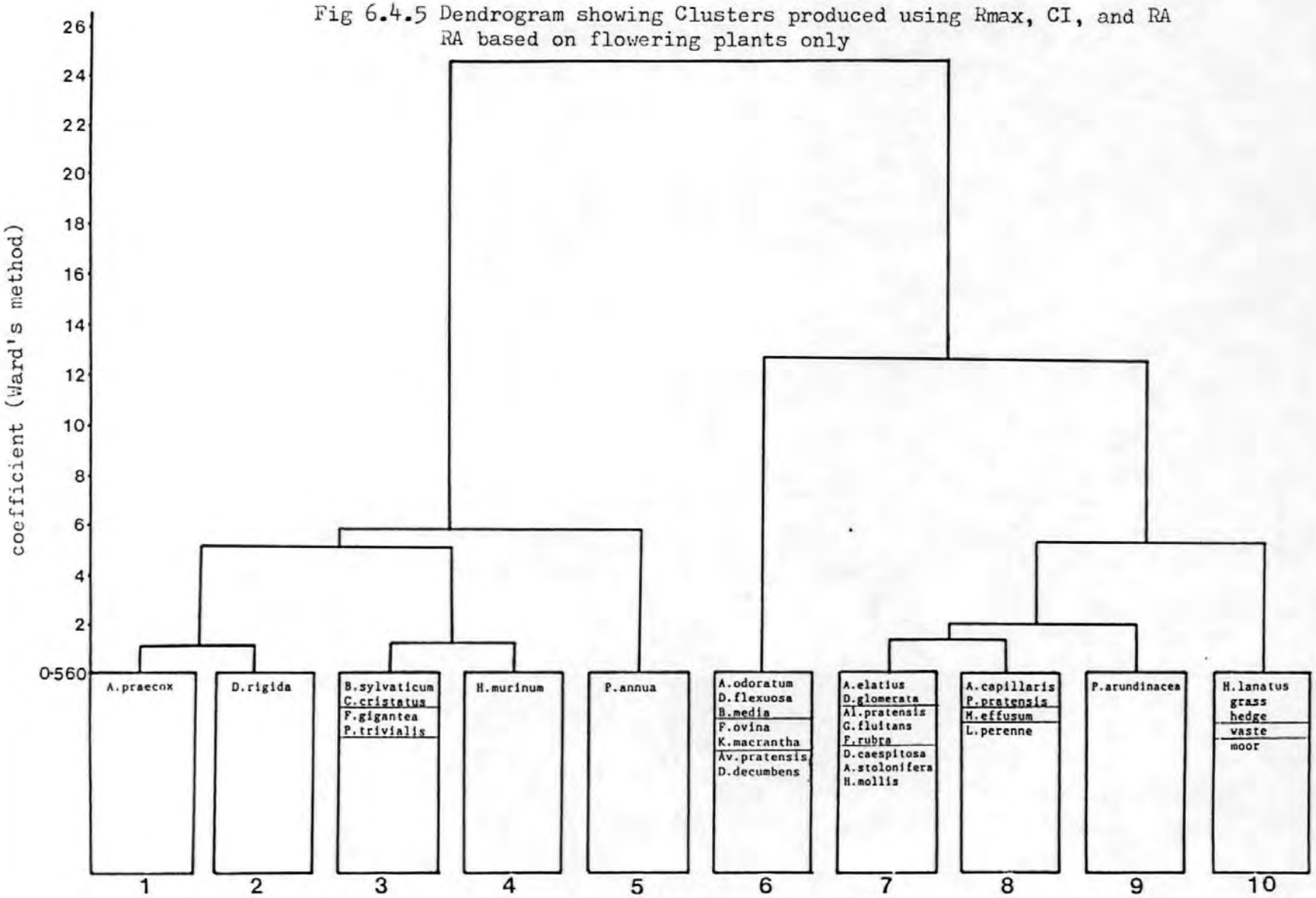


3 parameters would provide a less subjective method of assessing their value and also permit an integrated classification using all 3 parameters.

Clustan (Wishart 1982) was used to produce agglomerative polythetic classifications of the species using Ward's (1963) method. Ward's method is considered to be the preferable hierarchical, agglomerative method (Wishart 1982, Everitt 1979). Ward proposed that at any stage of the classification procedure, the loss of information which results from the grouping of individuals into clusters can be measured by the total sum of squared deviations of every point from the mean of the cluster to which it belongs. At each step in the analysis the combination of every possible pair of clusters is considered and the 2 clusters whose fusion results in the minimum increase in the error sum of squares are combined (Everitt 1980). The results can be summarised in the form of a dendrogram (figs 6.4.5-9).

Obviously the most robust classification will be that which includes the greatest amount of information. The classification analysis which uses all 3 parameters (Rmax, CI and RA) is shown in fig 6.4.5. The value of any 2 parameters in creating a classification can be judged against this integrated, comprehensive analysis. The main feature of this analysis is a division of species into ruderals in clusters 1-5 and the remaining competitive and stress-tolerant species in clusters 6-10. The ruderal group is characterised by species with high growth rates and reproductive allocations and includes all the annual species. The stress-tolerant ruderals Aira praecox and Desmazeria rigida show the most similarity. Within this group are a group of perennials (cluster 3) which are probably placed in this location because of their relatively high Rmax and/or RA values and moderate to low CI's. Poa

Fig 6.4.5 Dendrogram showing Clusters produced using Rmax, CI, and RA
RA based on flowering plants only



trivialis and Cynosurus cristatus can be regarded as competitive ruderals. However both Festuca gigantea and Brachypodium sylvaticum are characteristic of shady environments and their high RA is probably a consequence of their tufted growth form, as discussed earlier.

After this major differentiation of the ruderal species from the remaining species the next most significant division separates the stress-tolerators in cluster 6 from the remaining species. These stress-tolerant plants, Anthoxanthum odoratum, Deschampsia flexuosa, Briza media, Festuca ovina, Koeleria macrantha, Avenula pratensis and Danthonia decumbens all have relatively low Rmax's, CI's and RA's.

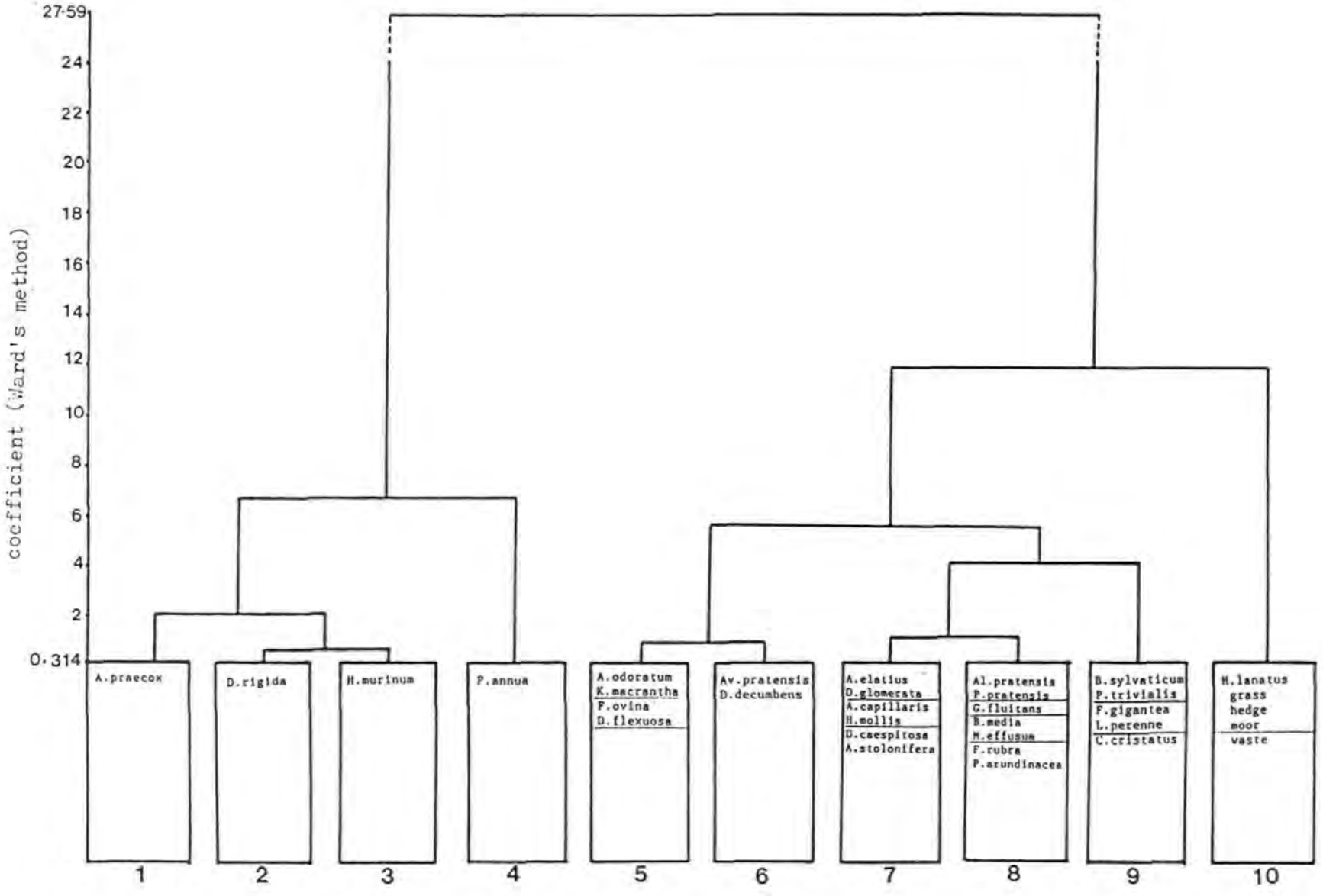
Below this division there is a significant separation of the four Holcus lanatus populations. It is evident from the sub-clusters that the Moorland and Hedgerow populations are the most similar (as would be expected from two stress-tolerant populations). In the classification using RA and CI for 41 species (fig 6.4.9) the Poly waste population is assigned to a different cluster from the other H. lanatus populations. This is undoubtedly a consequence of the significantly lower RA in the Poly population. A lower RA for a population on waste ground is not what would have generally been expected but as the plant was growing on dumped topsoil it is possible that it originated from a completely different habitat. Different 'biotypes' of a single species from different habitats have been found ie Taraxacum officinale (Gadgil and Solbrig 1972), Typha latifolia (Grace and Wetzel 1981) and Tussilago farfara (Bostock 1980). The grass Andropogon scoparius also showed some evidence of genetically based reduction in sexual RA with increasing age of field (Roos and Quinn 1977).

Within the remaining 'competitive' species in fig 6.4.5 Phalaris arundinacea is recognised as being distinctly dissimilar from the other species. This is probably attributable to its very high competitive index (7.5), which is the highest CI in the species under consideration. The final separation of the competitive species in clusters 7 and 8 does not seem to be based on any obvious strategic differences. The species in cluster 7 eg Arrhenatherum elatius, Holcus mollis and Deschampsia caespitosa all have CIs greater or equal to 5 whilst those in cluster 8 eg Millium effusum, Lolium perenne and Poa pratensis have CIs less than 5.

Thus the classification of species obtained using all of the 3 parameters can be satisfactorily explained in terms of species strategy. The few anomalies can be largely attributed to species structure and morphology and this area evidently requires further investigation. By comparing this comprehensive classification with the classifications obtained when one of the parameters is omitted, it is possible to determine the importance of each parameter in the interpretation of strategy. The most appropriate criteria would be those that lost the least amount of information compared with the integrated analysis.

Fig 6.5.6 shows the analysis using RA and Rmax. This classification is in fact, very similar to that in fig 6.4.5. The major division is again between the ruderals and the remaining species although in this case the ruderals are restricted to the annual species. Desmazeria rigida, Aira praecox and Hordeum murinum which are all found in similar dry, open habitats are most similar. The next major division is between the Holcus lanatus populations and the remaining species (when CI was included in the integrated classification stress-tolerant species with

Fig 6.4.6 Dendrogram showing Clusters produced using RA and Rmax
RA based on flowering plants only

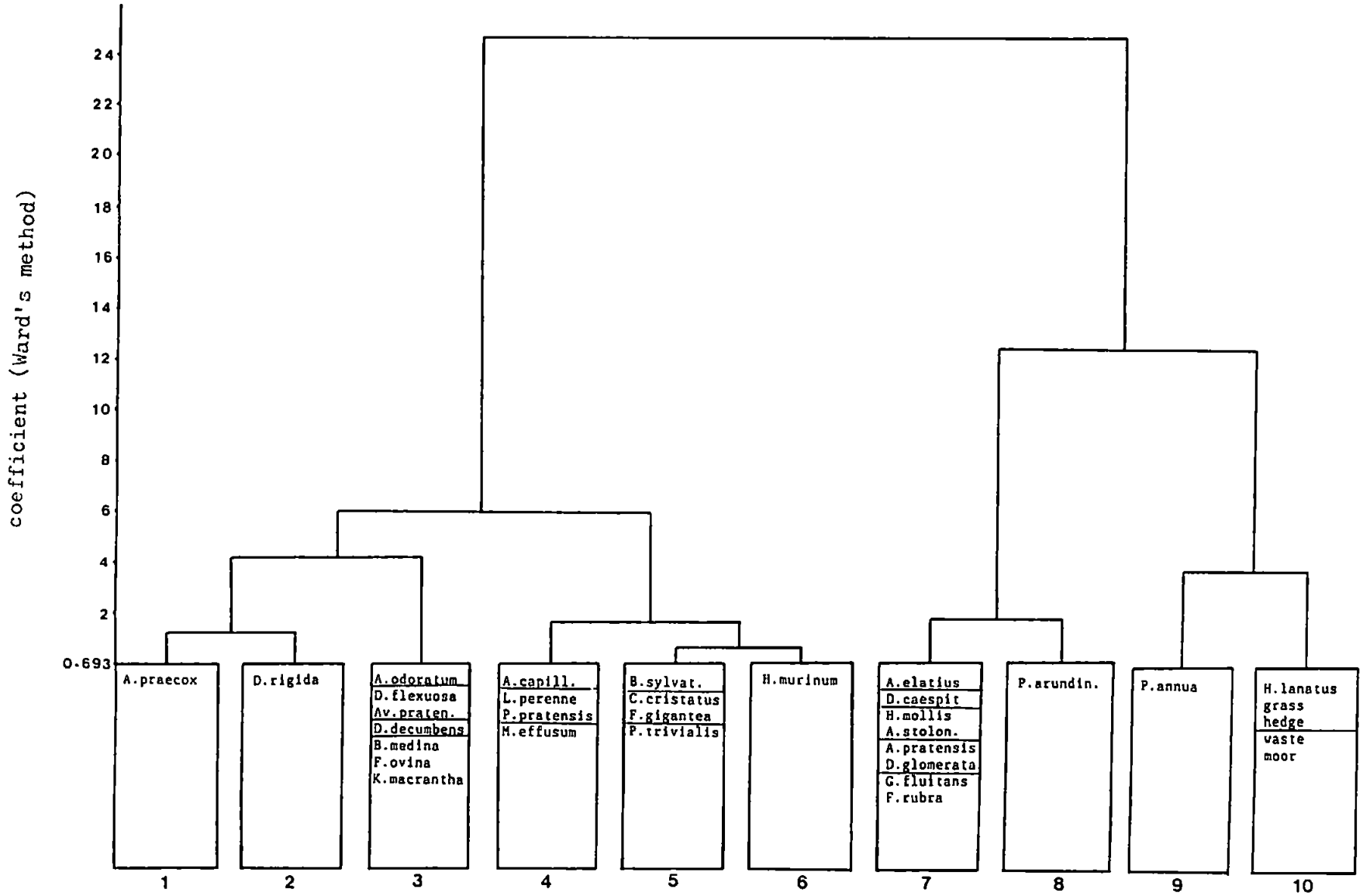


very low CIs were more dissimilar than the Holcus lanatus populations). This is followed by a division between the stress-tolerating plants in clusters 5 and 6 and the remaining competitive species. The 'ruderal competitive' group in cluster 9 had previously been included within the ruderals (fig 6.4.5) because of their relatively low CIs but with the omission of CI as an index they are allotted a 'competitive' position with Lolium perenne. Similarly Phalaris arundinacea is not identified as being significantly different because of its high CI, and in this classification is grouped with the other competitive species. The exclusion of CI as a factor also means that because Briza media has a slightly higher Rmax and a slightly lower RA than the other stress-tolerant species in clusters 5 and 6, it is grouped with the 'competitive' species in cluster 8. Therefore, although this classification identifies the same major groups that are present in the integrated classification, there are some slight discrepancies at the lower levels of the hierarchy.

Fig 6.4.7 shows the clusters obtained using Rmax and CI, the original axes of Grime's (1974) triangular ordination. In contrast with the previous 2 classifications, the main division in this analysis separates the competitive plants (clusters 7-10) from the remaining non-competitive ruderals and stress tolerators (clusters 1-6). The ruderal, Poa annua is located within the competitive group since its high RA is not taken into account in this analysis.

With the omission of RA as a criterion the 4 annual species are not grouped together (as in the previous classifications) but placed in positions dependent on their other characteristics. Hence Poa annua, with the highest ruderal Rmax is grouped with the competitive species whereas Aira praecox and Desmazeria rigida with the lowest ruderal CI

Fig 6.4.7 Dendrogram showing Clusters produced using Rmax and CI



and Rmax are grouped with the stress-tolerant species. Hordeum murinum, with a high CI and intermediate Rmax is placed in an intermediate position with the 'ruderal competitive' plants.

The analysis based on RA and CI in fig 6.4.8 is markedly dissimilar to the integrated classification in fig 6.4.5. Although the primary division separates off 3 ruderal species in cluster 1 ie Aira praecox, Desmazeria rigida and Poa annua, Hordeum murinum is omitted from this group. Within the remaining species the next division separates off the competitive plants in clusters 8-10. Arrhenatherum elatius is identified as being significantly different from the other species which was not evident in the integrated classification. The remaining clusters 2-7 are separated into ruderal competitors (2-4) and stress-tolerators (5-7). However the inclusion of Agrostis capillaris and Poa pratensis with the stress-tolerators seems somewhat dubious, and in fact the location of species at the lower levels of the hierarchy seems quite arbitrary. The effect of the inclusion of additional data on other species can be seen in fig 6.4.9. Although the basic structure of the classification remains the same, there are some refinements at the lower levels (eg Agrostis capillaris and Poa pratensis are included with the competitive plants) which makes the classification more comprehensible.

Each of these analyses is creating a classification on the basis of certain specified criteria and in terms of these specific criteria that classification is appropriate. The decision as to which classification is most appropriate remains a subjective one. Any simplification or summarisation of a set of data involves rejecting some of the information in the original data and the information that is retained depends on the chosen classification. A classification which retains

Fig 6.4.8 Dendrogram showing Clusters produced using RA and CI
RA based on flowering plants only

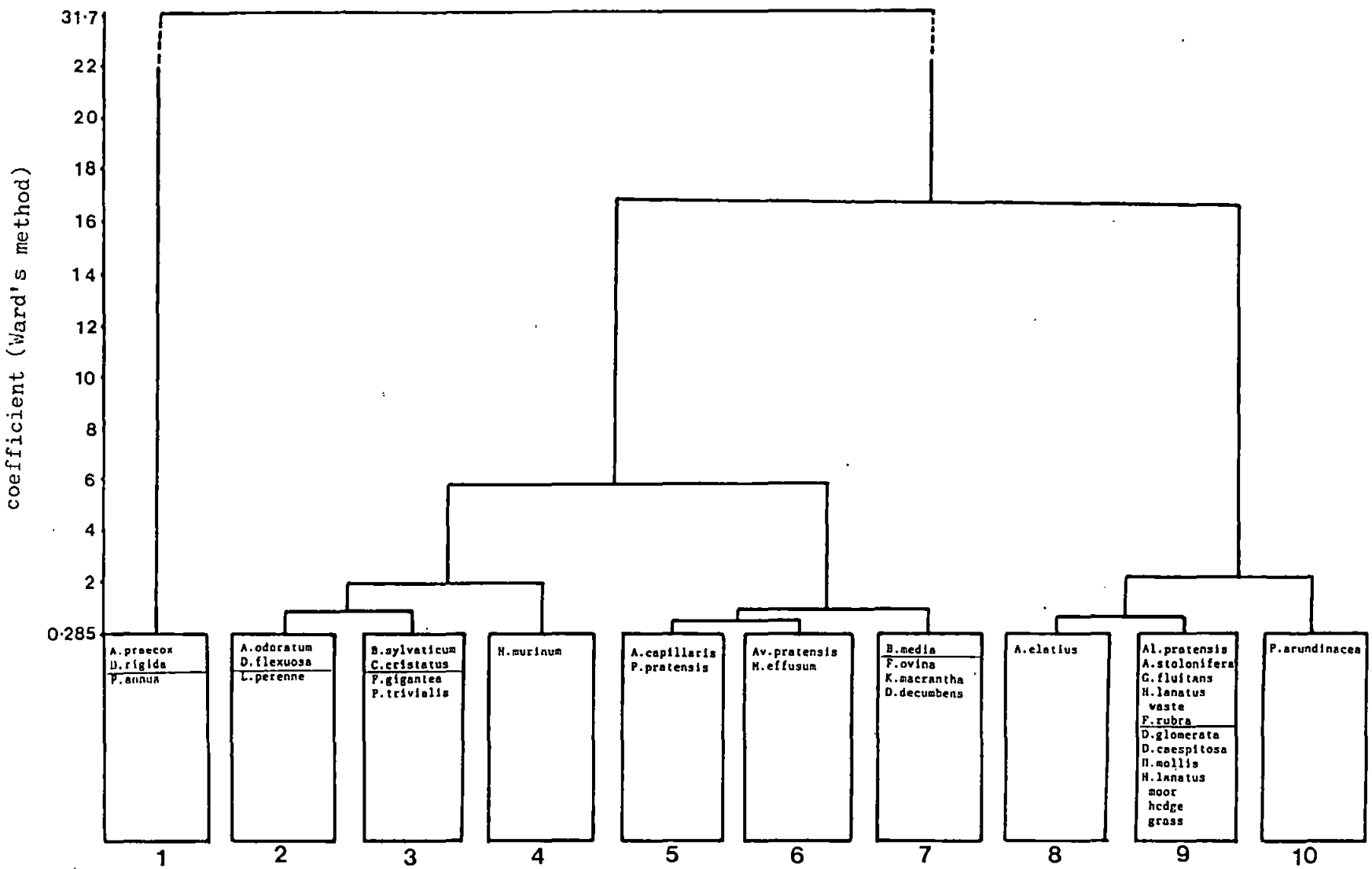
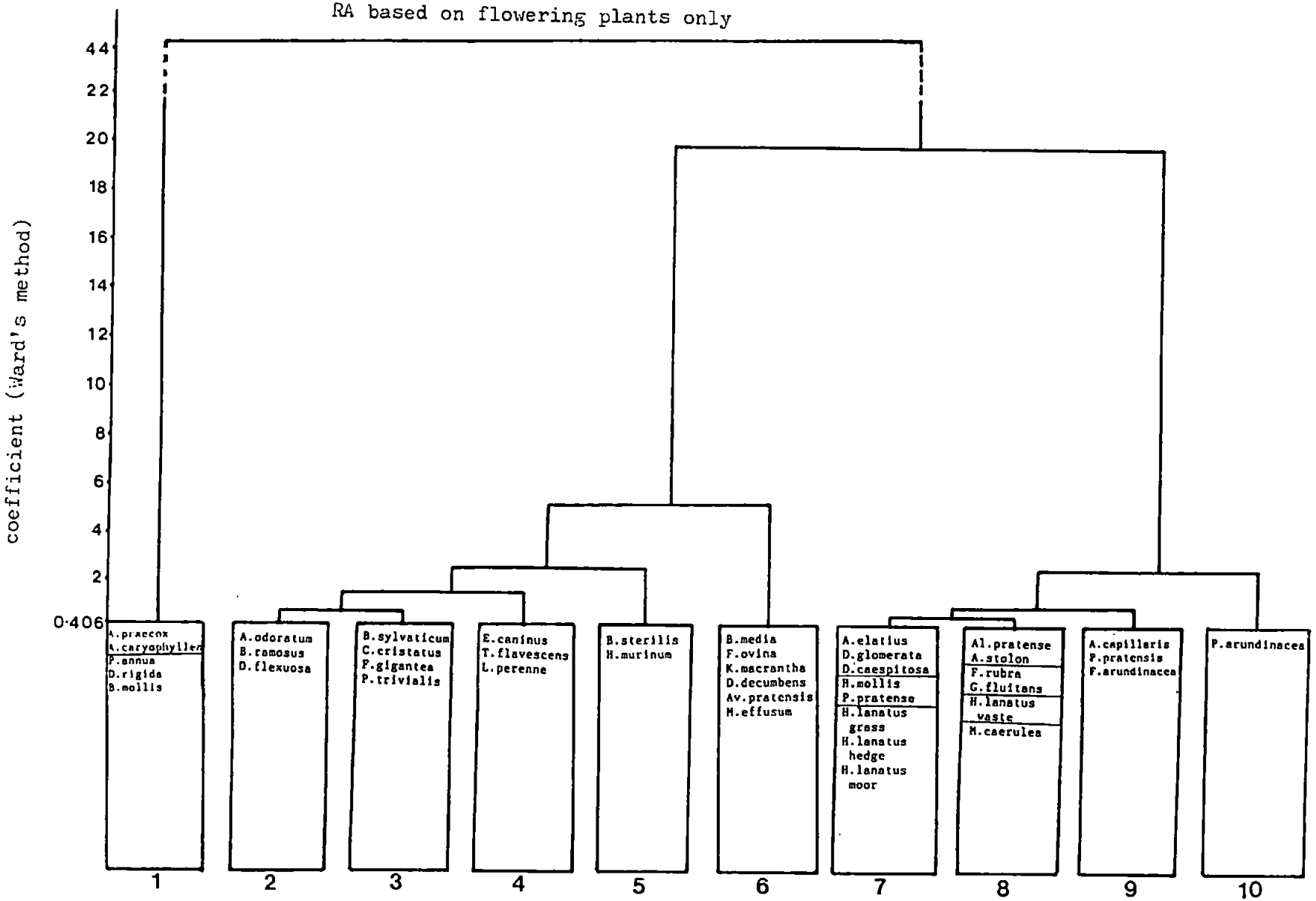


Fig 6.4.9 Dendrogram showing Clusters produced using all available values of RA and CI
RA based on flowering plants only



little information may be appropriate for a single, narrowly defined purpose but is unlikely to be generally useful. The decision as to precisely which information it is desirable to retain is a matter of opinion and may also vary with the use that is to be made of the classification. No classification can contain an infinite number of parameters on an infinite number of species and certain criteria should be selected on the basis of the amount of information that they impart. Reproductive allocation provides a very useful criterion by which plant strategy can be assessed. This is particularly true of the ruderal strategy and RA appears to be an appropriate index to use to emphasise the ruderal element of a plant's strategy. When used in conjunction with criteria such as CI and more especially Rmax it can create a meaningful classification of species which can be explained in terms of their ecological strategy. Obviously, of the various combinations of the 3 characteristics that were used to classify the data, the most satisfactory classification was that which included all 3 characteristics, Rmax, CI and RA. However, examination of the classifications produced using pairs of characteristics indicated that Rmax and RA produced more satisfactory classifications and consequently were more appropriate indices than CI.

RA and Rmax may be functionally more important in a plant's strategy than CI. CI is a composite index which takes into account the maximum height of the leaf canopy, lateral spread and the estimated maximum accumulation of persistent litter. These 3 characteristics are not necessarily correlated and two plants may have the same CI despite having quite different morphological attributes. However, height of canopy is given a greater weighting since the maximum possible score for height of canopy was arranged to be twice that allowed for either lateral spread or litter accumulation. In fact, height of canopy can

be a very plastic intraspecific character eg Arrhenatherum elatius showed polymorphism with respect to plant height (Mahmoud et al 1975) and even Mendel showed that stature could be a single character cross in Pisum (Briggs and Walters 1984). In contrast Rmax and RA are likely to be relatively fixed genetically since both are likely to represent the outcome of many interrelated features of a plant's biology eg Rmax represents the result of rate of protein synthesis, root/shoot ratio, various allocation patterns including leaf thickness and area, stomatal resistance, enzyme activities etc. Thus RA and Rmax are probably better indicators of strategy than height, which may be a single gene character. It seems possible therefore, that RA and Rmax are of more importance to a species in an evolutionary context and that this is why they are better indices of plant strategy.

Additional criteria such as on plant morphology and structure may also play an important part in vegetation strategies and the inclusion of data on additional species always improves a classification eg compare fig 6.4.9 with fig 6.4.7. Obviously further research is necessary before a comprehensive classification of plant strategies can be attempted but it seems evident that reproductive allocation should be an integral element in this classification.

CHAPTER 7 - CONCLUSION

One of the main aims of this thesis has been to address some of the conceptual problems related to the question of the best method by which to measure reproductive allocation, followed by the application of a 'best' method to a range of species of differing ecological strategies. Throughout the course of investigations into these problems a number of themes have frequently recurred. These themes, which are briefly summarised below, may be apparent in one or several experiments.

7.1 The response of RA to stress

Nutrient stress was selected as a relatively simple stress to apply to 2 different species Poa annua and Taraxacum officinale. In fact despite the 3 and 4 fold reductions in weight caused by a low nitrogen treatment neither species displayed a significant reduction in their biomass RA (51.7% for Taraxacum officinale and 36.9% for Poa annua) In annual or ruderal species like Poa annua and Taraxacum officinale the maintenance of a fixed proportion of biomass in reproduction despite environmental stress is an appropriate strategy. Had some other stress been applied, such as drought or shade, the response of the species may have differed. It seems likely that species have evolved appropriate responses to certain stresses which have habitually occurred in their evolutionary history.

When potassium and phosphorus were deficient, Taraxacum plants displayed an increased reproductive allocation of potassium and phosphorus. (Reproductive allocation behaviour in response to nutrient limitation may be species-specific (Williams and Bell 1981)). In Taraxacum there seemed to be a trend towards preferential allocation of K and P to reproductive structures. In ruderal species, therefore,

there is a growth response which maximises seed production and seed 'quality' at the expense of a rapid curtailment in vegetative development. Nevertheless, in extremely deficient conditions there must be a critical minimum level of vegetative development necessary to maintain the photosynthetic apparatus. This is evident in Taraxacum, particularly in the N deficient treatment where nutrient RA declines.

The response of RA to nutrient stress can therefore be both element and species specific. However it seems that in general under nutrient stress ruderal plants will maintain the proportion of resources devoted to reproduction despite reductions in total biomass and total nutrient content.

7.2 The relationship between nutrient and biomass RA

The nutrient allocation of N, P and K in Taraxacum officinale was found to be significantly different from that of biomass. When the mean reproductive allocations of all treatments were compared, KRA (71%) and PRA (66%) were significantly higher than BRA (51.7%). The high KRA was attributed to high concentrations of K in the scape sap. Biomass allocation, therefore, did not always reflect nutrient allocation. This was similar to the conclusion drawn by Abrahamson and Caswell (1982).

However, the extent of the difference between the various methods of measuring RA varied according to the treatment. In the control the difference between the methods was not significant, but in the 20%K and 20%P treatments the differences were highly significant, reflecting the higher allocation of K and P to reproduction in these treatments. Consequently, although it seems unwise to assume that the allocation of biomass and nutrients is similar, there is no obvious alternative

currency which is appropriate in all conditions. The relative contributions of biomass and nutrients to reproductive parts are qualitatively similar and are highly correlated. In optimal conditions biomass seems to be a reasonable currency by which to gauge RA since it is basically an integration of a number of physiological processes and often reflects the relative allocation of mineral nutrients. Moreover, biomass is undoubtedly easier to measure than nutrient allocation.

7.3 Reproductive cost

An alternative approach to the measurement of the evolutionary consequences of reproduction was suggested by Bell (1980). He argues that units of reproductive allocation are only of evolutionary significance if they are transformed into units of fitness. It is the cost to the plant of reproducing that it is important. This reproductive cost may be realised in terms of reduced future reproduction, survival or growth.

Prevention of flowering in Digitalis by manual excision of flower buds resulted in an increase in the number of axillary buds produced which was proportional to the number of flowers removed. Although there was a slight tendency for plants with higher RAs to be more susceptible to disease this was not statistically significant. In fact, this species behaved in a way that prevented any realisation of a reproductive cost. Any excess resources which may have been available to allow future growth were diverted into the production of axillary buds in the current season. Moreover, the optimal conditions in the experimental site where resources were abundant allowed plants sufficient resources to produce overwintering secondary rosettes. Any chance of a reproductive cost being observed in terms of reduced survival was consequently unlikely.

Similarly, in Plantago lanceolata removal of flowering buds resulted in an increased effort to produce flowering buds in that current year. Any resources which might have been diverted to reproduction in the second year were used in a 3-fold increase in current reproduction.

It seems therefore that although reproductive cost may be the more crucial measure of what is important to the plant in evolutionary terms, it may be very difficult to measure. Reproductive cost can also be expressed in numerous different ways in different species.

7.4 Individual variability and variability in the environment

The significance of variability in individual behaviour is apparent in many of the experiments. In the first experiment on the effect of nutrient stress on RA both Poa annua and Taraxacum officinale displayed wide variation in their individual reproductive allocation. Similarly Taraxacum plants in the reproductive cost experiment in Chapter 5.1 showed great variability, making any statistically significant conclusions impossible. Wide intraspecific variation was also evident in the comparative experiment (Chapter 6), increasing the standard deviation and reducing the significance of the results.

The use of conventional statistical techniques based on the population mean tends to mask this variability. The importance of individual variability has been stressed by Begon (1984) and Waite (1985). Increase or decrease in variability of RA in response to stress may itself be an adaptive strategy. Real (1980) has shown that a maximum principle for evolutionary processes based solely upon mean fitness of behaviours may, under certain circumstances, be misrepresentative and misleading in the analysis of biological systems.

The importance of variation in experimental situation was also evident in many of the experiments. In the reproductive cost experiment Taraxacum plants became much larger than was anticipated from observations in the field. This probably resulted in some intraspecific competition which may have increased the variability observed in the plants. Similarly Digitalis plants frequently die after flowering in the field but do not necessarily do so in optimal environmental conditions. This variability in behaviour dependent on experimental situation emphasises the need for controlled comparative experiments as advocated by Grime (1965).

7.5 The importance of plant morphology

The importance of plant morphology and structure and its influence on RA is evident in many of the experiments. RA measured in terms of biomass was positively correlated with total weight in Taraxacum whereas in Poa annua RA was negatively correlated with total weight in the first harvest and there was no relationship in the second harvest. From the available literature it is evident that species which show a positive correlation of RA with plant weight tend to have a consistent morphology, with large infloresences arising from a central rosette of leaves. Taraxacum can produce an indefinite number of flowers (given sufficient resources) with little change in the basic morphology or size of the rosette whereas in Poa annua any increase in reproductive parts automatically entails a corresponding increase in vegetative parts so that the relationship between the two remains constant.

In the final experiment where the value of RA as an ecological indicator is assessed the influence of plant morphology on RA is again apparent. Differences in plant morphology are used to explain why some anomalous species do not appear in the expected classes or categories

eg tufted perennial species characteristic of stressed environments often had higher RAs than expected, whereas rhizomatous or highly stoloniferous species often had lower RAs than expected.

The morphology of a particular species seems to influence the ratio of reproductive to vegetative parts. Morphology is taken into account in other indicators of ecological strategy such as CI but not in RA. It may be that certain types of morphology are more common in certain environments and that this may contribute to certain levels of RA being more prevalent in particular conditions.

7.6 RA as an indicator of strategy

The ultimate aim of this thesis was to conduct a comparative study of potential RA in species from different habitats (cf Grime and Hunt 1975). The general conclusion reached was that biomass allocation was an adequate means by which to gauge reproductive allocation. It was simpler and required less time and effort than many of the other currencies and the experimental evidence indicated that under optimum conditions biomass RA could be used in comparative experiments. Antonovics (1981) also suggested that in comparative experiments dry weight measurements of allocation were adequate.

When biomass RA was measured in a comparative analysis of different species of Gramineae it was obvious that RA can be a useful ecological index. In particular, it can be used to emphasise the ruderal element of a plant's strategy. In general, the reproductive behaviour of the Gramineae was consistent with that proposed for C, S and R strategies (Grime 1977). Ruderal species had high RAs (40.9 - 66.3%), stress-tolerant species had low RAs (0.02 - 5.2%) and competitive species had intermediate but very variable RAs (15%). RA compared favourably with

other indices of strategy (eg RMAX + CI) when plotted on triangular ordinations and used as a classification criterion.

Ideally, as many characters as possible should be used in classification of species strategies. However, in practice a compromise is often required and an index which 'loses' the least amount of information and is the simplest to measure is often most appropriate. The classification which contained the most information was the one using Rmax, CI and RA. On examination of the loss of information resulting from the exclusion of one or more of these characters it was evident that the classification using both RA and Rmax was most meaningful. CI is a composite index comprising of a number of morphological characteristics and it is argued that RA and Rmax may be more important to a species in an evolutionary context and are thus better indicators of plant strategy. Obviously RA alone cannot entirely describe a plant's strategy, but in conjunction with other parameters, particularly Rmax, RA produced a meaningful classification of species in terms of their ecological strategy.

ACKNOWLEDGEMENTS

I would like to thank the following people for their technical advice and practical assistance:

Dr K Alexander
Dr L Austin
Mr J Dight
Mr R Henderson
Mr A Hull
Mrs S Kaboche
Miss K Lacey
Mrs D Merrett
Mr S Newell
Dr K Thompson
Mrs A Torr
Dr D Wright

I am particularly grateful to Mrs E Glover for her time and patience whilst typing this manuscript. I also appreciate the understanding and encouragement shown to me by numerous friends and colleagues.
The project was carried out whilst in receipt of a SERC Research Studentship.

REFERENCES

Abrahamson, WG (1975). Reproduction of Rubus hispidus L in different habitats. American Midland Naturalist, 93, 471-478.

Abrahamson, WG (1979). Patterns of resource allocation in wildflower populations of fields and woods. American journal of botany 66, 71-79.

Abrahamson, WG and Caswell, H (1982). On the comparative allocation of Biomass, Energy and Nutrients in Plants. Ecology 63 (4), 982-991.

Abrahamson, WG and Gadgil, M (1973)). Growth form and reproductive effort in goldenrods (Solidago, Compositae). American naturalist, 107,651-661.

Abrahamson, WG and Hershey, B (1977). Resource allocation and growth of Impatients capensis (Balsaminaceae) in 2 habitats. Bulletin of the Torrey Botanical Club, 104, 160-164.

Aitchison, J (1982). The statistical analysis of compositional data JR Statist, Soc B 44 139-77

Aitchison, J (1983). Principal component analysis of compositional data Biometricity, 70,1, 57-65

Allen SE ed (1974). The chemical analysis of ecological materials. Oxford: Blackwell Scientific.

Alvey, Galway and Lane (1982). An introduction to Genstat, London Academic Press.

Antonovics, J (1980). Concepts of resource allocation and partitioning in plants. In Staddon JER Ed Limits to Action. The allocation of individual behaviour. Academic press. New York. 1-35.

Armstrong, RA (1982). A quantitative theory of reproductive effort in rhizomatous perennial plants. Ecology 63(3), 679-686.

Armstrong, RA (1984). On the quantitative theory of reproductive effort in clonal plants. Refinements of theory, with evidence from goldenrods and mayapples. Oecologia 63, 410-417.

Austin, RB (1966). The influence of the P and N of pea plants on the growth of their progeny. Plant and Soil 24, 359-368.

Avery, BW and Bascombe, CL (Ed) (1974) Soil Survey Laboratory methods 28-29.

Baker, RJ, Nelder, HA (1978). The Glim system manual numerical algorithms group. Banbury Rd, Oxford OX2 6NN.

Bateson, G (1963). The role of somatic change in evolution. Evolution, 17, 529-539.

Bazzaz, FA and Carlson RW (1979). Photosynthetic contribution of flowers and seeds to reproductive effort in an annual coloniser. New Phytologist, 82, 223-232.

Beasleigh, WG and Yarranton, GA (1974). Ecological strategy and tactics of Equisetum sylvaticum during a post-fire succession. Canadian Journal of Botany, 52, 2299-2318.

Begon, M (1984). Density and individual fitness. Asymmetric competition in evolutionary ecology Ed B Shorrocks. Blackwell Scientific Publications, Oxford

Begon, M and Mortimer A M (1981). Population Ecology. Blackwell Scientific Publications, Oxford.

Bell, G (1976). On breeding more than once. American Naturalist, 110, 57-77.

Bell, G (1980). The costs of reproduction and their consequences. Americal Naturalist, 116, 1, 45-76.

Bell, KL, Hiatt, HD and Niles WE (1979). Seasonal changes in biomass allocation in 8 winter annuals of the Mojave desert. Journal of Ecology, 67, 781-787.

Benzing, DH and Davidson EA (1979). Oligotrophic Tillandsia circinnata. Schlect (Bromeliaceae). An assessment of its patterns of mineral allocation and reproduction. Americal Journal of Botany, 66(4), 386-397.
Bierzychudek, P (1981). Pollinator Limitation of Plant Reproductive Effort. American Naturalist, 117, 838-840.
Bierzychudek, P (1982). The demography of jack-in-the-pulpit, a forest perennial that changes sex. Dissertation. Cornell University Ithaca, New York.
Bocher, TW and Larsen, K (1958). Geographical distribution of initiation of flowering, growth habit and other characteristics in Holcus Lanatus L. Botaniska Notiser, 111, 289-300.
Bostock, SJ (1978). Seed germination strategies of 5 perennial weeds. Oecologia, 36, 113-126.
Bostock, SD (1980). Variation in reproduction allocation in Tussilago farfara. Oikos, 34, 359-363.
Bostock, SJ and Benton, RA (1979). The reproductive strategies of 5 perennial Compositae. Journal of Ecology, 67, 91-107.
Bouma, D (1983). Diagnosis of mineral deficiencies using plant tests in inorganic plant nutrition. Ed A Lauchli and R L Bieleski, Springer-Verlag, Berlin.
Bradbury, IK and Hofstra, G (1976). The partitioning of net energy resources in 2 populations of Solidago canadensis during a single developmental cycle in Southern Ontario. Canadian Journal of Botany, 54, 2449-2456.
Bradshaw, AD (1965). Evolutionary significance of Phenotypic plasticity in plants. Adv. Genet., 13, 115-55.
Bradstreet, RB. (1965). The Kjeldahl method for Organic Nitrogen. Academic Press, New York.
Briggs, D and Walters, SM (1984). Plant Variation and Evolution, 2nd edit. Cambridge University Press.
Calow P (1973). The relationship between fecundity, phenology and longevity: a systems approach. American Naturalist, 107, 559-574.
Calow P (1978). Life Cycles. Chapman and Hall, London.
Caswell, H and Werner, PA (1978). Transient behaviour and life history analysis of teasel (Dipsacus sylvestris Huds). Ecology, 59,53-66.
Chapin, F Stuart, III (1980). The mineral nutrition of wild plants. Annual Review of Ecological Systematics, 11, 233-60.
Clapham, AR, Tutin TG and Warburg EF (1962). Flora of the British Isles, 2nd edition, Cambridge University Press.
Clark, SC (1980). Reproductive and vegetative performance in 2 winter annual grasses, Catapodium rigidum (L) CE Hubbard and C. Marinum (L) CE Hubbard. New Phytologist, 84, 59-78.
Clausen, J. Keck, DD and Hiesey, WM. (1940). Experimental studies on the nature of species. The effect of varied environments on North American plants. Carnegie Institute, Washington Publication no 520, 452pp.
Clay, K and Shaw, R (1981). An experimental demonstration of density dependent reproduction in a natural population of Diamorpha smallii - a rare annual. Oecologia, 51, 1-6.
Cody, ML (1966). A general theory of clutch size. Evolution, 20 174-184.
Cook, RE (1975). The photo-inductive control of seed weight in Chenopodium nibrum (short day weedy annual). Am J Bot 62,4,427-423.
Cunningham, GL, Syvertsen, JP, Reynolds, JF and Willson, JM (1979). Some effects of soil moisture availability on above ground production and reproductive allocation in Larrea tridentata (DC). Cov. Oecologia, 40, 113-123.

De Ridder, N, Seligman, NG and Van Keulen, H (1981). Analysis of Environmental and species effects on the magnitude of biomass investment in the RE of annual pasture plants. Oecologia, 49, 263-271.
Dittmer, HJ (1972). A method to determine root biomass including uncollected portions. Bulletin of the Torrey Botanical Club, 99, 146-147.
Donald, CM and Hamblin, J (1976). The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Advances in agronomy, 28, 361-405.
Douglas, DA (1981). The balance between vegetative and sexual reproduction of Mimulus primuloides (Scrophulariaceae) at different altitudes in California. Journal of Ecology, 69, 295-310.
Eis, S, Garman, EH and Ebell, LF (1965). Relation between cone production and diameter increment of douglas fir (Pseudotsuga menziesii (Mirb Franco), Grand fir (Abies grandis (Dougl) (Lindl) and Western White Pine (Pinus monticola, Doug). Canadian Journal of Botany, 43, 1553-.
Ellis, WM (1974). The breeding system and variation in populations of Poa annua L. Evolution, 27,656-652.
Epstein, E (1972). Mineral nutrition of plants. Principles and perspectives. NY Wiley, 412pp.
Ernst, WHO (1979). Population biology of allium ursinumin in Northern Germany. J Ecol 67 347-362.
Ernst, WHO (1981). Ecological implication of fruit variability in Phleum arenarium L, an annual dune grass. Flora, 171, 387-398.
Ernst, WHO (1983). Element nutrition of two contrasted dune annuals J Ecol, 71.1, 187-209.
Evans, DW and Canode, CL. (1971). Influence of N fertilization, gapping and burning on seed production of Newport Kentucky Bluegrass, agronomy Journal, 63, 575-80.
Everitt, B (1980). Cluster analysis 2nd edn. London, Heinemann. Educational for Social Science Research Council.
Faithfull, NT (1969). Laboratory Practice, 18, 1302.
Fenner, M (in press). The allocation of minerals to seeds in Senecio vulgaris subjected to nutrient stress.
Fenner, M (1985). Reproductive strategies in plants. In Seed Ecology, Chapman and Hall.
Filliben, JJ (1975). The probability plot correlation coeffient test for normality. Technometrics, 17 No 1, 111-117.
Fisher, RA (1930). The Genetical Theory of Natural Selection, Dover Press, New York, rev ed 1958, p47.
Fisher, RA and Yates, F (1974). Statistical Tables for Biological, Agricultural and Medical Research. Oliver and Boyd Ltd, Edinburgh (Longman).
Flinn, AM and Pate, JS (1970). A quantitative study of carbon transfer from pod and subtending leaf to ripening seeds of field pea (Pisum arvense L). Journal of Experimental Botany, 21, 72-82.
Gadgil, M and Solbrig, OT (1972). The concept of r- and k- selection: evidence from wild flowers and some theoretical considerations. American Naturalist, 106, 14-31.
Gaines, MS, Vogt, KJ, Hamrick, JL and Caldwell, J. (1974). Reprodutive strategies and growth patterns in sunflowers (Helianthus) American Naturalist, 108, 889-894.
Gerloff GC, Moore, DG, Curtis JT (1966). Selective absorption of mineral elements by native plants of Wisconsin Plant and Soil 25, 393-405.

Goodman, GT and Perkins (1959). Mineral uptake and retention in cotton grass (Eriophorum vaginatum L). Nature, 184, 467-468.
Grace, JB and Wetzel, RG (1981). Phenotypic and genotypic components of growth and reproduction in Typha latifolia: Experimental studies in marshes of different successional maturity. Ecology, 62, 789-801
Greenway, H and Pitman, MG (1965)..
Potassium retranslocation in seedlings of Hordeum vulgare. Aust J Biol. Sci. 18: 235-247 in Bouma.
Gregory, FG (1953). The control of growth and reproduction by external factors. Report of 13th Int Hort Congress. 96-105 London.
Grime, JP (1965). Comparative experiments as a key to the ecology of flowering plants. Ecology, 45, 513-515.
Grime, JP (1974). Vegetation, classification by reference to strategies. Nature, 250, 26-31.
Grime, JP (1977). Evidence for the existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist, 111, 1169-1194.
Grime, JP (1979). Plant strategies and vegetation processes, Wiley Chichester.
Grime, JP, Mason, G, Curtis, AV, Rodman J, Band SR, Mowforth, MAG, Neal, AM and Shaw, S (1981). A comparative study of germination characteristics in a local flora. J Ecol 69 1017-1060.
Grime, JP (1984). The ecology of species, families and communities of the contemporary Flora. New Phytol. 98, 15-33.
Grime JP, Hodgson, JG and Hunt, R (1985). Comparative plant ecology. A functional approach to common British species and communities. George Allen and Unwin Ltd, London.
Grime, JP and Hunt, R (1975). Relative growth rate: its range and adaptive significance in a local flora. J Ecol 63, 393-422.
Gross, HC (1972). Crown deterioration and reduced growth associated with excessive seed production by birch. Can.J.Bot 50, 2431-2437.
Gross, KL and Werner, PA (1982). Colonising abilities of 'biennial' plant species in relation to ground cover: implications for their distributions in a successional sere. Ecology 63(4). 921-931.
Grubb, PJ (1976). A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. Biological Conservation, 10, 53-76.
Harper, JL (1961). Approaches to the study of plant competition. Symp. Soc. Exptl. Biol. 151-39.
Harper, JL (1977). Population biology of plants. Academic press, London, England.
Harper, JL, Lovell, PH and Moore, KG (1970). The shapes and sizes of seeds. Annual Review of Ecology and Systematics, 1, 327-50.
Harper, JL and Ogden J (1970). The reproductive strategy of higher plants. The concept of strategy with special reference to Senecio vulgaris L. Journal of Ecology, 58, 681-698.
Harper, JL, and White, J (1974). The demography of plants. Annual Review of Ecology and Systematics, 5, 419-463.
Harris, GR and Lovell PH (1980). Growth and reproductive strategy in Veronica spp. Annals of Botany, 45, 447-458.
Hawthorn, WR and Cavers, PB (1978). Resource allocation in young plants of 2 perennial species of Plantago. Canadian Journal of Botany, 56, 2533, 2537.
Hawthorn, WR and Cavers, PB (1982). Dry weight and resource allocation patterns in populations of Plantago major and Plantago rugellii. Canadian Journal of Botany, 60, 2424, 2439.
Hewitt, LJ (1952). A biological approach to the problems of soil acidity. Transactions of the International Society of Soil Science Joint Meeting, Dublin, 1, 107-118.

Hewitt, EJ (1966). Sand and Water Culture Methods used in the Study of Plant Nutrition. Commonwealth Bureaux of Horticulture and Plantation crops. East Malling, Kent. Technical Communications No 22 (revised 2nd edition).

Hickman, JC (1975). Environmental unpredictability and plastic energy allocation patterns in the annual Polygonum cascadense (Polygonaceae) Journal of Ecology, 63, 689-701.

Hickman, JC (1977). Energy allocation and niche differentation in 4 co-existing annual species of Polygonum in western North America. Journal of Ecology, 65, 317-326.

Hickman, JC and Pitelka LF (1975). Dry weight indicated energy allocation in ecological strategy and analysis of plants. Oecologia, 21, 117-121.

Hiesey, WM, Clausen, J and Keck, DD (1942). Relations between climate and intraspecific variability in plants. American Naturalist, 76, 5-22.

Hill, J, Robson AD, Loneragan, JF (1978). The effect of Cu and N supply on the retranslocation of Cu in 4 culti vars of wheat. Austr.J.Agric.Res, 29, 925-939.

Hill, J, Robson, AD, Loneragan, JF (1979). The effects of Cu supply and shading on Cu retranslocation from old wheat leaves. Ann.Bot 43, 449-457.

Hirshfield, MF and Tinkle, DW (1975). Natural Selection and the Evolution of Reproductive Effort. Proceedings of the National Academy of Science, USA, 72-2227-2231.

Hocking PJ, and Pate JS (1978). Accumulation and distributions of min. elements in the Ann Lupins Pupinus albus L and Lupinus angus tifolius L. Aust.J.Agric.Res, 1978, 267-80.

Holler, LC and Abrahamson, WG (1977). Seed and vegetative reproduction in relation to density in Fragaria virginiana (Rosaceae). American Journal of Botany, 64, 1003-1007.

Holmsgaard, E (155). Tree ring analyses of Danish forest trees. Forstl. Forosksv. Dan, 183, 1-246.

Holt, BR (1972). Effect of arrival time on recruitment, mortality and reproduction in successional plant populations. Ecology 53: 668-673.

Hoskins, JL (1944). An interchangeable micro and macro steam distillation apparatus. Analyst, London, 69-271.

Hutchinson, CS and Seymour, GB (1982). Biological flora of the British Isles - Poa annua. J.Ecol 70, 887-907.

Jackson, ML (1958). Soil Chemical Analysis. Prentice Hall, London.

Jaksic, FM and Montenegro, G (1979). Resource allocation of Chilean herbs in response to climatic and microclimatic factors. Oecologia, 40, 81-88.

Johnson NC and Leone FC (1964). Statistics and Experimental Design in Engineering and Experimental Design in Engineering and the Physical Sciences Vol II.

Jolls, CL (1984). Contrasting resource allocation patterns in Sedum lanceolatum Torr: Biomass versus energy estimates. Oecologia, 63, 57-62.

Jurik, TW (1983). Reproductive Effort and CO2 dynamics of wild strawberry populations. Ecology, 64, 6, 1329-1342.

Kahn, AA and Sagar, GR (1969). Alteration of the pattern of distribution of photosynthetic products in the tomato by manipulation of the plants. Annals of Botany, 33, 753-763.

Kawano, S (1981). Trade-off relationships between some reproductive characteristics in plants with special reference to life history strategy. Botanical Magazine of Tokyo, 94, 295-294.

Kawano, S and Hayashi, S (1977). Plasticity in growth and reproductive allocation of Coix Ma-yuen Roman, cultivated at varying densities and nitrogen levels. Journal of the College of Liberal Arts, Toyama University, Japan, 10, 61-92.

Kawano, S and Masuda, J. (1980). The productive and reproductive biology of flowering plants. VII Resources allocation and reproductive capacity in wild populations of Heloniopsis orientalis (Thunb) C Tanaka (Liliaceae). Oecologia, 45, 307-317.

Kawano, S and Nagai, Y (1975). The productive and reproductive biology of flowering plants I Life history strategies of 3 Allium species in Japan Bot.Mag. Tokyo 88, 281-318.

Kawano, S, Hiratsaha, A, Hayashi, K (1982). The productive and reproductive biology of flowering plants V life history characteristics and survivorship of Erythronium japonicum Oikos, 38,129-149.

Lambert, DA (1968). Competition between plants of cocksfoot (Dactylis glomerata) grown for seed. J.Br.Grassld.Soc, 23, 274-79.

Langer, RHM (1956). Growth and nutrition of timothy (Phleum pratense) I the life history of individual tillers. Annals of Applied Biology, 44, 166-187.

Langer, RHM, Ryle, SM and Jewiss OR (1964). The changing plant and tiller populations of timothy and meadow fescue swards. I plant survival and the pattern of tillering. Journal of Applied Ecology, 1, 197-208.Law, R (1979b). The cost of reproduction in annual meadow grass. American Naturalist, 113, 3-16.

Law, R (1979a). Ecological Determinants in the Evolution of Life Histories in Population Dynamics, Ed Anderson, RM, Turner, BD and Taylor, LR, Blackwell Scientific Publications, Oxford.

Law, R, Bradshaw AD, Putwain, PD (1977). Life history variation in Poa annua. Evolution, 31, 233-246.

Lee, SM and Cavers PB (1981). The effects of shade on growth, development and resource allocation patterns of 3 species of foxtail (Setaria). Canadian Journal of Botany, 59, 1776-1786.

Lee, TD and Bazzaz, FA (1980). Effects of defoliation and competition on growth and reproduction in the annual plant Abutilon theophrasti. Journal of Ecology, 68, 813-821.

Leonard, ER (1962). Inter-relations of vegetative and reproductive growth, with special reference to indeterminate plants. The Botanical Review, 28, 3, 353-410.

Leopold, AC and Kriedemann, PE (1975). Plant growth and development. Second edition. McGraw-Hill, New York.

Linhart, YB (1974). Intra population differentation in annual plants 1. Veronica peregrina. L. raised under non-competitive conditions.

Loneragen, JF, Snowball, K, Robson AD (1976). Remobilisation of nutrients and its significance in plant nutrition. In Wardlaw F Passiour JB (eds). Transport and trasnfer processes in plants. Academic Press
NY p. 463-469.

Lotka, AJ (1922). Contribution to the energetics of evolution. Proceedings of the National Academy of Science of the USA, 8, 147-151.

Lovett-Doust, J (1980a). Experimental manipulation of patterns of resource allocation in the growth cycle and reproduction of Smyrnium olusatrum. Biological journal of the Linnean Society. 13, 155-166.

Lovett Doust, J (1980b). A comparative study of life history and resource allocation in selected umbelliferae. Biological Journal of the Linnean Society, 13, 139-154.

Lovett Doust, J and Cavers, PB (1982). Sex and gender dynamics in jack in the pulpit. Arisaema triphyllum (Araceae). Ecology, 63, 797-803.

Lovett Doust, J and Eaton, GW (1982). Demographic aspects of flower and fruit production in bean plants. Phaseolus vulgris L. American Journal of Botany, 69, 1156-1164.

Lovett Doust, J and Harper JC (1980). The resource costs of gender and maternal support in an andromonoecious umbellifer. Smyrnium olusatrum L. New Phytologist, 85, 251-264.

Luftensteiner (1980). The reproductive effort in four plant communities of Central Europe. Plant systematics and evolution 135, 235-251.

Ma, TS and Tuazaga, G (1942). Micro-kjeldahl determination of nitrogen. A new indicator and an improved rapid method. Industrial Engineering Chemical Analyst. Edn 14, 280-282.

Mackereth, FJH, Heron, J and Talling JF (1978). Water Analysis, Freshwater Biological Association, Scientific Publication No 36.

Mahmoud A, Grime, J Furness SP (1975). Polymorphism in Arrhenatherum elatius (L). The New Phytologist, 75, 269-276.

MacArthur, RH and Wilson EP. (1967). The theory of island Biogeography. Princeton University Press. Princeton, NJ.

McNamara, J and Quinn JA (1977). Resource allocation and reproduction in populations of Amphicarpum purshii (Graminae). American Journal of Botany, 64, 17-23.

McNaughton, SJ (1975). R and K- selection in Typha. American Naturalist, 109, 251-261.

Maun, MA (1974). Reproductive biology of Rumex crispus. Phenology, surface area of chlorophyll containing tissue and contribution of perianth to reproduction. Canadian Journal of Botany, 52, 2181-2187.

Maun, MA and Cavers PB (1971). Seed production and dormancy in Rumex crispus. II. The effects of removal of various proportions of flowers at anthesis. Can.J.Bot 49: 1841-1848.

Meagher, TR and Antonoviks, J (1982). The population biology of Chamaelirion luteum - a dioecious member of the lily family: life history studies. Ecology, 63, 1690-1700.

Mengel, K and Haeder, HE (1977). Effect of K supply on the rate of phloeum sap exudation and the composition of phloem sap of Ricinis communis. Plant Physiol 59: 2821284.

Mooney and Gulman (1979). Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants in topics in plant biology ed OT, Solbrig S, Jain, GB, Johnson and PH Raven, MacMillan.

Murdoch, WW (1966). Population stability and life history phenomena. American Naturalist, 100, 5-11.

Murphy, J and Riley, JP (1962). A modified single solution method for the determination of phosphate in natural waters. Analytica chim, Acta, 27, 31-36.

Newell, SJ and Tramer EJ (1977). Reproductive strategies in herbaceous plant communities during succession. Ecology, 59, 228-234.

Ogden J (1974). The reproductive strategy of higher plants. II The reproductive strategy of Tussilago farfara L. Journal of Ecology, 62, 291-324.

Oka, HI (1976). Mortality and adaptive mechanisms of Oryza perennis strains. Evolution, 30, 380-392.

Parry, GD (1981). The meanings of r- and K- selection. Oecologia, 48 260-264.

Pate, JS and Flinn, AM (1973). Carbon and nitrogen transfer from vegetative organs to ripening seeds of field pea (Pisum arvense L) J.Exp.Bot. Vol 24 No 83 pp 1090-1099.

Pearson, D (1976). The chemical analysis of foods, 6th edn, Longman.
Pianka, ER (1970). On r- and K- selection. American Naturalist, 104 592-597.
Pianka, ER. (1972) r- and K- selection or b and d selection? American Naturalist, 106, 581-588.
Pitelka, LF (1977). Energy allocation in annual and perennial lupines (Lupinus: Leguminosae). Ecology 58, 1055-1065.
Pitelka, LF, Stanton DS and Peckenham, MD (1980). Effects of light and density on resource allocation in a forest herb. Aster acuminatus (Compositae). American Journal of Botany, 67, 942-948.
Powell, CE, Ryle, GJA (1978). Effect of N deficiency on photosynthesis and the partitioning of c-labelled leaf assimilate in unshaded and partially shaded plants of Lolium temulentum. Ann appl Biol. 90: 241-248.
Powers, RF, Van Gent, DL and Townsend, RF (1981). Ammonia Electrode analysis of nitrogen in microkjeldahl digests of forest vegetation. Communications in soil science and plant analysis. 12(1), 19-30.
Primack, RB (1979). Reproductive effort in annual and perennial species of Plantago (Plantaginaceae). American Naturalist, 114, 51-62.
Raynal, DJ (1979). Population ecology of Hieracium florentinum (Compositae) in a central NY limestone quarry. Journal of Applied Ecology, 16, 287-298.
Raynal, DJ and Bazzaz FS (1975). The contrasting life cycle strategies of 3 summer annuals found in abandoned fields in Illinois. Journal of Ecology, 63, 587-596.
Real, LA (1980). Fitness, uncertainty and the role of diversification in evolution and behaviour. American Naturalist.
Reinartz, JA (1984). Life history variation of common mullein (Verbascum thapsus). II plant size, biomass partitioning and morphology. Journal of Ecology, 72, 913-925.
Robson, AD and Pitman, MG. 1983 interactions between nutrients in higher plants. P147-173 in Enclopaedia of plant physiol. Vol 15A.
Rodin, LE and Bazilevich, NI (1967). Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, Edinburgh.
Roos, FH and Quinn, JA (1977). Phenology and reproductive allocation in Andropogon scoparius (Graminae) populations in communities of different successional stages. American Journal of Botany, 64, 535-540.
Ryan, TA, Joiner, BL, Ryan, BF (1982). MINITAB Reference Manual.
Ryan, BF, Joiner, BL, Ryan, TA (1976). MINITAB Student Handbook. Duxbury Press. N Scituate, Massachussetts.
Sadhu, MK, Ghosh, SK and Bose TK (1975). Mineral nutrition of fruit plants. I effect of different levels of N, P and K on growth, flowering, fruiting and leaf composition of Phalsa (Grewia asiatica L). Indian Agric Vol 19 No 3, 319-324.
Sadhu, MK, Gosh, SK, Bose TK (1975). Effect of diff levels of N, P and K on growth, flowering, fruit set and mineral composition of pomegranate (Punica granatum L) in 'Recent Advances in Plant Sciences. Ed. Motial VS. Proceedings of conf. p 134-135.
Salisbury, EJ (1942). The reproductive capacity of plants. Bell, London.
Sarukahn, J (1974). Studies on plant demography: Ranunculus repens L R bulbosus L and R acris L. II reproductive strategies and seed population dynamics. Journal of Ecology, 62, 151-177.
Saruhkahn, K (1980). Demographic problems in tropical systems. Botanical monographs 15, 161-188.
Sarukahn, J and Harper, JL (1973). Studies in plant demography; Ranunaculus repens L, R bulbosus L, R acris L. J.Ecol. 61.675-716.

Schaffer, WM (1974). Selection for life histories: the effects of age structure. Ecology, 55. 291-303.
Schaffer, WM (1979). Equivalence of maximising reproductive value and fitness in the case of reproductive strategies. Proceedings of the National Academy of Sciences, USA, 76, 3567-3569.
Schaffer, WM (1983). The application of optimal control theory to the general life history problem. American Naturalist, 121, 418-431.
Schaffer, WM and Gadgil, M (1975). Selection for optimal life histories in plants. In Cody, ML and Diamond, JM. Ecology and evolution of communities, Belknap Press, Cambridge, Massachusetts, 142-157.
Schaffer, WM and Schaffer, MV (1977). The adaptive significance of variations in reproductive habit in the Agavaceae. In Stonehouse, B and Perrin, C eds. Evolutionary Ecology, University park press, Baltimore, USA, 261-276.
Shapiro, SS and Francia, RS (1972). Approximate analysis of variance test for normality (complete samples), Biometrika 52,591-611.
Shapiro, SS and Wilk, MB (1965). An analysis of variance test for normality. Biometrika 52, 591-612.
Shaver, GR, Chapin FSII (1980). Response to fertilisation by various plant growth forms in an Alastian tundra. Nutrient accumulation and growth. Ecology 61, No 3 in press, 662-675.
Shive, JW and Robbins, WR (1942). Bulletin of the New Jersey agricultural experimental station, 636. Methods of growing plants in solution and sand cultures.
Shiweizer, CJ and Reis, SK (1969). Protein content of seed. Increase improves growth and yield. Science, 165, 73-75.
Siccama, TG, Bormann, FH, Likens GE (1970). The Hubbard Brook Ecosystem study. Productivity and nut and phytosociology of the herbaceous layer. Ecol.Manag. 1970, Vol 40.
Silvertown, JW (1982). Introduction to Plant Population Ecology. Longman, London and New York.
Snedecor, GW and Cochran, WG (1980). Statistical methods 7th edn. Iowa State University Press.
Snell, TW and Burch (1975). The effects of density on resource partitioning in Chamaesyce hirta (Euphorbiaceae). Ecology, 56, 742-746.
Snell, TW and King, CE (1977). Lifespan and fecundity patterns in rotifers: the cost of reproduction, Evolution, 31, 882,890.
Sohn, JJ and Policansky D (1977). The costs of reproduction in the mayapple, Polophyllum peltatum (Berberidaceae). American Journal of Botany, 69, 615-622.
Solbrig, OT (1981). Energy, Information and plant evolution. Ch 11 in Physiological Ecology: An evolutionary approach to resource use. ed by CR Townsend and P Calow Blackwell Scientific Publications, Oxford.
Soule, JD and Werner PA (1981). Patterns of resource allocation in plants, with special reference to Potentilla recta L. Bulletin of the Torrey Botanical Club, 108, 311-319.
Southwood, TRE (1977). Habitat, the templet for ecological strategies Journal of Animal Ecology, 46, 337-365.
Spiertz, JHJ (1977). The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrogen economy of the Wheat plant.
Spratt, ED and Gasser, JKR (1970). Effects of fertiliser-N and water supply on distribution of dry matter and N between the different parts of wheat. Can.J.Plant Sci 50, 613-625.

Stark, RH, Hafenrichter, AL and Klages, KH (1949). The proceduction of seed and forage by mountain brome as influenced by nitrogen and age of stand. Agron, J 63,575-580.
Stearns, SC (1976). Life history tactics: a review of the ideas. Quarterly review of biology, 51, 3-47.
Stearns, SC (1977). The evolution of life history traits: a critique of theory and review of data. Annual Review of Ecology and Systematics, 8, 145-71.
Stebbins GL (1950). Variation and evolution in plants. Columbia University Press, New York and London.
Stern, WR and Beech, DF (1975). The growth of safflower (Carthamus tinctoris) in a low latitude environment. Aust.J.Agric.Res
Stewart, AJA and Thompson K (1982). Reproductive strategies of 6 herbaceous perennial species in relation to a successional sequence, Oecologia, 40, 81-88.
Struik, GJ (1965). Growth patterns of some native annual and perennial herbs in southern Wisconsin. Ecology, 46, 401-420.
Stuart, Chapin III, F (1980). The mineral nutrition of wild plants. Ann. Rev.Ecol.Syst. 11, 233-60.
Sutcliff, JF and Baker, DP (1974). Plants and mineral salts. Arnold, London.
Tamm, CO (1954). Some observations on the nutrient turnover in a bog community dominated by Eriophorum vaginatum. L Oikus 5, 189-194.
Thompson, K and Stewart, AJA (1981). The measurement and meaning of reproductive effort in plants. American Naturalist, 117, 205-211.
Tripathi, RS and Harper, JL (1973). The comparative biology of Agropyron repens and Agropyron caninum I. The growth of mixed populations established from tillers and from seeds. J Ecol, 61, 353-368.
Trivedi, S and Tripathi, RS (1982). Growth and reproductive strategies of 2 annual weeds as affected by soil nitrogen and density levels.
Tuomi, J, Niemela, P and Mannila, R (1983). Resource allocation on dwarf shoots of Birch (Betula pendula). Reproduction and leaf growth New Phytologist, 91, 482-487.
Twyford, IT, Walmsley, D (1974). The mineral composition of the Robusta Banana plant. III uptake and distribution of mineral constituents. Plant and soil 41, 471-491.
Ulrich, A and Hills, FJ (1973). Plant analysis as an aid in fertilising sugar crops. Part I. Sugar beets in soil testing and plant analysis, 271-288. Ed LM Walsh and JD. Beaton. Madison, Wisconsin: Soil science society of America.
Van Andel, J and Vera, F (1977). Reproductive allocation in Senecio sylvaticus and Chamaenerion angustifolium in relation to mineral nutrition. Journal of Ecology, 65, 747-758.
Van Baalen, J and Prinns, EGM (1983). Growth and reproduction of Digitalis purpurea in different stages of succession. Oecologia 58, 84-91.
Van Leeuwen (1981). The role of pollination in the population biology of the monocarpic species. Cirsium palustre and Cirsium vulgare. Oecologia 51, 28-32.
Waite, S and Hutchings, MJ (1982). Plastic energy allocation patterns in Plantago coronopus. Oikos, 38, 333-342.
Ward, JH (1963). Hierarchical grouping to optimise an objective function. J.ofAm.Statis.Assocation. 58, 236-244
Wareing, PF and Patrick J (1975). Source-sink relations and the partitioning of assimilates in the plant. In Cooper, JP Ed photosynthesis and productivity in different environments.

Watson, MA (1984). Developmental constraints: effect on population growth and patterns of resource allocation in a clonal plant. American Naturalist, 123, 411-426.
Weaver, SE and Cavers PB (1980). Reproductive effort in 2 perennial weed species in different habitats. Journal of applied ecology, 17, 505-513.
Werk, KS and Ehleringer, JR (1983). Photosynthesis by flowers in Encelia farinosa and Encelia californica (Asteraceae). Oecologia 57, 311-315.
Werner, PA (1975). Predictions of fate from rosette size in teasel (Dipsacus fullonum L). Oecologia, 20, 197-201.
Werner, PA (1976). Ecology of plant populations in successional environments, Systematic Botany. 1, 246-268.
Werner, PA and Platt WJ (1976). Ecological relationship of co-occurring goldenrods. American Naturalist 110, 959-971.
Whigham, D (1973). An ecological life history study of Uvularia perfoliata L. American Midland Naturalist, 91 343-59.
Wilbur, HM (1976). Life history evolution in 7 mildweeds of the genus Asclepias. Journal of Ecology, 64, 223-240.
Wilbur, HM, Tinkle, DW and Collins, JP (1974). Environmental certainty, trophic level and resource availability in life history evolution. American Naturalist, 108, 805-817.
Wilks, SS (1938). The large sample distribution of the likelihood ratio for testing composite hypotheses. Ann.Math.Statis, 9, 60-62.
Williams, GC (1966). Natural selection, the costs of reproduction and a refinement of Lack's principle. American Naturalist, 10, 687-690.
Williams, GC (1975). Sex and evolution. Princeton University Press * Princeton, NJ.
Williams, RF (1948). The effects of P supply on the rates of intake of P and N and on certain aspects of P metabolism in gramineous plants. Aust.J.Sci.Res. Ser B 1 333-61.
Williams, RF (1955). Redistribution of mineral elements during development. Annual Review of Plant Physiology, 6, 25-42.
Williams, DE (1961). The absorption of potassium as influenced by its concentration in the nutrient medium. 15, 387-399.
Willson, MF (1983). Plant reproductive ecology. John Wiley and Sons, NY.
Willson, MF and Price, PW (1979). Resource limitation of fruit and seed production in some Asclepias species. Canadian Journal of Botany, 58, 2229-2233.
Wilson, AM (1980). An investigation into reproductive effort in two successional stages using regression technique. MSc thesis, University of Durham.
Wishart, D. CLUSTAN User Manual.
Wishart, D (An algorithm for hierarchical classification. Biometrics 25, 165-170.
Woodwell, GM, Whittaker, RH, Houghton, RA (1975). Nutrient concentrations in plants in the Brookhaven oak-pine forest. Ecology 56, 318-32.
Zeide, B (1978). Reproductive behaviour of plants in time. American Naturalist, 112, 636-639.
* Williams, RB and Bell, KL (1981) Nitrogen allocation in Mojave Desert Winter Annuals. Oecologia 48, 145-50.

APPENDIX 1

Means of Harv one = ie mean wts/tray

LOGE Veg wt	All data	Veg wt	Rep wt	Total	RE	ASIN RE	LOGTEN RW
28	N	28	28	28	28	28	0.28
0.114	X	1.268	0.344	1.611	22.43	28.07	0.050
0.174	Med	1.190	0.356	1.576	21.94	27.93	0.076
0.518	SD	0.648	0.125	0.716	6.05	4.23	0.225
0.098	SE	0.122	0.024	0.135	1.14	0.80	0.043
1.217	Max	3.378	0.559	3.688	38.98	38.64	0.529
-0.906	Min	0.404	0.089	0.507	8.41	16.85	-0.394
0.413	Q3	1.512	0.422	1.912	26.17	30.77	0.179
-0.190	Q1	0.828	0.266	1.191	18.59	25.511	-0.081

Veg wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	1.350	0.829	0.4527	1.429	1.247	2.20	1.366
SD	0.144	0.205	0.0753	0.195	0.231	1.03	0.451
SE	0.072	0.103	0.0377	0.098	0.116	0.51	0.226

Rep wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	0.3515	0.2630	0.1100	0.4140	0.4009	0.448	0.4095
SD	0.0183	0.0368	0.0175	0.0201	0.102	0.109	0.0513
SE	0.0091	0.0184	0.0087	0.0100	0.051	0.055	0.0256

Total wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	1.702	1.092	0.5627	1.843	1.656	2.649	1.776
SD	0.147	0.211	0.0634	0.201	0.238	0.926	0.453
SE	0.074	0.106	0.0317	0.100	0.119	0.463	0.226

RE%

TR	1	2	3	4	5	6	7
N	20.75	24.56	19.86	22.64	24.90	20.3	23.99
X	4	4	4	4	4	4	4
SD	1.81	4.34	4.36	2.53	6.61	13.2	5.39
SE	0.91	2.17	2.18	1.26	3.30	6.6	2.7

ASIN RE

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	27.09	29.64	26.35	28.39	29.80	25.99	29.21
SD	1.29	2.98	3.26	1.70	4.29	9.17	3.78
SE	0.65	1.49	1.63	0.85	2.14	4.59	1.89

LOGTEN veg wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	0.1286	-0.090	-0.3483	0.1519	0.0902	0.296	0.120
SD	0.0461	0.100	0.0675	0.0609	0.0816	0.250	0.132
SE	0.0231	0.050	0.0337	0.0304	0.0408	0.125	0.066

Taraglin table of means

	Veg wt	Rep wt	Total wt	No Flows	RE%	ASIN RE	Veg wt NFs
N	28	20	28	28	28	28	28
X	0.796	1.333	2.128	6.06	61.49	51.71	1.234
Med	0.767	1.361	2.243	6.00	62.44	52.20	1.374
SD	0.335	0.593	0.870	2.75	7.58	4.46	0.470
SE	0.063	0.112	0.164	0.52	1.43	0.84	0.089
Max	1.429	2.661	3.913	11.33	72.08	58.10	1.884
Min	0.224	0.224	0.448	1.50	44.53	41.86	0.246

Effect of treatments

1. Total wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	2.638	1.392	0.596	2.396	2.679	2.527	2.670
SD	0.391	0.192	0.129	0.334	0.336	0.618	0.835
SE	0.196	0.096	0.065	0.167	0.168	0.309	0.417

2. Veg wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	1.131	0.5192	0.2775	0.7350	1.080	0.885	0.942
SD	0.249	0.0658	0.0768	0.0481	0.166	0.286	0.258
SE	0.125	0.0329	0.0384	0.0240	0.083	0.143	0.129

3. Rep wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	1.506	0.873	0.3185	1.661	1.599	1.642	1.729
SD	0.381	0.246	0.065	0.291	0.287	0.356	0.629
SE	0.191	0.123	0.0325	0.146	0.143	0.178	0.315

4. No of flowers

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	6.75	3.89	2.187	7.262	7.80	7.31	7.21
SD	3.04	1.31	0.625	0.899	2.73	3.10	1.51
SE	1.52	0.65	0.312	0.450	1.37	1.55	0.76

5. RE%

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	56.89	61.80	53.60	69.06	59.50	65.31	64.26
SD	9.13	9.51	4.96	2.73	6.15	3.76	6.04
SE	4.56	4.76	2.48	1.36	3.08	1.88	3.02

6. ASIN RE

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	49.00	51.92	47.07	56.22	50.51	53.94	53.33
SD	5.29	5.62	2.86	1.69	3.60	2.26	3.60
SE	2.64	2.81	1.43	0.85	1.80	1.13	1.80

7. Vet wt NFs

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	1.469	0.9505	0.2920	1.3880	1.585	1.5725	1.380
SD	0.201	0.0846	0.0556	0.0303	0.229	0.0825	0.364
SE	0.100	0.0423	0.0278	0.0151	0.114	0.0413	0.182

Taraxacum - non flowerers omitted

File = Taran Pk

RE	Arcsin	All Data	Veg wt	Rep wt	Total wt	NF
79	79	N	79	79	79	79
61.3	51.67	X	0.805	1.373	2.179	6.38
64.7	53.54	Med	0.777	1.341	2.223	6.00
15.0	9.31	SD	0.417	0.733	0.961	3.56
1.7	1.05	SE	0.047	0.082	0.108	0.40
87.5	69.32	Max	1.796	3.152	4.231	15.00
9.1	17.57	Min	0.105	0.120	0.331	1.00
71.8	57.94	Q3	1.057	1.991	2.829	9.00
52.5	46.44	Q1	0.453	0.913	1.596	4.00

Effect of treatments

1. Total wt

TR	1	2	3	4	5	6	7
N	11	11	10	14	11	9	13
X	2.873	2.411	0.579	2.380	2.654	2.632	2.630
SD	0.688	0.292	0.187	0.574	0.810	0.729	0.801
SE	0.207	0.088	0.059	0.153	0.244	0.243	0.222

2. Veg wt

TR	1	2	3	4	5	6	7
N	11	11	10	14	11	9	13
X	1.184	0.504	0.259	0.738	1.038	0.912	0.960
SD	0.418	0.141	0.103	0.223	0.424	0.314	0.372
SE	0.126	0.043	0.033	0.060	0.128	0.105	0.103

3. Rep wt

TR	1	2	3	4	5	6	7
N	11	11	10	14	11	9	13
X	1.578	0.907	0.320	1.642	1.616	1.720	1.670
SD	0.616	0.370	0.124	0.548	0.693	0.589	0.781
SE	0.186	0.112	0.039	0.147	0.209	0.196	0.217

4. No of flowers

TR	1	2	3	4	5	6	7
N	11	11	10	14	11	9	13
X	7.64	4.27	2.100	7.29	7.71	7.89	7.23
SD	4.15	1.90	0.876	2.81	3.77	3.66	3.06
SE	1.25	0.57	0.277	0.75	1.14	1.22	0.85

5. RE

TR	1	2	3	4	5	6	7
N	11	11	10	14	11	9	13
X	55.9	61.6	55.2	68.2	60.1	65.0	61.3
SD	18.3	18.5	6.47	10.2	15.4	8.78	18.1
SE	5.5	5.6	11.0	2.7	4.6	2.93	5.0

6. Arcsin RE

TR	1	2	3	4	5	6	7
N	11	11	10	14	11	9	13
X	48.2	51.8	48.10	55.91	50.87	53.82	51.9
SD	11.8	11.6	6.47	6.36	9.28	5.17	11.2
SE	3.5	3.5	2.05	1.7	2.8	1.72	3.1

7. Veg wt of non-flowerers

	Total	1	2	3	4	5	6	7
N	89	13	13	14	10	13	15	11
X	1.213	1.499	0.950	0.279	1.380	1.524	1.564	1.379
SD	0.527	0.287	0.316	0.121	0.145	0.309	0.218	0.466
SE	0.056	0.080	0.088	0.032	0.046	0.086	0.056	0.141

If use mean tray wt

X veg wt of	0.796
flowerers SD	0.063
SE	0.063
N	28

X veg wt	1.234
Non flowerers SD	
SE	0.089
N	29

X Total wt	2.030
Flowerers SD	
SE	0.14
N	28

Taraxacum - Non flowerers included

All data	Veg wt	Rep wt	Tot wt	RE	NFs	Arc RE
N	168	168	168	168	168	168
X	1.021	0.646	1.667	28.8	3.00	24.3
Med	1.003	0.000	1.588	0.000	0.00	0.00
SD	0.519	0.851	0.901	32.4	4.02	26.6
SE	0.040	0.066	0.069	2.5	0.31	2.1
Max	2.044	3.153	4.231	87.5	15.00	69.3
Min	0.027	0.000	0.027	0.00	0.00	0.00
Q3	1.455	1.300	2.184	0.643	5.00	5.33
Q1	0.641	0.000	1.096	0.00	0.00	0.00

Total wt

TR	1	2	3	4	5	6	7
N	24	24	24	24	24	24	24
X	2.078	1.161	0.404	1.963	2.042	1.965	2.057
SD	0.014	0.380	0.212	0.669	0.816	0.702	0.914
SE	0.166	0.078	0.043	0.137	0.167	0.143	0.187

Veg wt

TR	1	2	3	4	5	6	7
N	24	24	24	24	24	24	24
X	1.355	0.745	0.270	1.005	1.305	1.320	1.152
SD	0.380	0.335	0.112	0.375	0.435	0.409	0.460
SE	0.078	0.068	0.023	0.077	0.089	0.083	0.094

Rep wt

TR	1	2	3	4	5	6	7
N	24	24	24	24	24	24	24
X	0.723	0.416	0.134	0.958	0.740	0.645	0.90
SD	0.900	0.522	0.179	0.924	0.941	0.919	1.02
SE	0.184	0.107	0.037	0.189	0.192	0.188	0.21

NFs

TR	1	2	3	4	5	6	7
N	24	24	24	24	24	24	24
X	3.50	1.96	0.87	4.25	3.54	2.96	3.92
SD	4.75	2.51	1.19	4.09	4.65	4.46	4.29
SE	0.97	0.51	0.24	4.23	0.95	0.91	0.88

RE

TR	1	2	3	4	5	6	7
N	24	24	24	24	24	24	24
X	25.6	28.2	23.0	39.8	27.6	29.4	33.2
SD	30.9	33.7	28.7	35.2	32.2	32.6	33.9
SE	6.3	6.9	5.9	7.2	6.6	6.6	6.9

ARCSIN RE

TR	1	2	3	4	5	6	7
N	24	24	24	24	24	24	24
X	22.1	23.7	20.0	32.6	23.3	20.2	28.1
SD	25.7	27.4	24.6	28.6	26.6	26.8	27.6
SE	5.3	5.6	5.0	5.8	5.4	5.5	5.6

Poa first harvest

File = 'HARV ONE'

Non-flowering plants omitted

Derived from 'Poa n p k'

Characteristics of all data

	Veg wt	RE%	Rep wt	Total	Arcs in Trans RE
N	78 (6 non-flowerers)	78	78 (6 non-flowerers)	78 (6 non-flowerers)	78
Mean	1.273	22.92	0.341	1.614	28.22
Median	1.134	22.23	0.329	1.509	28.13
St Dev	0.315	7.59	0.158	0.869	5.64
SE mean	0.092	0.86	0.018	0.098	0.64
Max	5.279	48.43	0.680	5.313	44.10
Min	0.247	0.62	0.033	0.323	4.52
Q3	1.515	27.42	0.441	1.886	31.58
Q1	0.759	19.23	0.249	1.082	26.201

Appears to be slightly positively skewed

Poa first harvest - non flowers omitted

Effect of treatments

Total wt

TR	1	2	3	4	5	6	7
N	10	11	12	11	11	11	12
X	1.726	1.067	0.563	1.822	1.674	2.76	1.776
SD	0.327	0.228	0.164	0.465	0.369	1.21	0.760
SE	0.103	0.069	0.047	0.140	0.111	0.36	0.219

Veg wt

TR	1	2	3	4	5	6	7	Non-flowerers
N	10	11	12	11	11	11	12	6
X	1.373	0.803	0.453	1.410	1.257	2.32	1.366	4.74
SD	0.325	0.215	0.154	0.428	0.308	1.31	0.771	0.978
SE	0.103	0.065	0.045	0.129	0.093	0.40	0.223	0.399

Correl v wt and R wt = 0.254 sig at 0.05

Rep wt

TR	1	2	3	4	5	6	7
N	10	11	12	11	11	11	12
X	0.353	0.264	0.110	0.412	0.417	0.438	0.410
SD	0.055	0.073	0.030	0.095	0.142	0.174	0.147
SE	0.017	0.022	0.009	0.029	0.043	0.053	0.043

RE%

X	20.89	25.05	20.49	23.24	24.98	19.8	25.75
SD	3.76	6.43	5.40	5.23	6.88	12.2	9.19
SE	1.19	1.94	1.56	1.58	2.07	3.7	2.65

Arcs in trans RE

X	27.10	29.85	26.72	26.68	29.81	25.22	30.03
SD	2.81	4.41	3.96	3.63	4.51	9.72	6.72
SE	0.89	1.33	1.14	1.09	1.36	2.93	1.94

Log veg wt

TR	1	2	3	4	5	6	7
N	10	11	12	11	11	11	12
X	0.1286	-0.107	-0.367	0.134	0.0889	0.303	0.079
SD	0.0890	0.101	0.150	0.117	0.0979	0.249	0.233
SE	0.0281	0.031	0.043	0.035	0.0295	0.075	0.067

Log vet wt all data

Poa - second harvest

Non flowerers omitted

RE%	All data	Veg wt	Rep wt	Total	Arcs in RE
78	N	78	78	78	78
35.7	X	2.294	1.325	3.62	36.11
37.1	Med	2.324	1.409	4.16	37.50
13.0	SD	0.989	0.703	1.39	8.80
1.50	SE	0.112	0.080	0.16	1.00
62.8	Max	5.137	2.530	5.86	52.40
0.8	Min	0.543	0.034	0.065	5.20
45.5	Q3	2.882	1.874	4.61	42.40
27.0	Q1	1.718	0.691	2.74	31.32

TR	1	2	3	4	5	6	7
N	11	12	12	12	10	11	10
X	3.926	2.781	1.120	4.366	4.221	4.689	4.613
SD	0.904	0.760	0.293	0.787	0.378	0.740	0.552
SE	0.272	0.220	0.085	0.227	0.120	0.223	0.174

Veg wt

TR	1	2	3	4	5	6	7	Non Fs
N	11	12	12	12	10	11	10	6
X	2.222	1.797	0.733	1.797	2.580	3.183	2.97	5.165
SD	0.480	0.493	0.136	0.635	0.491	0.696	1.02	0.644
SE	0.145	0.142	0.039	0.183	0.155	0.210	0.32	0.263

Rep wt

TR	1	2	3	4	5	6	7
N	11	12	12	12	10	11	10
X	1.704	0.983	0.387	1.569	1.641	1.506	1.641
SD	0.682	0.421	0.254	0.608	0.367	0.707	0.654
SE	0.206	0.122	0.073	0.175	0.116	0.213	0.207

RE

X	42.0	34.46	31.6	35.1	39.05	31.6	36.7
SD	12.6	9.92	16.1	12.8	8.81	13.4	15.7
SE	3.8	2.86	4.7	3.7	2.79	4.0	5.0

Arcs in RE

X	40.21	35.76	33.3	35.92	38.58	33.1	36.4
SD	7.55	6.05	10.8	8.28	5.21	10.7	11.2
SE	2.28	1.75	3.1	2.39	1.65	3.2	3.5

Variance = ^{2}

SD =

$$d = \frac{^{2}1}{n1} + \frac{2}{n2}$$

SD = ^{2}

Variance = SD^2

	Arcs in trans
A X = 42.0	40.21
C X = 31.6	33.3
SDA = 12.6	7.55
SDC = 16.1	10.8

n A = 11 nC = 12

Variance =

$$d = \frac{12.6^2}{11} + \frac{16.1^2}{12}$$

$$= 14.43 + 21.6$$

$$= 6.002$$

$$t = \frac{40.0 - 31.6}{6.002}$$

t = 1.733 sig at 0.1 - only just

Means of Harv two = ie mean wts/tray

All Data	Veg wt	Rep wt	Total wt	RE	ASIN RE
N	28	28	28	28	28
X	2.347	1.357	3.70	36.24	36.89
Med	2.485	1.487	4.14	35.65	36.66
SD	0.901	0.573	1.32	7.95	4.86
SE	0.170	0.108	0.25	1.50	0.92
Max	4.040	2.320	5.54	53.06	46.76
Min	0.597	0.149	0.75	19.68	26.34
Q3	2.922	1.667	4.59	42.23	40.53
Q1	1.960	0.935	2.79	32.33	34.65

Prob plot ccr = 0.977 0.984 0.936

Veg wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	2.234	1.797	0.733	2.796	2.492	3.314	3.065
SD	0.229	0.412	0.124	0.271	0.340	0.549	0.678
SE	0.115	0.206	0.062	0.135	0.170	0.274	0.339

Rep wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	1.709	0.983	0.386	1.5690	1.754	1.506	1.588
SD	0.543	0.256	0.166	0.0956	0.388	0.482	0.449
SE	0.272	0.128	0.083	0.0478	0.194	0.241	0.224

Total wt

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	3.943	2.781	1.119	4.365	4.246	4.820	4.652
SD	0.722	0.579	0.252	0.359	0.208	0.741	0.325
SE	0.361	0.290	0.126	0.180	0.104	0.370	0.162

RE

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	42.42	35.37	33.2	36.00	41.22	31.02	34.5
SD	7.57	5.87	10.2	1.19	8.16	7.54	10.6
SE	3.79	2.94	5.1	0.60	4.08	3.77	5.3

ASIN RE

TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	40.59	36.45	34.97	36.867	39.90	33.73	35.75
SD	4.45	3.51	6.37	0.711	4.73	4.69	6.64
SE	2.23	1.76	3.18	0.356	2.37	2.35	3.37

LOGE VW							
TR	1	2	3	4	5	6	7
N	4	4	4	4	4	4	4
X	0.0296	-0.208	-0.802	0.350	0.208	0.682	0.275
SD	0.106	0.231	0.155	0.140	0.188	0.575	0.305
SE	0.053	0.115	0.078	0.070	0.094	0.287	0.152

APPENDIX 2

Correlation matrix - nutrient concentrations

Sig correls n = 27
.05 = .367 *
.01 = .470 **
.001 = .597 ***

	NFN	NFP	NFK	FVN	FVP	FVK	FRN	FRP
NFP	0.452 *							
NFK	0.198	0.121						
FVN	0.662 ***	0.392 *	0.029					
FVP	0.492 **	0.732 ***	0.058	0.777 ***				
FVK	-0.007	0.323	0.501 **	0.317	0.467			
FRN	0.102	0.117	-0.219	0.662 ***	0.553 **	0.275		
FRP	-0.067	0.548 **	0.047	0.312	0.600 ***	0.498 **	0.374 *	
FRK	-0.211	0.213	0.284	0.245	0.441 *	0.862 ***	0.461 *	0.648 ***

Correlation matrix - total amount of nutrients

If N = 27 sig correls
.05 = .367 *
.01 = .470 **
.001 = c .597 ***

	NFN	NFP	NFK	FVN	FVP	FVK	FRN	FRP
NFP	0.821 ***							
NFK	0.761 ***	0.656 ***						
FVN	0.782 ***	0.683 ***	0.562 **					
FVP	0.664 ***	0.730 ***	0.468 *	0.888 ***				
FVK	0.339	0.356	0.607 ***	0.509 **	0.571 **			
FRN	0.578 **	0.590 **	0.491 **	0.684 ***	0.642 ***	0.200		
FRP	0.421 *	0.558 **	0.392 *	0.588 **	0.664 ***	0.162	0.845 ***	
FRK	0.468 *	0.488 **	0.652 ***	0.517 **	0.538 **	0.391 *	0.872 ***	0.836 ***

Mean nutrient concentrations

Probability correlations

sig = 943

NFN	0.951
NFP	0.949
NFK	0.994
FVN	0.930
FVP	0.939
FVK	0.993
FRN	0.835
FRP	0.933
FRV	0.938

Correlations of nutrients concentrations

	Prob
NFP v NFN	5%
NFK v NFN	NS
FVN v NFN	1%
FVP v NFN	1%
FVN v NFP	5%
FVP v NFP	1%
FRP v NFP	1%
FVK v NFK	1%
FVP v FVK	5%
FVP v FVN	1%
FVK v FVP	5%
FRN v FVP	1%
FRP v FVP	1%
FRK v FVP	5%
FRK v FVK	5%
FRK v FVK	1%
FRP v FRN	5%
FRK v FRN	5%

Probability correlations for total nutrients

NFN	0.978
NFP	0.980
NFK	0.964
FVN	0.991
FVP	0.981
FVK	0.959
FRN	0.987
FRP	0.979
FRF	0.986

Analysis of variance tables

Twoway on concentrations

Nitrogen concentration

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	6.635	1.04	2.212	
Col stratum					
Treat	6	89.221	13.92	14.87	
Total					
Row col stratum					
Treat	6	97.041	15.14	16.174	0.780
Residual	12	248.780	38.82	20.732	
Total	18	345.822	53.97	19.212	
Row col units stratum					
FSM	2	25.767	4.02	12.883	3.945
Treat fsta	12	71.140	11.10	5.928	1.815
Resid	40(2)	130.619	20.38	3.265	
Total	54	227.526	35.51	4.213	
Grand total	81	669.203	104.44		

Means Grand mean = 1210

Treat	1	2	3	4	5	6	7
	12.21	11.83	10.89	12.34	12.34	11.1	14.64

FSTA	1	2	3
	11.33	12.36	12.60

FSM
Treat

1	11.45	12.06	13.12
2	10.96	12.45	12.10
3	10.54	10.66	11.49
4	11.92	12.67	12.44
5	9.05	10.90	13.36
6	10.07	11.74	13.14
7	15.28	16.07	12.57

SED
Treat = 1.987
Fsta 0.483
Treat 2.244
Fsta

P concentration

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.0010914	3.94	0.0003638	
Col stratum					
Treat	6	0.0020691	7.47	0.0003449	
Total	6				
Row col strat					
Treat	6	0.0103653	37.52	0.0017276	6.649
Residual	12	0.0031179	11.26	0.0002598	
Total	18	0.0134833	48.67	0.007491	
Row col units					
Fsta	2	0.0042645	15.39	0.0021322	16.734
Treat Fsta	12	0.0023343	8.43	0.0001945	1.527
Residual	40(2)	0.0050966	18.40	0.0001274	
Total	54	0.0116954	42.22	0.0002166	
Grand total	81	0.0283392	102.30		

GM = 0.0787

Treat	1	2	3	4	5	6	7
	0.0776	0.0826	0.0899	0.0791	0.0515	0.0813	0.0887

FSTA	1	2	3
	0.0730	0.0743	0.0887

FSTA				
1	0.0706	0.0796	0.0826	SED
2	0.0812	0.0805	0.0862	Treat = 0.00703
3	0.0831	0.0789	0.1076	Fsta = 0.00302
4	0.0716	0.0754	0.0904	Treat = 0.00959
5	0.0381	0.0422	0.0743	Fsta
6	0.0810	0.0762	0.0867	
7	0.0853	0.0876	0.0933	

K concentration

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	18.235	0.68	6.078	
Col stratum					
Treat	6	361.044	13.48	60.174	
Total	6				
Row col strat					
Treat	6	963.846	35.98	160.641	12.372
Residual	12	155.806	5.82	12.984	
Total	18	1119.652	41.79	62.203	
Row col units					
Fsta	2	779.592	28.80	385.796	77.458
Treat Fsta	12	264.616	9.88	22.051	4.427
Residual	40(2)	199.229	7.44	4.981	
Total	54	1235.437	46.11	22.878	
Grand total	81	2734.367	102.06		

GM = 1867

Treat	1	2	3	4	5	6	7
	18.23	21.78	24.57	20.12	28.03	14.66	13.33

Fsta	1	2	3
	17.68	15.56	22.78

Fsta Treat					
1	18.26	14.99	21.44	SEDs	
2	20.49	19.76	25.09	Treat	1.573
3	18.12	24.11	31.48	Fsta	0.596
4	20.26	17.08	23.03	Treat	2.033
5	17.76	13.25	23.07	Fsta	
6	14.91	8.34	16.74		

Anovas on total nutrients/tray

Non flowerers ie concn x biomass

N

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	41.99	3.45	14.00	
Col stratum					
Treat	6	358.46	59.76		
Total	6				
Row col strat					
Treat	6	630.79	51.79	105.07	6.771
Resid	12	196.20	15.30	15.52	
Total	18	816.60	67.09	45.37	
Grand total	27	1217.15	100.00		

Means	1	2	3	4	5	6	7
	15.9	10.35	4.23	15.55	14.11	16.67	21.62

SED = 2.978

P

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.0000972	0.25	0.0000324	
Col stratum					
Treat	6	0.0129816	33.93	0.0021636	
Total	6				
Row col strat					
Treat	6	0.0237124	61.97	0.0039521	32.206
Resid	12	0.0014725	3.85	0.0001227	
Total	18	0.0251849	65.82	0.0013992	
Grand total	27	0.0382636	100.00		

Means	1	2	3	4	5	6	7
	0.0991	0.0793	0.0311	0.0957	0.0610	0.1313	0.1141

SED = 0.00837

K

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	69.50	3.41	23.17	
Col stratum					
Treat	6	618.50	30.34	103.08	
Total	6				
Row col strat					
Treat	6	1188.39	58.3	198.06	14.684
Resid	12	161.86	7.94	13.49	
Total	18	1350.25	66.25	75.01	
Grand total	27	2038.24	100.00		

Means	1	2	3	4	5	6	7
	26.81	19.41	6.04	27.01	27.37	23.27	21.12

SED = 2.776

Total nutrients

Veg parts of flowerers

Source of variation	DF	SS	SS%	MS	VR
Row strat	3	48.984	9.59	16.328	
Col strat					
Treat	6	111.703	21.86	18.617	
Total	6				
Row col strat					
Treat	6	311.817	61.02	51.969	12.692
Resid	11(1)	45.041	8.81	4.095	
Total	17	356.857	69.84	20.992	
Grand total	26	517.544	101.29		

Means	1	2	3	4	5	6	7
	12.84	7.35	2.94	9.18	9.32	9.90	14.98

SED = 153

P

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.0023296	11.3	0.0007765	
Col stratum					
Treat	6	0.0057231	27.77	0.0009538	
Total					
Row col strat					
Treat	6	0.0110442	53.59	0.0018407	7.863
Resid	11(1)	0.0025752	12.50	0.0002341	
Total	17	0.0136194	66.09	0.0008011	
Grand total	26	0.0216721	105.16		

Means	1	2	3	4	5	6	7
	0.0862	0.0467	0.0241	0.0536	0.0379	0.0673	0.0822

SED = 0.01157

K

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	42.594	6.42	14.198	
Col stratum					
Treat	6	301.348	45.40	50.225	
Total	6				
Row col strat					
Treat	6	230.274	34.7	38.379	4.168
Resid	11(1)	101.296	15.26	9.209	
Total	17	331.57	49.96	19.504	
Grand total	26	675.512	101.78		

Means	1	2	3	4	5	6	7
	16.08	11.15	7.23	12.25	14.29	9.99	7.45

SED = 2.294

Concentrations

Treatment

		NFN	NFP	NFK	FVN	FVP	FVK	FRN	FRP	FRK
1	X	12.16	0.0742	19.43	12.77	0.0832	16.16	13.82	0.0862	22.61
	SD	2.64	0.0118	2.48	5.35	0.0197	2.44	4.29	0.0167	0.0608
	SE	1.32	0.0059	1.24	2.68	0.0098	1.22	2.15	0.0082	0.304
2	X	11.11	0.0797	20.41	12.60	0.0790	19.68	12.25	0.0847	25.010
	SD	2.64	0.0107	2.26	3.53	0.0102	3.99	0.0904	0.0149	0.528
	SE	1.32	0.0053	1.13	1.77	0.0051	2.00	0.452	0.0074	0.264
3	X	10.500	0.0825	18.16	10.62	0.0782	24.15	11.45	0.107	31.52
	SD	0.286	0.0114	3.64	1.69	0.0187	4.14	1.21	0.0217	3.77
	SE	0.143	0.0057	1.82	0.84	0.0094	2.07	0.60	0.0108	1.88
4	X	11.55	0.0722	19.87	12.30	0.0760	16.70	12.07	0.0910	22.65
	SD	2.23	0.0116	3.27	4.18	0.0112	5.81	1.09	0.0110	1.81
	SE	1.12	0.0058	1.64	2.09	0.0056	2.90	0.54	0.0055	0.90
5	N	4	4	4	3	3	3	3	3	3
	X	8.84	0.0390	17.70	9.450	0.0390	12.37	11.91	0.071	22.2
	SD	4.06	0.0102	2.48	0.350	0.0166	3.63	1.20	0.0078	10.529
	SE	2.03	0.0051	1.24	0.202	0.0096	2.10	0.70	0.00451	10.306
6	X	9.89	0.0797	13.475	11.55	0.07500	10.95	12.95	0.0855	18.175
	SD	1.22	0.0113	0.881	1.18	0.00849	3.02	0.639	0.0146	0.854
	SE	0.61	0.0056	0.440	0.59	0.00424	1.51	0.320	0.0073	0.427
7	X	15.22	0.08350	14.67	16.01	0.0857	8.10	12.51	0.0915	16.50
	SD	1.91	0.00493	2.74	2.40	0.0111	2.45	2.35	0.0101	2.03
	SE	0.95	0.00247	1.37	1.20	0.0055	1.22	1.17	0.0051	1.01
Overall Means		11.32	0.073	17.68	12.29	0.07504	15.56	12.44	0.08878	22.68
SD		2.85	0.0173	3.43	3.40	0.0184	6.20	1.97	0.01624	4.96

T-tests (concentrations)

Non flowering N v Flowering veg N	T = −1.14	P = 0.26
Flowering veg N v Flowering R N	T = 0.21	P = 0.84
Non flowering N v Rep N	T = 1.70	P = 0.096
Non flowering P v Veg P	T = −0.42	P = 0.67
Non flowering P v Rep P	T = −3.49	P = 0.0010*
Flowering veg P v Rep P	T = −2.92	P = 0.0052*
Non flowering K v veg K	T = 1.56	P = 0.13
Non flowering K v Rep K	T = −4.34	P = 0.0001
Flowering veg k v Flow rep K	T = −4.67	P = 0.0000

Flowering rep parts: P concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.0007210	10.60	0.0002403	
Col stratum					
Treat	6	0.0005173	7.60	0.0000862	
Total	6				
Row col strat					
Treat	6	0.0025876	38.04	0.0004313	1.435
Resid	11(1)	0.0033064	48.6	0.0003006	
Total	17	0.0058941	86.64	0.0003467	
Grand total	26	0.0071324	104.85		

Treat means	1	2	3	4	5	6	7
	0.0863	0.0857	0.1066	0.0693	0.0913	0.0843	0.0939

SED = 0.01311

Flowering rep parts: K concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	10.869	1.7	3.623	
Col stratum					
Treat	6	89.118	13.95	14.853	
Total	6				
Row col strat					
Treat	6	497.066	77.81	82.844	21.789
Resid	11(1)	41.823	6.55	3.802	
Total	17	538.889	84.36	31.699	
Grand total	26	638.877	100.01		

Means	1	2	3	4	5	6	7
	22.20	24.98	31.39	22.98	22.72	17.89	16.55

SED = 1.474

Treatment		RE% N	RE% P	RE% K	Asin RE N	Asin RE P	Asin RE K	RE Biomass	Asin RE Biomass
1	X	0.594	0.578	0.6477	50.45	49.57	53.71	56.89	49.00
	SD	0.101	0.106	0.0991	5.88	6.20	5.89	9.13	5.29
	SE	0.051	0.053	0.0495	2.94	3.10	2.94	4.56	2.64
2	X	0.615	0.631	0.671	51.81	52.74	55.24	61.80	51.92
	SD	0.114	0.113	0.112	6.74	6.76	6.88	9.51	5.62
	SE	0.057	0.056	0.056	3.37	3.38	3.44	4.76	2.81
3	X	0.552	0.6129	0.6017	48.20	51.56	50.90	53.60	47.07
	SD	0.0813	0.0555	0.0587	4.71	3.28	3.44	4.96	2.86
	SE	0.0407	0.0278	0.0293	2.35	1.64	1.72	2.48	1.43
4	X	0.6900	0.7275	0.7550	56.30	58.57	60.47	69.06	56.22
	SD	0.0857	0.0329	0.0674	5.24	2.13	4.34	2.73	1.69
	SE	0.0429	0.0165	0.0337	2.62	1.07	2.17	1.36	0.85
5	N	3	3	3	3	3	3		
	X	0.6484	0.7333	0.7275	53.66	59.09	58.65	59.50	50.51
	SD	0.0483	0.0855	0.0640	2.92	5.48	4.22	6.15	3.60
	SE	0.0279	0.0494	0.0369	1.69	3.17	2.44	3.08	1.80
6	X	0.6790	0.06774	0.7602	55.52	55.51	60.77	65.31	53.94
	SD	0.0368	0.0796	0.0505	2.26	4.90	3.43	3.76	2.26
	SE	0.0184	0.0398	0.0253	1.13	2.45	1.71	1.88	1.13
7	X	0.5832	0.6565	0.7822	49.84	54.20	62.55	64.26	53.33
	SD	0.0972	0.0731	0.0953	5.64	4.41	6.51	6.04	3.60
	SE	0.0486	0.0365	0.0476	2.82	2.21	3.25	3.02	1.80
Overall Means	X	0.6226	0.6567	0.7057	5.22	54.29	57.43	61.48	51.71
	SD	0.0897	0.6896	0.0964	5.31	5.43	6.11		

Total nutrients

Reproductive parts of flowerers

N

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	20.42	1.30	6.81	
Col stratum		213.55	13.64	35.59	
Treat	6				
Total	6				
Row col strat					
Treat	6	975.3	62.31	162.55	4.864
Resid	11(1)	367.6	23.49	33.42	
Total	17	1342.9	85.8	78.99	
Grand total	26	156.86	100.75		

Means	1	2	3	4	5	6	7
	21.0	11.3	3.2	19.4	17.4	20.4	22.1

SED = 4.37

P

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.003969	4.63	0.001323	
Col stratum					
Treat	6	0.012918	15.06	0.002153	
Total	6				
Row col strat					
Treat	6	0.04742	55.29	0.007903	3.679
Resid	11(1)	0.02363	27.55	0.002148	
Total	17	0.071050	82.84	0.004179	
Grand total	26	0.087936	102.53		

Means	1	2	3	4	5	6	7
	0.1394	0.0842	0.0301	0.1402	0.0919	0.1419	0.1690

SED = 0.03504

K

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	60.68	2.07	20.23	
Col stratum					
Treat	6	616.69	20.99	102.78	
Total	6				
Row col strat					
Treat	6	1694.16	57.67	282.32	5.444
Resid	11(1)	570.49	19.42	51.86	
Total	17	2264.65	77.09	133.21	
Grand total	26	2942.02	100.15		

Means	1	2	3	4	5	6	7
	34.4	22.9	9.9	35.3	33.5	29.6	29.5

SED = 5.44

Whole plants

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	113.25	3.43	37.75	
Col stratum					
Treat	6	498.49	15.11	83.08	
Total	6				
Row col strat					
Treat	6	2297.03	69.63	382.84	9.887
Resid	11(1)	425.93	12.91	38.72	
Total	17	2722.96	82.54	160.17	
Grand total	26	3334.7	101.9		

Means	1	2	3	4	5	6	7
	33.8	18.6	6.2	28.6	26.7	30.3	37.1

SED = 4.7

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.009735	6.00	0.003245	
Col stratum					
Treat	6	0.026050	16.6	0.004342	
Total	6				
Row col strat					
Treat	6	0.099124	61.11	0.016521	5.418
Resid	11(1)	0.033541	20.68	0.003049	
Total	17	0.132665	81.79	0.007804	
Grand total	26	0.168450	103.85		

Means	1	2	3	4	5	6	7
	0.266	0.131	0.054	0.194	0.130	0.209	0.251

SED = 0.0417

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	157.22	3.35	52.41	
Col stratum					
Treat	6	1242.6	26.48	207.1	
Total	6				
Row col strat					
Treat	6	2767.28	58.97	461.21	9.119
Resid	11(1)	556.36	11.85	50.58	
Total	17	3323.63	70.82	195.51	
Grand total	26	4723.45	100.65		

Means	1	2	3	4	5	6	7
	50.4	34.0	17.1	47.5	47.8	39.6	37.0

SED = 5.38

Total nutrients

	NFN	NFP	NFK	FVN	FVP	FVK	FRN	FRP	FRK
Treatment									
1									
X	17.62	0.1086	28.45	13.67	0.0915	18.18	20.48	0.01340	33.95
SD	2.55	0.0184	4.31	3.17	0.0160	4.67	6.15	0.0613	7.89
SE	1.28	0.0092	2.16	1.58	0.0080	2.34	3.07	0.0307	3.94
2									
X	10.68	0.0756	19.44	6.57	0.04058	10.28	10.55	0.0764	21.79
SD	3.40	0.0109	3.29	2.06	0.00272	2.67	2.40	0.0329	5.91
SE	1.70	0.0055	1.64	1.03	0.00136	1.33	1.20	0.0164	2.96
3									
X	3.076	0.02427	5.33	3.02	0.0227	6.91	3.589	0.03384	10.09
SD	0.664	0.00698	1.73	1.27	0.116	3.19	0.451	0.00953	2.75
SE	0.332	0.00349	0.87	0.63	0.0058	1.60	0.255	0.00477	1.38
4									
X	16.08	0.1005	27.65	9.04	0.05572	12.25	20.04	0.1494	37.30
SD	3.49	0.0179	5.10	3.06	0.00775	4.19	3.97	0.0193	4.51
SE	1.74	0.0089	2.55	1.53	0.00387	2.10	1.98	0.0096	2.25
5									
N		4	4	4	3	3	3	3	3
X	13.94	0.0616	27.96	10.21	0.0434	13.63	18.77	0.118	35.60
SD	6.15	0.0173	4.86	2.08	0.0249	6.04	2.57	0.0151	8.53
SE	3.07	0.0087	2.43	1.20	0.0144	3.49	1.49	0.0087	4.92
6									
X	15.58	0.1251	21.19	10.10	0.0675	9.56	21.31	0.1428	29.64
SD	2.35	0.0153	1.78	2.82	0.0277	3.64	5.10	0.0472	5.35
SE	1.18	0.0076	0.89	1.41	0.0139	1.82	2.55	0.0236	2.68
7									
X	21.47	0.1160	21.00	14.70	0.0811	7.38	21.41	0.1594	28.09
SD	3.78	0.0173	8.33	2.54	0.0246	2.47	7.51	0.0664	8.63
SE	3.78	0.0173	4.16	1.27	0.0123	1.24	3.76	0.0332	4.32
Overall									
X	14.06	0.0874	21.57	9.59	0.058	11.08	16.51	0.1155	27.8
SD	6.71	0.0376	8.69	4.43	0.0282	5.05	7.76	0.0574	10.6

Mean total amount of nutrients/tray

Treatment		N	P	K
1	X	34.16	0.2255	52.13
	SD	7.23	0.0637	5.84
	SE	3.61	0.0319	2.92
2	X	17.12	0.1169	32.07
	SD	1.86	0.0312	4.07
	SE	0.93	0.0156	2.04
3	X	6.61	0.0565	17.00
	SD	1.58	0.0211	5.75
	SE	0.79	0.0106	2.87
4	X	29.08	0.2051	49.54
	SD	4.34	0.0214	5.67
	SE	2.17	0.0107	2.84
5	X	28.99	0.1552	49.2
	SD	3.87	0.0385	13.4
	SE	2.23	0.0223	7.7
6	X	31.41	0.2103	39.19
	SD	7.60	0.0692	8.21
	SE	3.80	0.0346	4.11
7	X	36.10	0.02404	35.47
	SD	7.95	0.00823	7.31
	SE	3.98	0.0412	3.65
Overall means		26.1	0.01735	88.9
		11.3	0.0790	13.4

T-tests total amounts

NFN v FVN = T = 2.92 P = 0.0054*
NFN v FRN = T = 1.25 P = 0.22
FVN v FRN = T = -4.02 P = 0.0002*

NFK v FVK = T = 5.5 P = 0.0000*
NFK v FRK = T = -2.37 P = 0.022
FVK v FRV = T = -7.39 P = 0.0000*

NFP v FVP = T = 3.28 P = 0.0019*
NFP v FRP = T = 2.14 P = 0.038
FVP v FRP = T = -4.67 P = 0.0000*

Anovas on nutrient RAs

A. untransformed values

N

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.024338	11.87	0.008279	
Col stratum	6	0.065264	31.18	0.010877	
Total	6				
Row col strat					
Treat	6	0.045941	21.95	0.007657	1.143
Resid	11(1)	0.073717	35.22	0.006702	
Total	17	0.119658	57.17	0.007039	
Grand total	26	0.20976	100.22		

Means	1	2	3	4	5	6	7
	0.629	0.605	0.551	0.670	0.651	0.676	0.582

SED = 0.00619

P

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.03942	18.91	0.01314	
Col stratum					
Treat	6	0.075559	36.24	0.012593	
Total	6				
Row col strat					
Treat	6	0.051184	24.55	0.008531	1.854
Resid	11(1)	0.050615	24.28	0.004601	
Total	17	0.101799	48.22	0.005988	
Grand total	26	0.216778	103.97		

Means	1	2	3	4	5	6	7
	0.611	0.620	0.607	0.714	0.728	0.677	0.663

SED = 0.0513

K

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.005655	2.34	0.001885	
Col strat					
Treat	6	0.093707	38.74	0.015618	
Total	6				
Row col strat					
Treat	6	0.087594	36.22	0.014599	2.755
Resid	11(1)	0.658282	24.10	0.005298	
Total	17	0.145876	60.32	0.008581	
Grand total	26	0.245237	101.40		

Means	1	2	3	4	5	6	7
	0.690	0.665	0.593	0.730	0.6990	0.757	0.791

SED = 0.0550

Asin trans RA

N

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	88.15	12.02	29.38	
Col stratum					
Treat	6	227.82	31.08	37.97	
Total	6				
Row col strat					
Treat	6	161.92	22.09	26.99	1.154
Resid	11(1)	257.27	35.09	23.39	
Total	17	419.2	57.18	24.66	
Grand total	26	735.16	100.28		

Means	1	2	3	4	5	6
	52.50	51.16	48.00	53.14	53.9	55.35

SED = 2.656

P

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	142.00	18.54	47.33	
Col strat					
Treat	6	278.28	36.34	46.38	
Total	6				
Tow col strat					
Treat	6	192.34	25.12	32.06	1.908
Resid	11(1)	184.8	24.13	16.8	
Total	17	377.13	49.25	22.18	
Grand total	26	797.42	104.14		

Means	1	2	3	4	5	6	7
	51.60	52.06	51.22	57.76	58.78	55.46	54.59

SED = 3.098

K

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	16.04	1.65	5.35	
Col stratum		389.56	40.08	64.93	
Treat	6				
Total	6				
Row col strat					
Treat	6	354.57	36.48	59.09	2.82
Resid	11(1)	230.55	23.72	20.96	
Total	17	585.12	60.20	34.42	
Grand total	26	990.72	101.94		

Means	1	2	3	4	5	6	7
	56.47	54.88	50.35	58.90	56.72	60.45	63.11

SED = 2.461

Anovas on concentrations

Non flowering: N concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	7.304	3.35	2.435	
Col stratum					
Treat	6	36.834	16.89	6.139	
Total	6	36.834	16.89	6.139	
Row col stratum					
Treat	6	113.598	52.08	18.933	2.822
Resid	11(1)	73.802	33.83	6.709	
Total	17	187.401	85.91	11.024	
Grand total	26	231.539	106.15		

Means	1	2	3	4	5	6	7
	11.53	11.16	10.74	11.27	7.61	10.22	15.48

Rep = 4
SED = 1.958

Non flowering: P concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.0002558	3.36	0.00008519	
Col strat					
Treat	6	0.00133770	17.57	0.00022295	
Total	6				
Row col stratum					
Treat	6	0.00666496	87.56	0.00111083	28.69
Resid	22(1)	0.00709719	93.24	0.00041748	
Grand total	26	0.00869048	114.17		

Mean treat	1	2	3	4	5	6	7
	0.0699	0.0838	0.0846	0.0695	0.0351	0.0814	0.0840

SED Rep = 4
SED = 0.00474

Non flowering: K concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	5.45	1.75	1.817	
Col stratum					
Treat	6	112.663	36.16	18.777	
Total	6				
Tow col stratum					
Treat	6	116.340	37.34	19.39	2.66
Resid	11(1)	80.194	25.74	7.290	
Total	17	196.535	63.08	11.561	
Grand total	26	314.647	100.98		

Means	1	2	3	4	5	6	7
	18.63	20.69	18.24	19.73	16.87	14.43	14.93

SED = 2.041

Flowering veg parts: N concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	14.89	4.96	4.96	
Col stratum					
Treat	6	35.21	11.73	5.87	
Total	6				
Row col strat					
Treat	6	120.29	40.07	10.05	1.51
Resid	11(1)	146.03	48.64	13.28	
Total	17	266.32	88.71	15.67	
Grand total	26	316.43	105.40		

Mean treat	1	2	3	4	5	6	7
	11.89	12.68	10.15	12.66	9.18	11.72	16.71

SED = 2.754

Flowering veg parts: P concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.000591	6.74	0.000197	
Col stratum					
Treat	6	0.0019871	22.65	0.0003312	
Total	6				
Row col strat					
Treat	6	0.0061391	69.98	0.0010232	5.083
Resid	11(1)	0.0022144	25.24	0.0002013	
Total	17	0.0083535	95.22	0.004914	
Grand total	26	0.0109316	124.61		

Mean treat	1	2	3	4	5	6	7
	0.0787	0.0804	0.0770	0.0746	0.0364	0.0762	0.0902

SED = 0.01073

Flowering veg parts: K concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	10.6	1.06	3.53	
Col stratum					
Treat	6	302.40	30.29	50.4	
Total	6				
Row col strat					
Treat	6	569.41	57.04	94.9	8.974
Resid	11(1)	116.32	11.65	10.57	
Total	17	685.74	68.69	40.34	
Grand total	26	998.74	100.04		

Means	1	2	3	4	5	6	7
	13.98	19.78	23.97	17.53	13.65	11.54	8.63

SED = 2.458

Flowering rep parts: N concn

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	7.419	7.38	2.473	
Col stratum					
Treat	6	28.124	27.99	4.687	
Total	6				
Row col strat					
Treat	6	12.423	12.37	2.070	0.419
Resid	11(1)	54.312	54.06	4.937	
Total	17	16.735	66.43	3.926	
Grand total	26	102.278	101.80		

Means	1	2	3	4	5	6	7
	13.82	12.27	11.18	12.49	12.26	12.40	12.234

SED = 1.68

Flowering rep parts: N concn logten trans f

Source of variation	DF	SS	SS%	MS	VR
Row stratum	3	0.006523	6.73	0.002174	
Col stratum					
Treat	6	0.028192	29.10	0.004699	
Total	6				
Row col strat					
Treat	6	0.010985	11.34	0.001831	0.385
Resid	11(1)	0.052338	54.02	0.004758	
Total	17	0.063323	65.36	0.003725	
Grand total	26	0.098038	101.19		

Means	1	2	3	4	5	6	7
	1.127	1.089	1.049	1.094	1.087	1.095	1.083

SED = 0.0521