

## CHAPTER THREE

### PLANT ATTRIBUTES OF THE SPECIES AT NEWHOLME

#### 3.1 INTRODUCTION

The use of plant attributes to simplify complex data and make generalisations about vegetation is not new. Plant attributes such as growth form (forb, grass, sedge and rush), species origin (native and exotic) and plant life cycle (annual, biennial and perennial) form simple classifications which are universally used and understood. The literature review (Section 1.1.1) demonstrated that plant communities can be successfully characterized by the prevalence of species with particular attributes. Due to the frequent correlations among plant attributes, studies examining the relationship between an environmental factor and a large number of plant attributes simultaneously are more robust than those examining single attributes in isolation.

A problem fundamental to the study of plant attributes is which attributes to choose. The chosen attributes may be of a morphological or a functional nature. Based on comments by Montalvo *et al.* (1991), functional attributes are defined here as those attributes which directly influence species survival, growth and reproduction, while morphological attributes are defined as those attributes concerned with the form and structure of the plant. Morphological attributes have the advantage of being universally available (as a by-product of taxonomy), but are of uncertain relevance to vegetation prediction (Grime *et al.* 1993). Attributes may be chosen on the basis that they play an important adaptive role in the environment in which the plants live (Raunkiaer 1934; Noble & Slatyer 1977, 1980; Keddy 1992) or because they are relevant to a particular management purpose or study objective (Friedel *et al.* 1988; Epp & Aarssen 1989; Diaz *et al.* 1992). Both adult and juvenile plant attributes need to be examined because adult and juvenile attributes vary independently and the ability of a plant to successfully produce a new generation depends on attributes possessed throughout its life cycle (Fenner 1978; Shipley *et al.* 1989). Here 'juvenile' or 'regenerative' attributes are defined as those concerned with colonizing a site (e.g. seed mass, seed dispersal, germination characteristics, type of vegetative propagule), while 'adult' or 'established phase' attributes are those concerned with maintaining an existing site (e.g. growth form, Raunkiaer life form, leaf life span, root morphology).

In this study a balance of morphological, functional, adult and juvenile attributes were selected. Most of the attributes were determined from individuals growing in the field because for the plant attribute approach to be useful for management it must be robust enough to cope with environmental complexity. However, some investigators believe that plant attributes should be determined under standardized conditions to allow comparisons among sites, regions and continents (Grime & Hunt 1975; Orshan 1982; Hendry & Grime 1993).

Maximum relative growth rate (and other growth parameters) of the Newholme species was measured under standard glasshouse conditions similar to those used by Grime and Hunt (1975), to allow comparison.

The functional approach of plant growth analysis was used because of the problems inherent in the classical approach (Causton 1991). The functional approach involves fitting mathematical functions to the primary data from a number of harvests and the resulting 'growth curves' are used to obtain instantaneous values of growth (Hunt 1982). The relative growth rate (RGR) of a plant is defined as the rate of increase in plant dry weight per unit of plant weight already present (Lambers & Poorter 1992). RGR can be broken down into a 'physiological' component, the net assimilation rate (NAR), and a 'morphological' component, the leaf area ratio (LAR) (Lambers & Dijkstra 1987).

$$\text{That is, } \quad \text{RGR} = \text{NAR} \times \text{LAR} \quad (3.1)$$

NAR (or its synonym, the unit leaf rate, ULR) is largely the balance of photosynthesis and respiration in the entire plant and is defined as the rate of increase in plant weight per unit leaf area (Lambers & Poorter 1992). LAR is defined as the amount of leaf area per unit total plant weight. The maximum relative growth rate (R<sub>max</sub>) is defined as the highest instantaneous relative growth rate value obtained during the period of observation (Grime & Hunt 1975).

The specific objectives of this chapter are to examine:

1. whether the vegetation of the study site can be described by the presence of species with particular plant attributes; and
2. the associations and correlations amongst the plant attributes of species.

## **3.2 METHODS**

Most of the plant attributes were chosen on the basis of the key for C-S-R strategies developed by Grime and his colleagues, and the attributes they found to be important in their cluster analysis of a large number of attributes of herbaceous species (Grime *et al.* 1988). The work of numerous other authors (e.g. Rogers & Whalley 1989; Montalvo *et al.* 1991; Lambers & Poorter 1992) also influenced the choice of attributes investigated in this study.

### **3.2.1 General Attributes and Attributes Measured in the Field**

The origin and life cycle of each species common at the study site (Table 3.2 in Section 3.3.1) were determined from the literature (Harden 1990 - 1993). The few biennial species present were classified as annuals. The growth form of each species was classified as either grass (members of the Poaceae), sedge or rush (members of the Cyperaceae, Lomandraceae and Juncaceae) or forb (herbaceous plant other than a grass, sedge or rush).

## (a) Whole Plant Morphology Attributes

To remove the chance of phenotypic responses to fertilization and soil disturbance, and to standardise the collection of plant attribute data in the field, individuals were examined from an area where growing conditions were similar (i.e. unfertilized, low disturbance). Ten to 20 individuals of each species were chosen from quadrats (0.25 m<sup>2</sup>) selected at random on a 5 x 2 m grid established upslope of the experimental plots and within the fenced enclosure. One individual was selected per quadrat and marked with a wooden skewer. If fewer than ten individuals could be located at random, further individuals were selected arbitrarily from the enclosed area or, if necessary, outside the enclosed area (< 50 m away). For example, sufficient numbers of the sown species (*Lolium perenne*, *Dactylis glomerata*, *Sanguisorba minor* and *Plantago lanceolata*), *Vulpia myuros* and *V.bromoides* could only be found in highly disturbed plots. The marked individuals were used to examine Raunkiaer life form, stem structure, height, width, persistent litter, inflorescence form, leaf size, leaf shape, leaf texture, leaf hairiness and to monitor leaf life span, as follows:

### *Raunkiaer Life Form*

The species were examined in the unfavourable season (winter) and classified according to the life forms developed by Raunkiaer (1934) and Orshan (1982):

1. Phanerophytes - surviving buds or shoot-apices borne on shoots projecting into air higher than 80 cm.
2. Chamaephytes - surviving buds or shoot-apices borne on shoots very close to ground (< 25 cm temperate climates; < 80 cm in arid or tropical zones).
3. Hemicryptophytes - surviving buds or shoot-apices situated in soil surface.
4. Cryptophytes (Geophytes) - surviving buds or shoot-apices buried underground at a distance from the surface, which varies in different species.
5. Therophytes - renewal buds located in seed, i.e. annuals.
6. Amphiphytes - plants with more than one type of renewal bud location.

### *Stem Structure*

The stem structure of each species was assigned to one of the categories developed by Gimingham (1951):

1. Tussocks - dome-shaped in outline.
2. Tufted growth - similar in outline to a tussock but on a smaller scale. Includes grasses and small plants with petiolate radical leaves densely aggregated, or aggregated aerial shoots and small leaves.
3. Branched forms - much branched.
4. Erect forms - branching restricted.

5. Rosettes - all leaves radical; forming a radiating cluster.
6. Partial rosettes - most leaves are radical; the aerial shoots also bear leaves (cauline), but are smaller than the radical leaves.
7. Prostrate forms - stems prostrate, spreading from centre, leaves without long petioles. Single stem or matted stems.
8. Twining - stems that twine around others rather than prostrate.
9. Arcuate - main stem (or above ground axis) arching.

### *Plant Height and Width*

The maximum vegetative height, reproductive height and the diameter of the densest part of the plant (usually vegetative) was measured on each individual. Species demonstrating a positive response to fertilization were measured under both fertilized and unfertilized conditions.

### *Persistent Litter*

Following Grime (1974), the depth of persistent litter (including standing dead) was measured for each species and classified as:

1. Absent.
2. Up to 1 cm in depth.
3. Up to 5 cm in depth.
4. Up to 10 cm in depth.
5. Up to 20 cm in depth.
6. > 20 cm in depth.

## **(b) Inflorescence Attributes**

### *Inflorescence Form*

The inflorescence form of each individual was examined and classified (based on definitions of Harden 1990) into:

1. Capitulum - dense cluster of more or less sessile flowers on a common receptacle.
2. Spike-like - a simple inflorescence, terminating in a floral bud and with sessile flowers.
3. Panicle-like - a compound inflorescence with a main axis and lateral branches.
4. Cyme-like - inflorescence in which main axis ends in a flower and further growth is by one or more branches which end in a flower.
5. Solitary - flowers borne singly, not in an inflorescence.

### *Commencement of Flowering*

From June 1993 until June 1994, the untreated areas within the experimental enclosure were surveyed each month (on or about the 15th) for species in bud, flower or fruit. For a few of the less common species, observations of known populations outside the enclosure were made (< 50 m away), e.g. a population of *Drosera burmannii* in a drainage line. In the case of graminoids, flowering was defined by the occurrence of anthers exerted beyond the bracts (Wheeler *et al.* 1990). Two attributes were derived from this survey, the number of months over which a species flowered (flowering period duration) and the month in which flowering commenced. Note that flowering period duration was the number of months in which any individual of the species was found in flower, not the number of months over which a particular individual continued to flower.

### **(c) Leaf Attributes**

#### *Leaf Size, Shape, Texture and Hairiness*

The leaf size of each species was estimated in the field using the diagram provided by Raunkiaer (1934). Leaf size was classified as either leptophyll (< 25 mm<sup>2</sup>), nanophyll (25 - 225 mm<sup>2</sup>), microphyll (225 - 2025 mm<sup>2</sup>), mesophyll (2025 - 18225 mm<sup>2</sup>) or macrophyll (18225 - 164025 mm<sup>2</sup>). Leaflet size was used for those species with compound leaves. Leaf shape was classified as either filiform, linear, oblong, trifid, elliptic, circular, lanceolate, hastate, oblanceolate or obovate according to the definitions of Harden (1990). Leaf texture was classified as either soft or fibrous/thick. Leaves were defined as hairy if greater than 50% of the leaf surface was seen to be covered by hairs with the naked eye and were classified into:

1. Glabrous.
2. Lower side of leaf hairy.
3. Upper side of leaf hairy.
4. Both sides hairy.
5. Leaf edges hairy.

#### *Leaf Life Span*

About ten of the individuals of each species selected to assess plant morphology attributes were used to estimate leaf life span. Between two to six young leaves per individual (depending on the species) were marked with small loops of electrical wire (0.8 mm or 1.5 mm in diameter). For small-leaved species such as *Wahlenbergia planiflora*, *Hypericum*

*gramineum* and *Richardia stellaris*, the wire was looped around the stem below the first four young leaves. The number of tagged leaves alive was recorded every two weeks. Following Hodgson and Booth (1993), a leaf was regarded as dead if less than 25% of its length was green. The tagged leaves were monitored from 6 October 1993 until 15 June 1994, by which time all of the tagged leaves had died.

#### **(d) Root Attributes**

##### *Underground Storage Organs*

Individuals of each species were arbitrarily selected from the area above the experimental plots and were removed intact within a plug of soil about 15 cm deep. Confirmation was sometimes made using road cuttings nearby. Based on the categories of Grace (1993), the underground storage organs of each species were classified into:

1. Runners - a slender prostrate stem having a bud at the end which sends out leaves and roots.
2. Stolons - a more or less horizontal stem growing above the ground and rooting at the nodes.
3. Rhizomes - an underground stem, usually growing horizontally (bearing buds in axils of reduced scale-like leaves).
4. Stem tubers - swollen end of underground stem bearing buds in axils of scale-like leaves.
5. Bulbs - modified shoots consisting of a shortened stem enclosed by fleshy scale-like leaves or leaf-bases.
6. Corms - swollen stem base containing food reserves and bearing buds in the axils of scale-like remains of leaves of previous season's growth.
7. Taproot - the main descending root of a plant that has a single, dominant root system.
8. Root tubers - underground storage organ formed by swelling of a root.

#### **(e) Diaspore Attributes**

##### *Diaspore Mass*

Diaspores were collected from plants within the fenced enclosure during December 1992 to February 1993. Four replicates of 50 diaspores each were weighed using a micro-balance (Sartorius 2405). Due to the difficulty in removing the ancillary structures in some species, only diaspore mass was determined.

## *Diaspore Number*

About ten individuals of each species were arbitrarily selected within the fenced enclosure. The inflorescences of each selected individual were removed and placed in separate paper bags. The total number of diaspores per individual were counted, or estimated by mass when the number was large (using mean diaspore mass determined above). Where required (a small number of forb species), the mean diaspore number per flower was used to calculate the contribution made by flowers present but not yet in fruit. This may have resulted in an over-estimate of diaspore number if the flowers aborted.

## *Diaspore Morphology*

The morphology of the diaspores collected for diaspore mass was determined under a dissecting microscope and assigned to one of the classes (Table 3.1) described by Grime *et al.* (1981).

**Table 3.1:** Classes describing diaspore morphology. Lenticular = circular outline, doubly convex lens; reniform = kidney-shaped in cross section; subulate = narrow, gradually tapering to fine apex; rugose = wrinkled, covered with coarse lines or furrows; tuberculate = rough with small wart-like outgrowths; reticulate = forming a network; striate = parallel arrangement of lines, ridges, grooves, or dots and mucilaginous = slimy, gummy substance.

Diaspore Shape	Diaspore Dispersal Morphology	Diaspore Hairs or Teeth	Diaspore Surface Texture
Spherical;	Absent;	More or less absent;	More or less smooth;
Ovoid, rhomboidal or turbinate (top-shaped);	Straight awn(s) or spine(s);	Radial or irregular;	Rugose, tuberculate or reticulate;
Trigonous or triquetrous;	Hygroscopic awn(s) or spine(s);	Antrorse (turned towards the apex).	Striate;
Lenticular, reniform or subulate;	Pappus or persistent calyx;		Hairy or bristly;
Cylindrical or ligulate (strap-shaped);	Hook(s) or barbed spine(s);		Striate and hairy;
Clavate (club-shaped);	Elaiosome;		Mucilaginous.
Winged;	Inflorescence breaks free;		
Tadpole-shaped;	Dust-like diaspores;		
Conical.	Explosive fruits.		

### 3.2.2 Attributes Measured in the Glasshouse

#### (a) Growth Analysis of Seedlings

Glasshouse experiments were conducted to estimate the mean relative growth rate ( $\bar{R}$ ), maximum relative growth rate ( $R_{max}$ ), root:shoot ratio, allometric constant ( $K$ ) and leaf area ratio (LAR) of a number of species. Each experiment consisted of growing five replicates of six or seven plant species at two nutrient concentrations for 7, 14, 21, 28 and 35 days. The pots were completely randomized within five blocks and the position of the blocks were rotated each week. Since five experiments were required to examine all of the species, *Lolium perenne* was used as a reference species in each experiment to determine differences in growing conditions.

Species abundant in the field experiment, a few less common species and the sown species were chosen for growth analysis. Seed availability was rarely a problem, but choice of species was limited by the poor germinability and unknown germination requirements of some species (e.g. *Panicum effusum*, *Digitaria brownii*, *Schoenus apogon*, *Carex breviculmis*, *Haloragis heterophylla*, *Drosera peltata*, *Tricoryne elatior*, *Microtis unifolia*, *Zornia dyctiocarpa* and *Fimbristylis dichotoma*). Therefore, selection of species for growth analysis was biased towards species that germinated relatively easily.

#### *Growing Medium and Planting*

To avoid the contamination of the harvested plant roots by soil, screened concrete sand was used as the growing medium. Square PVC seedling tubes (5 cm wide and 12.5 cm deep) were lined with PVC mesh, filled with sand and flushed thoroughly with water before planting. Where necessary, seeds were scarified using sandpaper or stratified at 4°C for two weeks. The time taken to germinate had been previously determined for each species so that germination, could be synchronized. Seed of the different species were placed onto moistened sand in the germination cabinet and, upon germination, three individuals were transplanted into each pot in the glasshouse. To reduce transplant shock, a constant humid environment was provided by inverting clear plastic cups over the seedlings for a few days (Booth *et al.* 1993). A few days after transplantation, two of the least vigorous individuals were removed leaving one individual per pot.



## *Temperature and Light*

Two different temperature regimes were required to provide optimal growth conditions for the cool-season (C3) species and warm-season (C4) species. For the C3 species (Experiment 1 - 4) the temperature in the glasshouse was set at 15°C/25°C, while the temperature for the C4 species (Experiment 5) was set at 20°C/35°C. The temperature and humidity in each experiment was monitored using a thermohydrograph (Appendix 4A).

In their initial study of seedling growth rates, Grime and Hunt (1975) used an 13 hour day in order to maximise growth, while day lengths of 14 or 16 hours have generally been used in other studies. Thus a day length of 16 hours was used here, to maximise growth without being too unrealistic. The lights in the glasshouse experiments 1 - 4 were tungsten incandescent reflector lights (250W). Since the temperature requirements for Experiment 5 contrasted to that required by other glasshouse users, an alternative glasshouse was used. The lights in the latter glasshouse were of the HLRG reflector type (400W). Due to the large number of species being examined, the five experiments were run in succession from September 1993 to May 1994. To monitor differences in light conditions in the different glasshouses and over the study period, the short-wave radiation, 2 cm above the pot surface, was measured twice a week with a Quantum light photometer/radiometer (Appendix 4A).

## *Nutrients and Watering*

Plant nutrients were supplied as a modified 'Long Ashton' nutrient solution, following Grime and Hunt (1975). Hereafter the nutrient concentrations used are described relative to the strength of the standard 'Long Ashton' nutrient solution (Appendix 4B). Each species was grown at two nutrient concentrations which were likely to be near optimal and supra-optimal. A trial found that the growth of *Lolium perenne* and *Dactylis glomerata* was reduced by the application of four times the standard strength Long Ashton (as used by Austin & Austin 1980) and that a choice of half strength, standard strength and double strength Long Ashton would suit the range of species in this study. The trial also indicated that the seedlings should be acclimatised by diluting the first nutrient addition by half and applying it 3 or 4 days after germination. Thereafter the nutrient solutions were applied twice weekly in 20 ml aliquots, which was just enough to drain out of the pots. The nutrient solutions were prepared from separate macronutrient stock solutions and a micronutrient stock solution, which were frequently renewed. The pH of the nutrient solutions, determined using a glass electrode assembly, was 7.25 for the half strength solution, 6.77 for the standard solution and 6.50 for the double strength solution. The pots were hand-watered with tapwater until the water just flushed through the drainage holes, as often as required (usually every second day but sometimes daily), to minimise nutrient build-up. Tapwater was considered to be adequate

because the aim was to provide nutrient levels optimal for the growth, rather than to relate growth to specific nutrient levels.

### *Harvesting*

Five replicates (pots) of each species were harvested at 7, 14, 21, 28 and 35 days after germination. Unhealthy replicates suffering from fungus or insect attack were omitted. The sand was carefully washed from the roots. Using a dissecting microscope, the roots were separated from the shoots by dividing the non-green parts from the green parts of the plant. The leaves were separated at the petiole for dicots and at the ligule for grasses. The sheath of the monocots and the petioles of the dicots were included in with the stem fraction because they perform a similar supporting function. A Delta-T Area Meter was used to measure the total leaf-lamina area of each individual. The root, stem and leaf fractions were oven-dried at 80°C for 48 hours and placed in a desiccator before weighing. A micro-balance (Sartorius 2405) was used to weigh small samples.

### *Calculation of Growth Parameters*

#### Mean Relative Growth Rate

The mean relative growth rate,  $\bar{R}$ , of each species was calculated for each harvest interval ( $\bar{R}_{1-2}$ ,  $\bar{R}_{2-3}$ ,  $\bar{R}_{3-4}$ ,  $\bar{R}_{4-5}$  and  $\bar{R}_{1-5}$ ) using Fisher's equation:

$$\bar{R}_{1-2} = \frac{\ln W_2 - \ln W_1}{T_2 - T_1} \quad (3.2)$$

where  $W_1$  is the dry weight at time  $T_1$ ,  $W_2$  the dry weight at time  $T_2$  (Hunt 1982).

#### Maximum Relative Growth Rate

The maximum relative growth rate,  $R_{max}$ , is defined as the highest instantaneous relative growth rate value obtained during the period of observations (Grime & Hunt 1975). The instantaneous relative growth rate,  $R$ , is equivalent to:

$$R = \frac{d(\ln W)}{dT} \quad (3.3)$$

That is, the instantaneous relative growth rate is the slope of the plot of the natural logarithm of  $W$  against  $T$  and is obtained by fitting the simplest function to the plot using regression

analysis (Hunt 1982). When the best fit is a linear function, both  $R$  and  $R_{max}$  are equal to the slope of this regression line because  $R$  (the slope) has not changed over time (Grime & Hunt 1975).  $R_{max}$  is also approximately equal to  $\bar{R}^{-1.5}$  (as determined by Fisher's equation) when the plot of the natural logarithm of  $W$  against  $T$  is linear (Grime & Hunt 1975).

### Root to Shoot Ratio

The root:shoot ratio of each species was calculated for each harvest interval as:

$$\frac{R_w}{S_w} \quad (3.4)$$

where  $R_w$  and  $S_w$  are root and shoot dry weights, respectively (Hunt 1978).

### Allometric Constant

The allometric constant,  $K$ , is defined as:

$$\ln R_w = \ln b + K \ln S_w \quad (3.5)$$

That is, the allometric constant is the slope of the linear regression of the natural logarithm of root dry weight ( $R_w$ ) against the natural logarithm of shoot dry weight ( $S_w$ ) over the period of observations (Hunt 1978). The allometric constant describes whether a plant is allocating more of its biomass to the roots or to the shoots, as it grows over time.

### Leaf Area Ratio

The leaf area ratio,  $LAR$ , of those species whose leaf area was large enough to be estimated by the leaf area meter, was calculated for each harvest interval as:

$$LAR = \frac{L_A}{W} \quad (3.6)$$

where  $L_A$  and  $W$  are total leaf area and whole plant dry weight respectively (Hunt 1978).

## (b) Root Number in Experimental Root-tubes

A root-tube experiment was established to investigate the root morphology of some of the more common species in the study. The use of glass-fronted root-observation tubes followed the methods of Harradine and Whalley (1981) and avoided the difficulties inherent in observing plant roots *in situ* (Bohm 1979). Six species were chosen to cover a range of growth forms, life cycles and origin. The species were *Aristida ramosa*, *Sporobolus creber*,

*Vulpia bromoides*, *Acetosella vulgaris*, *Hypochaeris radicata* and *Wahlenbergia planiflora*. There were four replicates of each species making a total of 24 root-tubes (except for *H. radicata* and *A. vulgaris* which had five and three replicates, respectively due to germination of seed present in the soil and mistaken identification of seedlings). Although *A. ramosa* and *S. creber* are warm-season (C4) species, all of the root-tubes were grown at a temperature of 15°C/25°C because differences in root morphology, rather than root growth rate, were of primary interest. The temperature, humidity and light conditions were the same as described for Experiment 1 as the two experiments were run concurrently (Appendix 4A).

The root-tubes consisted of a polyethylene tube (90 cm long and with an internal diameter of 16.5 cm) which had been sawn longitudinally in half. The bottom of the tube was sealed with a semi-circle of Perspex with drainage holes and a rectangular piece of glass was clamped onto the front of the tube to allow the soil and roots to be viewed. Light was excluded from the tubes by panels of galvanised iron which slid in front of the glass and were removed to make measurements.

A sandy loam soil, collected from the A horizon of the Newholme site, was mixed, dried and sieved through a 5.6 mm sieve. To avoid differences in bulk densities when filling the root-tubes, each root-tube was laid down horizontally and a layer of dampened soil was placed into the tube and stamped down with a wooden stamper (Bohm 1979). Then the topmost few millimetres of the soil surface was loosened and a new layer of soil added and stamped down (Bohm 1979). This process was repeated until the tube was full and the soil came into contact with the glass panel placed on top. Once the root-tube was clamped together, the soil column was thoroughly saturated with half strength 'Long Ashton' nutrient solution (Appendix 4B).

Seeds of each species were germinated on sand in a germination cabinet and three seedlings were transplanted into each tube on 2 September 1993. Once established, the plants were thinned to one individual per root-tube. The root-tubes were inclined (glass face down) so that the roots would grow towards the glass surface. The tubes were originally inclined at an angle of 45° from the vertical. However after three weeks, the angle was altered to 20° from the vertical to allow better access to the glass panel for measurement. This angle was also more in keeping with other studies which use glass-faced tubes inclined at angles of about 3° - 25° from the vertical (Bohm 1979). Each week the root-tubes were watered with tapwater until it flushed through the drainage holes and every four weeks they were fertilized with quarter strength 'Long Ashton' nutrient solution.

Twice a week, root density was estimated by counting the number of roots intersecting lines drawn horizontally across the glass panel at 10 cm intervals. The maximum depth reached by the roots was also recorded and the leaf stage noted. After 4 weeks (1 October 1993), an outline of the roots was traced onto transparent film. After 12 weeks the plants were harvested, with the above-ground parts separated into shoots and reproductive parts, while the roots were harvested at 10 cm intervals. The soil was washed from the roots and the harvested plants were oven-dried at 80°C to constant mass before weighing.

### 3.2.3 Data Analysis

Significant differences between the mean relative growth rate (untransformed) of the reference species, *Lolium perenne*, in the five growth analysis experiments was determined by analysis of variance (anova) using SYSTAT (Wilkinson *et al.* 1992). Significant differences between species in their mean total root number (log transformed), mean maximum root depth (untransformed) and the mean time taken for the first lateral root (log transformed) to form in the root-tube experiment were determined by anova. Pairwise comparisons of the means were made using Bonferroni tests. The data were transformed where necessary to meet the assumptions of normality and after anova the residuals were examined for outliers and normality (Tabachnick & Fidell 1989).

The association of categorical plant attributes with other categorical plant attributes was determined using contingency tables and chi-squared ( $\chi^2$ ) statistical tests. A significant overall chi-square test for an  $r \times c$  contingency table indicates non-independence of the two variables (Everitt 1977). The plant attribute categories were cross-tabulated and the tables were standardized by row percentages using SYSTAT (Wilkinson *et al.* 1992). The chi-squared distribution is a derived approximation for the distribution of the statistic  $\chi^2$  and is made under the assumption that the expected values are not too small (Everitt 1977). Therefore, chi-squared tests are only reliable when no expected value is smaller than about five (Everitt 1977; Bailey 1981). When more than 25% of the values in a large contingency table were less than five, some of the plant attribute categories were combined. For the  $r \times c$  contingency tables the Pearson chi-square test of significance was used (Wilkinson *et al.* 1992). When the expected cell values were small in the  $2 \times 2$  contingency tables, Fisher's exact test of significance was used because it counts all the possible outcomes exactly and is not subject to assumptions regarding small expected values (Bailey 1981; Wilkinson *et al.* 1992). The degree of association amongst the continuous plant attributes was determined by correlation using SYSTAT (Wilkinson *et al.* 1992). The more robust non-parametric Spearman rank correlation coefficient was used to protect against outliers and violation of the assumption of homogeneity of variance.

### 3.3 RESULTS

#### 3.3.1 General Attributes and Attributes Measured in the Field

##### (a) Whole Plant Morphology Attributes

Fifty-four species were found in enough numbers in the field and were present on the experimental plots (Table 3.2). Thirty-five (65%) of the species were native, while nineteen (35%) species were exotic. Forty-three (80%) species had a perennial life cycle, while eleven (20%) were annual or biennial. Most species were forbs, followed by grasses and then sedges or rushes (Table 3.3).

**Table 3.2:** The species in the Newholme field experiment for which the plant attributes were examined in the field.

Family	Species	Family	Species
Anthericaceae	<i>Tricoryne elatior</i>	Poaceae (cont.)	<i>Sorghum leiocladum</i>
Cyperaceae	<i>Carex breviculmis</i>		<i>Sporobolus creber</i>
	<i>Carex inversa</i>		<i>Vulpia bromoides</i>
Juncaceae	<i>Fimbristylis dichotoma</i>		<i>Vulpia myuros</i>
	<i>Schoenus apogon</i>	Asteraceae	<i>Conyza albida</i>
	<i>Juncus bufonius</i>		<i>Gnaphalium coarctatum</i>
	<i>Juncus capitatus</i>		<i>Hypochoeris radicata</i>
	<i>Juncus homalocaulis</i>	Campanulaceae	<i>Wahlenbergia planiflora</i>
Orchidaceae	<i>Juncus subsecundus</i>	Clusiaceae	<i>Hypericum gramineum</i>
	<i>Luzula flaccida</i>	Droseraceae	<i>Drosera burmannii</i>
	<i>Microtis unifolia</i>		<i>Drosera peltata</i>
Poaceae	<i>Pterostylis bicolor</i>	Euphorbiaceae	<i>Phyllanthus virgatus</i>
	<i>Aira cupaniana</i>	Fabaceae	<i>Glycine clandestina</i>
	<i>Aristida ramosa</i>		<i>Glycine tabacina</i>
	<i>Aristida vagans</i>		<i>Trifolium dubium</i>
	<i>Aristida warburgii</i>		<i>Trifolium repens</i>
	<i>Bothriochloa macra</i>		<i>Zornia dyctiocarpa</i>
	<i>Briza minor</i>	Gentianaceae	<i>Centaurium erythraea</i>
	<i>Cymbopogon refractus</i>		<i>Centaurium tenuiflorum</i>
	<i>Dactylis glomerata</i>	Haloragaceae	<i>Haloragis heterophylla</i>
	<i>Dichelachne micrantha</i>	Onagraceae	<i>Epilobium billardierianum</i>
	<i>Digitaria brownii</i>	Oxalidaceae	<i>Oxalis exilis</i>
	<i>Elymus scaber</i>	Plantaginaceae	<i>Plantago lanceolata</i>
	<i>Eragrostis leptostachya</i>	Polygonaceae	<i>Acetosella vulgaris</i>
	<i>Eragrostis species 'red'</i>		<i>Rumex brownii</i>
<i>Lolium perenne</i>	Rosaceae	<i>Sanguisorba minor</i>	
<i>Panicum effusum</i>	Rubiaceae	<i>Richardia stellaris</i>	

**Table 3.3:** The number and percentage (in bold) of species assigned to each growth form category (n = 54).

	Growth Form		
	Forbs	Grasses	Sedges/rushes
	26	19	9
	<b>48</b>	<b>35</b>	<b>17</b>

The distribution amongst the Raunkiaer life forms showed that most species were hemicryptophytes (Table 3.4). Therophytes were also well represented, while geophytes and amphiphytes were less common. There were no "pure" chamaephyte species, but the two amphiphyte species had renewal buds close to the ground (as for chamaephytes) as well as in the ground (as for hemicryptophytes). Most species had a tussock or tufted stem structure, while semi-rosette and erect habits were also well represented (Table 3.5). Species with a rosette, prostrate, twining, or branched stem structure were less common.

**Table 3.4:** The number and percentage (in bold) of species assigned to each of the Raunkiaer life forms (n = 54).

Raunkiaer Life Forms			
Amphiphytes	Geophytes	Hemicryptophytes	Therophytes
2	4	37	11
<b>4</b>	<b>7</b>	<b>69</b>	<b>20</b>

**Table 3.5:** The number and percentage (in bold) of species assigned to each of the stem structure categories (n = 54).

Stem Structure								
Tussock	Tuft	Rosette	Semi-rosette	Branched	Erect	Single prostrate	Matted prostrate	Twining
14	14	4	8	1	6	4	1	2
<b>26</b>	<b>26</b>	<b>7</b>	<b>15</b>	<b>2</b>	<b>11</b>	<b>7</b>	<b>2</b>	<b>4</b>

Distribution of the mean vegetative height of the species was negatively skewed, with most species being 10.1 - 20 cm tall, while species less than 5 cm and between 20.1 - 30 cm in height were also well represented (Table 3.6a). Mean vegetative height of the species examined ranged from a low of 4 mm for *Centaureum tenuiflorum* to a high of 63.4 cm for *Conyza albida* (Appendix 5A). The distribution of the mean reproductive height of the species was slightly positively skewed, with most species being 30.1 - 50 cm tall, while the 10.1 - 20 cm and the 20.1 - 30 cm height classes were also well represented (Table 3.6b). Mean reproductive height of the species examined ranged from a low of 1.8 cm for *Richardia stellaris* to a high of 87.2 cm for *Conyza albida* and *Sorghum leiocladum*.

**Table 3.6:** The number and percentage (in bold) of species assigned to each of the height classes. (a) vegetative height (n = 54); (b) reproductive height (n = 52).

	Height Class (cm)						
	≤ 5	5.1 - 10.0	10.1 - 20.0	20.1 - 30.0	30.1 - 50.0	50.1 - 70.0	> 70
(a) Vegetative	10	4	24	13	1	1	0
	<b>19</b>	<b>8</b>	<b>45</b>	<b>24</b>	<b>2</b>	<b>2</b>	<b>0</b>
(b) Reproductive	3	3	11	10	15	6	4
	<b>6</b>	<b>6</b>	<b>21</b>	<b>19</b>	<b>29</b>	<b>11</b>	<b>8</b>

Distribution of the mean width of the species was negatively skewed, with widths of less than 5 cm and between 10.1 - 20 cm being common, while species greater than 50 cm wide were uncommon (Table 3.7). The mean width of the species ranged from 1.3 cm for *Centaureum tenuiflorum* to 64.3 cm wide for *Sorghum leiocladum* (Appendix 5B).

**Table 3.7:** The number and percentage (in bold) of species assigned to each of the width classes (n = 54).

Width Class (cm)					
≤ 5	5.1 - 10.0	10.1 - 20.0	20.1 - 30	30.1 - 50.0	> 50.0
14	8	16	8	7	1
<b>26</b>	<b>15</b>	<b>29</b>	<b>15</b>	<b>13</b>	<b>2</b>

Distribution of the mean height:width ratio of the species was negatively skewed, with most of the species having a ratio between 0.51 - 0.7, while ratios greater than 2.1 were less common (Table 3.8). That is, species tended to be greater in width than in height. Mean height:width ratio of the species ranged from 0.27 for the low and wide *Sanguisorba minor* to 8.67 for the tall and narrow *Microtis unifolia* (Appendix 5B).

**Table 3.8:** The number and percentage (in bold) of species assigned to each of the height:width ratio classes (n = 54).

Height:Width Class					
≤ 0.5	0.51 - 0.7	0.71 - 1.0	1.1 - 2.0	2.1 - 5.0	> 5.0
10	12	11	11	4	6
<b>19</b>	<b>22</b>	<b>20.5</b>	<b>20.5</b>	<b>7</b>	<b>11</b>

Most species did not possess persistent litter (Table 3.9). For those species which did possess litter, depths of up to 1 cm, 5 cm and 20 cm were equally well represented. *Juncus subsecundus*, *Lolium perenne* and *Sporobolus creber* were the only species with persistent litter greater than 20 cm in depth (Appendix 5A).

**Table 3.9:** The number and percentage (in bold) of species assigned to each of the persistent litter classes (n = 54).

Persistent Litter Class					
Absent	up to 1 cm	up to 5 cm	up to 10 cm	up to 20 cm	> 20 cm deep
19	9	9	5	9	3
<b>35</b>	<b>17</b>	<b>17</b>	<b>9</b>	<b>17</b>	<b>5</b>



**(b) Inflorescence Attributes**

Most species had spike-like inflorescences, while species with panicle-like and solitary inflorescences were also well represented (Table 3.10). Most species investigated began to flower in November or December, while species commencing flowering in August or February were uncommon. The first species to flower at Newholme was *Carex breviculmis* in August, while the last two species to flower were *Eragrostis leptostachya* and *Phyllanthus virgatus* in February (Appendix 5B).

**Table 3.10:** The number and percentage (in bold) of species assigned to each of the inflorescence forms (n = 54).

Inflorescence Form				
Capitulum	Spike-like	Panicle-like	Cyme-like	Solitary
6	17	13	6	12
<b>11</b>	<b>31</b>	<b>24</b>	<b>11</b>	<b>22</b>

**Table 3.11:** The number and percentage (in bold) of species which commenced flowering in each month (n = 54).

Commencement of Flowering						
August	September	October	November	December	January	February
1	3	6	20	16	6	2
<b>2</b>	<b>5</b>	<b>11</b>	<b>37</b>	<b>30</b>	<b>11</b>	<b>4</b>

Flowering period duration of the species demonstrated a negatively skewed distribution, with the greatest number of species flowering for only one month. Species flowering for two, three, four or five months were also well represented (Table 3.12). Species flowering for more than five months were uncommon. Species flowering for one month were *Drosera burmannii*, *Sorghum leiocladum*, *Juncus homalocaulis*, *Juncus subsecundus*, *Elymus scaber* and the exotic annuals (*Aira cupaniana*, *Briza minor* and *Vulpia* spp.). The native annual, *Schoenus apogon*, was the only annual with a flowering period longer than one month. The native forbs, *Wahlenbergia planiflora* and *Oxalis exilis*, had the longest flowering period of eight and nine months, respectively (Appendix 5A).

**Table 3.12:** The number and percentage (in bold) of species assigned to each of the flowering period duration classes (n = 54).

Flowering Period Duration							
1 month	2 months	3 months	4 months	5 months	6 months	7 months	8 - 9 months
12	8	9	6	9	4	4	2
<b>22</b>	<b>15</b>	<b>17</b>	<b>11</b>	<b>17</b>	<b>7</b>	<b>7</b>	<b>4</b>

(c) Leaf Attributes

Distribution of the mean leaf life span of the species was negatively skewed, with most of the species having a leaf life span of between 75.1 - 100 days or 100.1 - 125 days (Table 3.13). *Aira cupaniana* had the shortest mean leaf life span of 28.6 days, while *Carex inversa* had the longest mean leaf life span of 204.9 days (Appendix 5C). During the monitoring of leaf life span some forbs, *Hypericum gramineum*, *Wahlenbergia planiflora* and *Haloragis heterophylla*, died back to ground level during summer (late December 1993) after a relatively dry spring (October and November 1993). Some of these individuals sprouted again about a month later (early February 1994) after above average rainfall in December and January and temperatures started to decline (Fig. 2.1). *Acetosella vulgaris*, *H. heterophylla*, *H. gramineum*, and *W. planiflora* were prone to herbivory by insects, as were *Lolium perenne*, *Dactylis glomerata* and *Briza minor* to a lesser degree.

**Table 3.13:** The number and percentage (in bold) of species assigned to each of the leaf life span classes (n = 31).

Leaf Life Span (days)						
25 - 50	50.1 - 75	75.1 - 100	100.1 - 125	125.1 - 150	150.1 - 200	200.1 - 250
3	5	9	9	2	2	1
<b>10</b>	<b>16</b>	<b>29</b>	<b>29</b>	<b>6.5</b>	<b>6.5</b>	<b>3</b>

Most species had leaves in the nanophyll size class, while species with leaves in the microphyll and the leptophyll size classes were more or less equally represented (Table 3.14). Almost three-quarters of the species had leaves of a soft texture, while leaves of a fibrous or thick texture were less common (Table 3.15). More than half of the species had linear shaped leaves, while the other leaf shape categories were more or less equally represented (Table 3.16). Almost three-quarters of the species had glabrous leaves, while most species with hairy leaves were hairy on both sides of the leaf (Table 3.17).

**Table 3.14:** The number and percentage (in bold) of species assigned to each of the leaf size classes (n = 54).

Leaf Size		
Leptophyll	Nanophyll	Microphyll
11	29	14
<b>20</b>	<b>54</b>	<b>26</b>

**Table 3.15:** The number and percentage (in bold) of species assigned to each of the leaf texture classes (n = 54).

Leaf Texture	
Fibrous or thick	Soft
15	39
<b>28</b>	<b>72</b>

**Table 3.16:** The number and percentage (in bold) of species assigned to each of the leaf shape classes (n = 54).

Leaf Shape						
Filiform	Linear	Elliptic	Circular	Lanceolate	Oblanceolate	Obovate
4	29	5	4	6	3	3
7	<b>54</b>	<b>9</b>	7	<b>11</b>	<b>6</b>	<b>6</b>

**Table 3.17:** The number and percentage (in bold) of species assigned to each of the leaf hairiness classes (n = 54).

Leaf Hairiness				
Glabrous	Lower side hairy	Upper-side hairy	Both sides hairy	Edges hairy
40	4	1	7	2
<b>74</b>	7	<b>2</b>	<b>13</b>	<b>4</b>

#### (d) Root Attributes

Almost half of the species lacked underground storage organs (Table 3.18). For those species with storage organs, most had short rhizomes, while species with stolons were uncommon.

**Table 3.18:** The number and percentage (in bold) of species assigned to each of the underground storage organ categories (n = 54).

Underground Storage Organs						
Absent	Stolons	Long rhizomes	Short rhizomes	Stem tubers	Taproot	Root tubers
25	2	5	10	4	5	3
<b>46</b>	<b>4</b>	<b>9</b>	<b>19</b>	7	<b>9</b>	<b>6</b>

#### (e) Diaspore Attributes

Most species had ovoid-shaped diaspores, while species with trigonous, tadpole and conical-shaped diaspores were also well represented (Table 3.19). Most species did not have a diaspore morphology indicative of a particular dispersal strategy (Table 3.20). However, for those species which did, most had dust-like diaspores while species with straight awns were also well represented. About two-thirds of the species had glabrous diaspores, while most of the species with hairy diaspores had hairs of the antrorse type (Table 3.21). Most species had

diaspores with a smooth surface texture, while rugose diaspores were also well represented (Table 3.22). Diaspores with striate, hairy and mucilaginous surface textures were less common.

**Table 3.19:** The number and percentage (in bold) of species assigned to each of the diaspore shape categories (n = 54). Ovoid = ovoid/rhomboidal/turbinate; Trigonous = trigonous/triangular; Lenticular = lenticular/reniform subulate; Cylindrical = cylindrical/ligulate.

Diaspore Shape								
Spherical	Ovoid	Trigonous	Lenticular	Cylindrical	Clavate	Winged	Tadpole	Conical
1	17	10	5	4	1	1	8	7
<b>2</b>	<b>31</b>	<b>19</b>	<b>9</b>	<b>7</b>	<b>2</b>	<b>2</b>	<b>15</b>	<b>13</b>

**Table 3.20:** The number and percentage (in bold) of species assigned to each of the diaspore dispersal categories (n = 54). Awn = straight awn/spine; Hygroscopic awn = hygroscopic awn/spine; Pappus = pappus/persistent calx; Hook = hook/barbed spine.

Diaspore Dispersal Morphology							
Absent	Straight awn	Hygroscopic awn	Pappus	Hook	Inflorescence breaks	Dust-like diaspores	Explosive
19	7	4	5	2	1	12	4
<b>35</b>	<b>13</b>	<b>7.5</b>	<b>9</b>	<b>4</b>	<b>2</b>	<b>22</b>	<b>7.5</b>

**Table 3.21:** The number and percentage (in bold) of species assigned to each of the diaspore hairiness categories (n = 54).

Diaspore Hairiness		
Glabrous	Antrorse	Radial
35	15	4
<b>65</b>	<b>28</b>	<b>7</b>

**Table 3.22:** The number and percentage (in bold) of species assigned to each of the diaspore surface texture categories (n = 54).

Diaspore Surface Texture				
Smooth	Rugose	Striate	Hairy	Mucilaginous
28	20	4	1	1
<b>52</b>	<b>37</b>	<b>7</b>	<b>2</b>	<b>2</b>

The distribution of mean diaspore mass of the species on a logarithmic scale was unimodal and truncated-normal. The modal class of diaspore mass was 0.0001 to 0.001 g (Fig. 3.1). Mean diaspore mass ranged from a minimum of 0.001 mg for *Microtis unifolia* and *Pterostylis bicolor* to a maximum of 8.4 mg for *Glycine tabacina* (Appendix 5C).

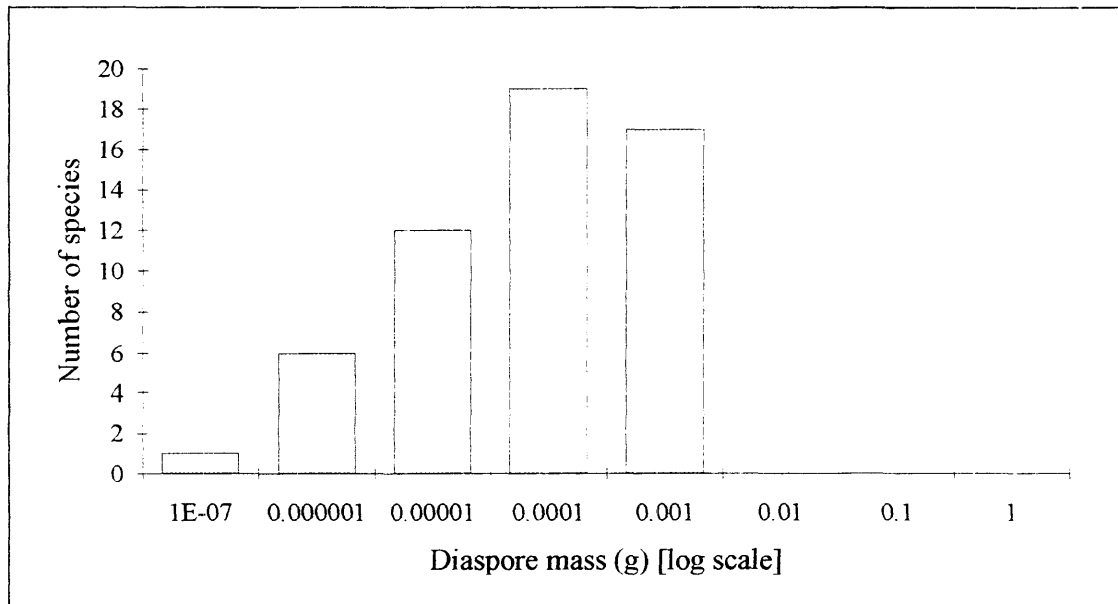


Fig. 3.1: The distribution of diaspore mass (g) of the Newholme species on a logarithmic scale.

Mean diaspore number per plant of the species was negatively skewed, with the modal class being 501 to 1000 diaspores per individual (Table 3.23). Mean diaspore number ranged from as few as 5 diaspores per individual for *Oxalis exilis* to as many as 34 700 diaspores per individual for *Conyza albida* (Appendix 5C).

Table 3.23: The number and percentage (in bold) of species assigned to each of the diaspore number categories (n = 48).

Diaspore Number (per individual)						
< 50	51 - 150	151 - 500	501 - 1000	1001 - 5000	5001 - 10000	> 10000
7	7	10	11	8	3	2
<b>14.5</b>	<b>14.5</b>	<b>21</b>	<b>23</b>	<b>17</b>	<b>6</b>	<b>4</b>

### 3.3.2 Attributes Measured in the Glasshouse

#### (a) Growth Analysis of Seedlings

Growth analysis data was obtained for 22 species (Table 3.25). Differences in the mean relative growth rate of *Lolium perenne* over the five week observation period ( $\bar{R}_{1-5}$ ) indicated that the conditions for growth in Experiment 2 were more favourable than in Experiment 1, 4 and 5 (Table 3.24). Conditions for growth in Experiment 3 were more favourable than in Experiment 5. Temperature cannot explain the difference in growth rate of

*L. perenne* as they were similar in the first four experiments. However, the higher humidity levels in Experiment 2 and 3 compared to the other experiments may have resulted in an increased growth rate. The combination of the high light levels and low humidity may have been responsible for the poor growth of *L. perenne* in Experiment 1. As expected, the relative growth rate of *L. perenne* (a C3 species) was reduced at the higher temperature regime required for the C4 species in Experiment 5. Despite this, the relative growth rate of *L. perenne* in Experiment 5 was not significantly different from that in Experiment 1 and 4. Thus, the maximum relative growth rate of the species examined in Experiment 1 and 4 may have been underestimated.

**Table 3.24:** Mean ( $\pm$  standard error) relative growth rate of the reference species, *Lolium perenne*, for each experiment. The temperature and humidity range and the mean ( $\pm$  standard error) light levels for each experiment is also given. Mean relative growth rates with different superscripts were significantly different at the  $p < 0.05$  level (Bonferroni tests). Individuals were supplied with the standard strength Long Ashton nutrient solution.

Experiment	$\bar{R}_{1-5}$ (week <sup>-1</sup> )	Temperature	Relative Humidity	Light levels (W m <sup>-2</sup> )
1	1.19 $\pm$ 0.134 ab	15°C to 28°C	40% to 70%	579.6 $\pm$ 269.7
2	1.46 $\pm$ 0.071 c	15°C to 27°C	45% to 80%	301.1 $\pm$ 201.7
3	1.32 $\pm$ 0.145 bc	20°C to 28°C	50% to 80%	312.2 $\pm$ 145.9
4	1.12 $\pm$ 0.117 ab	20°C to 26°C	50% to 70%	276.5 $\pm$ 128.2
5	1.03 $\pm$ 0.173 a	25°C to 33°C	35% to 50%	341.6 $\pm$ 235.3

Forbs with small diaspores, such as *Centaurium tenuiflora*, *Wahlenbergia planiflora* and *Gnaphalium coarctatum* tended to have a high mortality rate in the glasshouse experiments, as did *Richardia stellaris*. Due to the high loss of replicates of *W. planiflora* and *R. stellaris*, growth analysis was repeated using ten replicates (instead of five) grown at the nutrient concentration found to be optimal in the first attempt. The loss of replicates of *Eragrostis* 'red', *Sporobolus creber*, *Aristida warburgii* and *Bothriochloa macra* in Experiment 5 may have been due to the low humidity in this glasshouse (Appendix 4A).

Maximum relative growth rates ranged from a low of 0.27 mg/mg/week for *Richardia stellaris* to a high of 1.79 mg/mg/week for *Capsella bursa-pastoris* (Table 3.25). For most of the species examined the greatest growth rate was achieved at the standard Long Ashton nutrient level. However, the greatest growth rate was achieved at the half strength nutrient level for *R. stellaris*, *Aristida warburgii*, *A. ramosa* and *Sanguisorba minor*, while the growth rate of *Plantago lanceolata*, *Lolium perenne* and *Capsella bursa-pastoris* was greatest at the double strength nutrient level.

**Table 3.25:** Mean ( $\pm$  standard error) maximum relative growth rate (Rmax), root:shoot ratio (R:S), allometric constant (K) and leaf area ratio (LAR) of species. \* = exotic species. Species are listed from lowest to highest Rmax. Root:shoot ratio and leaf area ratio after 35 days is given, with the exception of R:S for *S.creber* and LAR for *A.vulgaris* which are after 21 days. Exp = the experiment the species was grown in (for the experimental conditions see Appendix 4A). The highest growth rate estimate and the nutrient strength at which it was obtained are given; half = half strength Long Ashton nutrient solution; standard = standard strength Long Ashton nutrient solution; double = double strength Long Ashton nutrient solution. <sup>a</sup> = Rmax may be underestimated (see text for explanation).

Species	Exp	Nutrient	Rmax (week-1)	Root:Shoot	K	LAR. (cm <sup>2</sup> /mg)
* <i>Richardia stellaris</i>	4 <sup>a</sup>	half	0.26 $\pm$ 0.049	1.41 $\pm$ 0.673	-	0.09 $\pm$ 0.025
<i>Wahlenbergia planiflora</i>	4 <sup>a</sup>	standard	0.36 $\pm$ 0.056	0.54 $\pm$ 0.473	-	-
<i>Aristida warburgii</i>	5	half	0.40 $\pm$ 0.073	0.99 $\pm$ 0.117	1.43 $\pm$ 0.106	-
<i>Luzula flaccida</i>	4 <sup>a</sup>	standard	0.61 $\pm$ 0.052	0.31 $\pm$ 0.083	0.78 $\pm$ 0.047	0.23 $\pm$ 0.015
<i>Aristida ramosa</i>	5	half	0.64 $\pm$ 0.060	1.09 $\pm$ 0.236	0.97 $\pm$ 0.178	-
<i>Cymbopogon refractus</i>	5	standard	0.71 $\pm$ 0.051	0.48 $\pm$ 0.157	0.85 $\pm$ 0.052	0.11 $\pm$ 0.014
<i>Carex inversa</i>	3	standard	0.81 $\pm$ 0.057	0.43 $\pm$ 0.048	1.02 $\pm$ 0.062	0.05 $\pm$ 0.012
<i>Dichelachne micrantha</i>	4 <sup>a</sup>	double	0.82 $\pm$ 0.046	0.65 $\pm$ 0.095	1.00 $\pm$ 0.031	0.14 $\pm$ 0.004
* <i>Vulpia bromoides</i>	2	standard	0.89 $\pm$ 0.055	0.41 $\pm$ 0.087	0.91 $\pm$ 0.040	-
<i>Elymus scaber</i>	2	standard	0.96 $\pm$ 0.057	0.56 $\pm$ 0.079	1.04 $\pm$ 0.026	0.06 $\pm$ 0.014
* <i>Sanguisorba minor</i>	1 <sup>a</sup>	half	1.02 $\pm$ 0.040	0.56 $\pm$ 0.062	1.00 $\pm$ 0.020	0.10 $\pm$ 0.007
* <i>Aira cupaniana</i>	1 <sup>a</sup>	standard	1.03 $\pm$ 0.082	0.46 $\pm$ 0.153	1.01 $\pm$ 0.089	-
* <i>Juncus bufonius</i>	3	standard	1.04 $\pm$ 0.067	0.48 $\pm$ 0.116	0.88 $\pm$ 0.051	-
<i>Bothriochloa macra</i>	5	standard	1.07 $\pm$ 0.054	0.68 $\pm$ 0.066	1.00 $\pm$ 0.039	0.12 $\pm$ 0.020
<i>Sporobolus creber</i>	5	standard	1.09 $\pm$ 0.108	0.29 $\pm$ 0.027	0.78 $\pm$ 0.041	-
* <i>Hypochaeris radicata</i>	2	standard	1.14 $\pm$ 0.071	0.62 $\pm$ 0.138	0.92 $\pm$ 0.044	0.19 $\pm$ 0.026
* <i>Vulpia myuros</i>	2	standard	1.17 $\pm$ 0.063	0.59 $\pm$ 0.091	0.98 $\pm$ 0.024	-
* <i>Acetosella vulgaris</i>	1 <sup>a</sup>	standard	1.21 $\pm$ 0.087	0.45 $\pm$ 0.063	0.89 $\pm$ 0.039	0.43 $\pm$ 0.270
* <i>Dactylis glomerata</i>	2	standard	1.31 $\pm$ 0.054	0.56 $\pm$ 0.113	0.95 $\pm$ 0.027	0.09 $\pm$ 0.013
* <i>Plantago lanceolata</i>	3	double	1.36 $\pm$ 0.055	0.34 $\pm$ 0.084	0.89 $\pm$ 0.034	0.15 $\pm$ 0.016
* <i>Lolium perenne</i>	2	double	1.49 $\pm$ 0.054	0.52 $\pm$ 0.084	0.97 $\pm$ 0.032	0.13 $\pm$ 0.011
* <i>Capsella bursa-pastoris</i>	4 <sup>a</sup>	double	1.79 $\pm$ 0.074	0.28 $\pm$ 0.043	0.96 $\pm$ 0.030	0.26 $\pm$ 0.062

Most species had a mean root:shoot ratio of between 0.41 and 0.5 or 0.51 and 0.6 (Table 3.26). That is, after 35 days of growth, the seedlings of most species had partitioned about one third of their dry mass into their roots. The mean root:shoot ratio ranged from a minimum of 0.28 for *Capsella bursa-pastoris* to a maximum of 1.41 for *Richardia stellaris* (Table 3.25): *C. bursa-pastoris* seedlings only allocated about one quarter of their biomass to their roots, while *R. stellaris* seedlings allocated about two thirds of their biomass to their roots. Out of the native species, *Aristida ramosa* and *A.warburgii* seedlings allocated about one half of their biomass to their roots, while *Sporobolus creber* and *Luzula flaccida* seedlings allocated about one quarter of their biomass to their roots.

**Table 3.26:** The number and percentage (in bold) of species assigned to each of the root:shoot ratio categories (n = 22).

Root:Shoot Ratio					
$\leq 0.4$	0.41 - 0.5	0.51 - 0.6	0.61 - 0.8	0.81 - 1.0	$> 1.0$
4	6	6	3	1	2
<b>18</b>	<b>27</b>	<b>27</b>	<b>14</b>	<b>5</b>	<b>9</b>

Half of the species had mean allometric constants between 0.91 and 1.0 (Table 3.27). Thus most of the species allocated a slightly greater proportion of new biomass to their shoots rather than their roots, as they grew over the 35 days. The mean allometric constant ranged from a minimum of 0.78 for *Sporobolus creber* and *Luzula flaccida* to a maximum of 1.43 for *Aristida warburgii* (Table 3.25). *S. creber* and *L. flaccida* seedlings allocated a greater proportion of their biomass to their shoots over time. Those species with an allometric constant greater than one, *A. warburgii*, *Carex inversa*, *Dichelachne micrantha*, *Elymus scaber* and *Sanguisorba minor* seedlings, allocated a greater proportion of their biomass to their roots over time.

**Table 3.27:** The number and percentage (in bold) of species assigned to each of the allometric constant categories (n = 20).

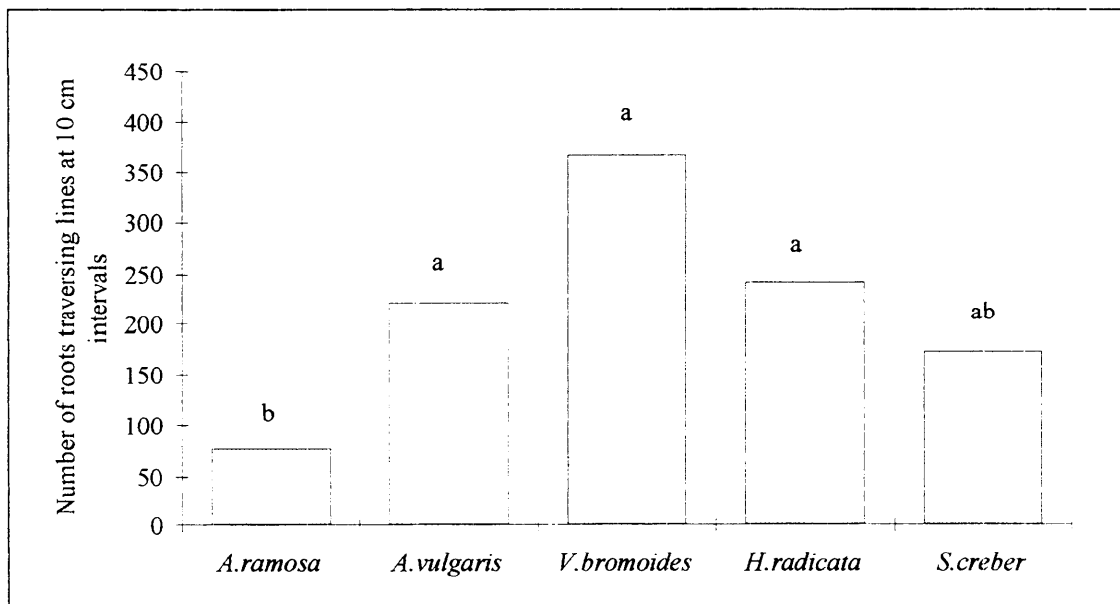
Allometric Constant			
0.41 - 0.8	0.81 - 0.9	0.91 - 1.0	> 1.0
2	4	10	4
<b>10</b>	<b>20</b>	<b>50</b>	<b>20</b>

The sample of species for which the mean leaf area ratio was obtained was biased towards larger-leaved species because small leaves failed to register on the leaf area meter. The mean leaf area ratio ranged from a minimum of 0.05 cm<sup>2</sup> mg<sup>-1</sup> for *Carex inversa* to a maximum of 0.43 cm<sup>2</sup> mg<sup>-1</sup> for *Acetosella vulgaris* (Table 3.25). Thus, the leaves of *C. inversa* had a small area for the amount of biomass invested, while the leaves of *A. vulgaris* had a large area for the amount of biomass invested.

#### (b) Root Number in Experimental Root-tubes

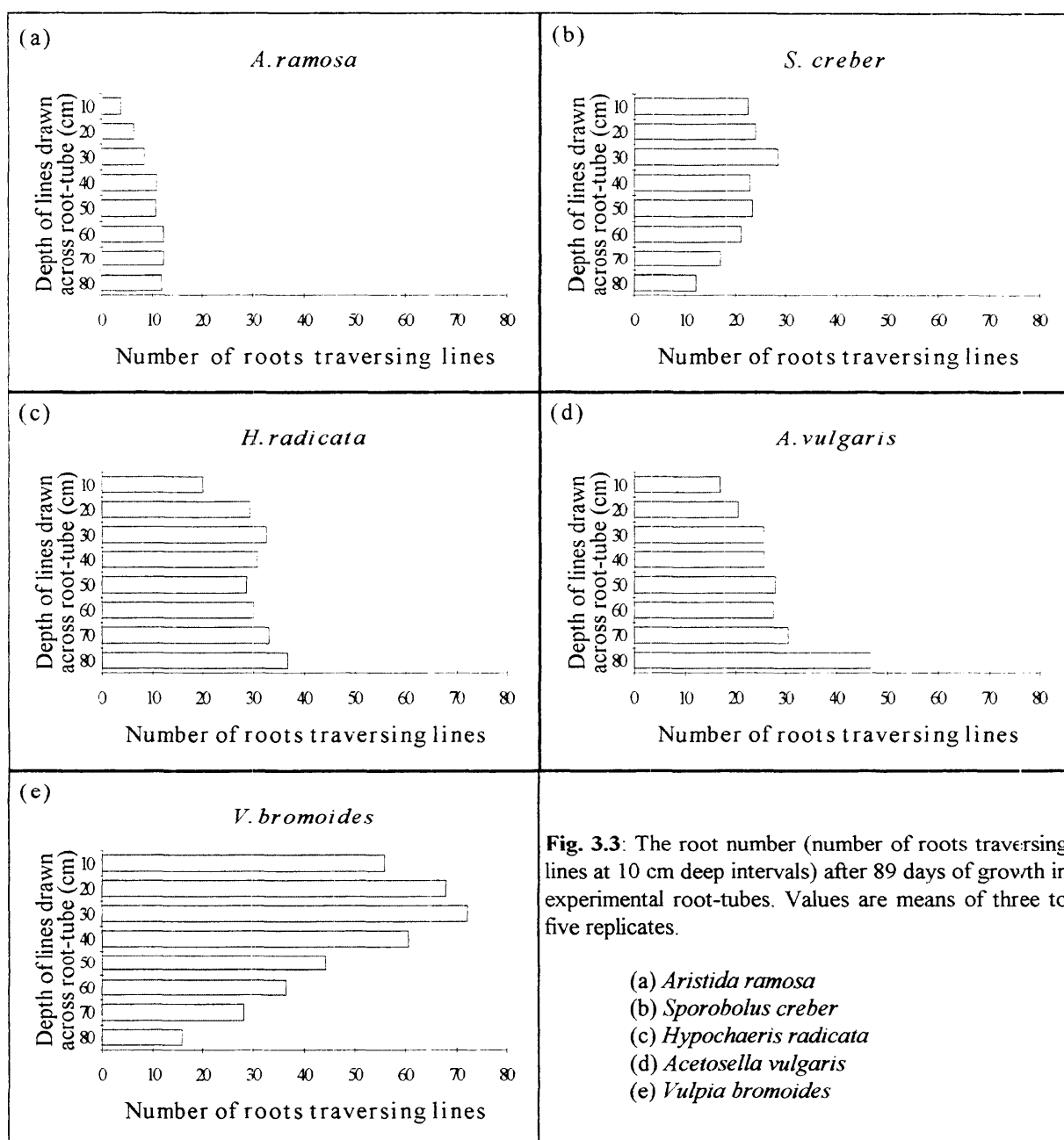
After 89 days of growth, *Vulpia bromoides* had the greatest number of roots traversing the eight lines drawn horizontally across the glass panel at 10 cm intervals down the root-tube. The total number of roots traversing the lines in the root-tubes occupied by *Acetosella vulgaris*, *V. bromoides*, *Hypochaeris radicata* and *Sporobolus creber* was not significantly different from each other (Fig. 3.2). The total root number of *Aristida ramosa* was significantly lower than that of *Acetosella vulgaris*, *V. bromoides* and *Hypochaeris radicata*, but was similar to that of *S. creber*. The root number of *Wahlenbergia planiflora* is not presented because only two of the three replicates established.





**Fig. 3.2:** Total root number (number of roots traversing eight lines placed at 10 cm intervals down the root-tube) of *Aristida ramosa*, *Acetosella vulgaris*, *Vulpia bromoides*, *Hypochaeris radicata* and *Sporobolus creber* in experimental root-tubes after 89 days of growth. Values are means of three to five replicates. Species with different subscripts had significantly different total root densities at the  $p < 0.05$  level (Bonferroni tests).

The distribution of roots down the profile of the root-tubes after 89 days showed that root number of *Aristida ramosa* and *Acetosella vulgaris* increased with depth and was maximal at 60 - 70 cm and 80 cm, respectively (Fig. 3.3a and 3.3d). Similarly the root number of *Hypochaeris radicata* was greatest towards the bottom of the root-tubes, but a peak in root number occurred at a depth of 30 cm as well as 80 cm (Fig. 3.3c). In contrast, the greatest number of the roots of *Sporobolus creber* and *Vulpia bromoides* occurred at shallower depths (30 cm) and root number decreased with soil depth (Fig. 3.3b and e). The root number of *V. bromoides* decreased rapidly with depth. One month after germination, the maximum root depth of *H. radicata* was significantly greater than that of *V. bromoides*, *A. ramosa* and *S. creber*, but was similar to that of *A. vulgaris* (Table 3.28). Further, the maximum root depth of *A. vulgaris* was significantly greater than that of *A. ramosa* and *S. creber*. By two and three months after germination, the maximum depths reached by the roots of all five species were not significantly different.



**Table 3.28:** Mean ( $\pm$  standard error) maximum root depth (cm) reached after 29, 60 and 89 days in root-tubes. Maximum root depth with different letters (across each row) were significantly different at the  $p < 0.05$  level (Bonferroni tests).  $n$  = number of replicate plants. See text for full specific names.

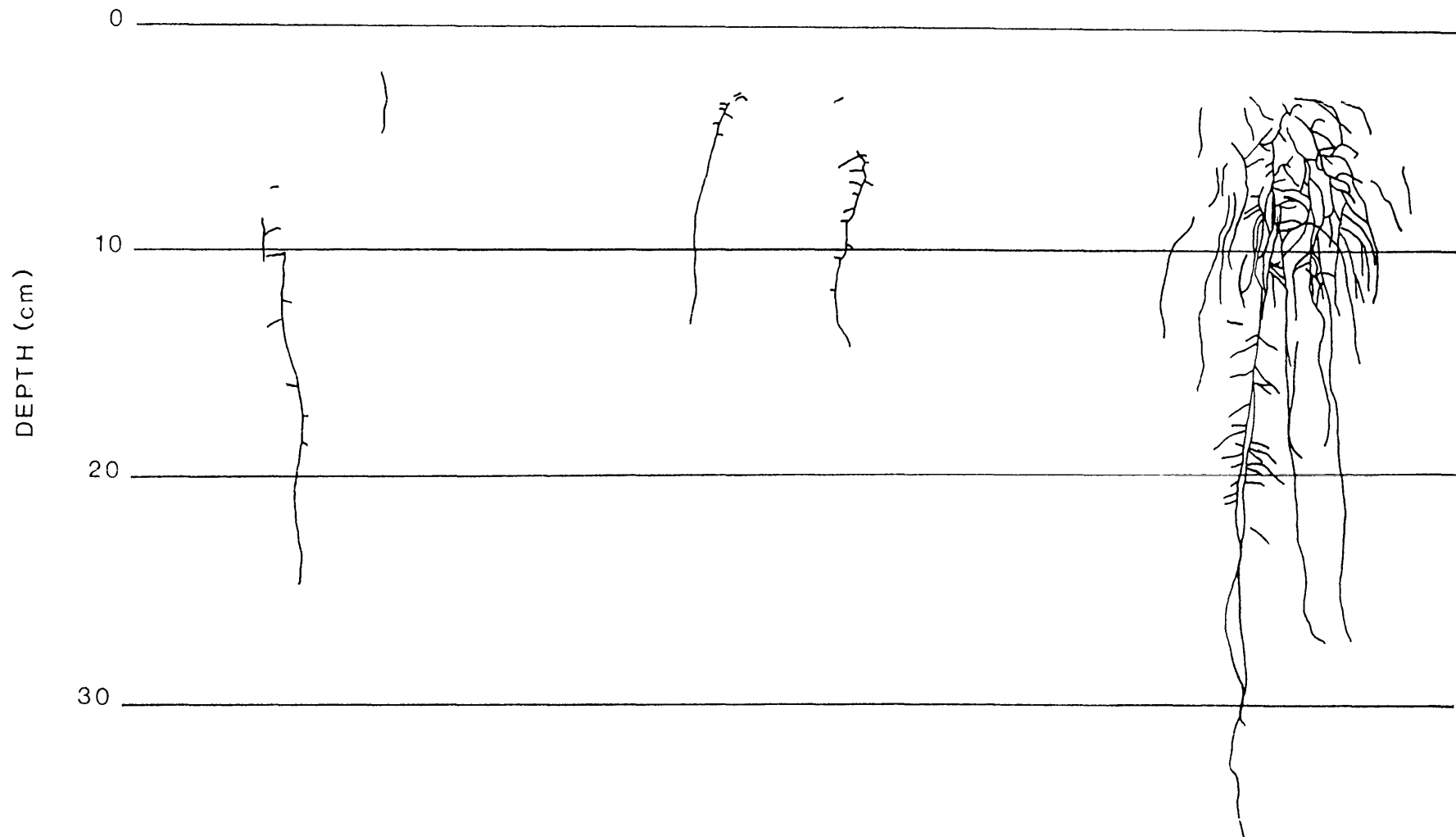
Time after germination (months)	Mean Maximum Root Depth (cm)				
	<i>A. vulgaris</i>	<i>V. bromoides</i>	<i>H. radicata</i>	<i>A. ramosa</i>	<i>S. creber</i>
$n$	3	4	5	4	4
1	$53.6 \pm 14.63$ ac	$27.4 \pm 11.88$ ab	$52.5 \pm 10.19$ c	$24.1 \pm 11.31$ b	$16.7 \pm 4.30$ b
2	$83.4 \pm 0.40$ a	$61.2 \pm 17.66$ a	$84.0 \pm 0.68$ a	$59.5 \pm 28.91$ a	$55.6 \pm 19.02$ a
3	$83.4 \pm 0.40$ a	$81.1 \pm 3.18$ a	$84.1 \pm 0.70$ a	$83.3 \pm 0.61$ a	$83.5 \pm 0.58$ a

The mean time from germination to the appearance of the first lateral root (i.e. side branching) at the soil-glass interface (Table 3.29) was significantly shorter for *A.vulgaris*, *V.bromoides* and *H.radicata* (the C3 species) than for *S.creber* (a C4 species). Further, the mean time from germination to the appearance of the first lateral root was significantly shorter for *V.bromoides* than for *A.ramosa* (a C4 species). By the end of the experiment all of the species had reached the bottom of the root-tube, except for *V.bromoides*.

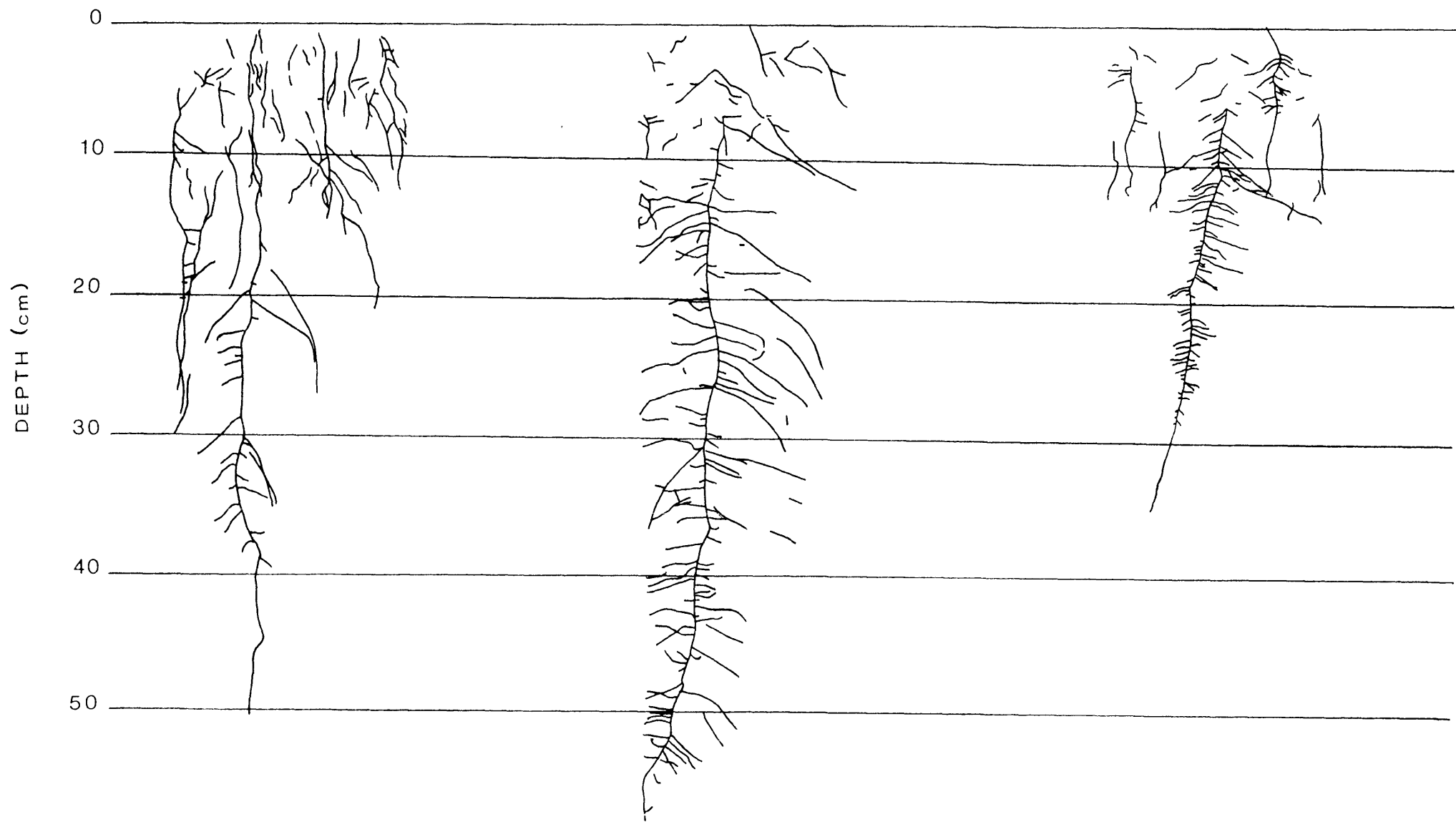
**Table 3.29:** Mean ( $\pm$  standard error) time from germination to the appearance of the first lateral root at the soil-glass interface (in days) in the experimental root-tubes. Mean times with different superscripts were significantly different at the  $p < 0.05$  level (Bonferroni tests). See text for full specific names.

	Time to first lateral root (days)				
	<i>A.vulgaris</i>	<i>V.bromoides</i>	<i>H.radicata</i>	<i>A.ramosa</i>	<i>S.creber</i>
n	3	4	5	4	4
Mean Time	17.7 $\pm$ 2.31 ab	16.0 $\pm$ 2.0 b	16.8 $\pm$ 3.19 ab	29.3 $\pm$ 8.85 ac	36.5 $\pm$ 13.40 c

Figure 3.4 illustrates that after four weeks of growth, *Aristida ramosa* and *Sporobolus creber* had a similar root morphology with a primary axis and the beginnings of a herringbone root system. In contrast, *Vulpia bromoides* had a random dense pattern of fine root. Figure 3.5 illustrates that after four weeks of growth, *Acetosella vulgaris* developed several thick axis roots associated with each rhizome and running parallel to each other, while the longest axis root was developing a herringbone pattern. *Hypochaeris radicata* had a strong herringbone root pattern with a single thick primary axis and many long lateral roots. The root pattern of the native forb, *Wahlenbergia planiflora*, was intermediate between that of *A.vulgaris* and *H.radicata*. *W.planiflora* had axis roots associated with each rhizome and a herring-bone pattern consisting of a primary axis with many short lateral roots. The roots of *W.planiflora* were finer than those of *A.vulgaris* and *H.radicata*.



**Fig. 3.4:** Root patterns of *Aristida ramosa*, *Sporobolus creber* and *Vulpia bromoides* (from left to right) at the soil-glass interface of the root tubes, four weeks after emergence. Scale of the root trace is 36% of actual size.



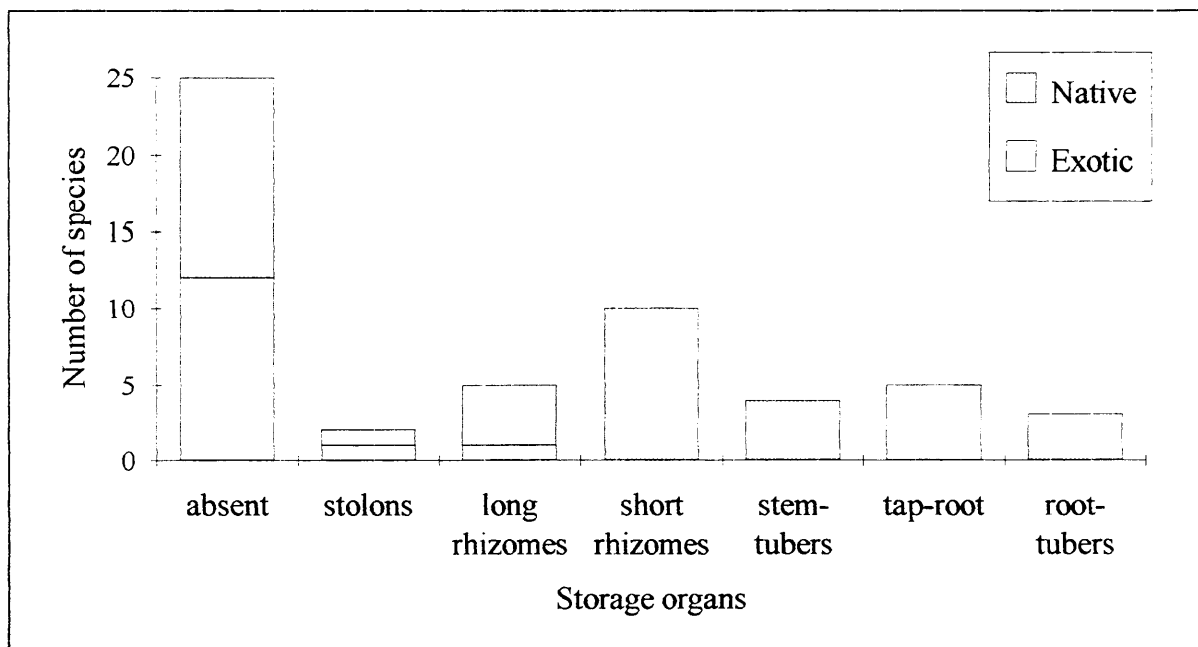
**Fig. 3.5:** Root patterns of *Acetosella vulgaris*, *Hypochaeris radicata* and *Wahlenbergia planiflora* (from left to right) at the soil-glass interface of the root tubes, four weeks after emergence. Scale of the root trace is 25% of actual size.

### 3.3.3 Relationships Among Plant Attributes

There was a significant ( $p < 0.001$ ) association between origin and life cycle of the 54 species examined, indicating that most of the annual species were exotic while the majority of the perennial species were native (Table 3.30). Most exotic species either lacked storage organs or possessed taproots, while exotic species with stolons or long rhizomes were less common (Fig. 3.6). Most native species either lacked storage organs or had short rhizomes. Native species with long rhizomes, stem-tubers, root-tubers and stolons were less common. Species with short rhizomes, stem-tubers or root-tubers were exclusively native, while species with taproots were exclusively exotic. When the underground storage organ categories, were combined into three there was a significant ( $p < 0.05$ ) association between species origin and the presence of underground storage organs (Table 3.31). More than half of the exotic species lacked these organs, while most native species possessed stolons or rhizomes.

**Table 3.30:** The relationship between species origin and life cycle. Values are the number and percentage (in bold) of species in each category ( $n = 54$ ).  $\chi^2 = 18.81$ ,  $df = 1$ ,  $p < 0.001$  (Fisher's exact two-tail test).

Origin	Annual	Perennial
Exotic	10	9
	<b>91</b>	<b>21</b>
Native	1	34
	<b>9</b>	<b>79</b>



**Fig. 3.6:** The relationship between species origin and the presence of underground storage organs of the Newholme species ( $n = 54$ ).

**Table 3.31:** The relationship between species origin and the presence of underground storage organs. Values are the number and percentage (in bold) of species in each category (n = 54).  $\chi^2 = 6.11$ , df = 2,  $p < 0.05$ .

Storage Organs	Exotic	Native
Absent	12 <b>63</b>	13 <b>37</b>
Stolons or Rhizomes	2 <b>11</b>	15 <b>43</b>
Stem/Root tubers or Taproot	5 <b>26</b>	7 <b>20</b>

Leaf texture was significantly ( $p < 0.01$ ) associated with species origin (Table 3.32). Most species with fibrous or thick leaves were native, while species with soft leaves were equally represented by exotic and native species. Leaf texture was also significantly ( $p < 0.05$ ) associated with species life cycle (Table 3.33). That is, all of the species with fibrous or thick leaves were perennial, while species with soft leaves were either annual or perennial. Further, leaf texture was significantly ( $p < 0.05$ ) associated with the growth form of species (Table 3.34). More than half of the species with fibrous or thick leaves were grasses, while most of the species with soft leaves were forbs. Leaf texture was also significantly ( $p < 0.05$ ) associated with the presence of persistent litter (Table 3.35). More than half of the species with fibrous or thick leaves had persistent litter greater than 5 cm in depth, while most of the species with soft leaves either did not have persistent litter or had litter up to 5 cm in depth.

**Table 3.32:** The relationship between species origin and leaf texture. Values are the number and percentage (in bold) of species in each category (n = 54).  $\chi^2 = 7.41$ , df = 1,  $p < 0.01$ .

Origin	Fibrous or thick	Soft
Exotic	1 7	18 <b>46</b>
Native	14 <b>93</b>	21 <b>54</b>

**Table 3.33:** The relationship between species life cycle and leaf texture. Values are the number and percentage (in bold) of species in each category (n = 54).  $\chi^2 = 5.31$ , df = 1,  $p < 0.05$  (Fisher's exact two-tail test).

Life cycle	Fibrous or thick	Soft
Annual	0 <b>0</b>	11 <b>28</b>
Perennial	15 <b>100</b>	28 <b>72</b>

**Table 3.34:** The relationship between the growth form and leaf texture of a species. Values are the number and percentage (in bold) of species in each category (n = 54).  $\chi^2 = 6.61$ , df = 2, p < 0.05.

Growth Form	Fibrous or thick	Soft
Forb	3 <b>20</b>	23 <b>59</b>
Grass	8 <b>53</b>	11 <b>28</b>
Sedge and rush	4 <b>27</b>	5 <b>13</b>

**Table 3.35:** The relationship between the leaf texture and the depth of persistent litter. Values are the number and percentage (in bold) of species in each category (n = 54).  $\chi^2 = 8.46$ , df = 2, p < 0.05.

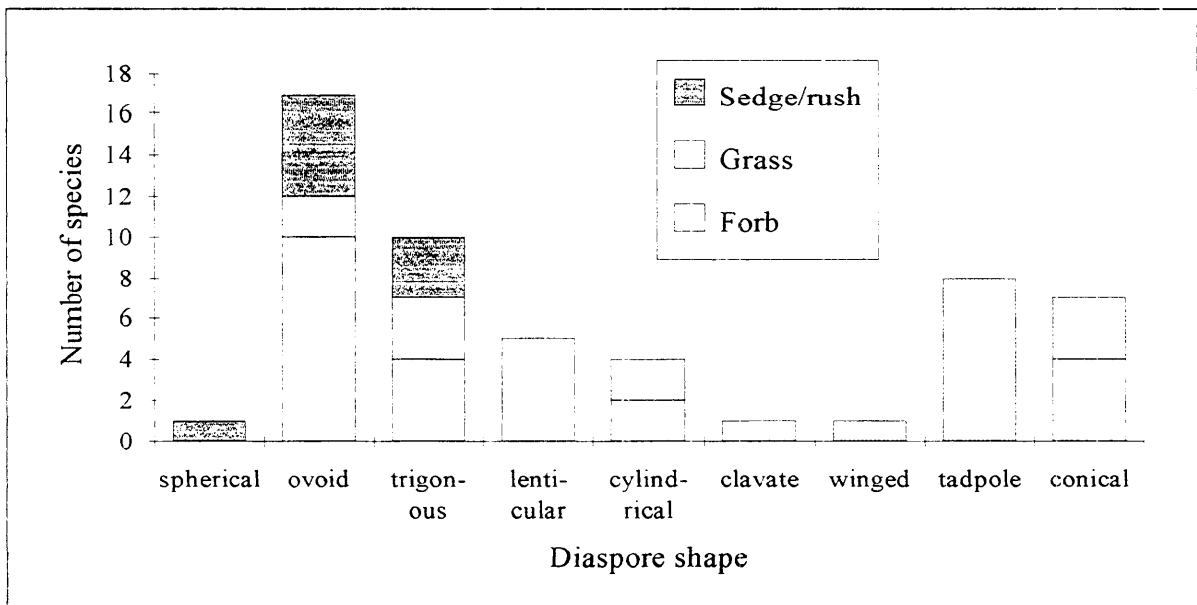
Persistent Litter	Fibrous or thick	Soft
Absent	2 <b>13</b>	17 <b>44</b>
Up to 5 cm	4 <b>27</b>	14 <b>36</b>
> 5 cm deep	9 <b>60</b>	8 <b>20</b>

The most common diaspore shape for forb species was ovoid, while species with lenticular and clavate shaped diaspores were exclusively forbs (Fig. 3.7). Tadpole shape was the most common diaspore shape of grass species and was exclusive to grasses. The diaspores of sedge and rush species were predominantly ovoid, spherical, or trigonous in shape, while species with spherical-shaped diaspores were exclusively sedge and rush species. When the diaspore shape categories were combined to make two categories, a significant association between the growth form and diaspore shape of a species was demonstrated (p < 0.01). Most forb species and all of the sedge and rush species had spherical-shaped diaspores, while most grass species had cylindrical-shaped diaspores (Table 3.36).

**Table 3.36:** The relationship between species growth form and diaspore shape. Values are the number and percentage (in bold) of species in each category (n = 54).  $\chi^2 = 14.46$ , df = 2, p < 0.01. Spherical = spherical, ovoid, rhomboidal, turbinate, trigonous, triquetrous, lenticular or winged. Cylindrical = cylindrical, ligulate, clavate, tadpole or conical.

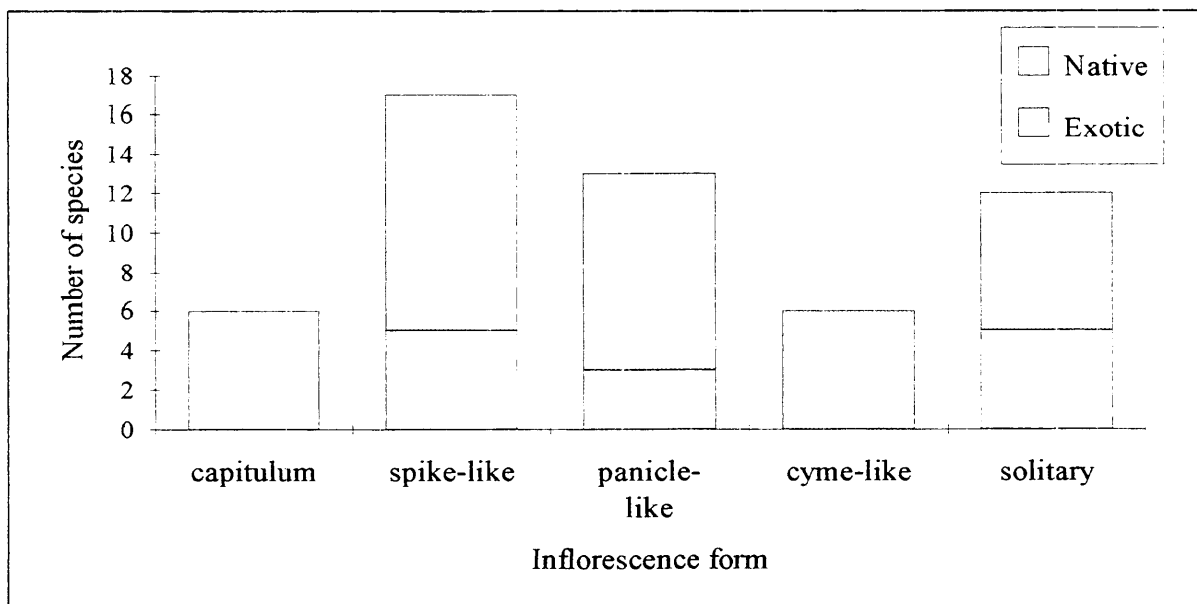
Diaspore Shape	Forb	Grass	Sedge/rush
Spherical	19 <b>73</b>	6 <b>32</b>	9 <b>100</b>
Cylindrical	7 <b>27</b>	13 <b>68</b>	0 <b>0</b>



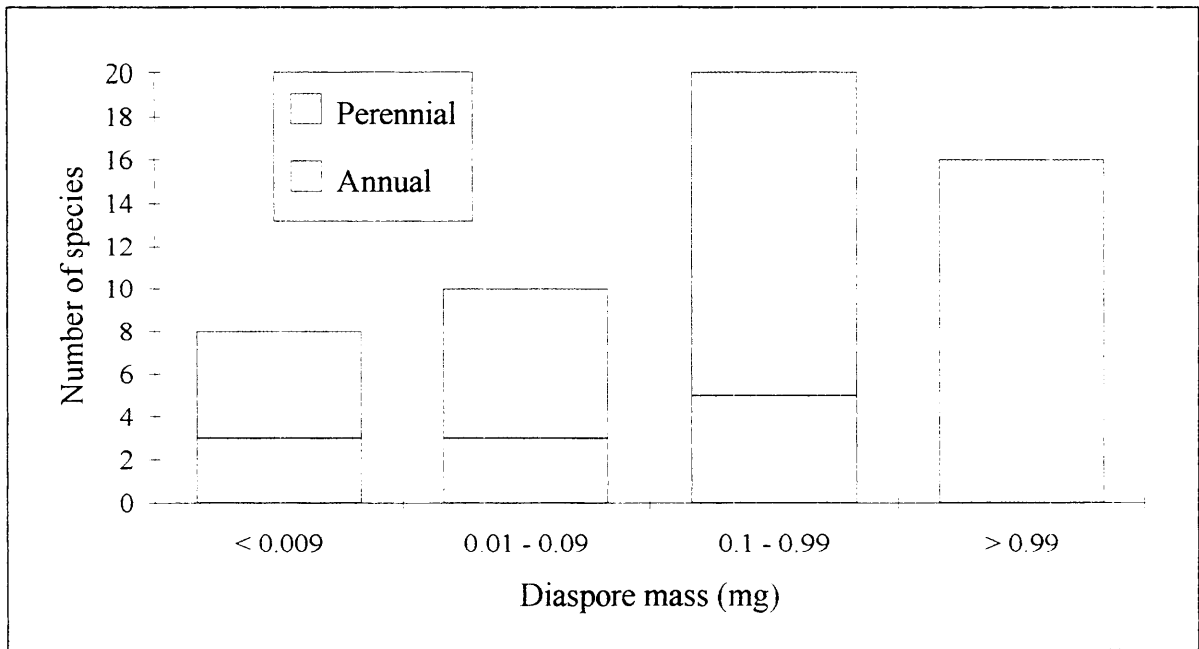


**Fig. 3.7:** The relationship between species growth form and diaspore shape of the species recorded in the experimental plots (n = 54). Ovoid = ovoid, rhomboidal or turbinate; Trigonous = trigonous or triquetrous; Lenticular = lenticular, reniform or subulate; Cylindrical = cylindrical or ligulate.

All of the species with a capitulum inflorescence form were exotic, while all of the species with cyme-like inflorescences were native (Fig 3.8). Three native Asteraceae were recorded on the plots, *Chrysocephalum semipapposum*, *Gnaphalium gymnocephalum* and *Triptilodiscus pygmaeus*, but their low abundance prevented the assessment of their plant attributes. Species with spike-like, panicle-like and solitary inflorescence types were represented by both native and exotic species. The range of diaspore mass of perennial species was wide, whereas no annual species had a diaspore mass greater than 0.99 mg (Fig 3.9).

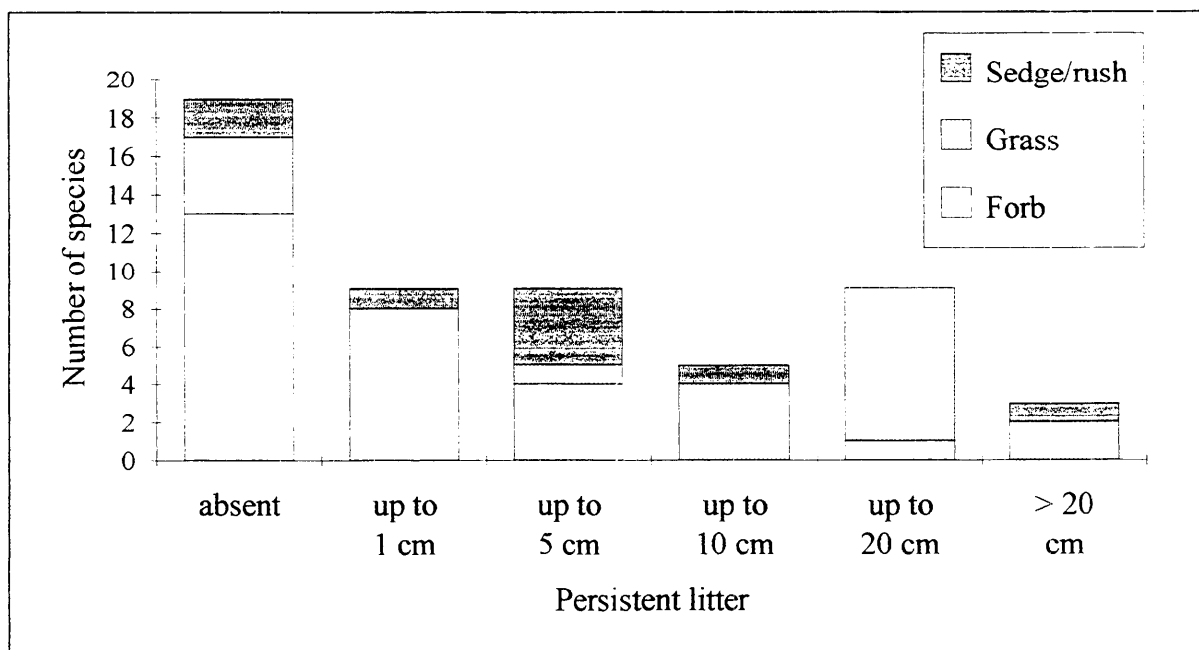


**Fig. 3.8:** The relationship between species origin and inflorescence form of the species recorded in the experimental plots (n = 54).

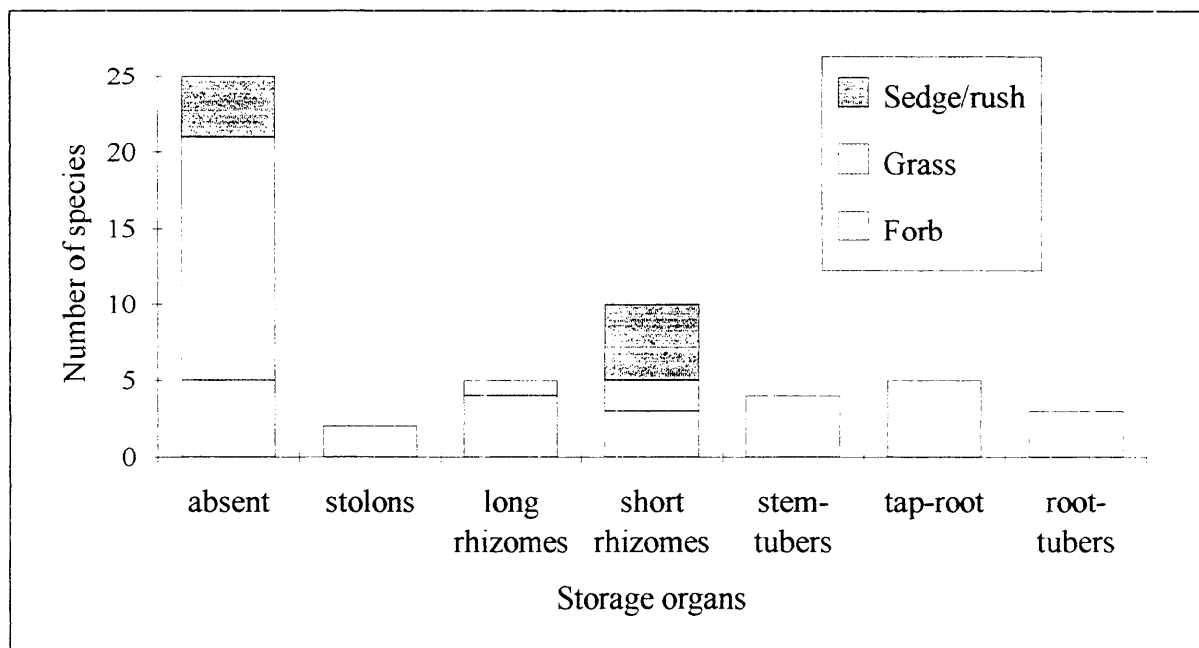


**Fig. 3.9:** The relationship between species life cycle and mean diaspore mass of the species recorded in the experimental plots (n = 54).

Species that lacked persistent litter were most commonly forbs and forbs rarely had litter greater than 5 cm in depth (Fig 3.10). Sedge and rush species were represented in most of the litter classes, but generally had litter up to 5 cm in depth. Grass species also had a wide range of litter depths, but most grass species had litter up to 20 cm in depth. Forbs possessed a diverse range of underground storage organs, while sedge and rush species either lacked storage organs or had short rhizomes (Fig. 3.11). Most grass species lacked storage organs, but those grass species that did had rhizomes.



**Fig. 3.10:** The relationship between species growth form and depth of persistent litter of the species recorded in the experimental plots (n = 54). Litter included standing dead.

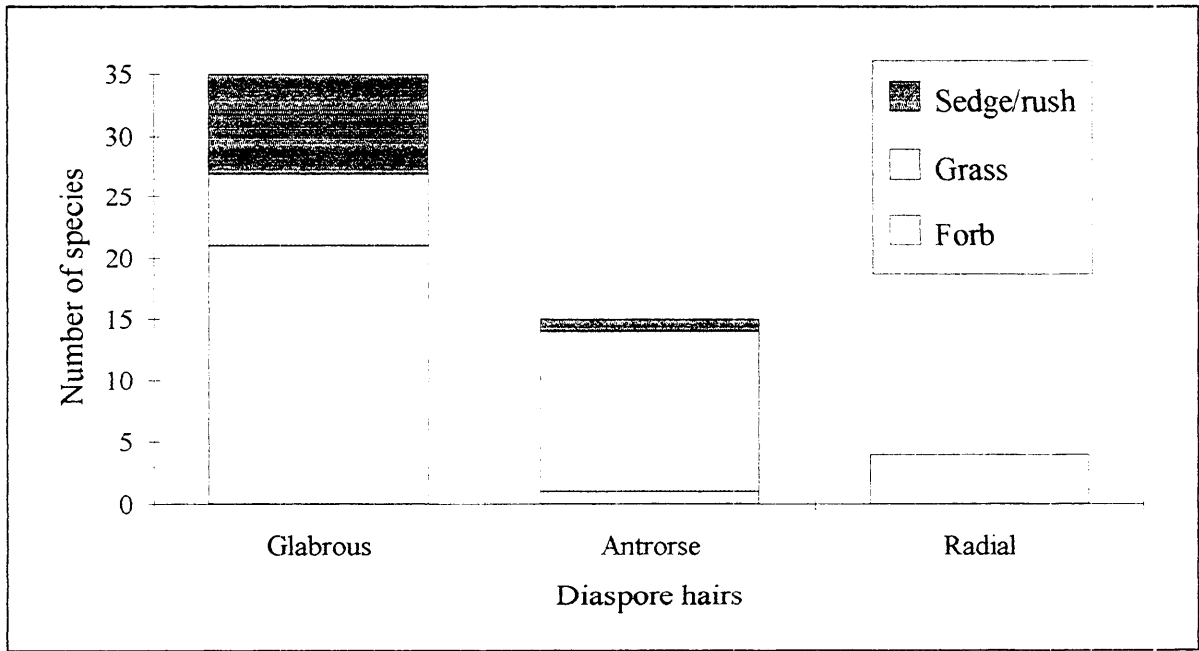


**Fig. 3.11:** The relationship between species growth form and the presence of underground storage organs of the species recorded in the experimental plots (n = 54).

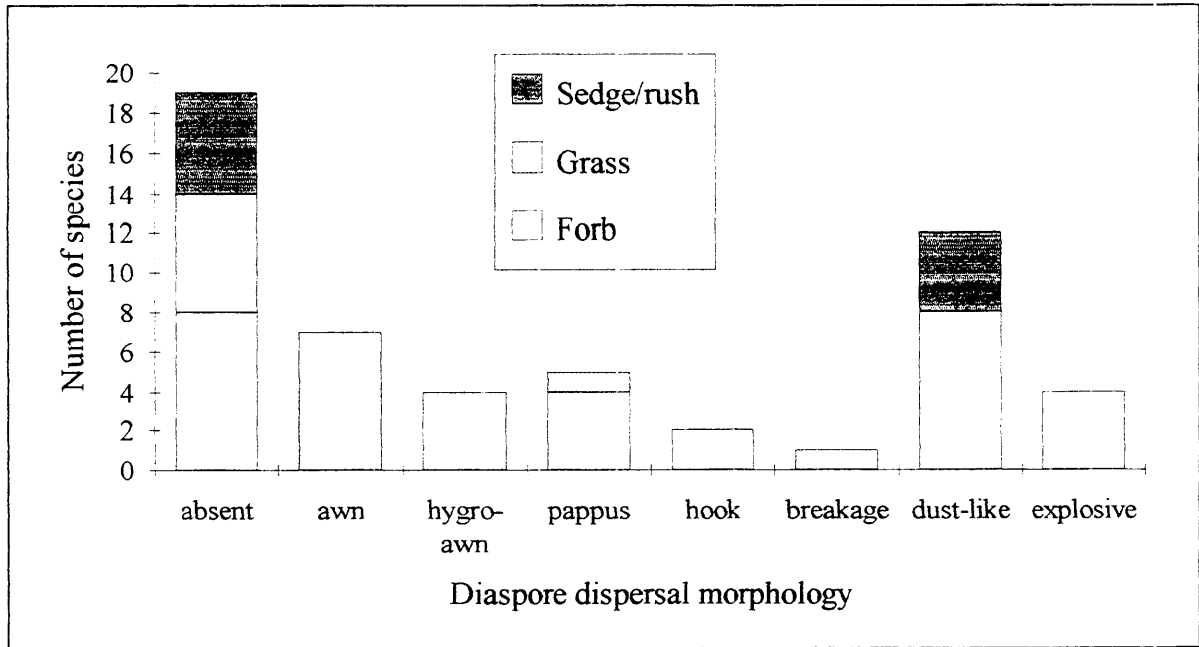
Most species with glabrous diaspores were forbs, while species with radial or irregular hairs on their diaspores were exclusively forbs (Fig. 3.12). Most species with antrorse diaspore hairs were grasses, while most sedge and rush species had glabrous diaspores. Species lacking a diaspore morphology associated with dispersal were evenly represented by forbs, grasses and sedges/rushes (Fig. 3.13). Forbs displayed a diverse range of diaspore dispersal morphology, with dust-like diaspores being the most common attribute. Species with hooks on their diaspores or explosive fruits were exclusively forbs. Most grass species possessed straight or hygroscopic awns, while grass species with a persistent calyx or an inflorescence that breaks free were less common. Sedge and rush species either did not possess a diaspore morphology associated with dispersal or had dust-like diaspores.

Both of the amphiphyte species had long flowering periods, while all four geophyte species had short flowering periods (Fig. 3.14). About half of the hemicryptophytes had flowering periods of a moderate duration, while hemicryptophytes with short or long flowering periods were equally represented. Most therophytes had short flowering periods, but one therophyte, *Centaureum tenuiflora*, had a flowering period of six months.

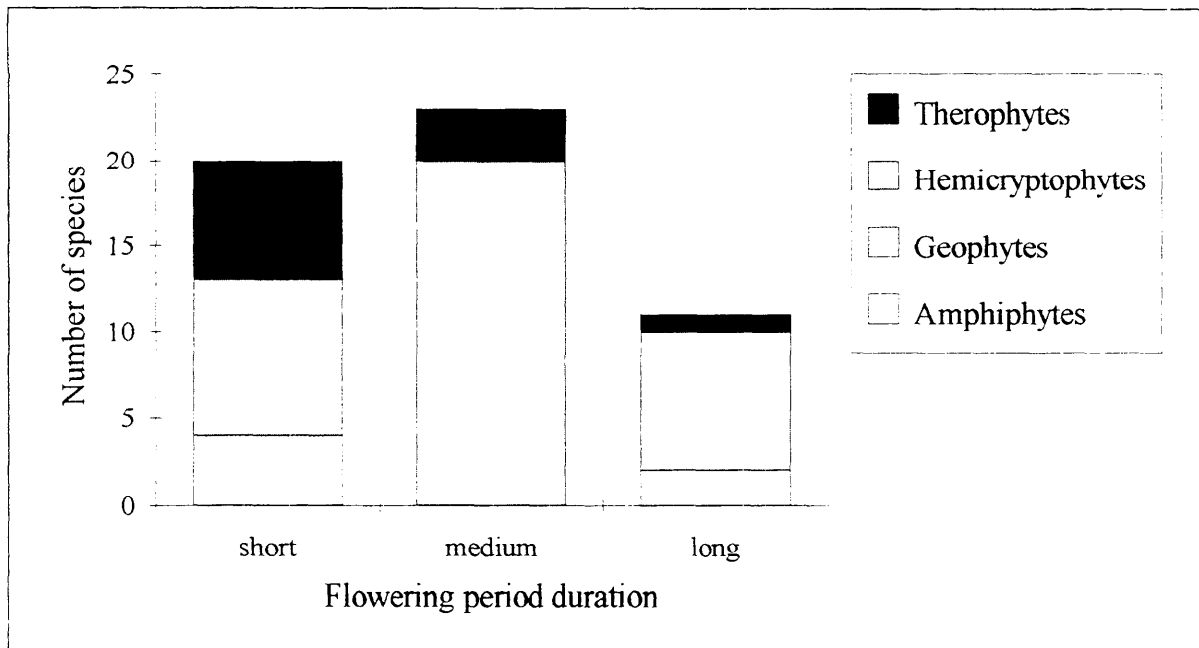
Most species with a tussock or tufted stem structure had persistent litter greater than 5 cm in depth (Fig. 3.15). Most species with a rosette or semi-rosette stem structure lacked persistent litter and most of the remainder had litter up to 5 cm in depth were also common: one species had litter greater than 5 cm in depth. Species with branched, erect, prostrate or twining stem structures either lacked persistent litter or had litter up to 5 cm in depth.



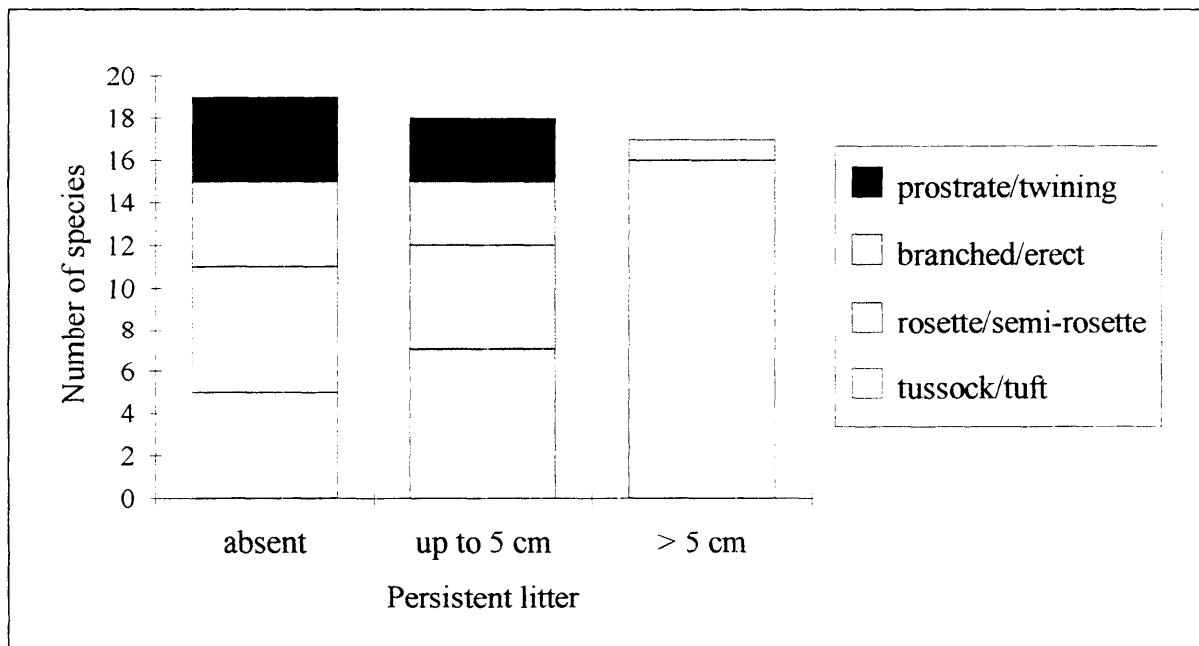
**Fig. 3.12:** The relationship between species growth form and the presence of hairs on their diaspores of the species recorded in the experimental plots (n = 54). Radial = radial or irregular.



**Fig. 3.13:** The relationship between species growth form and diaspore dispersal morphology of the species recorded in the experimental plots (n = 54). Awn = straight awn or spine; Hygro-awn = hygroscopic awn or spine; Pappus = pappus or persistent calx; Hook = hook or barbed spine; Breakage = inflorescence breaks free.



**Fig. 3.14:** The relationship between the Raunkiaer life forms of species and flowering period duration of the species recorded in the experimental plots (n = 54). Short = < 2 months; Medium = 2 - 5 months; Long = > 5 months.

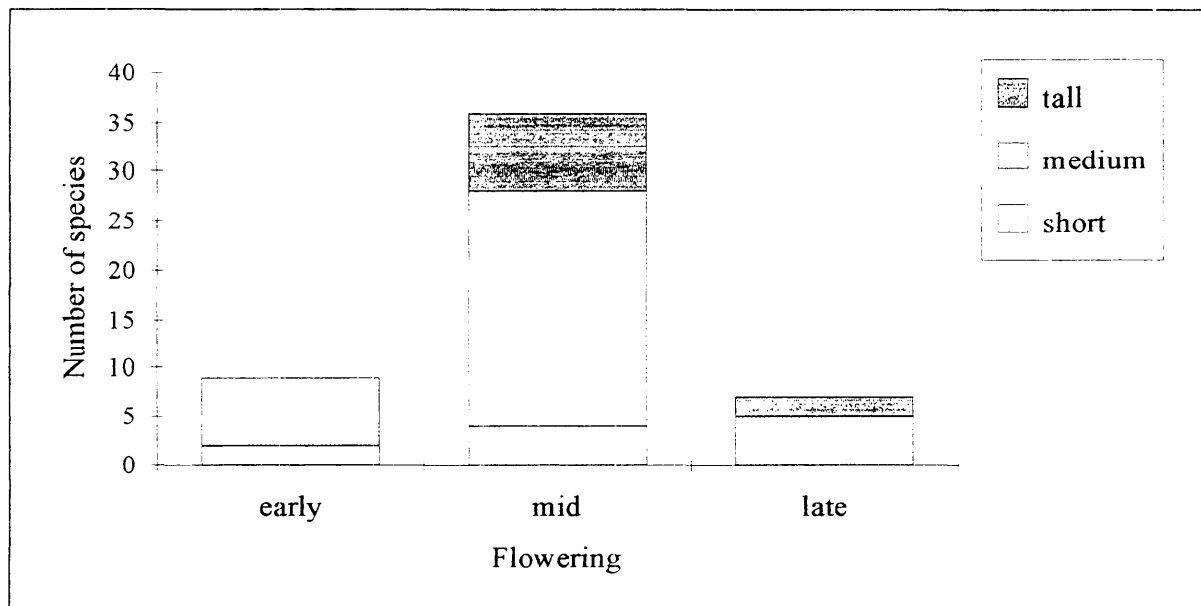


**Fig. 3.15:** The relationship between the stem structure of species and the presence of persistent litter of the species recorded in the experimental plots (n = 54). Litter included standing dead.

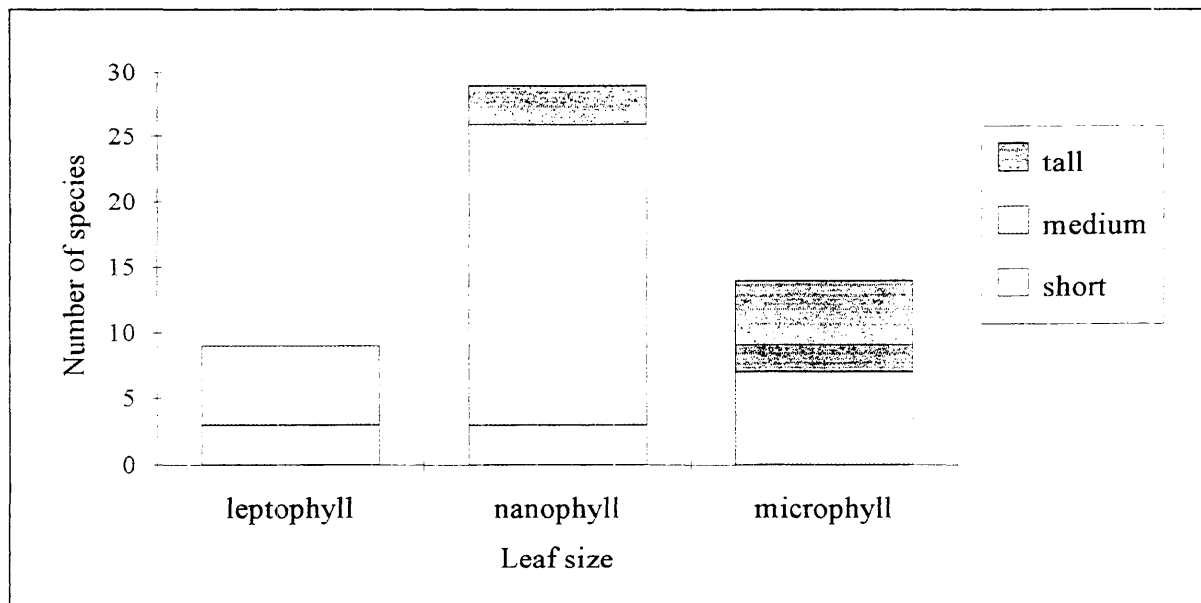
Species of low stature tended to either commence flowering early or mid-season (Fig. 3.16), while tall species tended to commence flowering either mid or late season. Most species of medium stature began to flower mid-season, but some species of medium stature commenced flowering early or late in the season. Short species tended to have small (leptophyll) to medium (nanophyll) sized leaves, while tall species had medium (nanophyll)

to large (microphyll) sized leaves (Fig. 3.17). Species of medium stature were represented in all three leaf size categories, but most of them had medium (nanophyll) sized leaves.

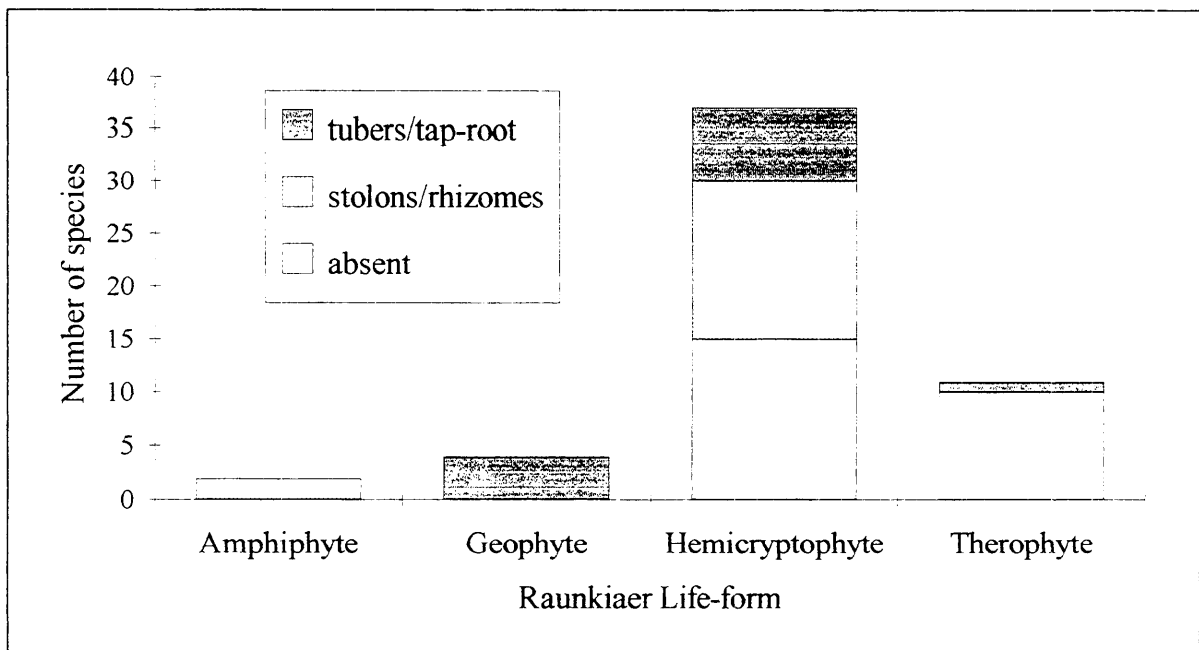
Both of the amphiphyte species possessed stolons or rhizomes, while all four geophytes possessed stem tubers (Fig. 3.18). In general, therophyte species lacked underground storage organs, while hemicryptophyte species were represented all three categories (absent, tubers or taproot, and stolons or rhizomes).



**Fig. 3.16:** The relationship between species reproductive height and the commencement of flowering of the species recorded in the experimental plots (n = 54). Early = Aug - Oct; Mid = Nov - Dec; Late = Jan - Feb; Short = < 10 cm; Medium = 10 - 50 cm; Tall = > 50 cm.

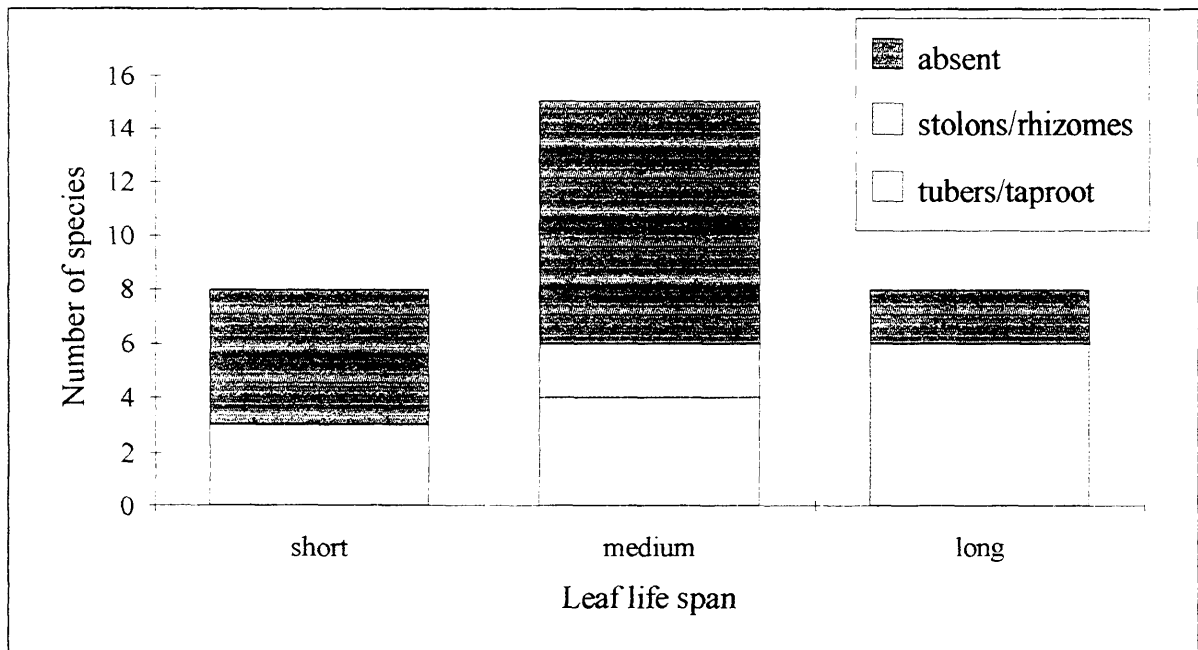


**Fig. 3.17:** The relationship between species reproductive height and leaf size of the species recorded in the experimental plots (n = 54). Leptophyll < 25 mm<sup>2</sup>; Nanophyll = 25 - 225 mm<sup>2</sup>; Microphyll = 225 - 2050 mm<sup>2</sup>; Short = < 10 cm; Medium = 10 - 50 cm; Tall = > 50 cm.

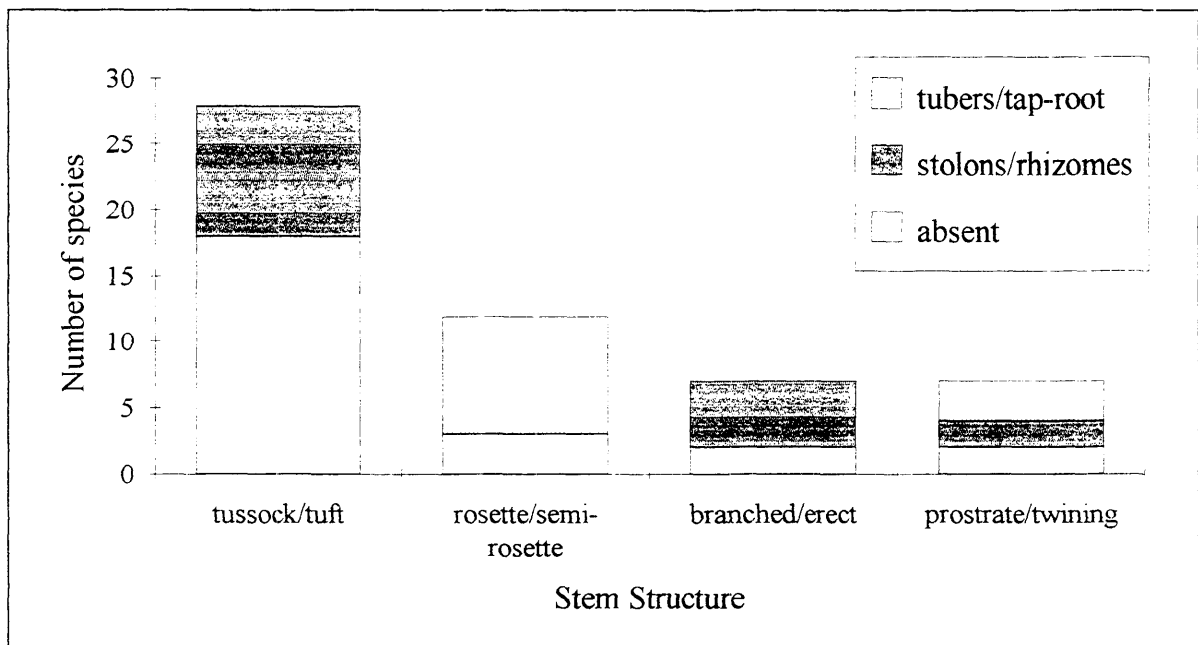


**Fig. 3.18:** The relationship between Raunkiaer life forms and the presence of underground storage organs in the species recorded in the experimental plots ( $n = 54$ ). Tubers include both stem and root tubers. Rhizomes include both short and long rhizomes.

Species with short leaf life spans either lacked underground storage organs or had stem-tubers or taproots (Fig. 3.19). Most species with long leaf life spans possessed stolons or rhizomes. Species with medium leaf life spans were represented in all three underground storage organ categories. Most of the species with a tussock or tufted stem structure lacked underground storage organs, while those with stolons or rhizomes were common (Fig. 3.20). No species with tussock or tufted stem structure possessed tubers or taproots. Most species with a rosette or semi-rosette stem structure possessed tubers or taproots; the remainder lacked storage organs. No rosette or semi-rosette species possessed stolons or rhizomes. Prostrate or twining species were equally represented in all three storage organ categories. Most of the species that commenced flowering early in the season (August - October) possessed stolons or rhizomes, while most of the species that commenced flowering late (January - February) lacked underground storage organs (Fig. 3.21). Species which began flowering mid-season (November - December) were well represented by all three storage organ categories.

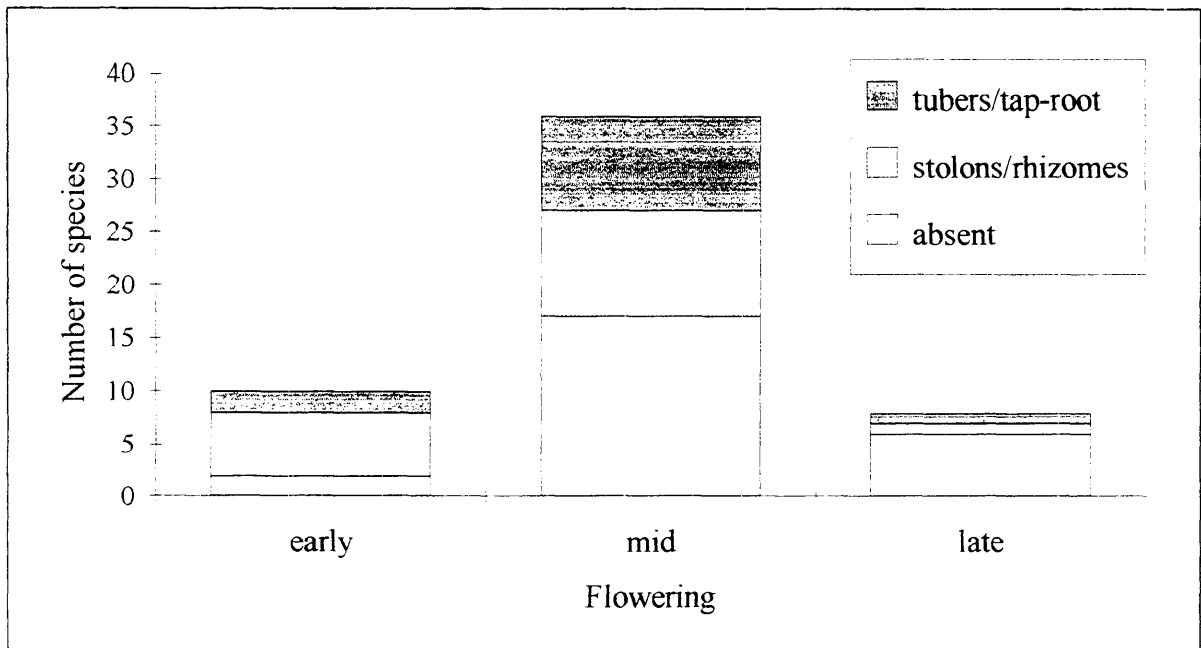


**Fig. 3.19:** The relationship between leaf life span and the presence of underground storage organs of the species recorded in the experimental plots (n = 31). Tubers include both stem and root tubers. Rhizomes include both short and long rhizomes. Short = < 70 days; Medium = 70 - 110 days; Long = > 110 days.



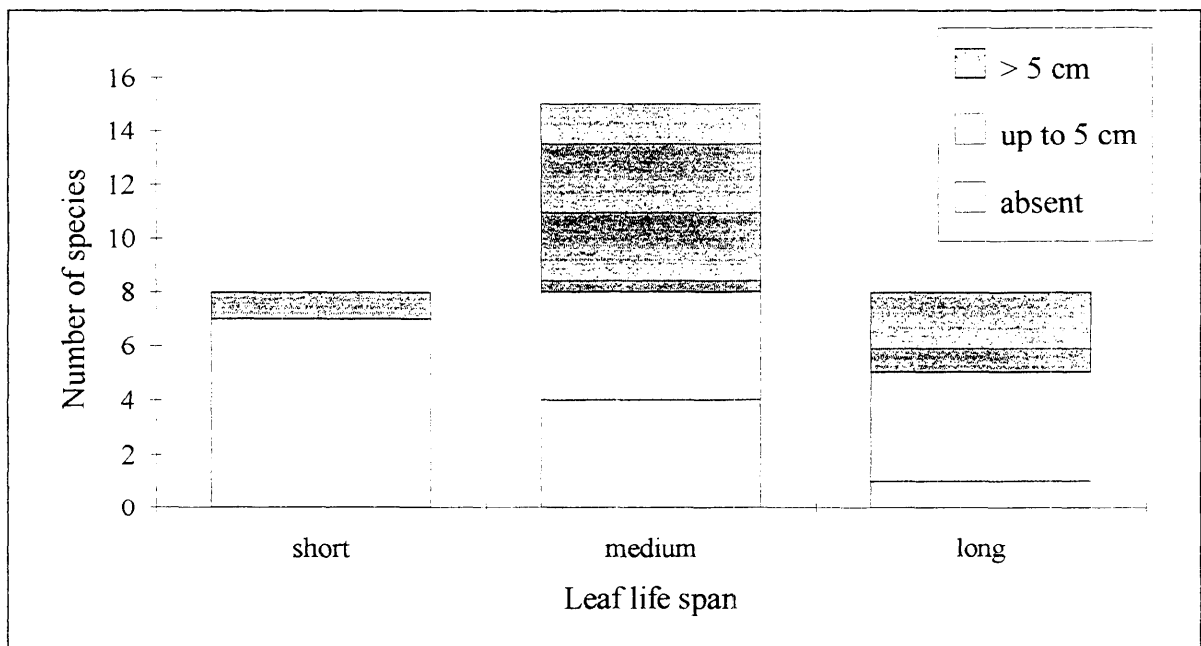
**Fig. 3.20:** The relationship between stem structure and the presence of underground storage organs of the species recorded in the experimental plots (n = 54). Tubers include both stem and root tubers. Rhizomes include both short and long rhizomes. Prostrate included both single and matted prostrate.





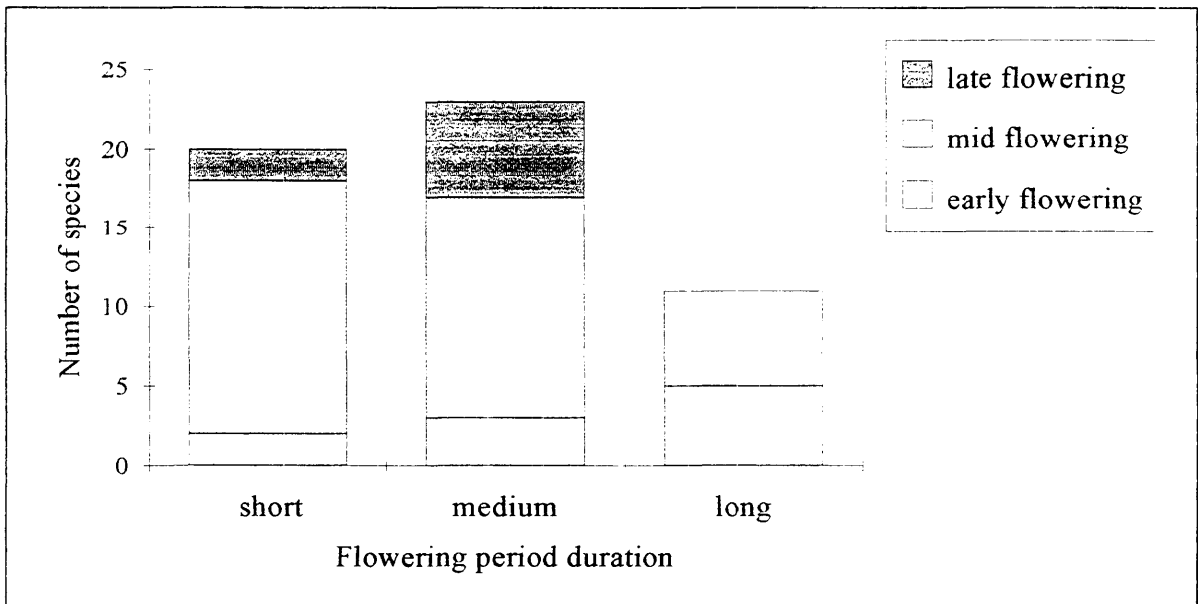
**Fig. 3.21:** The relationship between the presence of underground storage organs and the commencement of flowering of the species recorded in the experimental plots (n = 54). Tubers include both stem and root tubers. Rhizomes include both short and long rhizomes. Early = Aug - Oct; Mid = Nov - Dec; Late = Jan - Feb.

Most species with short leaf life spans (< 70 days) also lacked persistent litter (Fig. 3.22). Species with long leaf life spans (> 110 days) usually possessed persistent litter either up to or greater than 5 cm in depth. Species with medium leaf life spans (70 - 110 days) were represented by all three of the litter classes.

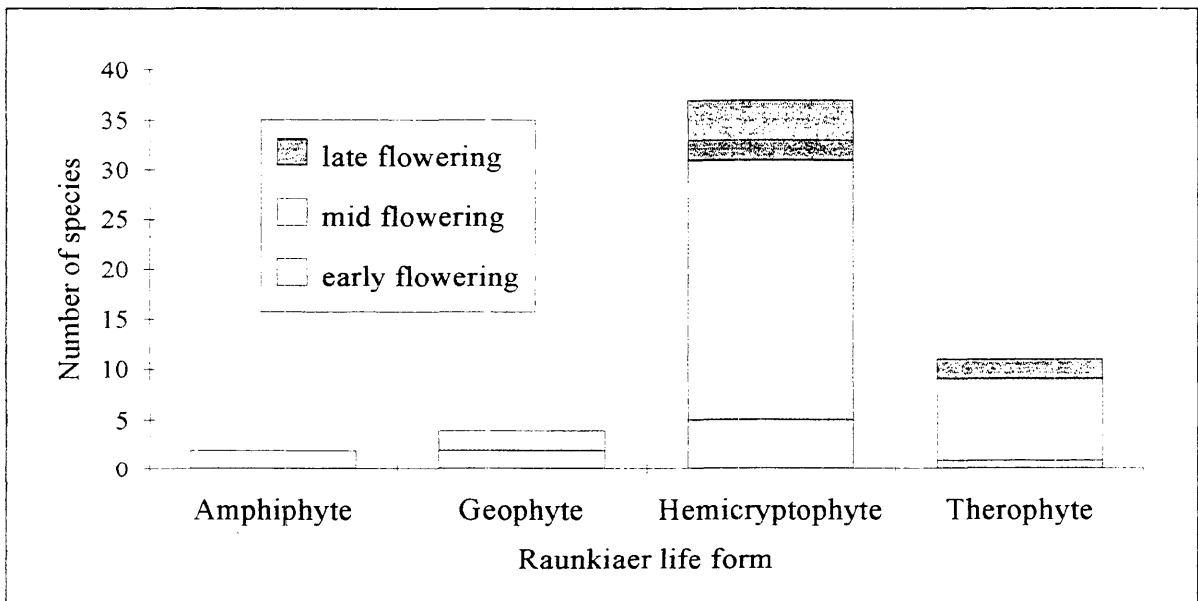


**Fig. 3.22:** The relationship between leaf life span and the presence of persistent litter of the species recorded in the experimental plots (n = 31). Short leaf life span < 70 days; Medium leaf life span = 70 - 110 days; Long leaf life span > 110 days. Litter included standing dead.

Half of the species that commenced flowering early also had a long flowering period (> 5 months) (Fig. 3.23). Species that began to flower mid-season had flowering periods of a short, medium and, to a lesser extent, long duration. None of the species that commenced flowering late in the season had a long flowering period. Both of the amphiphyte species commenced flowering early in the season, while the geophytes began to flower early or mid-season (Fig. 3.24). Most of the hemicryptophytes and the therophytes commenced flowering mid-season, while the species that began to flower late in the season were either hemicryptophytes or therophytes.

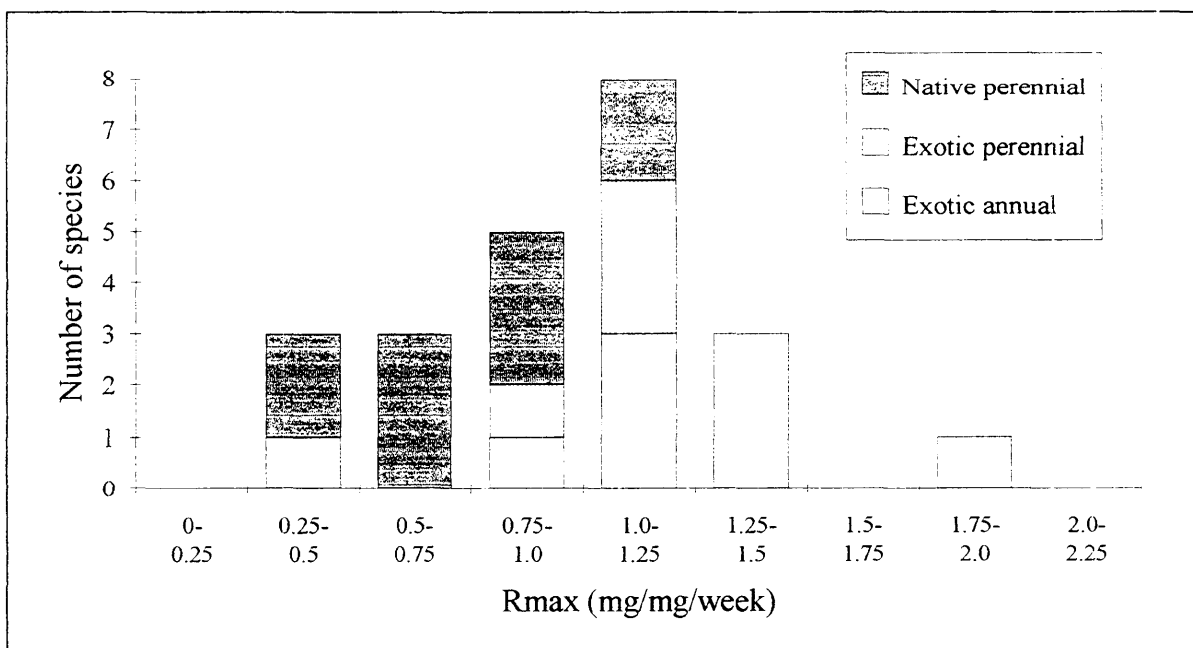


**Fig. 3.23:** The relationship between commencement of flowering and flowering period duration of 54 of the species recorded in the experimental plots (n = 54). Early = Aug - Oct; Mid = Nov - Dec; Late = Jan - Feb. Short < 2 months; Medium = 2 - 5 months; Long > 5 months.



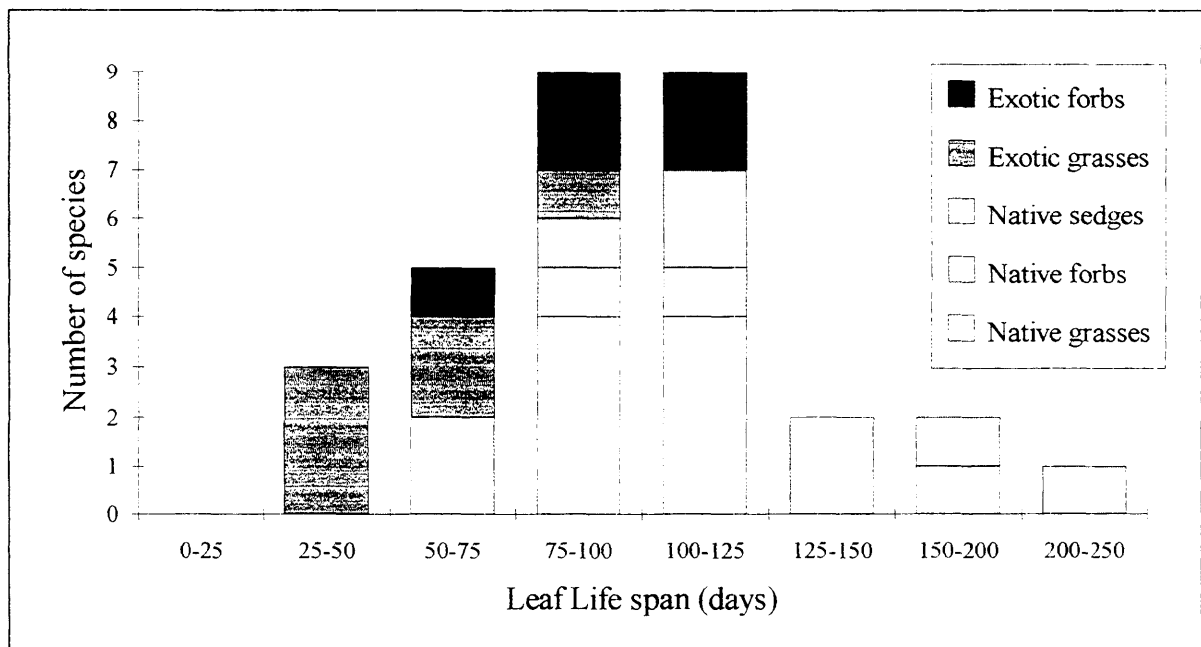
**Fig. 3.24:** The relationship between the commencement of flowering and Raunkiaer life form of the species recorded in the experimental plots (n = 54). Early = Aug - Oct; Mid = Nov - Dec; Late = Jan - Feb.

The maximum relative growth rates ( $R_{max}$ ) of the species examined were more or less normally distributed, with the greatest number of the species having a growth rate between 1.1 and 1.25 mg/mg/week (Fig. 3.25). There was a trend for the seedlings of native species to have low to medium  $R_{max}$ , while exotic species tended to have medium to high  $R_{max}$ . The exception to this was *R.stellaris* which was the only exotic species with a low  $R_{max}$  ( $0.26 \pm 0.049 \text{ week}^{-1}$ ). Of the native species, *Bothriochloa macra* and *Sporobolus creber* had the highest  $R_{max}$  ( $1.07 \pm 0.054$  and  $1.09 \pm 0.108 \text{ week}^{-1}$ , respectively). The seedlings of annual species, which were all exotic, tended to have medium to high maximum relative growth rates, while native perennial species had low to medium maximum  $R_{max}$  (Fig. 3.25). Exotic perennial species had the widest range of  $R_{max}$  values.



**Fig. 3.25:** The number of native perennial, exotic perennial and exotic annual species in each maximum relative growth rate category. Growth rate was measured for 22 of the species recorded in the experimental plots.

Species with short-lived leaves tended to be exotic, while species with long-lived leaves were predominantly native (Fig. 3.26). All of the species with leaf life spans shorter than 50 days were exotic, while all of the species with leaf life spans greater than 125 days were native. Species with leaf life spans of a moderate length were equally represented by exotic and native species. The leaf life spans of forbs tended to be within the middle range of 50 - 150 days, while native sedges had particularly long-lived leaves. Grasses demonstrated the widest range of leaf life spans with exotic grasses having short-lived and native grasses having long-lived leaves. As a consequence of their short life cycle, annual species generally had shorter leaf life spans than perennial species (Appendix 5C).



**Fig. 3.26:** The number of exotic forb, exotic grass, native sedge and rush, native forb and native grass species in each leaf-life span category. Leaf life span was measured for 31 of the species recorded in the experimental plots.

The correlations between reproductive and vegetative height, vegetative height and the height:width ratio, width and the height:width ratio, and the allometric constant and root:shoot ratio were significant because the variables in each of these pairs were related or derived from each other (Table 3.37). Wide species were also tall species, while narrow species were short species. Short wide species had a long flowering period, while tall narrow species had a short flowering period. Narrow species had short-lived leaves, while wide species had long-lived leaves. Species with long-lived leaves also had a long flowering period duration, while species with short-lived leaves had a short flowering period.

Tall narrow species tended to produce a large number of diaspores per individual, while short wide species produced a small number of diaspores per individual (Table 3.37). Tall narrow species also had light diaspores and short wide species had heavy diaspores. Seedlings of tall narrow species allocated a greater proportion of their biomass to shoots over time (high allometric constant), while the seedlings of short wide species allocated a greater proportion of their biomass to roots over time (low allometric constant). Species with a short flowering period produced a large number of diaspores per individual, while species with long flowering periods produced a small number of diaspores per individual. Species with short-lived leaves produced a large number of diaspores per individual, while species with long-lived leaves produced a small number of diaspores per individual. Tall species had heavy diaspores while short species had light diaspores. Wide species had heavy diaspores while narrow species had light diaspores. The diaspores of species producing a large number of diaspores were small, while the diaspores of species producing a small number of diaspores were large.

**Table 3.37:** Spearman Rank correlation coefficients amongst continuous plant attributes. Significant correlations are marked in bold. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ . VH = vegetative height (n=54); RH = reproductive height (n=54); W = width (n=54); H:W = vegetative height width ratio (n=54); FD = flowering period duration (n=54); LLS = leaf life span (n=31); SN = diaspore number/individual (n=54); SW = diaspore mass (n=54); RGR = maximum relative growth rate (n=22); R:S = root:shoot ratio (n=22); LAR = leaf area ratio (n=14); AC = allometric constant (n=20).

	RH	W	H:W	FD	LLS	SN	SW	RGR	R:S	LAR	AC
VH	<b>0.67</b> ***	<b>0.63</b> ***	<b>0.36</b> **	-0.09	0.20	0.23	<b>0.32</b> **	-0.06	-0.05	-0.29	0.02
RH		<b>0.65</b> ***	-0.02	-0.01	0.03	0.11	<b>0.45</b> ***	0.11	0.20	-0.23	-0.02
W			<b>-0.39</b> **	0.15	<b>0.32</b> *	-0.14	<b>0.64</b> ***	0.10	-0.01	-0.13	-0.28
H:W				<b>-0.27</b> *	-0.18	<b>0.30</b> *	<b>-0.29</b> *	-0.14	-0.25	0.01	<b>0.42</b> *
FD					<b>0.50</b> **	<b>-0.27</b> *	0.14	-0.10	0.08	0.35	-0.34
LLS						<b>-0.41</b> *	-0.04	<b>-0.56</b> **	0.05	<b>-0.55</b> *	0.06
SN							<b>-0.59</b> ***	0.19	-0.35	0.38	-0.10
SW								-0.06	0.31	<b>-0.57</b> *	0.34
RGR									-0.27	0.43	-0.33
R:S										-0.27	<b>0.39</b> *
LAR											<b>-0.64</b> **

Species with fast growing seedlings had adults with short-lived leaves, while those with slow growing seedlings had adults with long-lived leaves (Table 3.37). At the seedling stage, species with a high leaf area ratio had adults with short-lived leaves, while seedlings with a small leaf area ratio had adults with long-lived leaves. Species with a high leaf area ratio as seedlings also had small diaspores and species with a low leaf area ratio had large diaspores. Species with a low leaf area ratio as seedlings also allocated a greater proportion of their biomass to shoots over time (high allometric constant) and species with a high leaf area ratio allocated a greater proportion of their biomass to roots over time (low allometric constant).

## 3.4 DISCUSSION

### 3.4.1 General Attributes and Attributes Measured in the Field

#### (a) Plant Morphology Attributes

Similar to previous studies in temperate Australian grassland communities (reviewed by Trémont & McIntyre 1994), most of the species encountered in the present study were forbs. Most of the species were native and perennial, in agreement with other work on the Northern Tablelands (Whalley *et al.* 1978; McIntyre *et al.* 1993; Trémont 1993). The paucity of the annual native flora at Newholme is probably due to the introduction of livestock grazing, a change in the fire regime, and the immigration of exotic annuals associated with European settlement (Whalley 1991). Prior to European settlement, the fire regime consisted of irregular burning in summer by aborigines (Norton 1971). Thus, the timing of the opening of vegetation was suited to the establishment of summer annuals. The introduction of grazing and periodic (often annual) late-winter burning by pastoralists on the Northern Tablelands in the nineteenth century prevented the accumulation of biomass during spring, enabling the germination in the autumn and establishment of cool-season annuals in the spring (Norton 1971; Whalley *et al.* 1978). The fire regime was no longer suited to the establishment of summer annuals, either native or exotic. As a result, most exotic annuals were adapted to spring growth, i.e. cool-season. The three native annual grasses present at Newholme were the common species *Schoenus apogon* (spring - summer) and the uncommon species *Agrostis venusta* (spring) and *Agrostis avenacea* (spring - summer). Thus, the remaining native annual flora are also adapted spring growth. Further, the immigration of cool-season exotic annuals that accompanied European settlement may have reduced cool-season native annuals because exotics are better adapted to conditions associated with trampling by hard-hoofed grazers (e.g. higher seedling growth rates or earlier germination than the native cool-season annuals). For example, the seedlings of the native annual, *A.avenacea*, appear in the autumn, grow slowly during the winter and make rapid growth in spring (Lodge & Whalley 1989).

Most of the species were hemicryptophytes, which is consistent with earlier reports for grasslands on the Northern Tablelands (Trémont 1994; McIntyre *et al.* 1995) and for Britain (Duffy *et al.* 1974). Hemicryptophytes survive the seasonal climate (cold winters) on the Northern Tablelands by protecting their buds from frosts in the soil or litter (Trémont & McIntyre 1994). The hemicryptophyte habit may also protect the buds from desiccation because some individuals (e.g. *Hypericum gramineum*, *Wahlenbergia planiflora* and *Haloragis heterophylla*) died back to ground level during summer (late December) after a relatively dry spring and re-sprouted about a month later in response to rainfall and declining air temperatures. Trémont (1993) also noted that some *Hypericum gramineum* individuals

appeared 'dead' after a hot dry period in late January and early February on the Northern Tablelands. These observations are consistent with the summer dormancy described by McWilliam (1978) that enables survival under conditions of heat and moisture stress. The hemicryptophyte habit may also be an adaptation to survive fire because soil is an effective insulator and protects the growing buds during fire (Gill 1981; Specht & Rayson 1957). *Aristida ramosa* is a hemicryptophyte without underground storage organs and its increased distribution in response to regular burning (Lodge & Whalley 1989) suggests that it has the capacity to resprout from renewal buds protected from fire in the soil surface. Alternatively, hemicryptophytes are prevalent in grasslands because the position of their apical meristems in the soil or litter makes them less susceptible to damage by grazing (Duffy *et al.* 1974).

The classification of species in Raunkiaer life forms is not always straight forward. For example, three of the species on the Northern Tablelands were classified differently by different researchers. *Acetosella vulgaris* and *Trifolium repens*, were classed as amphiphytes in this study because they were observed (during late winter) to have renewal buds both in the ground (hemicryptophyte) and near the ground surface (< 25 cm above the ground: chamaephyte). However, *A. vulgaris* was classified as a chamaephyte by Trémont (1994) and as a hemicryptophyte by McIntyre *et al.* (1995), while *T. repens* was classified as a hemicryptophyte by both Trémont (1994) and McIntyre *et al.* (1995). In this study, *Oxalis exilis* was classified as a hemicryptophyte because buds were only observed in the ground, whereas it was classified as a chamaephyte by both Trémont (1994) and McIntyre *et al.* (1995). The division between hemicryptophytes and chamaephytes used by McIntyre *et al.* (1995) differed from that used here and by Trémont (1994), in that plants with persistent buds < 1 cm above the ground surface were classed as hemicryptophytes rather than as chamaephytes. The latter classification makes ecological sense if litter provides the same degree of protection of the perennating buds as soil.

The significant number of therophytes (annuals) and the paucity of geophytes was similar to that found by Duffy *et al.* (1974) in open grasslands on nutrient-poor soils in Britain. Therophytes are prevalent in open, nutrient-poor grasslands because there is a high frequency of open sites suitable for the regular germination and establishment from seed required by therophytes. Nutrient-poor grazed grasslands may contain few geophytes because sustained defoliation may deplete the stored reserves of underground tubers, upon which next season's growth relies. In nutrient-rich grasslands the reserves stored by geophytes may be greater, enabling them to tolerate defoliation. Only two species were chamaephytes. Chamaephytes are less frequent in moist, temperate grasslands than in drier, warmer climates (Duffy *et al.* 1974). The location of the buds of chamaephytes above-ground means they are unprotected from frosts. Chamaephytes may be uncommon in grazed grassland because the location of meristematic tissue above ground makes them susceptible to defoliation and trampling (Trémont 1994). Alternatively, the location of perennating buds above-ground in chamaephytes makes them susceptible to damage by fire.

The classifications of Raunkiaer life forms and storage organs were related because by definition, therophyte species perennate only by seed, while stem tubers are the means by which some geophytes locate their perennating organs deep below the ground. For this reason, therophytes generally lacked underground storage organs, all of the geophytes possessed stem tubers and both amphiphyte species possessed stolons or rhizomes. Overlap between classifications may be responsible for the significant association between Raunkiaer life form and root morphology found by Floret *et al.* (1987) in a Mediterranean coppice.

The vegetative height of most species was between 10 and 20 cm, although there was a group of smaller species. Few species were less than 10 cm high in their reproductive state, reflecting the considerable advantage of height for pollination and seed dispersal. Most species were slightly wider than they were taller possibly because in herbaceous plants the absence of lignification is a structural constraint limiting their height. The constraints of the herbaceous habit may also be responsible for the trend for tall species to be wide species and short species to be narrow species. Alternatively, the equal occupation of vertical and horizontal space (box-like growth form) rather than a predominance in either direction may be advantageous in a moderately grazed, low fertility environment. Tall species have greater access to light than short species, but if the tall species are narrow the neighbouring foliage may easily negate the height advantage. On the other hand, great width is of little benefit to short species if they live in low light environments.

#### (b) Flowering Attributes

Most of the species had spike-like inflorescences which may be advantageous in relatively short vegetation (grassland) because neighbouring foliage (or their own inflorescence branches) will not obstruct access by pollinators and seed dispersal. The flowering period of most species was only one month, while 35% of the species had a flowering period of five months or longer. An extended flowering period means that seed is available over a longer period and seeds are present to exploit any infrequent disturbances (Odgers & Rogers 1993). Many species flowered into late summer or autumn; *Wahlenbergia planiflora*, *Hypochaeris radicata*, *Sanguisorba minor*, *Aristida ramosa*, *Trifolium repens*, *Rumex brownii*, *Dichelachne micrantha* and *Conyza albida* were still flowering in May.

Most of the species that began flowering early in the season possessed rhizomes or stolons, while most of the species that began flowering later lacked underground storage organs. The climate on the Northern Tablelands consists of cold winters and a variable rainfall pattern, therefore photosynthesis early in the season may be limited by low temperatures or soil-moisture availability. Flowering relies on sufficient vegetative growth being achieved, from which nutrients and sugars are drawn upon by the developing flowers and fruits (Salisbury & Ross 1985). Thus, the stored food reserves in rhizomes (Grace 1993) may enable species with rhizomes to commence flowering early in the season. Flowering may



be delayed in species without storage organs until temperatures or soil-moisture availability is adequate to support energy production prior to flowering. Consistent with this idea, rainfall during the study period was below average. Most of the species that commenced flowering early in the season also had a long flowering period in contrast to those flowering later. Flowering had ceased by May, probably due to a combination of photo-period and temperature requirements (Salisbury & Ross 1985). The cessation of flowering in May means that those species that commence flowering late in the season (mainly C4 species) had a relatively short duration available for flowering.

Both amphiphyte species possessed rhizomes or stolons and commenced flowering early in the season. As a consequence, the amphiphyte species were able to flower for a long period. All four of the geophyte species had short flowering periods even though they began flowering early or mid-season. The short flowering period of the geophytes was due to their above-ground parts dying back to their underground tubers each summer. None of the geophytes flowered after December, suggesting that the limited time spent above-ground is a strategy to avoid summer desiccation. Most of the therophytes (annuals) commenced flowering mid-season. Therophytes are probably unable to flower early in the season because they must germinate from seed and produce sufficient growth to support flowering without the benefit of the previous year's growth or storage. Most therophytes had short flowering periods, probably because the costs of enduring soil moisture stress during summer are greater than the benefits of a longer flowering period.

Species with short leaf life spans either lacked underground storage organs or possessed tubers or taproots. Tubers and taproots may enable a series of less costly short-lived leaves to be produced in response to defoliation from grazing and soil disturbance. On the other hand, most species with long leaf life spans possessed stolons or rhizomes. The costly construction of long-lived leaves will only be of benefit if the plant persists at the site. For species that do not invest in long-term persistence, short-lived leaves are more cost effective. Stolons and rhizomes enhance long-term persistence by functioning to anchor the plant, store food reserves, protect meristems and enable vegetative reproduction (Grace 1993).

Species of low stature commenced flowering either early or mid-season, while tall species commenced flowering either mid or late season. For example, the first species to flower at the site (in August), *Carex breviculmis*, had inflorescences close to the ground within its tufted growth form. Since bare ground decreased over the growing season, the accessibility of the flowers of small-statured species also decreased, thus species of low reproductive height would be favoured by flowering early. Although seed production and dispersal may not directly follow flowering, early flowering indicates the potential for early seed production and dispersal. As bare ground decreases through the growing season, the chance of foliage obstructing seed dispersal through the air increases and the availability of safe sites (e.g. gaps) decreases. Thus, the probability of successful seed dispersal and establishment from short plants decreases through the growing season. Forbs tend to flower earlier than grasses on the Northern Tablelands (Trémont & McIntyre 1994), possibly because

many forbs are of small stature and would be favoured by flowering and dispersing seeds before biomass accumulates.

Short wide species tended to have long flowering periods and, if it is assumed that seed dispersal occurs directly after flowering, they also have a long time available for seed dispersal. Species investing in lateral spread, rather than height, reduce access by pollinators and the distance over which seeds are dispersed. Therefore a longer flowering (and dispersal) period will increase the chances of pollinators finding the flowers and will increase the chance that a suitable micro-site (e.g. gap) will become available close to the parent plant. On the other hand, tall narrow species tended to have short flowering (and dispersal) period. Species that invest in height rather than width, enhance access by pollinators and enable seeds to be dispersed farther. As the area over which seeds are dispersed increases, the chance of a suitable micro-site becoming available at a particular time also increases. Therefore, when seeds are dispersed from height the cost of a long flowering (and dispersal) period outweigh the benefit because the chance of landing in a suitable micro-site is high despite a short-time being available.

### (c) Leaf Attributes

The Newholme species spanned three of the smallest leaf size classes developed by Raunkiaer, but most of the species had leaves in the nanophyll size class. Leaf size tends to increase with vegetation height and with soil fertility (Raunkiaer 1934; Beadle 1966; Givnish 1982). Thus the tendency for the species to have small leaves reflects the absence of shrubs and trees and the low fertility of the study site. Short species tended to have relatively small (leptophyll) to medium (nanophyll) sized leaves and tall species had medium (nanophyll) to relatively large (microphyll) sized leaves, demonstrating that the relationship between leaf size and vegetation height also occurs within herbaceous vegetation. The relatively small stature of grassland species means that the costs of constructing, supporting and defending large leaves would outweigh the benefits of a greater area to intercept light because they experience lower levels of radiation.

Most species had linear leaves because grasses, sedges and rushes combined made up the greatest number of species at the site. Erect linear leaves achieve the greatest height advantage for a given amount of biomass (without investment in branches and petioles), enabling greater access to light. Most species had soft leaves, possibly because herbaceous species have short life spans relative to trees and so benefit less from strengthening or defending their leaves. Leaf texture was significantly associated with life span in the present study, in agreement with the study by Floret *et al.* (1987). Species with fibrous or thick leaves were perennial, while species with soft leaves were either annual or perennial. Most species with fibrous or thick leaves were also native, while species with soft leaves were equally represented by exotic and native species. Thus, annual and exotic species do not invest in

structural compounds, such as lignin, to strengthen their leaves. Further, more than half of the species with fibrous or thick leaves were grasses, while most of the species with soft leaves were forbs. These results are consistent with the observation that many native perennial grasses common on infertile soils on the Northern Tablelands are unpalatable (Whalley *et al.* 1978).

Most species had a leaf life span between 75 and 125 days. The leaves of herbaceous perennials generally functioned for more than 3 months, which was slightly longer than that found in meadow and fen vegetation (Diemer *et al.* 1992), but shorter than in British chalk grassland (Sydes 1984). Extended leaf longevity may enable herbaceous plants to survive in resource-poor habitats by using resources conservatively (Grime 1977; Diemer *et al.* 1992; Reich *et al.* 1992). The species with the longest leaf life span in this study and in a British grassland (Sydes 1984) was of the genus *Carex*.

Species with short-lived leaves tended to be exotic, while species with long-lived leaves were predominantly native. Longer-lived leaves slows the rate of nutrient cycling between the plant and the soil, thereby reducing the risk of nutrient loss (Grime 1977; Chabot & Hicks 1982). Most of the native species were also perennial and their long-lived leaves enable them to use nutrients conservatively and persist at the site. The risk of biomass loss in the disturbed habitats occupied by many exotic species is high. Thus exotic species may reduce the cost of a disturbance event by producing short-lived leaves because they are less expensive to replace. Native grasses and sedges invest in long-lived leaves because a conservative use of nutrients enable them to survive periods of environmental stress (nutrients and water). The short-lived leaves of the exotic grasses is associated with their short life spans, which enable them to avoid environmental stress or the loss of biomass from disturbance. Species with a short life span had short-lived leaves, flowered for a short duration and had a small lateral spread. These attributes are consistent with the idea that short leaf life spans evolved as a means of avoiding environmental stresses (Chabot & Hicks 1982). In contrast, species with longer life span had longer-lived leaves, flowered for a longer duration and had a greater lateral spread. The benefits of possessing long-lived leaves and a long flowering period only outweigh the costs when a species persists at a site and the chance of environmental stress is high (Chabot & Hicks 1982; Reich *et al.* 1992).

Most species lacked persistent litter, which is consistent with forbs being the most common growth form and accumulating little litter. Grass, sedge and rush species generally possessed litter, while it was mainly the grasses that accumulated deep litter (> 10 cm). The exception was that annual grasses tended to lack persistent litter. Species with fibrous or thick leaves tended to accumulate deeper litter than species with soft leaves because tough leaves, high in lignin and other structural compounds, are often associated with slow decomposition and mineralization (Chabot & Hicks 1982). The differences in litter depths between the growth forms is consistent with forbs and annual grasses having soft leaves which decompose rapidly. Species with tussock or tufted stem structure tended to have deeper persistent litter than species with rosette, semi-rosette, branched, erect, prostrate or winding habits.

Accumulation of persistent litter by rosette, semi-rosette, or prostrate species would be a disadvantage because it would hinder photosynthesis. All of the species with short leaf life spans also lacked persistent litter, while species with long leaf life spans often accumulated litter greater than 5 cm in depth. Litter accumulates in species with long-lived leaves because they have higher concentrations of fibre (Coley 1987) which decomposes slowly (Chabot & Hicks 1982).

#### (d) Root Attributes

Most of the species with underground storage organs had short rhizomes probably because rhizomatous species are more resistant to grazing than upright species (Moore & Biddiscombe 1964; Davidson 1978). Short rhizomes enable a species to tolerate grazing because they provide anchorage, protect meristems and allow recovery from defoliation using stored food reserves (Grace 1993). About half of the species possessed underground storage organs and were capable of vegetative reproduction or regeneration. Most exotic species either lacked storage organs or had taproots, while most native species either lacked storage organs or possessed short rhizomes. Taproots enabled exotic species (mostly perennial) to resist soil disturbance and regenerate after damage using stored reserves (Grace 1993). Rhizomes enable native species and graminoid species to resist uprooting by grazing, to recover from defoliation using stored reserves and reduce the risk of juvenile mortality in resource-poor environments by providing energy for their establishment (Grace 1993).

Most rosette or semi-rosette species had tubers or taproots and none of them had stolons or rhizomes. The low position of the leaves of rosette and semi-rosette species means that they often experience low light levels and their storage needs can be achieved with tubers or taproots, but not with stolons or rhizomes. Alternatively, the possession of stolons or rhizomes by rosette or semi-rosette species would interfere with their leaf arrangement which minimises leaf overlap and self-shading. Tussock, tufted, branched and erect species often possessed stolons or rhizomes making them capable of vegetative reproduction and dispersal as well as performing storage, protection and anchorage functions (Grace 1993). An ability to resist uprooting, recover from defoliation and expand horizontally rather than vertically is an advantage to species with tussock, tufted, branched and erect stem structures because the elevated position of their foliage means they are more susceptible to grazers. Leaf overlap and self-shading is common in tussock, tufted, branched and erect stem structures, thus the cost of further self-shading associated with rhizomes would be small, especially as these stem structures often have access to high light conditions. On the other hand, few species with tussock, tufted, branched or erect stem structures possessed tubers or taproots suggesting that their access to resources is satisfactory and they do not require a substantial storage facility.

#### (e) Diaspore Attributes

Most of the species had seeds with a smooth texture. Smooth seeds have a high seed-water contact which enhances germination (Harper *et al.* 1970) which may be advantageous in habitats experiencing moisture stress. The only species with a mucilaginous seed coat was the native annual *Schoenus apogon*. Mucilage also increases seed-water contact so that water uptake becomes greater than water loss (Harper *et al.* 1970). Whether or not the mucilaginous seed coat of *S. apogon* enables it to germinate later than the other annuals, at times of water stress, is worthy of further investigation because there are few native annuals at the site.

Most species did not have a seed morphology indicative of any particular dispersal strategy, similar to an earlier study in Central Australia (Jurado *et al.* 1991). Round seeds without dispersal appendages become easily buried in the soil and the soil provides protection against fire, anchors the germinating seed and protects their radicles from desiccation (Peart 1979; Peart & Clifford 1987). Thus, species with diaspores without dispersal appendages may be adapted to survive regular burning associated with white settlement or periods of moisture stress. Only 18% of species in this study had wind dispersed diaspores (when dust-like seeds were omitted) compared to 38% in Central Australia (Jurado *et al.* 1991) which is consistent with the percentage of wind dispersed species increasing with decreasing annual rainfall (Howe & Smallwood 1982). Jurado *et al.* (1991) suggested that the prevalence of wind-dispersed seeds in arid habitats may relate to wind being a more successful dispersal agent in sparse vegetation.

Species with awns on their diaspores were common, in contrast to the species of Central Australia. Jurado *et al.* (1991) suggested that the paucity of species with awns on their diaspores in arid Central Australia may be due to its lower density of mammals because seeds with awns are often dispersed by adhesion to animals. Alternatively, the soil surface at Newholme would be more compacted by livestock than the soil in Central Australia and awns assist the callus of diaspores to become embedded in compacted soil surfaces, but are of little advantage on soft soils (Peart 1981). Awned diaspores may be less common in Central Australia because they are less likely to be passively buried than unawned diaspores (Peart 1984) and would remain unprotected from the extreme temperatures.

Species with dust-like seeds (e.g. *Centaurium* spp., *Drosera* spp., *Juncus* spp., *Hypericum gramineum*, *Wahlenbergia planiflora*, *Microtis unifolia* and *Pterostylis bicolor*) were common. These species generally possessed dehiscent fruits, where the capsule splits and the seeds are released. Due to the small size of the capsule openings the seeds are released slowly, increasing the chance that some seeds will be released at a time when conditions are favourable for germination. Small seeds travel farther than large seeds when they are of similar shape, structure and released from the same height (Thompson & Rabinowitz 1989). Thus, species with dust-like seeds may disperse long distances, increasing the chance that they will land in a suitable micro-site.

Most grass species possessed straight or hygroscopic awns, while most of the species with antrorse hairs on their diaspores were grasses. Spreading passive awns orientate the fall of the diaspore so that the callus becomes embedded in the soil surface and antrorse hairs anchor the diaspore as the radicle penetrates the soil surface preventing desiccation (Peart 1981). Hygroscopic awns propel the diaspore across the soil surface until they become lodged in a crack and are, for this reason, favoured on cracking or crumbly soil surfaces (Peart 1981). Only four species had hygroscopic awns in the present study probably because hygroscopic awns are of little advantage on loose-grained soil types. Most sedge and rush species had spherical, glabrous diaspores that lacked dispersal appendages; attributes which are conducive to passive burial.

The distribution of mean diaspore mass of the species was similar to that in other habitats (Jurado *et al.* 1991), with the exception that the highest classes of the normal distribution were truncated. That is, no species had a diaspore mass greater than 0.01g. The absence of heavy diaspores reflects the absence of shrubs and trees at the site because trees generally have bigger seeds than shrubs which in turn have bigger seeds than herbs (Baker 1972; Thompson & Rabinowitz 1989). The modal class of diaspore mass was lower (0.0001 to 0.001 g) than that in Central Australia (0.001 to 0.005 g), consistent with previous comparisons between seed mass mode in arid Australia and temperate higher rainfall areas (Jurado *et al.* 1991). In contrast to the Central Australian distribution, but similar to two other temperate higher rainfall data sets (Jurado *et al.* 1991), diaspores in this study were found in the smallest diaspore mass class. Seed mass increases as the likelihood of exposure to drought increases (Baker 1972) because the larger food reserves in larger seeds allow the root system to develop rapidly increasing the seedling survivorship in drought conditions (Rogers & Whalley 1989; Grime *et al.* 1993).

There was no association between diaspore mass and plant life span, in agreement with previous studies (Mazer 1989; Jurado *et al.* 1991; Gleeson & Tilman 1994). The perennial species examined had a wide range of diaspore mass, while all annual species had a diaspore mass less than 0.99 mg. Other studies have found a tendency for annuals to have smaller seeds than longer-lived species (Baker 1972; Silvertown 1981). Although life span partially accounts for variation in diaspore mass, other factors such as family (Mazer 1989) and plant height (see below) complicate the relationship between diaspore mass and life span. Similarly, no significant association was found in the present study between diaspore mass and species origin probably because the relationship depends upon the family (Mazer 1989).

Thompson and Rabinowitz (1989) postulated that seed mass and plant height is related because heavy seeds disperse farther from taller plants. However, they found that the correlation between plant height and seed mass was only significant in some families (Poaceae, Carophyllaceae and Fabaceae). Poaceae made a large contribution in this study and diaspore mass was positively correlated with both vegetative and reproductive height. Diaspore mass was positively correlated with plant width, in agreement with Fernández Alés *et al.* (1993). Diaspore mass was also negatively correlated with height:width ratio. Thus, an

exception to the positive relationship between plant size (height and width) and diaspore size is that species exploiting the horizontal environment (short wide species) had heavy diaspores, while species exploiting the vertical environment (tall narrow species) had light diaspores.

Diaspore number was inversely related to diaspore mass, in agreement with previous studies (Harper *et al.* 1970; Fenner 1983; Fernández Alés *et al.* 1993). The prevalence of species that produce a large number of small diaspores supports the suggestion by Jurado *et al.* (1991) that a strategy of scattering seeds over a large number of locations to increase the chance of landing in a suitable micro-site is favoured over producing seeds large enough to cope with poor locations. Further, some species (e.g. orchids) succeed in nutrient-poor habitats by forming mycorrhizal associations and scattering seeds over a large number of locations may increase the chance of contact with mycorrhiza (Grime 1979). Tall narrow species tended to produce a large number of small diaspores per individual, while short wide species produced a small number of heavy diaspores per individual. A seed dispersing from a short wide species is more likely to land in the area vegetated by the parent plant (or its litter) than in a gap. Thus a larger seed would be advantageous because it increases survival in vegetated areas. However, large seeds are expensive to produce so only a few can be produced for a given amount of resources. On the other hand, a seed dispersing from a tall narrow species is more likely to be dispersed past the area vegetated by the parent plant and land in a gap. As competition for resources are not as great in non-vegetated areas, seeds with small reserves can establish. As small seeds are less expensive to produce, a large number can be produced.

Species with short flowering periods produced a large number of diaspores per individual, while species with long flowering periods produced a small number of diaspores per individual. If it is assumed that seed dispersal occurs directly after flowering, then species with a short flowering period only have a short time over which to disperse their seeds. As the chance of a suitable micro-site (e.g. gap) becoming available near the parent plant in the short-term is small, scattering a large number of small seeds over a large area will increase the chance of landing in a suitable micro-site. On the other hand, the chance of a micro-site becoming available near the parent plant increases over time. Thus, for species dispersing fewer heavier seeds over a short distance the chance of their seeds landing in a suitable micro-site will be increased if they have a long flowering (and dispersal) period. Species with short-lived leaves produced a large number of diaspores per individual, while species with long-lived leaves produced a small number of diaspores per individual. This association between leaf life span and diaspore number may be due to the developing flowers and fruits drawing on the nutrients and sugars of the leaves and hastening their death (Bazzaz & Harper 1977; Salisbury & Ross 1985).

### 3.4.2 Attributes Measured in the Glasshouse

#### (a) Growth Analysis of Seedlings

The maximum relative growth rate ( $R_{max}$ ) of the species examined in the present study ranged from a minimum of 0.26 g/g/week (*Richardia stellaris*) to a maximum of 1.79 g/g/week (*Capsella bursa-pastoris*), which is within the range (0.22 g/g/week to 2.70 g/g/week) found by Grime and Hunt (1975). However, the  $R_{max}$  of the two slowest growing species in this study may have been underestimated due to the sub-optimal growing conditions of that experiment. Further the probable absence of mycorrhiza in the growing media means that the experiments probably underestimated growth rates experienced by some species in the field.

The maximum relative growth rate of *Dactylis glomerata* and *Lolium perenne* in this study was 1.31 g/g/week and 1.49 g/g/week, respectively. These results compare well with the  $R_{max}$  values of 1.31 g/g/week and 1.30 g/g/week, respectively, obtained by Grime & Hunt (1975). The  $R_{max}$  of *Sanguisorba minor* found here was 1.02 g/g/week compared to a range of 0.5 - 0.9 g/g/week reported by Grime *et al.* (1988). The  $R_{max}$  of *Plantago lanceolata* (1.36 g/g/week) and *Acetosella vulgaris* (1.21 g/g/week) in this study were lower than that found in Britain (1.70 g/g/week and 1.55 g/g/week, respectively) by Grime and Hunt (1975).

The distribution of seedling growth rates was similar to that found by Grime and Hunt (1975) for limestone pasture and pastures on acidic strata in Britain, with the modal number of species having seedling growth rates of less than 1.0 g/g/week. This differed to the distribution found in other habitat types (e.g. verges, paths, soil heaps, manure and sewage waste, meadows), where the greatest number of species had seedling growth rates between 1.25 - 1.44 g/g/week (Grime & Hunt 1975). Thus, the relatively low growth rates of the species in this study is consistent with species of relatively unproductive, undisturbed habitats having slow maximum potential growth rates (Grime 1979). Low growth rates may also be favoured under conditions of moisture stress which often occur at the site. For example, *Aristida ramosa's* ability to deplete available water slowly has been attributed to its slow growth rate (Harradine & Whalley 1979).

Seedlings of native species tended to have low to moderate  $R_{max}$ , while exotic species had moderate to high  $R_{max}$ . The slow growth rates of the native species enable a conservative use of resources which is favoured in the nutrient-poor environment of the study site. The invasion of exotic species into grasslands on the Northern Tablelands is associated with the introduction of grazing and regular burning (Whalley *et al.* 1978). High growth rates would enable these exotic species to rapidly pre-empt the gaps created by defoliation and soil disturbance or to complete their life cycle rapidly to avoid disturbance. Similar to the study by Gleeson and Tilman (1994), the  $R_{max}$  values of perennials and annuals in this study were not significantly different, nor were those of forbs and grasses. However, when comparisons are



made within the same genus the relative growth rates of annual grasses are higher than perennial grasses (Garnier 1992). There was a trend for seedlings of annual species (which were all exotic) to have medium to high  $R_{max}$  values.

The  $R_{max}$  of seedlings was inversely related to adult leaf life span, in agreement with Reich *et al.* (1992). Species with fast-growing seedlings had adults with short-lived leaves, while species with slow-growing seedlings had adults with long-lived leaves. Species with long-lived leaves high in lignin, probably have low  $R_{max}$  because increased investment in support and defence compounds may be at the expense of photosynthetic capacity (Coley 1987; Poorter & Remekes 1990; Niemann *et al.* 1992). There was no significant correlation between diaspore mass and maximum relative growth rate, in agreement with Shipley and Peters (1990a). However, several other studies have found that seed size is negatively correlated with growth rate (Gleeson & Tilman 1994; Marañón & Grubb 1993; Fenner 1983). Shipley and Peters (1990b) examined seven published data sets and found that the correlation between seed size and relative growth rate was of variable strength, indicating that other factors contribute to the variation in relative growth rate.

Leaf area ratio was negatively correlated with leaf life span, in agreement with the findings of Reich *et al.* (1992). Species with a high leaf area ratio as seedlings had adults with short-lived leaves, while those with a small leaf area ratio had adults with long-lived leaves. Species with short-lived leaves are favoured if they maximize light interception by investing in a large leaf area rather than structural and defence compounds, which are of little benefit when leaves are short-lived. On the other hand, the benefits of structure and defence outweigh the costs of a reduction in the area available to intercept light because long-lived leaves are more likely to encounter damage or herbivory over their life-time. Species with a high leaf area ratio as seedlings also had small seeds, while species with a low leaf area ratio had heavy seeds. Upon germination, species investing in leaf structure and defence at the expense of leaf area (i.e. low leaf area ratio) may experience an initial deficit period until the benefits of increased leaf longevity outweigh the costs of small leaf area. Thus, the larger food reserves in heavy seeds may assist seedlings with low leaf area through this initial deficit period. Alternatively, the negative correlation between leaf area ratio and seed mass may be related to the negative correlations between leaf life span and seed mass and leaf life span and leaf area ratio.

After 35 days of growth under optimal conditions, most species partitioned twice as much dry weight into their shoots as into their roots. Most species allocated a slightly greater proportion of new biomass to shoots than to roots as they grew over the 35 days, in agreement with an earlier study on British grassland species (Hunt *et al.* 1987). Thus although seedlings initially invested in root growth to anchor the plant and gain access to soil resources, they increasingly invested in shoot growth to gain access to light until shoot biomass was twice that of the roots. These results are consistent with species from nutrient-poor habitats having low root:shoot ratios (Elberse & Berendse 1993). However, there is also a phenotypic trend

for species to allocate more biomass to the shoot than to the root in response to fertilization (Tilman & Wilson 1991; Elberse & Berendse 1993).

Seedlings of tall narrow species allocated a greater proportion of new biomass to their shoots over time (high allometric constant), while the seedlings of short wide species allocated a greater proportion of new biomass to their roots over time (low allometric constant). Similar to the study by Garnier (1992), no significant relationship between maximum relative growth rate and the allometric constant was found here. Other studies (Hunt *et al.* 1987; Shipley & Peters 1990a) have found a positive correlation between maximum relative growth rate and the allometric constant, possibly because they examined species from a wider range of habitats. At the seedling stage, species allocating a greater proportion of new biomass to their shoots over time (high allometric constant) had a low leaf area ratio, while species allocating a greater proportion of their biomass to their roots over time had a high leaf area ratio (low allometric constant). This apparent contradiction suggests that biomass invested in the shoot is being devoted to other purposes besides increased leaf area (e.g. structural and defence compounds).

#### (f) Root Number in Experimental Root-tubes

Total root number (intersecting the lines drawn across the glass face of the root-tubes) decreased in the order *Vulpia bromoides* > *Hypochaeris radicata* > *Acetosella vulgaris* > *Sporobolus creber* > *Aristida ramosa*. These results suggest a trend for the root number of exotic annuals > exotic perennials > native perennials. The relatively low number of roots for *A. ramosa* suggests that it could have a low demand for resources (associated with low growth rate), a slowly developing root system, or long-lived roots. Initially the maximum root depth of *H. radicata* and *A. vulgaris* was greater than that of *S. creber* and *A. ramosa*, but this effect had diminished by two months after germination. Secondary root development in the cool-season (C3) species (*V. bromoides*, *H. radicata* and *A. vulgaris*) began before the warm-season (C4) species (*S. creber* and *A. ramosa*). However, comparisons of growth are only reliable within the same photosynthetic pathway because the glasshouse temperature (15°C to 28°C) was mid-way between conditions suitable for C3 and C4 species.

Initially *A. ramosa* and *S. creber* seedlings invested their root biomass into downward elongation and as a result their lateral roots were small. Early development of one main primary root protects the seedlings of these two species against moisture stress (Harradine & Whalley 1981). The roots of *A. ramosa* and *S. creber* elongated to a similar depth, but they differed in that *S. creber* had a greater root number at shallower depths than *A. ramosa*. A greater number of roots at shallow depths allows greater access to applied fertilizer and moisture from light rainfall (Harradine & Whalley 1981). Thus, *S. creber* may have access to applied fertilizer and light rainfall. Greater root number in deeper layers enables *A. ramosa* to access subsoil water, thereby avoiding water shortages (Harradine & Whalley 1979). Field

studies by Harradine and Whalley (1981) confirmed that mature *A.ramosa* plants have a maximum rooting depth in excess of 1 m providing access to subsoil water when rainfall is low. By the end of the experiment the roots of *S.creber* had reached a similar depth to *A.ramosa* in the root-tubes and thus may also have access to subsoil water. Alternatively *S.creber* may survive moisture stress by using water conservatively (unlikely because *S.creber* has a high relative growth rate), tolerating water stress or acclimatising to water stress (Harradine & Whalley 1979).

The roots of *A.vulgaris* and *H.radicata* elongated downwards at a similar rate and secondary root development began at a similar time. The high root number of these two species in the deeper soil layers suggest that they may avoid water shortages by accessing subsoil water reserves. *H.radicata* probably has access to light rainfall as well because it has a high root number in the upper soil profile. The time taken for *V.bromoides* to invest in secondary root development was similar to that of *A.vulgaris* and *H.radicata*. Initially the maximum depth of the roots of *H.radicata* was greater than that of *V.bromoides*, but this effect had diminished by two months after germination. On the Northern Tablelands, *Vulpia* spp. germinate after suitable rainfall throughout January to September (Jones & Whalley 1993). Rapid downward elongation of the roots to protect the *Vulpia* spp. seedling against moisture stress may not be required because germination occurs when the risk of moisture stress is low. By the end of the experiment *V.bromoides* was the only species that had not reached the bottom of the root-tube. Instead of investing in great root depth, annuals such as *V.bromoides* avoid water stress by completing their life cycle before the risk of moisture stress is high (i.e. summer). The root number of *V.bromoides* at shallow depths was greater than that of *H.radicata* and *A.vulgaris*, suggesting that *V.bromoides* would have greater access to applied fertilizer and light rainfall. The relatively shallow root depth of *V.bromoides* has been previously noted and is consistent with the observed drought susceptibility of this species (Ozanne *et al.* 1965).

*Hypochaeris radicata*, *A.ramosa* and *S.creber* all developed herringbone root systems, but *H.radicata* had a much thicker primary axis (taproot) and much longer lateral roots than the other two species. Herringbone root patterns are suited to conditions of limiting soil resources because they are most effective for the exploration and exploitation of the soil (Fitter 1987). However, herringbone root patterns are also expensive (Fitter 1987) and therefore are not cost effective for short-lived species such as *V.bromoides*. *Acetosella vulgaris* had several thick axis roots running parallel to each other, while its longest axis root had a somewhat herringbone pattern. *A.vulgaris* may form a sequence of herringbone roots associated with the production of rhizomes across the soil surface, giving it the capacity to explore and exploit the soil. In contrast, *V.bromoides* had a random dense pattern of fine roots which is consistent with the prediction that annuals have nearly random or even dichotomous root systems (Fitter *et al.* 1988).

Species investing root biomass in thin roots tend to take up more of the available nutrients (Boot 1989). Therefore the relatively fine roots of *V.bromoides* and *Wahlenbergia*

*planiflora* may enable them to take up more available nutrients. A capacity for high nutrient uptake is particularly advantageous for annual species such as *V.bromoides* as it enables them to complete their life cycle rapidly. *H.radicata* and *A.vulgaris* had relatively thick roots which have greater transport capacity, are less susceptible to herbivory and mechanical damage, are longer lived and play a greater anchoring role than thin roots (Boot 1989). These two deep-rooted species may have thick roots because they are more favourable than thin roots in deeper soil layers where anaerobic conditions may prevail due to water logging (Boot 1989).

### 3.4.3 Conclusion

The study site can be described in terms of the predominance of species with particular plant attributes (Table 3.38). The presence of species with these attributes can be explained in terms of the environmental conditions of the site (e.g. fertility and climate) and its land-use history.

**Table 3.38:** Summary of the predominant plant attributes of the species at the Newholme site.

Type of Attribute	Predominant Attribute (based on number of species)
Growth Form	Forbs > Grasses > Sedges/Rushes
Life-cycle	Perennial > Annual
Species Origin	Native > Exotic
Raunkiaer Life-form	Hemicryptophytes > Therophytes > Geophytes > Amphiphytes
Stem Structure	Tussock & Tuft > Semi-rosette > Erect > Prostrate > Rosette > Twining
Vegetative Height	10 - 20 cm
Reproductive Height	30 - 50 cm
Width	10 - 20 cm
Persistent Litter	Absent > Present
Inflorescence Type	Spike-like > Panicle-like & Solitary > Capitulum & Cyme-like
Month of Flowering	November > December > January & October > February, August & September
Flowering Duration	1 month > 2 to 5 months > 6 to 9 months
Leaf Texture	Soft > Fibrous/thick
Leaf hairiness	Glabrous > Hairy
Leaf Size	Nanophyll > Microphyll > Leptophyll
Leaf Shape	Linear > Lanceolate > Elliptic > Filiform & Circular > Oblanceolate & Obovate
Leaf Life Span	75 - 125 days
Seedling Growth Rate	< 1.0 g/g/week
Root:shoot Ratio	0.41 - 0.6
Storage Organs	Absent > Rhizomes > Taproots, Stolons, Stem tubers & Root tubers
Diaspore Texture	Smooth > Rugose > Striate > Other
Diaspore Shape	Ovoid > Trigonus > Tadpole > Conical > Lenticular > Other
Diaspore Hairiness	Glabrous > Antrorse > Radial
Dispersal Morphology	Absent > Dust-like > Awns > Pappus & Explosive > Other
Diaspore Size	0.0001 - 0.001g
Diaspore Number	501 - 1000 diaspores per individual

Most of the continuous plant attributes investigated in the present study were inter-correlated: plant height, width, diaspore number, diaspore mass, leaf life-span, flowering duration, relative growth rate, leaf area ratio, root:shoot ratio and allometric constant. There were also strong associations between species origin, life-cycle, the absence or presence of storage organs, leaf texture, growth form, the absence or presence of litter and diaspore shape. Often a functional explanation for these correlations could be evoked, but experimentation is required to test these hypotheses.

The aim of this chapter was to describe the study site in terms of the presence of species with particular plant attributes and to examine the associations amongst plant attributes. Using pattern analysis, the plant attribute data in this chapter could be synthesised into a number of "guilds", "syndromes" or "strategies". However, a synthesis of plant attributes into 'strategies' is deferred until Chapter 6. Strategies formed on the basis of attribute data alone may not bear any relationship to the environment nor to the mechanisms which determine vegetation pattern. There is a greater likelihood of finding the mechanisms by which plant attributes determine vegetation pattern, if the attributes are examined in conjunction with the environment they inhabit. In Chapter 6, discriminant function analysis is used to determine if plant attributes discriminate between the different fertilization and disturbance treatments. Thus, the strategies described in Chapter 6 are associated with particular environmental conditions (i.e. level of fertility and disturbance regime).

## CHAPTER FOUR

### EFFECTS OF FERTILIZATION AND SOIL DISTURBANCE ON PLANT ATTRIBUTE COMPOSITION

#### 4.1 INTRODUCTION

Interest in the use of plant attributes as an alternative, but complementary, method of characterising plant communities and their relationship to the environment is growing. Over time, the focus of research has changed from descriptive studies, which characterize continents and communities by certain plant attributes (e.g. Gimingham 1951; Floret *et al.* 1987; Danin & Orshan 1990), to studies examining the relationship between plant attributes and environmental factors (e.g. Montalvo *et al.* 1991; Díaz *et al.* 1992; McIntyre *et al.* 1995). In Chapter 3, the Newholme study site was characterized by the presence of particular plant attributes. The literature review (Section 1.1.1) demonstrated that the prevalence of species with particular plant attributes is often predictably related to environmental factors and this chapter goes on to explore this further.

The most important limitations of the plant attribute approach are that plant attributes are frequently correlated with other plant attributes and the adaptive significance of a particular plant attribute may be unknown (Section 1.1.1). Prior knowledge of the correlations that exist between the plant attributes enables a more reliable interpretation of the adaptive significance of relationships between attributes and environmental factors. Correlations amongst the attributes in this study were explored in Chapter 3. The literature review (see Section 1.1.1) also demonstrated that the use of multivariate techniques on a large number of plant attributes has the advantage of being able to discern which plant attributes are most strongly related to a particular environmental factor. However, potentially useful information has been lost from some studies (Gomez Sal *et al.* 1986; Montalvo *et al.* 1991; Díaz *et al.* 1992) by the reliance on multivariate techniques alone. To ensure that full use was made of the data set in this study, the effect of soil disturbance and fertilization on the prevalence of species with each plant attribute was examined separately.

The aim of this chapter was to investigate whether the abundance of species with particular plant attributes can be associated with soil disturbance and fertilization. The specific question addressed was: Does soil disturbance, fertilization or sowing significantly affect the prevalence (number or cover) of herbaceous plant species with the attributes discussed in Chapter 3.

## 4.2 METHODS

A completely randomised block experiment with three factors, soil disturbance, fertilization and sowing, was established in an area of natural grassland on the Northern Tablelands (Section 2.2.2). There were three levels of soil disturbance (none, hand-hoed and rotary-hoed), two levels of fertilization (none and fertilized) and two levels of sowing (none and sown). The treatments were arranged randomly within each block, with each block replicated five times (Appendix 1B). Percentage canopy cover of each species was determined in each permanent 1 x 1 m plot using the point-quadrat method (Goodall 1952). Using a frame of 80 points arranged systematically (10 cm apart), the presence or absence of each species at each point was expressed as a percentage of the total number of points used. This data provided the species (cover or presence) x plots matrix. The plant attribute data for each species were collected from individuals growing in the field under nutrient-poor, low disturbance conditions (Section 3.2). For a small number of species which did not grow in sufficient number under nutrient-poor, low disturbance conditions, the plant attribute data was collected on individuals growing under more specific conditions (e.g. the sown species on the highly disturbed, fertilized plots). Growth parameters such as maximum relative growth rate, root:shoot ratio and leaf area ratio were determined in the glasshouse. This data provided the species x attribute matrix.

The species x plots matrix multiplied by the species x attributes matrix produced a matrix of attributes x plots. In other words, the relative cover of species with a particular categorical plant attribute was determined by summing together the canopy cover of each species in the plot with the attribute and expressing it as a percentage of the total canopy cover of the vegetation in the plot. The relative number of species with a particular plant attribute was determined by summing together the number of species in the plot with the attribute and expressing it as a percentage of the total number of species in the plot. Absolute cover and absolute number of species was not used here because it would merely reflect the fact that vegetation cover and species richness on the highly disturbed plots was low. In other words, high soil disturbance would *always* produce a significant decrease in the absolute cover or number of *all* of the attributes examined because few species survived high soil disturbance.

The effect of soil disturbance, fertilization and sowing on the relative cover and the relative number of species with particular categorical plant attributes was determined by a fully factorial analysis of variance at each of the four sampling times (Section 2.2.5) using SYSTAT (Wilkinson *et al.* 1992). The three factors, disturbance, fertilization and sowing, together with all of the interaction terms (i.e. disturbance x fertilization, disturbance x sowing, fertilization x sowing and disturbance x fertilization x sowing) were examined. All of the three factors are considered to be fixed and therefore the conclusions drawn from the analysis apply only to the specific treatments considered in the study (Underwood 1981).



There were five replicates for each treatment. Dependence of one plant attribute category on another (e.g. relative cover of exotic and native species) was not a problem because anovas were carried out separately for each category of a plant attribute. Estimates of percentage cover (expressed as proportions) were arcsin-transformed where necessary to meet the assumptions of normality (Goodall 1952). After analysis of variance, residuals were examined for outliers and normality (Tabachnick & Fidell 1989) using the normal probability plots in SYSTAT. Changes in treatment effects over time were assessed using anova with repeated measures and trend analysis. The Greenhouse-Geiser and Huynh-Feldt statistics were used in the repeated measures anovas to adjust for the violation of homogeneity of covariance (Tabachnick & Fidell 1989). For the commencement of flowering attribute, the November 1992 sampling period was omitted from the analysis because cover of the individual *Aristida* spp. was not separated and they differed in commencement of flowering. Further detail of the rationale of the data analysis used here is given in Section 2.2.5.

The effect of soil disturbance, fertilization and sowing on the continuous plant attributes was determined by correlating canopy cover of the species in each treatment (averaged over five replicates) with the mean of their plant attributes (which were measured independent of the experimental treatments) using SYSTAT (Wilkinson *et al.* 1992). As the correlations were within each treatment rather than between the treatments, absolute cover was used. The more robust non-parametric Spearman rank correlation coefficient was used to protect against outliers and violation of the assumption of homogeneity of variance. Both the November 1993 and February 1994 sampling periods were analysed to observe any seasonal differences in the abundance of certain plant attributes.

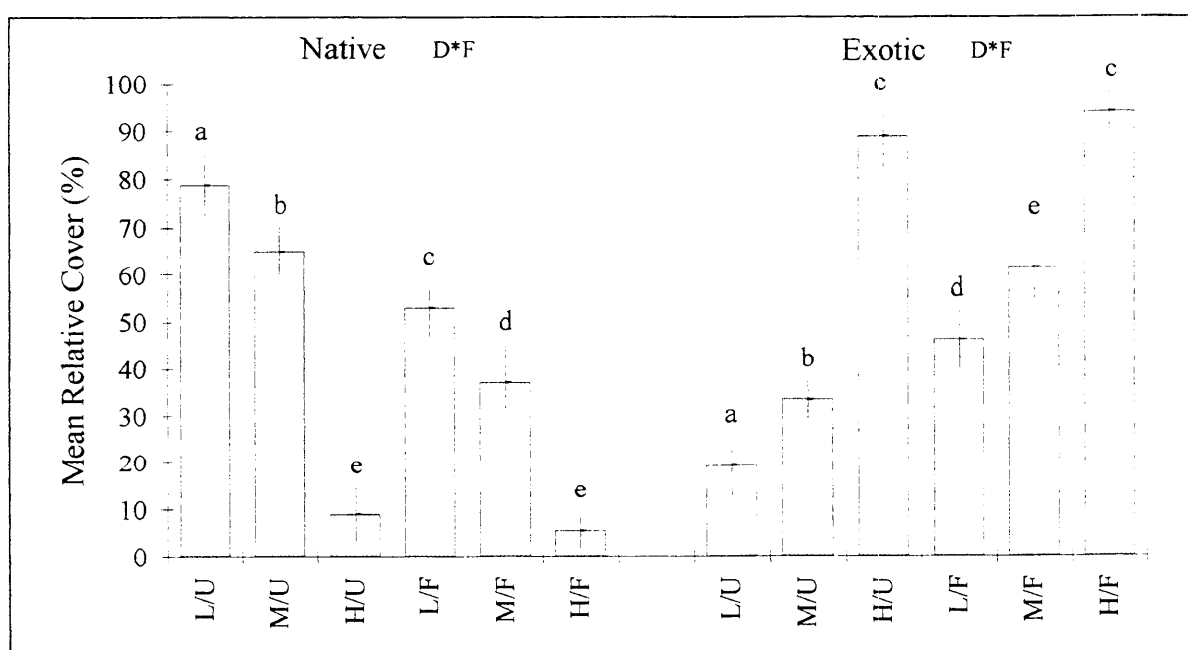
## 4.3 RESULTS

### 4.3.1 Species Origin

Anova revealed a significant disturbance x fertilization interaction for relative cover of native and exotic species in February 1994 (Table 4.1). At low and moderate levels of soil disturbance, fertilization significantly decreased the relative cover of natives and increased the relative cover of exotics (Fig. 4.1). Fertilization had no effect in highly disturbed plots. The effect of the disturbance x fertilization interaction increased linearly over time (Appendix 7). The sown treatment did not significantly affect the relative cover of native and exotic species at any time during the study.

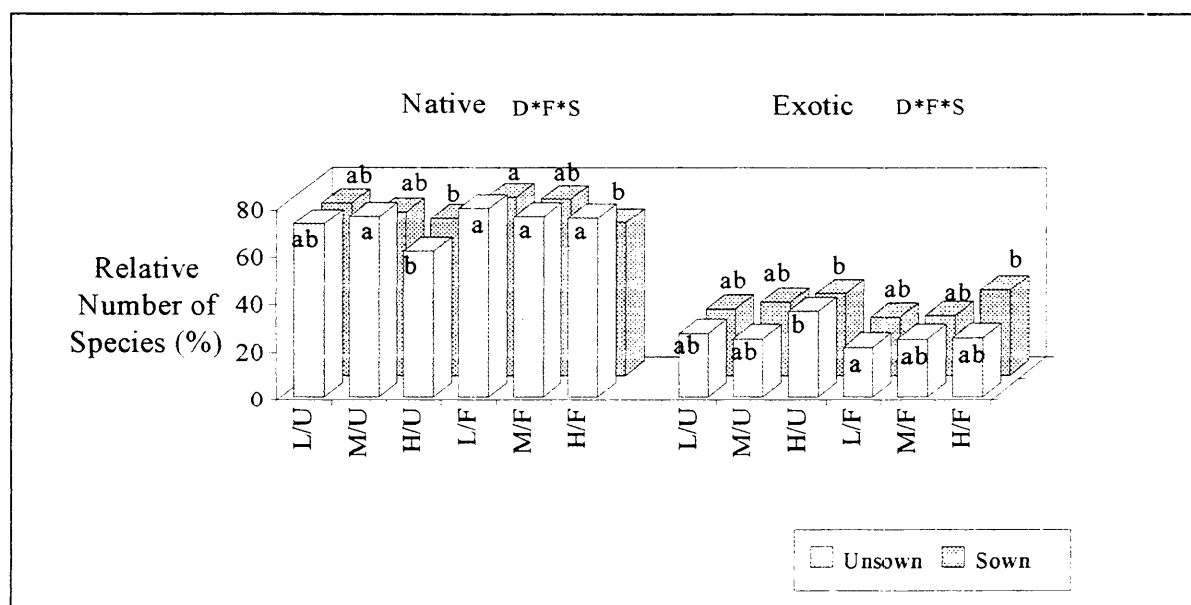
**Table 4.1:** Analysis of variance (F values) of exotic and native relative cover (%) and relative species richness (%) with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown and fertilization x sown interactions were not significant. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Relative Cover (%)		Relative Number of Species (%)	
		Native	Exotic	Native	Exotic
Disturbance	2/48	512.17***	508.62***	11.54***	11.04***
Fertilization	1/48	151.62***	165.17***	9.15**	7.45**
Sown	1/48	0.01	0.53	4.60*	5.55*
Disturbance x Fertilization	2/48	<b>25.34***</b>	<b>22.81***</b>	0.44	0.16
Disturbance x Fertilization x Sown	2/48	1.08	1.00	<b>4.20*</b>	<b>3.21*</b>



**Fig. 4.1:** Mean relative cover (%) of exotic and native species in each of the six treatments in February 1994. The sown treatment was not significant and is therefore not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the means of the native species and between the means of the exotic species.

Anova detected a significant disturbance x fertilization x sown interaction for the relative number of native and exotic species in February 1994 (Table 4.1). The relative number of native species in highly disturbed unfertilized unsown plots was lower than in moderately disturbed unfertilized unsown plots, while the number in highly disturbed fertilized sown plots was lower than in low disturbance fertilized sown plots (Fig. 4.2). The relative number of exotic species in the low disturbance fertilized unsown plots was lower than in highly disturbed unfertilized and highly disturbed fertilized sown plots. The effect of the disturbance x fertilization x sown interaction remained consistent over time (Appendix 7).



**Fig. 4.2:** Mean relative number (%) of exotic and native species in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized, F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the means of the native species and between the means of the exotic species.

A weak positive correlation was found between the absolute number of exotic species and native species within a plot (Spearman rank coefficient,  $r = 0.272$ ;  $p < 0.05$ ). Native species richness was positively correlated with total, dead and live biomass and was negatively correlated with light penetration (Table 4.2). Exotic species richness was weakly negatively correlated with total and live biomass and soil phosphorus.

**Table 4.2:** Spearman Rank correlation coefficients between absolute native and exotic species number and environmental variables in February 1994 ( $n = 60$ ). \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

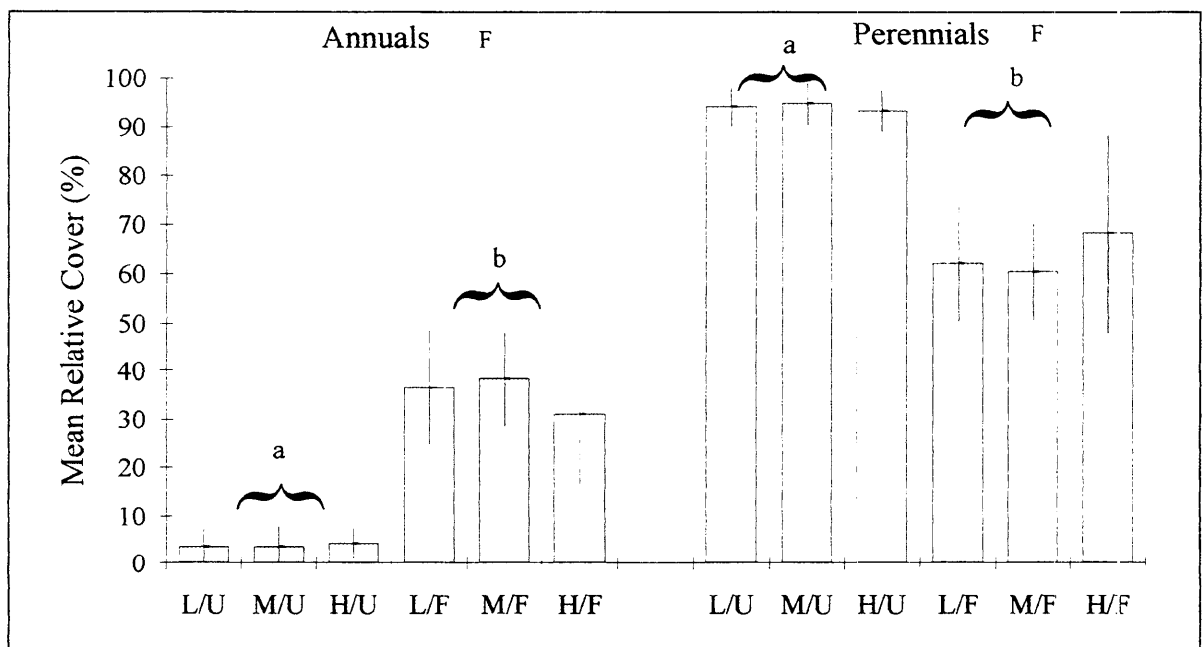
	Species Richness	
	Native	Exotic
Total Biomass	<b>0.359**</b>	- <b>0.245*</b>
Dead Biomass	<b>0.422***</b>	- 0.192
Live Biomass	<b>0.288*</b>	- <b>0.233*</b>
Light penetration	- <b>0.477***</b>	0.002
Phosphorus	0.082	- <b>0.257*</b>
pH	0.008	0.187

### 4.3.2 Life Cycle

The relative cover of annual and perennial species was not significantly affected by soil disturbance in February 1994 (Table 4.3). The effect of soil disturbance on annual and perennial cover was greater in spring than in summer, with high soil disturbance decreasing the relative cover of annuals and increasing the cover of perennials in spring (Appendix 7). Fertilization significantly increased the relative cover of annuals and decreased perennials in February 1994 (Fig. 4.3). A significant disturbance x fertilization x sown interaction for the relative cover of perennials was detected early in the study, but the effect diminished over time. Sowing had no significant effect on the relative cover of annual and perennial species at any time during the study.

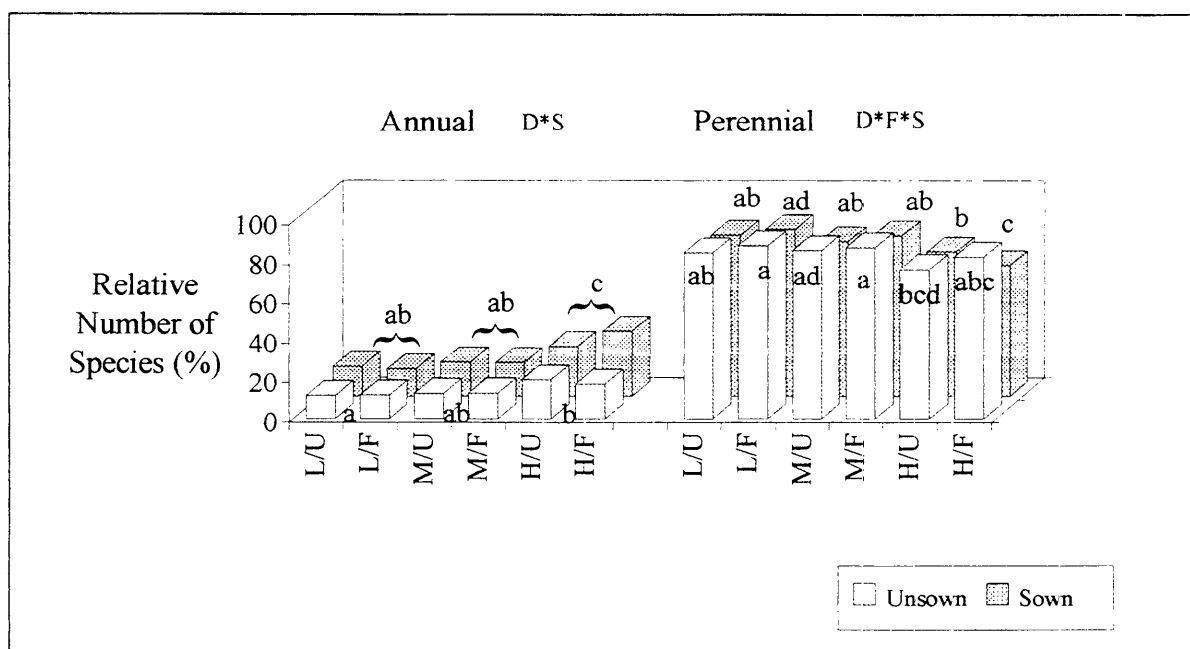
**Table 4.3:** Analysis of variance (F values) of annual and perennial relative cover (%) and relative species richness (%) with disturbance, fertilization & sown as factors in February 1994. Disturbance x fertilization and fertilization x sown interactions were not significant. ↑ - increased; ↓ - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Relative Cover (%)		Relative Number (%)	
		Annuals	Perennials	Annuals	Perennials
Disturbance	2/48		0.20	27.54***	25.84***
Fertilization	1/48	↑ 147.35***	↓ 126.92***	0.37	2.13
Sown	1/48	0.45	1.48	22.55***	22.77***
Disturbance x Sown	2/48	0.39	0.22	3.50*	2.12
Disturbance x Fertilization x Sown	2/48	0.25	0.58	2.08	3.57*



**Fig. 4.3:** Mean relative cover (%) of annual and perennial species in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the means of the annual species and between the means of the perennial species.

There is a significant disturbance x sown interaction for the relative number of annual species and a significant disturbance x fertilization x sown interaction for the relative number of perennial species in February 1994 (Table 4.3). High soil disturbance increased the relative number of annual species only in sown plots (Fig. 4.4). Fertilization had no significant effect on the relative number of annuals in February 1994, but did significantly increase annuals in November 1993 (Appendix 7). Fertilization decreased the relative number of perennial species only in highly disturbed sown plots in February 1994.



**Fig. 4.4:** Mean relative number (%) of annual and perennial species in each of the twelve treatments in February 1994. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the means of the annual species and between the means of the perennial species.

Total, dead and live biomass was weakly negatively correlated with the absolute number of annual species and positively correlated with perennial species richness (Table 4.4). Perennial species richness was also negatively correlated with light penetration.

**Table 4.4:** Spearman Rank correlation coefficients between annual and perennial species number and environmental variables in February 1994 ( $n = 60$ ). \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

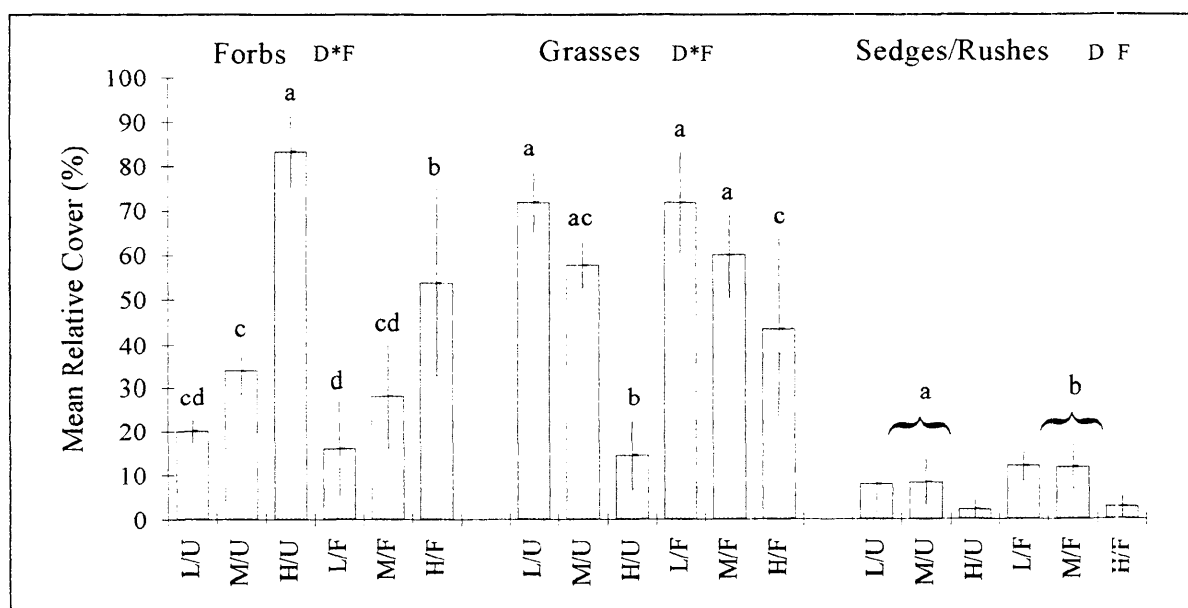
	Species Richness	
	Annual	Perennial
Total Biomass	- 0.242*	0.355**
Dead Biomass	- 0.220*	0.418***
Live Biomass	- 0.265*	0.296*
Light penetration	0.115	- 0.491***
Phosphorus	- 0.072	0.070
pH	- 0.035	0.006

### 4.3.3 Growth Form

Anova revealed a significant disturbance x fertilization interaction for the relative cover of forbs and grasses in February 1994 (Table 4.5). The increase in forb cover and decrease in grass cover with high soil disturbance was especially marked in unfertilized plots (Fig. 4.5). Fertilization significantly increased the relative cover of sedges and rushes. The effect of fertilization on the relative cover of sedges and rushes was greater in summer than spring (Appendix 7). The relative cover of sedge and rush species was lower in highly disturbed plots than in low disturbance plots (2,48 df;  $p < 0.001$ , Bonferroni test) and moderately disturbed plots (2,48 df;  $p < 0.001$ , Bonferroni test). Sowing did not significantly affect the relative cover of forbs, grasses or sedges/rushes at any time during the study.

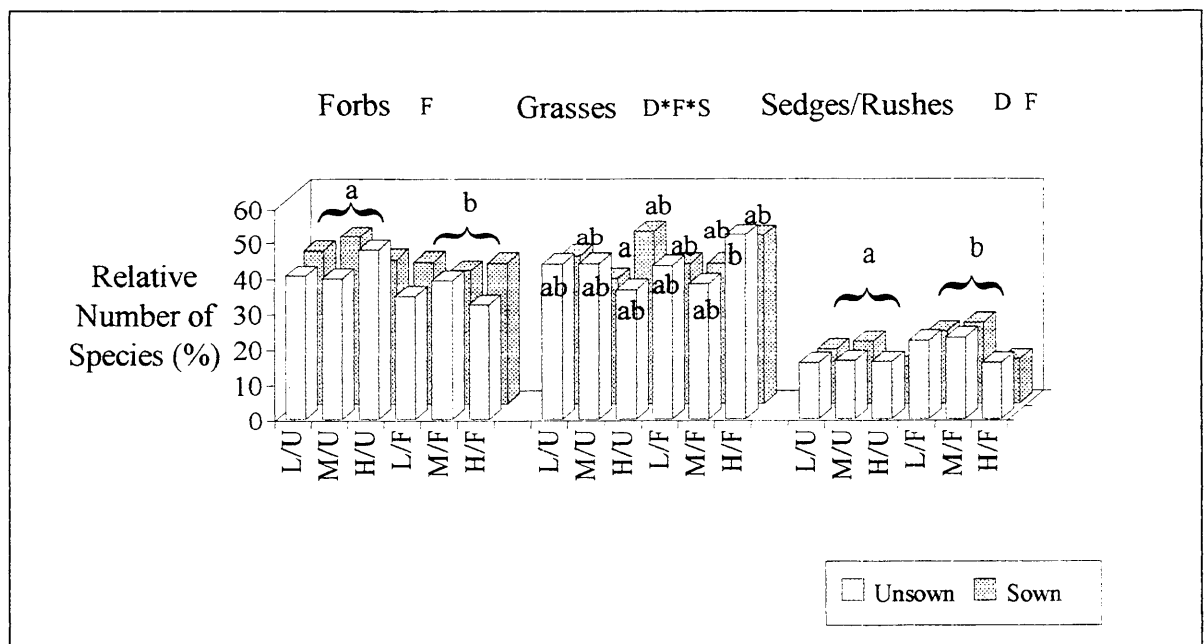
**Table 4.5:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of forb, grass and sedge/rush species with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown and fertilization x sown interactions were not significant. Disturbance x fertilization x sown interaction not significant for relative cover and disturbance x fertilization interaction not significant for relative number of species.  $\uparrow$  - increased;  $\downarrow$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Forbs	Grasses	Sedges/rushes
<b>Relative Cover (%)</b>				
Disturbance	2/48	92.17***	69.61***	$\downarrow$ 19.20***
Fertilization	1/48	17.23***	11.71**	$\uparrow$ 5.34*
Sown	1/48	0.03	0.72	3.24
Disturbance x Fertilization	2/48	6.83**	9.37***	0.91
<b>Relative Number of Species (%)</b>				
Disturbance	2/48	0.19	4.64*	$\downarrow$ 8.68**
Fertilization	1/48	$\downarrow$ 8.65**	0.78	$\uparrow$ 10.78**
Sown	1/48	1.66	0.20	1.74
Disturbance x Fertilization x Sown	2/48	2.95	4.25*	0.24



**Fig. 4.5:** Mean relative cover (%) of forb, grass and sedge/rush species in each of the six treatments in February 1994. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each growth form category.

Anova revealed that fertilization significantly decreased the relative number of forb species in February 1994 (Table 4.5; Fig. 4.6). Soil disturbance did not significantly affect the relative number of forbs in February 1994, but significantly decreased forbs in spring (Appendix 7). There was a significant disturbance x fertilization x sown interaction for the relative number of grass species in February 1994. The relative number of grass species in moderately disturbed unfertilized sown plots was significantly lower than in highly disturbed fertilized unsown plots. Fertilization significantly increased the relative number of sedge and rush species. The relative number of sedge and rush species was lower in highly disturbed plots than in low disturbance plots (2,48 df;  $p < 0.05$ , Bonferroni test) and moderately disturbed plots (2,48 df;  $p < 0.01$ , Bonferroni test). Sowing had no significant effect on the relative number of forbs or sedges/rushes in February 1994, but sowing increased the relative number of forbs in November 1992 and decreased the number of sedges and rushes in November 1992 and March 1993.



**Fig. 4.6:** Mean relative number (%) of forb, grass and sedge/rush species in each of the twelve treatments in February 1994. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each growth form storage category.

The absolute numbers of forb, grass and sedge/rush species were negatively correlated with light penetration (Table 4.6). Grass and sedge/rush species richness were positively correlated with dead and live biomass, while sedge/rush richness was positively correlated with total biomass and negatively correlated with soil phosphorus.

**Table 4.6:** Spearman Rank correlation coefficients between forb, grass and sedge/rush species number and environmental variables in February 1994 (n = 60). \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

	Species Richness		
	Forbs	Grasses	Sedges/rushes
Total Biomass	0.013	0.210	<b>0.472***</b>
Dead Biomass	0.078	<b>0.230*</b>	<b>0.533***</b>
Live Biomass	- 0.044	<b>0.226*</b>	<b>0.333**</b>
Light penetration	- <b>0.255*</b>	- <b>0.293*</b>	- <b>0.534***</b>
Phosphorus	- 0.135	- 0.076	- <b>0.247*</b>
pH	0.114	0.073	- 0.179

#### 4.3.4 Raunkiaer Life Form

Fertilization significantly increased the relative cover of amphiphyte species and therophytes, but decreased the relative cover of hemicryptophytes in February 1994 (Table 4.7; Fig. 4.7). The effect of fertilization on the relative cover of amphiphytes, therophytes and hemicryptophytes increased linearly over time (Appendix 7). The relative cover of amphiphytes was greater in highly disturbed plots than in low disturbance plots (2,48 df; p < 0.01, Bonferroni test) and moderately disturbed plots (2,48 df; p < 0.01, Bonferroni test). The relative cover of hemicryptophytes was lower in highly disturbed plots than in low disturbance plots (2,48 df; p < 0.001, Bonferroni test) and moderately disturbed plots (2,48 df; p < 0.01, Bonferroni test). The effect of soil disturbance on amphiphyte and hemicryptophyte cover increased linearly over time.

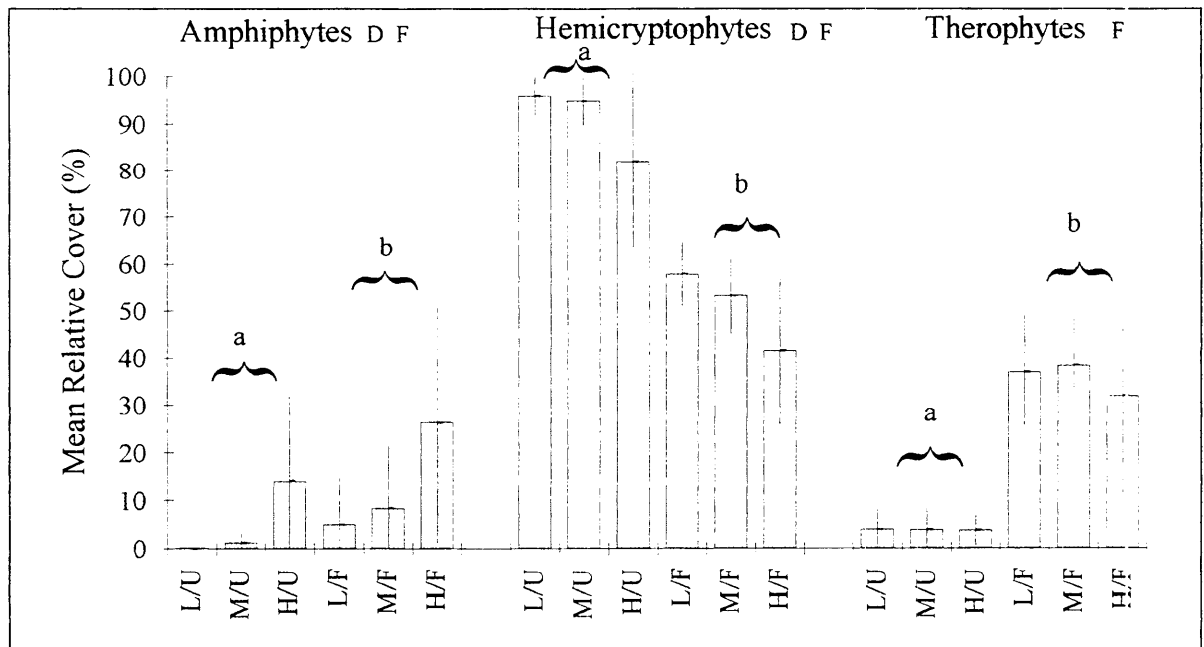
**Table 4.7:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of the Raunkiaer life form categories with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown, fertilization x sown and disturbance x fertilization x sown interactions were not significant. Disturbance x fertilization interaction was not significant for relative cover. ↑ - increased; ↓ - decreased. \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

	df	Amphiphyte	Hemicryptophyte	Therophyte
<b>Relative Cover (%)</b>				
Disturbance	2/48	↑ <b>9.05***</b>	↓ <b>10.05***</b>	0.39
Fertilization	1/48	↑ <b>4.75*</b>	↓ <b>204.32***</b>	↑ <b>142.01***</b>
Sown	1/48	0.02	1.56	0.58
<b>Relative Number of Species (%)</b>				
Disturbance	2/48	↑ <b>12.86***</b>	11.75***	1.43
Fertilization	1/48	2.27	15.17***	↑ <b>11.52**</b>
Sown	1/48	0.17	0.16	0.31
Disturbance x Fertilization	2/48	2.05	<b>4.83*</b>	1.66

Disturbance and sowing did not affect the relative cover of therophytes in February 1994 (Table 4.7), but high soil disturbance decreased their cover in November 1992, March 1993 and November 1993, and there was a significant disturbance x fertilization x sown interaction in March 1993 (Appendix 7). Sowing did not effect relative cover of amphiphytes



and hemicryptophytes in February 1994, nor at any other time during the study. The relative cover of geophyte species was too low to analyse in February 1994. However, the relative cover of geophytes in highly disturbed plots was lower than in low disturbance plots (2,48 df;  $p < 0.001$ , Bonferroni test) and moderately disturbed plots (2,48 df;  $p < 0.01$ , Bonferroni test) in both November 1992 and 1993.

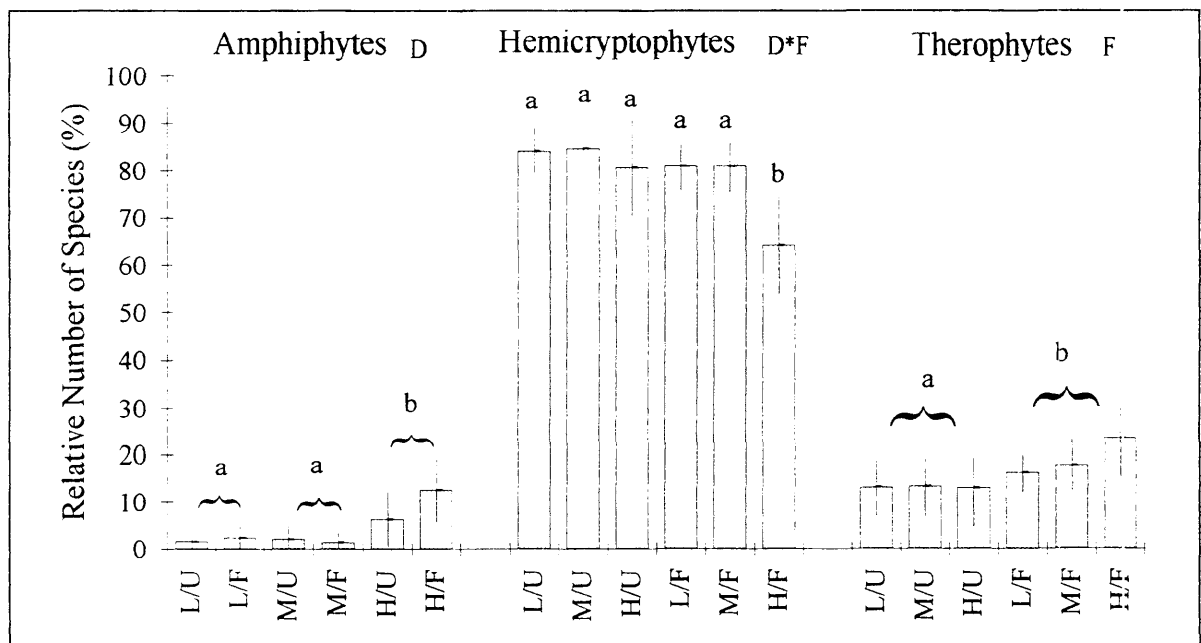


**Fig. 4.7:** Mean relative cover (%) of amphiphyte, hemicryptophyte and therophyte species in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the treatments means of each Raunkiaer life form category.

High soil disturbance significantly increased the relative number of amphiphyte species in February 1994 (Table 4.7; Fig. 4.8). The effect of soil disturbance on amphiphytes increased linearly over time, while the effect of fertilization was not significant at any time during the study (Appendix 7). There was a significant disturbance  $\times$  fertilization interaction for the relative number of hemicryptophyte species. High soil disturbance decreased the relative number of hemicryptophytes in fertilized plots only. The effect of the disturbance  $\times$  fertilization interaction on hemicryptophytes increased linearly with time. Fertilization increased the relative number of therophyte species in February 1994. The effect of fertilization on therophytes was greater in summer than in spring.

Disturbance did not affect the relative number of therophytes in February 1994, but high soil disturbance significantly decreased their number in March 1993 and increased their number in November 1993 (Appendix 7). Sowing did not significantly affect the relative number of amphiphytes, hemicryptophytes and therophytes in February 1994. However,

sowing decreased the relative number of therophytes and increased hemicryptophytes in November 1992 and March 1993. The relative number of geophytes was too low to analyse in February 1994. However, the relative number of geophytes in highly disturbed plots was lower than in low disturbance plots (2,48 df;  $p < 0.001$ , Bonferroni test) and moderately disturbed plots (2,48 df;  $p < 0.01$ , Bonferroni test) in both November 1992 and 1993. Fertilization decreased the relative number of geophytes in November, but not significantly (1,48 df;  $p = 0.05$ , Bonferroni test).



**Fig. 4.8:** Mean relative number (%) of amphiphyte, hemicryptophyte and therophyte species in each of the six treatments in February 1994. Note the change in order of treatments for amphiphytes. The sown treatment was not significant and therefore is not shown. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each Raunkiaer life form category.

#### 4.3.5 Height, Width and Height:Width Ratio

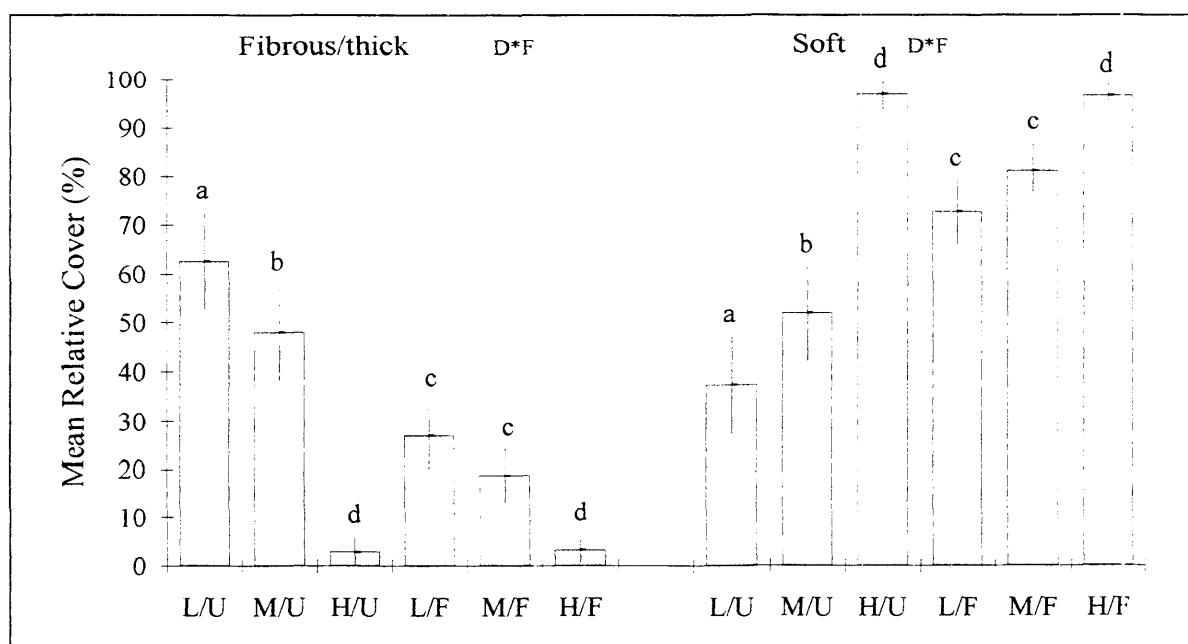
The canopy cover of species was negatively correlated with their vegetative height in fertilized, highly disturbed plots in November 1993 (Table 4.8). In February 1994, canopy cover of species was positively correlated with their vegetative height in fertilized, low disturbance plots. The canopy cover of species was inversely related to their reproductive height in unfertilized moderately disturbed plots and inversely related to their width in the moderately disturbed and the unfertilized low disturbance plots in November 1993. The canopy cover of species was positively correlated with their height:width ratio in the low and moderately disturbed plots in November 1993. By summer, the positive correlation was only significant in the fertilized, low and moderately disturbed plots.

**Table 4.8:** Spearman Rank correlation coefficients between size attributes of species and their absolute cover (%) in each treatment in November 1993 and February 1994. Significant correlations are marked in bold. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

Plant Attribute	n		L/U	M/U	H/U	L/F	M/F	H/F
Vegetative Height	51	Nov. 1993	-0.056	-0.122	-0.033	0.043	-0.064	<b>-0.198*</b>
	50	Feb. 1994	0.038	0.052	-0.050	<b>0.207*</b>	0.082	-0.131
Reproductive Height	50	Nov. 1993	-0.133	<b>-0.206*</b>	-0.002	-0.071	-0.049	-0.033
	49	Feb. 1994	0.050	-0.023	0.029	-0.021	0.031	-0.021
Width	51	Nov. 1993	<b>-0.221*</b>	<b>-0.255*</b>	-0.064	-0.113	<b>-0.221*</b>	-0.082
	50	Feb. 1994	0.046	0.073	0.019	0.115	0.056	-0.061
Height:Width	51	Nov. 1993	<b>0.237*</b>	<b>0.249*</b>	0.078	<b>0.323**</b>	<b>0.339***</b>	-0.038
	50	Feb. 1994	0.048	0.100	0.127	<b>0.273**</b>	<b>0.203*</b>	0.093

### 4.3.6 Leaf Texture

Anova detected a significant disturbance x fertilization interaction for the relative cover of species with fibrous or soft leaves in February 1994 (Table 4.9). Both moderate and high soil disturbance decreased the relative cover of fibrous-leaved species and increased the cover of soft-leaved species to a greater extent in unfertilized than fertilized plots (Fig. 4.9). The effect of the disturbance x fertilization interaction increased linearly over time (Appendix 7). The sown treatment did not significantly affect the relative cover of species with fibrous or soft leaves at any time during the study.

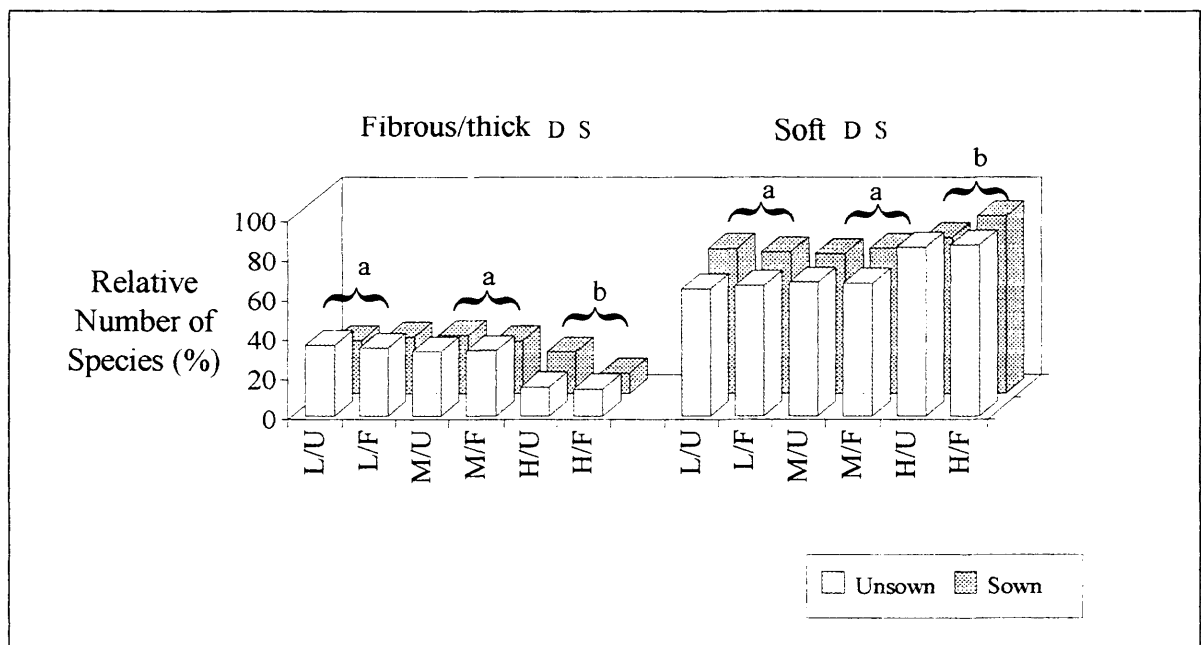


**Fig. 4.9:** Mean relative cover (%) of species with fibrous/thick or soft leaves in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the means of species with fibrous/thick leaves and between the means of species with soft leaves.

**Table 4.9:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species with fibrous/thick or soft leaves with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown, fertilization x sown and disturbance x fertilization x sown interactions were not significant.  $\hat{\downarrow}$  - increased;  $\hat{\uparrow}$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Relative Cover (%)		Relative Number of Species (%)	
		Fibrous	Soft	Fibrous	Soft
Disturbance	2/48	222.87***	222.87***	$\hat{\downarrow}$ 44.54***	$\hat{\uparrow}$ 44.54***
Fertilization	1/48	89.71***	89.71***	2.09	2.09
Sown	1/48	0.02	0.02	$\hat{\downarrow}$ 4.83*	$\hat{\uparrow}$ 4.83*
Disturbance x Fertilization	2/48	29.14***	29.14***	1.35	1.35

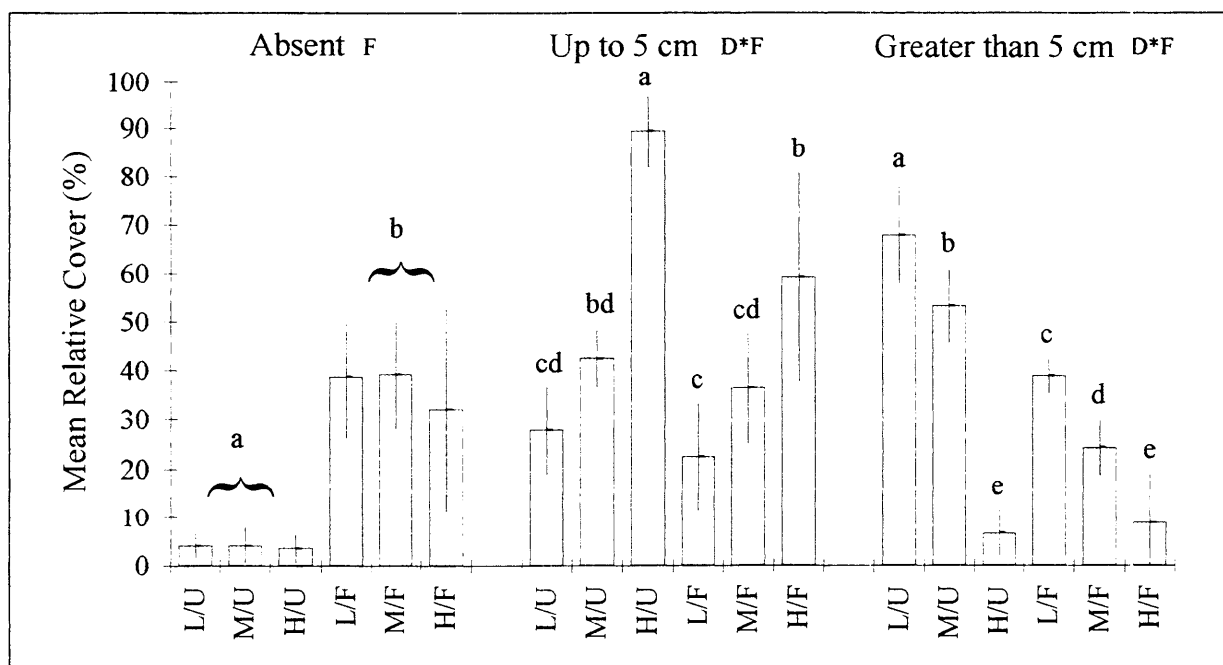
High soil disturbance decreased the relative number of species with fibrous leaves and increased the number of species with soft leaves (Table 4.9; Fig. 4.10). The effect of soil disturbance increased linearly over time (Appendix 7). Fertilization did not significantly affect the relative number of species with fibrous or soft leaves at any time during the study. The relative number of species with fibrous leaves was greater in unsown plots than sown plots (1,48 df;  $p < 0.05$ , Bonferroni test), while the number of soft-leaved species was greater in sown plots than unsown plots (1,48 df;  $p < 0.05$ , Bonferroni test).



**Fig. 4.10:** Mean relative number (%) of species with fibrous/thick or soft leaves in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the means of the species with fibrous/thick leaves and between the means of the species with soft leaves.

### 4.3.7 Persistent Litter

Fertilization significantly increased the relative cover of species without persistent litter in February 1994 (Fig. 4.11; Table 4.10). Disturbance did not significantly affect the relative cover of species without persistent litter in February 1994, but did decrease cover in November 1992, March 1993 and November 1993 (Appendix 7). Anova revealed a significant disturbance x fertilization interaction for the relative cover of species with persistent litter up to 5 cm and species with persistent litter greater 5 cm in depth. High soil disturbance increased the relative cover of species with persistent litter up to 5 cm to a greater extent in unfertilized plots. Moderate and high soil disturbance decreased the relative cover of species with persistent litter greater 5 cm to a greater extent in fertilized plots. The effect of the disturbance x fertilization interaction for species with persistent litter up to 5 cm increased linearly over time. Sowing did not significantly affect the relative cover of species without litter, species with litter up to 5 cm and species with litter greater than 5 cm in February 1994. However, there was a significant disturbance x fertilization x sown interaction for the relative cover of species with litter up to 5 cm in November 1992 and species with litter greater than 5 cm in November 1993.

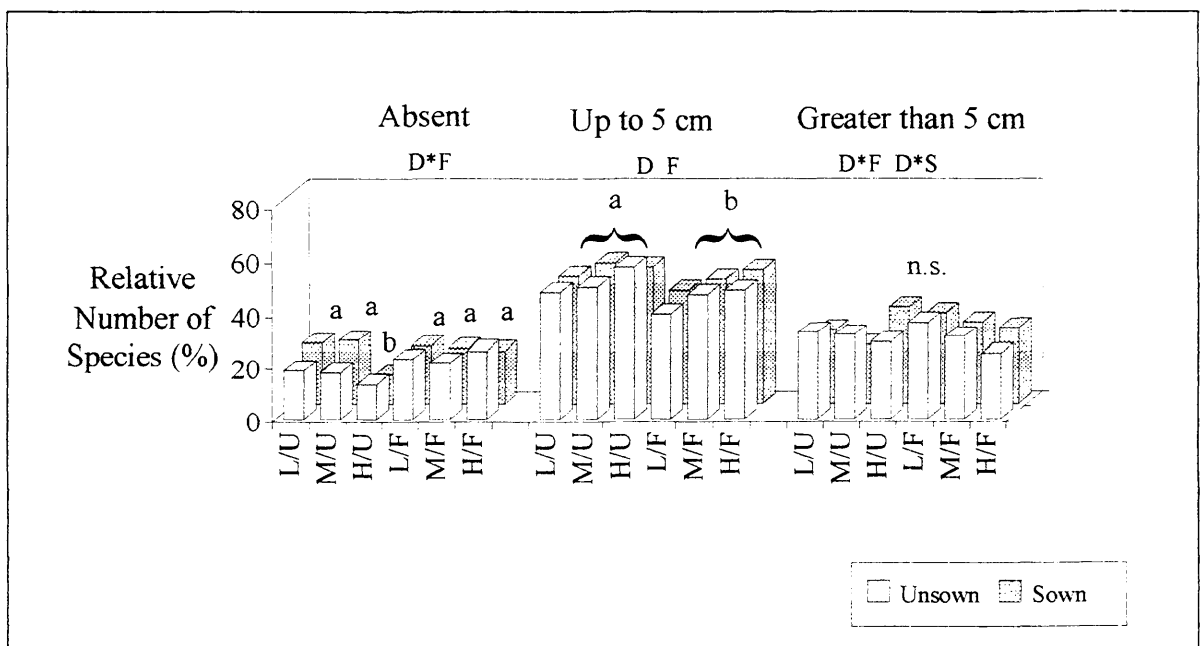


**Fig. 4.11:** Mean relative cover (%) of species without persistent litter, with litter up to 5 cm in depth or with litter greater than 5 cm in depth in each of the treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each litter category.

**Table 4.10:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species without persistent litter, with litter up to 5cm in depth or with litter greater than 5cm in depth with disturbance, fertilization & sown as factors for February 1994. Fertilization x sown and disturbance x fertilization x sown interactions were not significant. Disturbance x sown interaction was not significant for relative cover.  $\hat{\uparrow}$  - increased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Absent	Litter up 5cm	Litter > 5cm
<b>Relative Cover (%)</b>				
Disturbance	2/48	1.13	79.08***	191.05***
Fertilization	1/48	$\hat{\uparrow}$ 154.97***	17.80***	92.43***
Sown	1/48	0.08	0.21	1.66
Disturbance x Fertilization	2/48	0.42	6.17**	27.90***
<b>Relative Number of Species (%)</b>				
Disturbance	2/48	2.96	4.56*	1.66
Fertilization	1/48	9.41**	7.66*	0.23
Sown	1/48	0.06	0.05	0.13
Disturbance x Fertilization	2/48	5.32**	0.14	3.56*
Disturbance x Sown	2/48	2.38	0.38	3.35*

Anova revealed a significant disturbance x fertilization interaction for the relative number of species without persistent litter in February 1994 (Table 4.10). The effect of the disturbance x fertilization interaction was greater in summer than in spring (Appendix 7). The relative number of species without litter was decreased by high soil disturbance in unfertilized plots, but was unaffected in fertilized plots (Fig. 4.12). Fertilization significantly decreased the relative number of species with persistent litter up to 5 cm in depth in February 1994. The effect of fertilization on species with persistent litter up to 5 cm increased linearly over time. High soil disturbance significantly increased the relative number of species with persistent litter up to 5 cm (2,48 df;  $p < 0.05$ , Bonferroni test).



**Fig. 4.12:** Mean relative number (%) of species without persistent litter, litter up to 5 cm in depth and with litter greater than 5 cm deep in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each litter category.

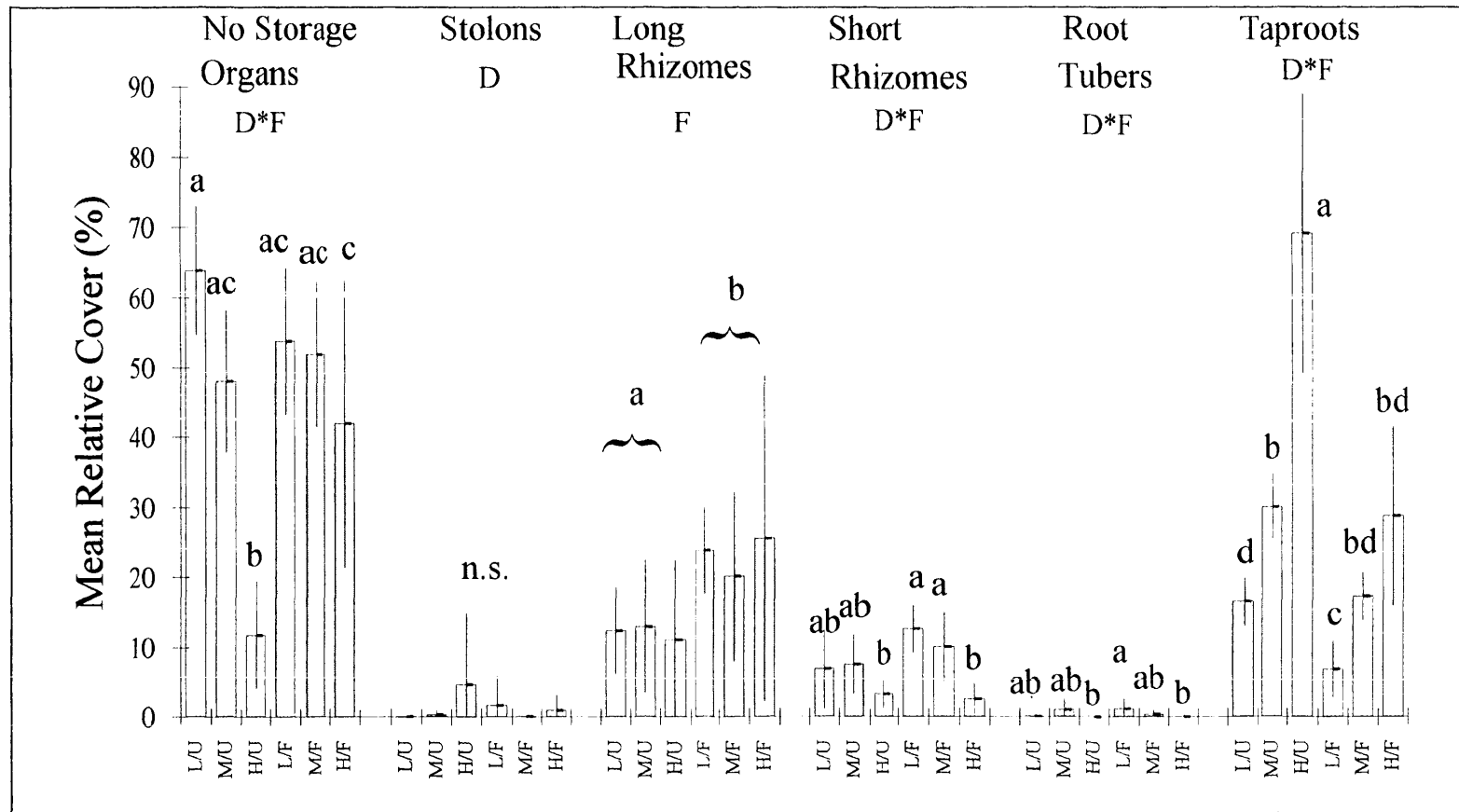
Although anova revealed a significant disturbance x fertilization interaction and a disturbance x sown interaction for the relative number of species with litter greater than 5 cm, pairwise comparisons using Bonferroni adjustment revealed no significant differences between the treatment means (Table 4.10) because pairwise comparisons are more conservative than the F-ratio in anova (Underwood 1981). Sowing did not significantly affect the relative number of species without persistent litter in February 1994, but sowing increased their number in November 1992 (Appendix 7). Sowing did not significantly affect the relative number of species with litter up to 5 cm at any time during the study.

#### 4.3.8 Underground Storage Organs

There was a significant disturbance x fertilization interaction for the relative cover of species without underground storage organs, with short rhizomes, root tubers and with taproots in February 1994 (Table 4.11). High soil disturbance decreased the relative cover of species without underground storage organs to a greater extent in unfertilized plots (Fig. 4.13). The effect of the disturbance x fertilization interaction for the relative cover of species without underground storage organs increased linearly over time. Both moderate and high soil disturbance increased the relative cover of species with taproots to a greater extent in unfertilized plots. The disturbance x fertilization interaction species with taproots diminished over time (Appendix 7). High soil disturbance decreased the relative cover of species with short rhizomes only in fertilized plots. The relative cover of species with root tubers in highly disturbed fertilized plots was lower than in low disturbance fertilized plots.

**Table 4.11:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species in the underground storage organ categories, with disturbance, fertilization and sowing as factors for February 1994. Fertilization x sown and disturbance x fertilization x sown interactions were not significant. Disturbance x sown interaction was not significant for relative cover. † - increased; ‡ - decreased. \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

	df	Absent	Stolons	Long Rhizomes	Short Rhizomes	Root Tubers	Taproots
<b>Relative Cover (%)</b>							
Disturbance	2/48	33.65***	1.96	0.11	17.40***	4.62*	72.85***
Fertilization	1/48	5.93*	0.50	† 10.13**	6.03*	1.17	69.79***
Sown	1/48	0.40	2.50	0.01	1.88	0.03	0.05
Disturbance x Fert	2/48	12.96***	1.90	0.38	3.28*	3.67*	9.71***
<b>Relative Number (%)</b>							
Disturbance	2/48	0.37	† 4.69*	0.04	0.40	‡ 6.93**	1.21
Fertilization	1/48	0.04	0.96	‡ 5.32*	6.52*	0.51	1.23
Sown	1/48	0.26	0.12	9.90**	2.32	0.02	55.78***
Disturbance x Fert	2/48	0.44	2.32	1.59	5.60**	2.75	1.63
Disturbance x Sown	2/48	0.89	2.32	4.55*	1.75	0.02	4.79*



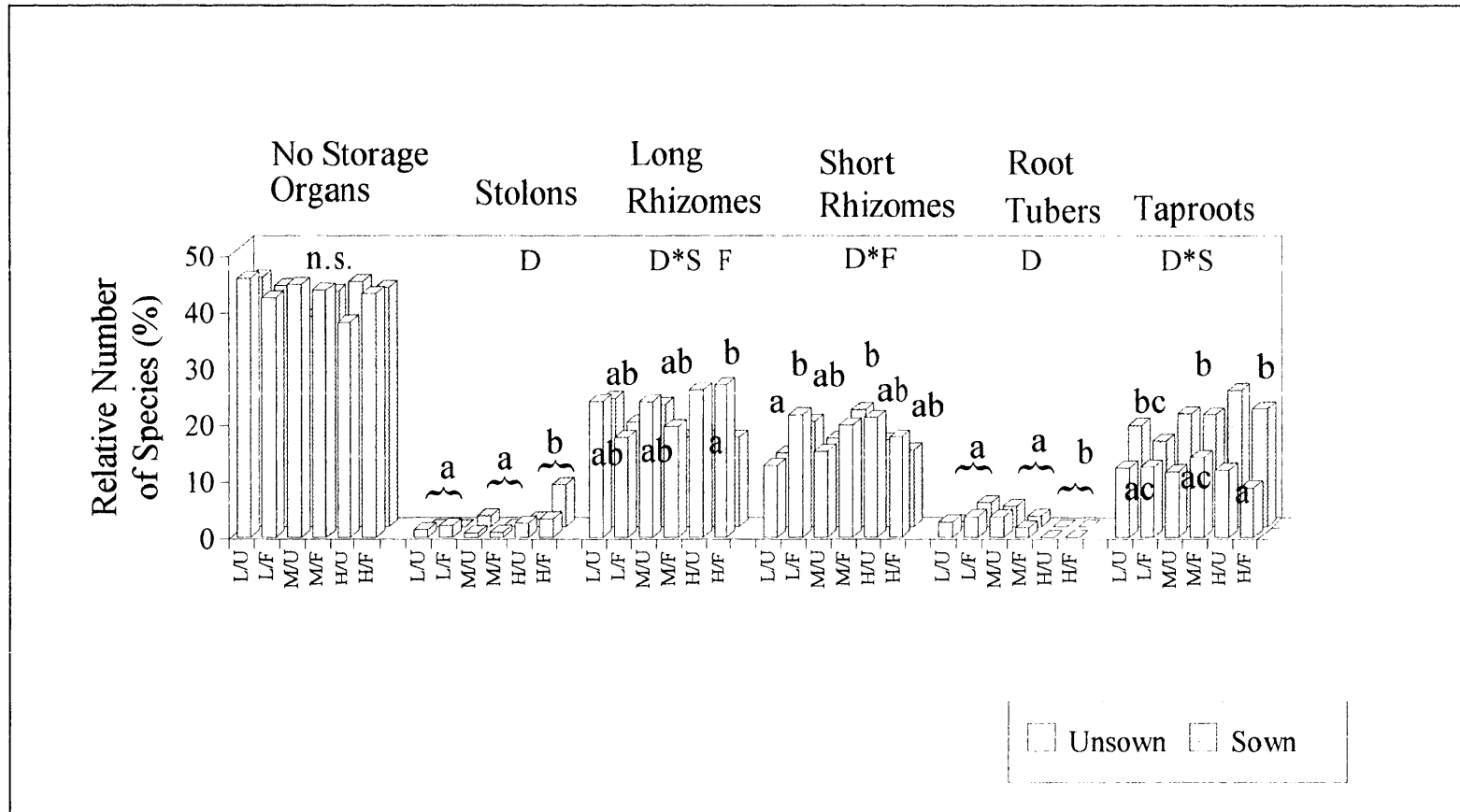
**Fig. 4.13:** Mean relative cover (%) of species without storage organs or with stolons, long rhizomes, short rhizomes, root tubers or taproots in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each underground storage organ category.



The relative cover of species with stolons and long rhizomes was not significantly affected by soil disturbance at any time during the study (Appendix 7). Fertilization significantly increased the relative cover of species with long rhizomes in February 1994 (Table 4.11; Fig. 4.13), but the effect had diminished over time. The relative cover of species with stem tubers was too low to analyse in February 1994, but their relative cover in highly disturbed plots was lower than in low disturbance (2,48 df;  $p < 0.001$ , Bonferroni test) and moderately disturbed (2,48 df;  $p < 0.001$ , Bonferroni test) plots in spring. Fertilization decreased the cover of species with stem tubers (1,48 df;  $p < 0.01$ , Bonferroni test) in March 1993. Fertilization did not affect the relative cover of species with stolons at any time during the study. The sown treatment did not significantly affect the relative cover of species without underground storage organs, with stolons, long rhizomes, short rhizomes, root tubers and taproots at any time during the study.

The relative number of species without underground storage organs was not significantly affected by soil disturbance, fertilization and sowing in February 1994 (Table 4.11), nor at any other time during the study (Appendix 7). High soil disturbance significantly increased the relative number of species with stolons and decreased the number of species with root tubers in February 1994 (Fig. 4.14). There was a significant disturbance  $\times$  fertilization interaction for the relative number of species with short rhizomes. Fertilization increased the relative number of species with short rhizomes only in low disturbance plots. Fertilization did not significantly affect the relative number of species with stolons, root tubers or taproots in February 1994, nor at any other time during the study.

There was a significant disturbance  $\times$  sown interaction for the relative number of species with long rhizomes or taproots in February 1994 (Table 4.11). Sowing decreased the relative number of species with long rhizomes only in highly disturbed plots (Fig. 4.14). Sowing significantly increased the relative number of species with taproots only in moderately and highly disturbed plots. The relative number of species with long rhizomes was significantly decreased by fertilization in February 1994 (1,48 df;  $p < 0.05$ , Bonferroni test). The relative number of species with stem tubers was too low to analyse in February 1994, but their relative number in highly disturbed plots was lower than in low disturbance (2,48 df;  $p < 0.001$ , Bonferroni test) and moderately disturbed (2,48 df;  $p < 0.001$ , Bonferroni test) plots in November 1992. However over time the effect of disturbance became dependent on the level of fertilization (March 1993) and on the level of fertilization and sowing (November 1993). The sown treatment did not significantly affect the relative number of species with stolons, short rhizomes, stem tubers or root tubers at any time during the study (Appendix 7).



**Fig. 4.14:** Mean relative number (%) of species without underground storage organs or with stolons, long rhizomes, short rhizomes, stem tubers, root tubers or taproots in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each of the underground storage organ categories.

### 4.3.9 Diaspore Number and Diaspore Mass

The canopy cover of species was positively correlated with their diaspore number per individual in highly disturbed plots in November 1993 (Table 4.12). The correlations between the diaspore mass of species and their canopy cover were not significant in any treatments in both November 1993 and February 1994.

**Table 4.12:** Spearman Rank correlation coefficients between continuous diaspore attributes of species and their absolute cover (%) in each treatment in November and February 1994. Significant correlations are marked in bold. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

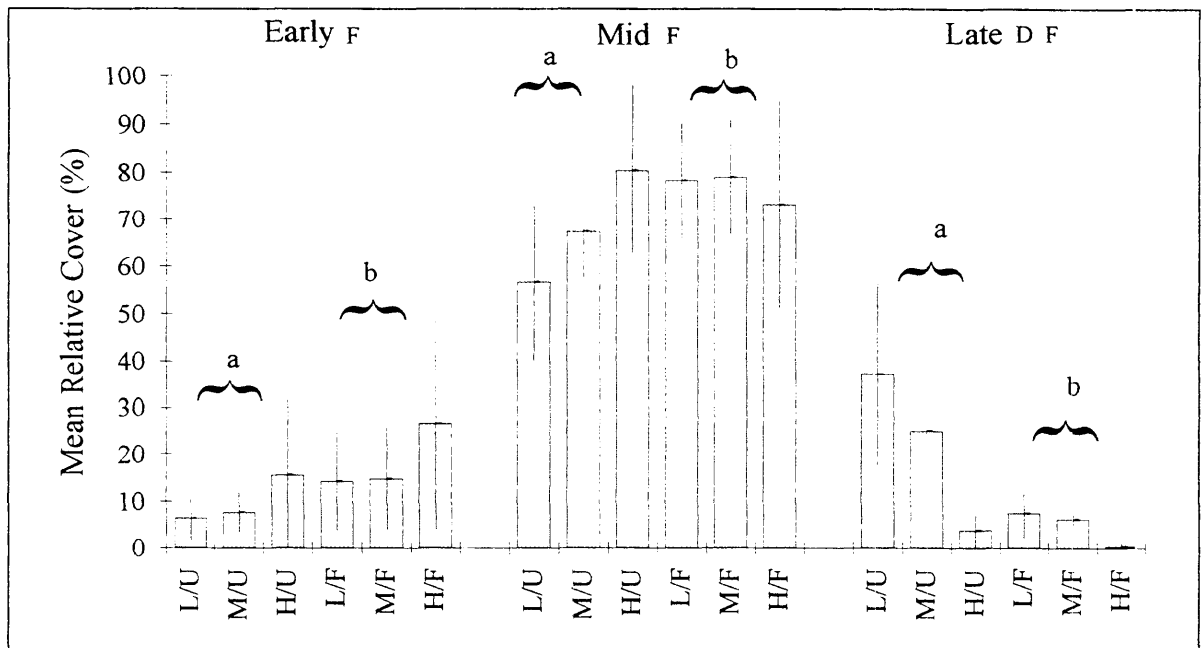
Plant Attribute	n		L/U	M/U	H/U	L/F	M/F	H/F
Diaspore Number	47	Nov. 1993	-0.076	0.038	<b>0.214*</b>	0.115	0.053	<b>0.250*</b>
	47	Feb. 1994	-0.164	-0.146	0.097	-0.015	-0.049	0.132
Diaspore Mass	51	Nov. 1993	-0.039	-0.174	0.063	0.005	-0.008	-0.010
	50	Feb. 1994	0.077	0.060	0.062	0.103	0.158	-0.050

### 4.3.10 Commencement of Flowering

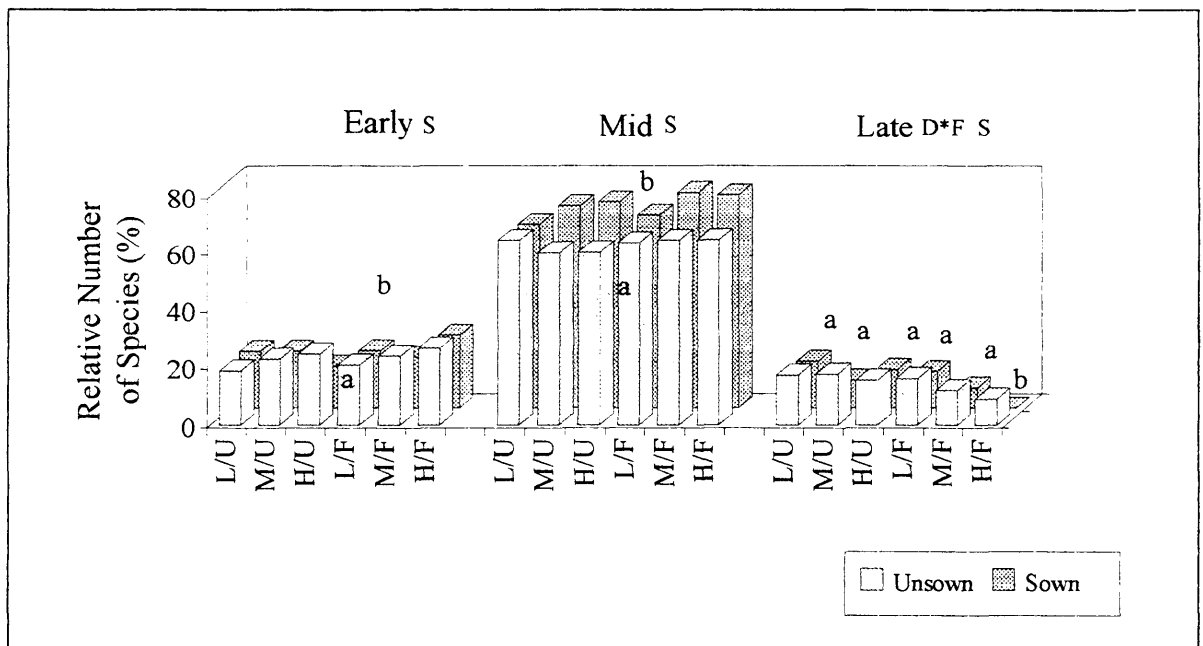
In February 1994, fertilization significantly increased the relative cover of species that commenced flowering early (August - October) and mid-season (November - December) and decreased the cover of species that commenced flowering late (January - February) (Fig. 4.15; Table 4.13). Disturbance did not significantly affect the relative cover of early and mid-flowering species at any time during the study (Appendix 7). In February 1994, the relative cover of late flowering species in highly disturbed plots was lower than in low disturbance plots (2,48 df;  $p < 0.001$ , Bonferroni test) and moderately disturbed plots (2,48 df;  $p < 0.001$ , Bonferroni test). Sowing did not significantly affect the relative cover of early, mid or late-flowering species at any time during the study.

**Table 4.13:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of the commencement of flowering categories with disturbance, fertilization & sown as factors for February 1994. Early = Aug - Oct; Mid = Nov - Dec; late = Jan - Feb. Disturbance x sown, fertilization x sown and disturbance x fertilization x sown interactions were not significant. Disturbance x fertilization interaction was not significant for relative cover.  $\uparrow$  - increased;  $\downarrow$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Early	Mid	Late
<b>Relative Cover (%)</b>				
Disturbance	2/48	1.79	2.32	$\downarrow$ <b>28.91***</b>
Fertilization	1/48	$\uparrow$ <b>5.85*</b>	$\uparrow$ <b>4.07*</b>	$\downarrow$ <b>48.11***</b>
Sown	1/48	1.14	0.05	0.31
<b>Relative Number of Species (%)</b>				
Disturbance	2/48	0.79	1.17	9.08***
Fertilization	1/48	1.74	2.80	18.96***
Sown	1/48	$\downarrow$ <b>4.24*</b>	$\uparrow$ <b>17.82***</b>	10.16**
Disturbance x Fertilization	2/48	1.52	0.30	<b>5.42**</b>



**Fig. 4.15:** Mean relative cover (%) of early (Aug - Oct), mid-season (Nov - Dec) and late (Jan - Feb) flowering species in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means in each flowering category.



**Fig. 4.16:** Mean relative number (%) of early (Aug - Oct), mid-season (Nov - Dec) and late (Jan - Feb) flowering species in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each flowering category.

Disturbance and fertilization did not significantly affect the relative number of early or mid-flowering species at any time during the study (Appendix 7). Sowing significantly decreased the relative number of early flowering species and increased the number of mid-

flowering species (Table 4.13; Fig. 4.16). Anova revealed a significant disturbance x fertilization interaction for the relative number of late flowering species. High soil disturbance decreased the relative number of late flowering species only in fertilized plots. The effect of the disturbance x fertilization interaction for late flowering species was greater in summer than in spring. Sowing significantly decreased the relative number of late flowering species in February 1994 (1,48 df;  $p < 0.01$ , Bonferroni test).

#### 4.3.11 Flowering Period Duration

The canopy cover of species was positively correlated with their flowering period duration in unfertilized plots in February 1994 (Table 4.14).

**Table 4.14:** Spearman Rank correlation coefficients between the flowering duration of species and their absolute cover (%) in each treatment in November 1993 and February 1994. Significant correlations are marked in bold. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

Flowering Duration	n	L/U	M/U	H/U	L/F	M/F	H/F
November 1993	51	0.122	0.165	0.137	0.068	0.116	-0.010
February 1994	50	<b>0.237*</b>	<b>0.281*</b>	<b>0.241*</b>	0.115	0.152	0.175

#### 4.3.12 Leaf Life span

The canopy cover of species was negatively correlated with their leaf life span in highly disturbed plots and moderately disturbed fertilized plots in November 1993 (Table 4.15). By February 1994, the negatively correlation only remained significant in highly disturbed fertilized plots, while there was a significant positive correlation in low disturbance unfertilized plots.

**Table 4.15:** Spearman Rank correlation coefficients between the leaf life span of species and their absolute cover (%) in each treatment in November 1993 and February 1994. Significant correlations are marked in bold. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

Leaf life span	n	L/U	M/U	H/U	L/F	M/F	H/F
November 1993	30	0.023	-0.126	<b>-0.259*</b>	-0.168	<b>-0.261*</b>	<b>-0.451***</b>
February 1994	29	<b>0.317**</b>	0.104	-0.099	-0.034	-0.126	<b>-0.385**</b>

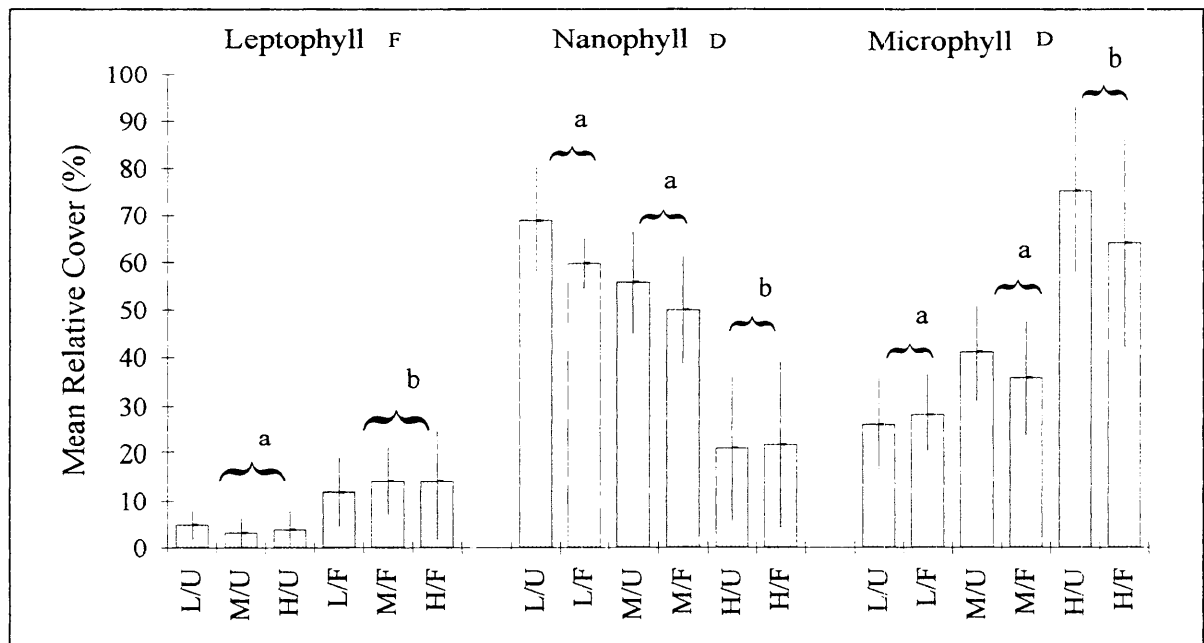
#### 4.3.13 Leaf Size

Fertilization significantly increased the relative cover of species with leptophyll (< 25 mm<sup>2</sup>) sized leaves in February 1994 (Table 4.16; Fig. 4.17). The effect of fertilization on the relative cover of species with leptophyll leaves was greater in spring than in summer (Appendix 7). High soil disturbance decreased the relative cover of species with nanophyll

(25 - 225 mm<sup>2</sup>) sized leaves and increased the cover of species with microphyll (225 - 2025 mm<sup>2</sup>) sized leaves in February 1994. The effect of disturbance on the relative cover of species with nanophyll leaves diminished over time, while the effect on species with microphyll leaves was greater in spring than in summer.

**Table 4.16:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species in the leaf size categories with disturbance, fertilization & sown as factors for February 1994. Leptophyll = < 25 mm<sup>2</sup>; nanophyll = 25 - 225 mm<sup>2</sup>; microphyll = 225 - 2025 mm<sup>2</sup>. Disturbance x sown and disturbance x fertilization x sown interactions were not significant. Disturbance x fertilization and fertilization x sown interactions were not significant for relative cover. ↑ - increased; ↓ - decreased \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

	df	Leptophyll	Nanophyll	Microphyll
<b>Relative Cover (%)</b>				
Disturbance	2/48	0.07	↓ 53.83***	↑ 43.71***
Fertilization	1/48	↑ 30.34***	1.43	1.58
Sown	1/48	0.09	0.02	0.03
<b>Relative Number of Species (%)</b>				
Disturbance	2/48	6.69**	4.26*	↑ 21.41***
Fertilization	1/48	4.39*	0.36	7.21*
Sown	1/48	1.23	1.51	5.32*
Disturbance x Fertilization	2/48	4.14*	0.38	1.36
Fertilization x Sown	1/48	0.40	14.60***	12.28**

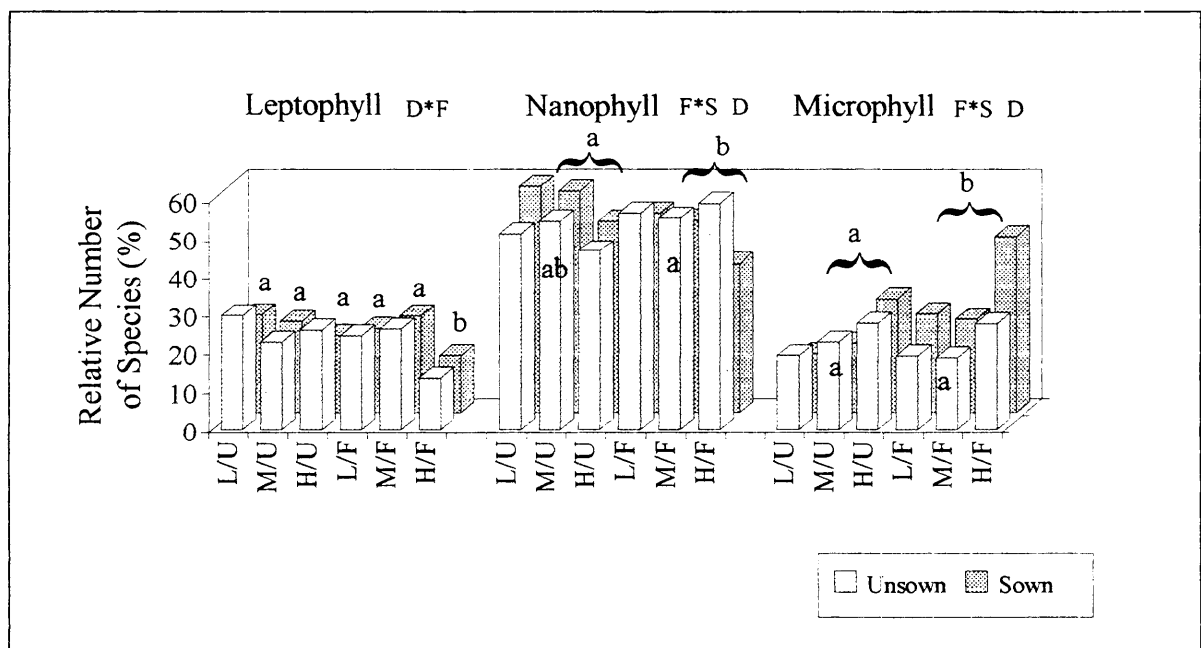


**Fig. 4.17:** Mean relative cover (%) of species with leptophyll (< 25 mm<sup>2</sup>), nanophyll (25 - 225 mm<sup>2</sup>) or microphyll (225 - 2025 mm<sup>2</sup>) sized leaves in each of the treatments in February 1994. Note the change in order of the treatments for species with leptophyll leaves. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent ± 1 standard error. Different letters denote significant differences (p < 0.05 level) between the treatment means of each leaf size category.

Disturbance did not significantly affect the relative cover of species with leptophyll leaves in February 1994, but there was a significant disturbance x fertilization interaction in

spring (Appendix 7). Fertilization did not significantly affect the relative cover of species with nanophyll leaves in February 1994, nor at any other time during the study. Fertilization decreased the relative cover of species with microphyll leaves in November 1993 only. The sown treatment did not significantly affect the relative cover of species with leptophyll, nanophyll or microphyll leaves at any time during the study.

Anova revealed a significant disturbance x fertilization interaction for the relative number of species with leptophyll leaves in February 1994 (Table 4.16). High soil disturbance decreased the relative number of species with leptophyll leaves only in fertilized plots (Fig. 4.18). Sowing did not significantly affect the relative number of species with leptophyll leaves in February 1994, but did decrease their number in November 1992 and there was a significant disturbance x fertilization x sown interaction in March 1993 and November 1993 (Appendix 7). There was a significant fertilization x sown interaction for the relative number of species with nanophyll or microphyll leaves. Fertilization decreased the relative number of species with nanophyll leaves and increased species with microphyll leaves only in sown plots. The relative number of species with nanophyll leaves in highly disturbed plots was lower than in low disturbance plots (2,48 df;  $p < 0.05$ , Bonferroni test). The relative number of species with microphyll leaves in highly disturbed plots was greater than in low disturbance plots (2,48 df;  $p < 0.001$ , Bonferroni test) and moderately disturbed plots (2,48 df;  $p < 0.001$ , Bonferroni test). The effect of disturbance and the fertilization x sown interaction on the relative number of species with nanophyll or microphyll leaves increased linearly over time.



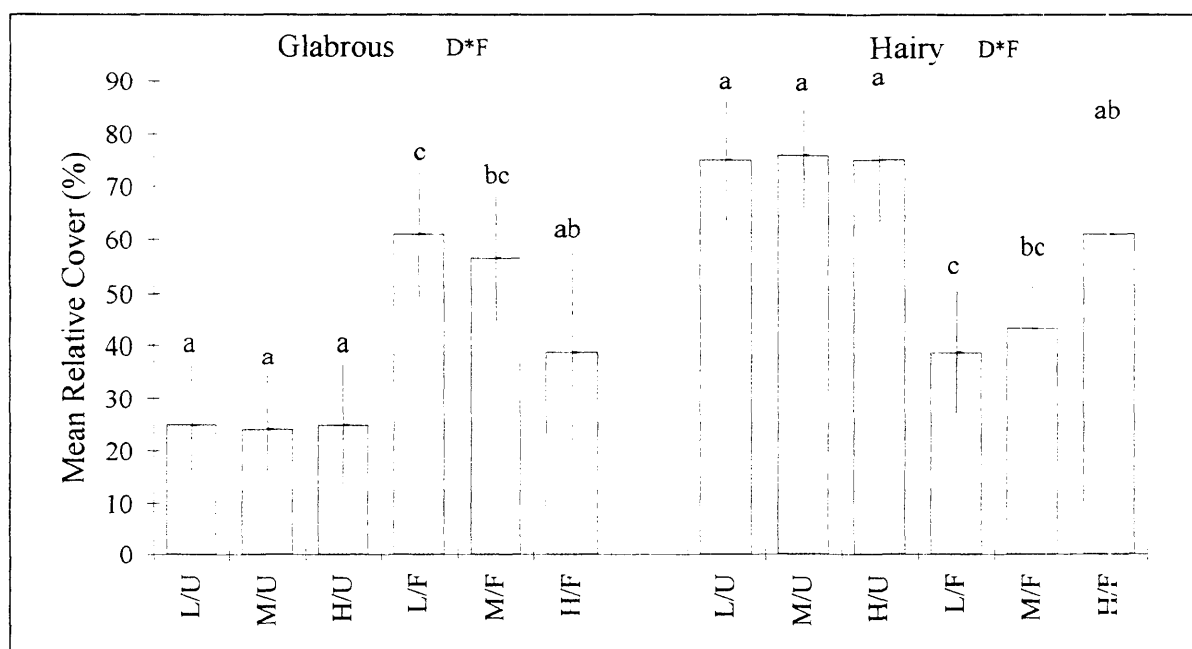
**Fig. 4.18:** Mean relative number (%) of species with leptophyll (< 25 mm<sup>2</sup>), nanophyll (25 - 225 mm<sup>2</sup>) or microphyll (225 - 2025 mm<sup>2</sup>) sized leaves in each of the treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each leaf size category.

### 4.3.14 Diaspore Hairiness

There was a significant disturbance x fertilization interaction for the relative cover of species with glabrous or hairy diaspores in February 1994 (Table 4.17). Fertilization increased the relative cover of species with glabrous diaspores and decreased species with hairy diaspores in low and moderately disturbed plots, but not in highly disturbed plots (Fig. 4.19). The relative cover of species with glabrous or hairy diaspores was not significantly affected by sowing at any time during the study (Appendix 7).

**Table 4.17:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species with glabrous or hairy diaspores with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown, fertilization x sown and disturbance x fertilization x sown interactions were not significant.  $\hat{\uparrow}$  - increased;  $\hat{\downarrow}$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

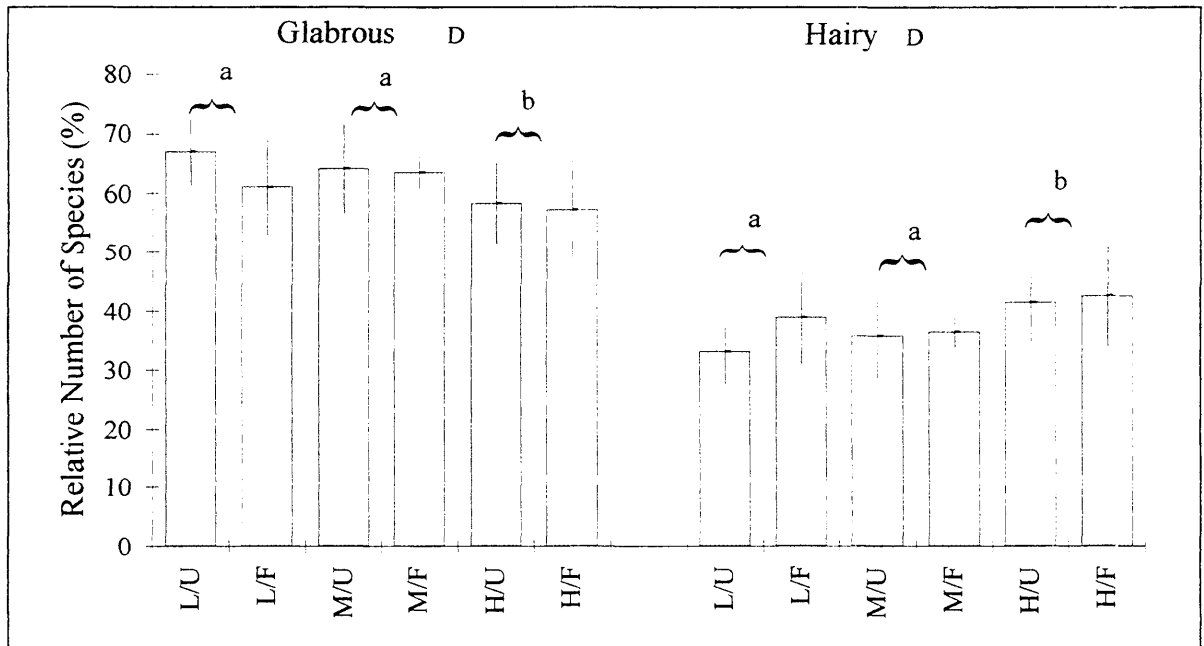
	df	Relative Cover (%)		Relative Number of Species (%)	
		Glabrous	Hairy	Glabrous	Hairy
Disturbance	2/48	3.61*	3.61*	$\hat{\downarrow}$ 4.61*	$\hat{\uparrow}$ 4.61*
Fertilization	1/48	57.75***	57.75***	1.91	1.91
Sown	1/48	0.39	0.39	0.02	0.02
Disturbance x Fertilization	2/48	<b>3.21*</b>	<b>3.21*</b>	0.83	0.83



**Fig. 4.19:** Mean relative cover (%) of species with glabrous or hairy diaspores in each of the treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the means of the species with glabrous diaspores and between the means of the species with hairy diaspores.



High soil disturbance decreased the relative number of species with glabrous diaspores and increased species with hairy diaspores in February 1994 (Fig. 4.20; Table 4.17). Fertilization significantly increased the relative number of species with glabrous diaspores and decreased species with hairy diaspores in November 1992, but the effect diminished over time (Appendix 7) until no significant effect was detected in February 1994. The relative number of species with glabrous or hairy diaspores was not significantly affected by sowing at any time during the study.



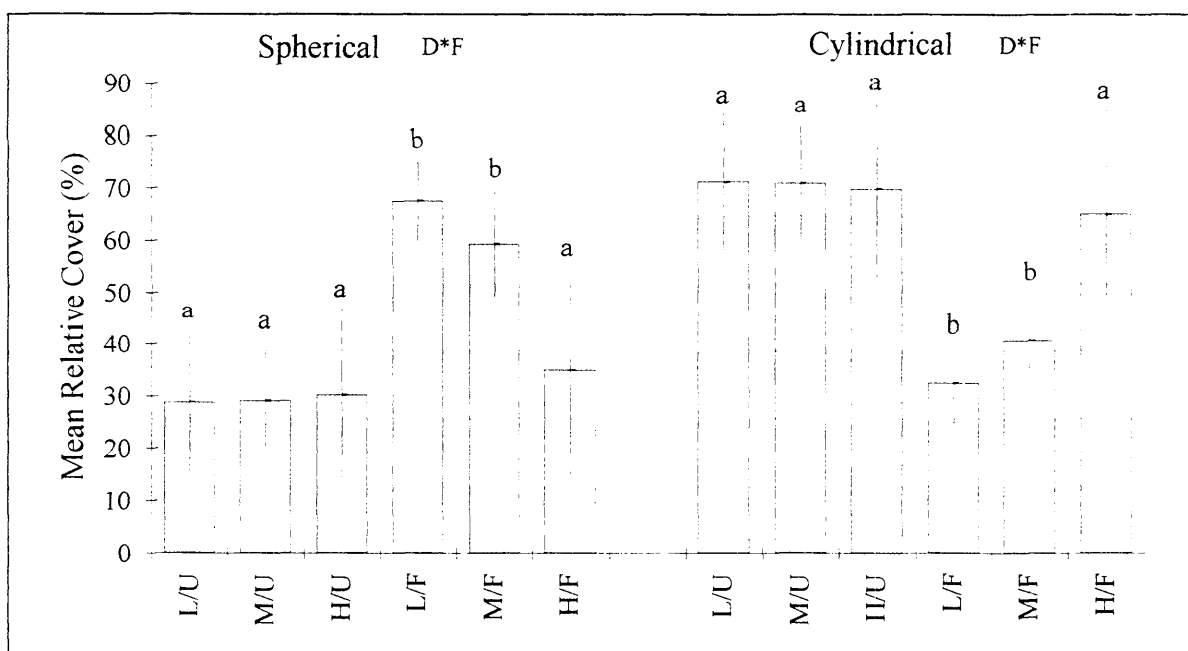
**Fig. 4.20:** Mean relative number (%) of species with glabrous or hairy diaspores in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the means of the species with glabrous diaspores and between the means of the species with hairy diaspores.

#### 4.3.15 Diaspore Shape

Anova revealed a significant disturbance  $\times$  fertilization interaction for the relative cover of species with spherical or cylindrical diaspores in February 1994 (Table 4.18). The increase in the relative cover of spherical diaspores and the decrease in species with cylindrical diaspores with fertilization diminished with increasing soil disturbance (Fig. 4.21). High soil disturbance decreased the relative cover of species with spherical diaspores and increased species with cylindrical diaspores only in fertilized plots. The relative cover of species with spherical or cylindrical diaspores was not significantly affected by sowing at any time during the study (Appendix 7).

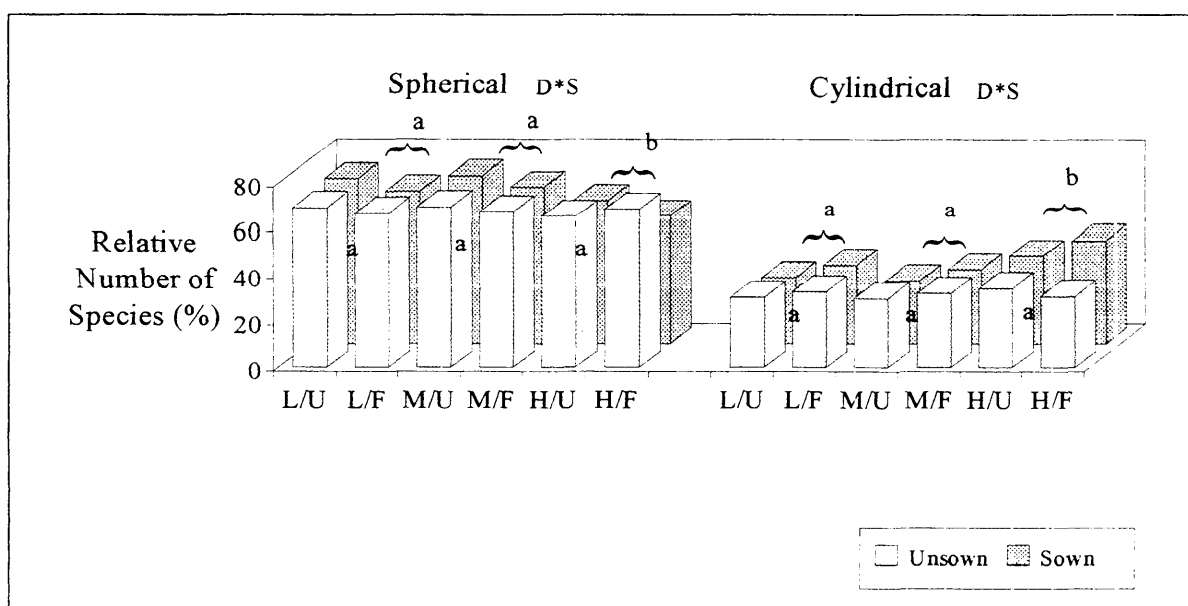
**Table 4.18:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species with spherical or cylindrical shaped diaspores with disturbance, fertilization & sown as factors for February 1994. Fertilization x sown and disturbance x fertilization x sown interactions were not significant. ↑ - increased; ↓ - decreased. \* p < 0.05; \*\* p < 0.01; \*\*\* p < 0.001.

	d.f	Relative Cover (%)		Relative Number of Species (%)	
		Spherical	Cylindrical	Spherical	Cylindrical
Disturbance	2/48	6.17**	6.17**	5.77**	5.77**
Fertilization	1/48	40.52***	40.52***	3.17	3.17
Sown	1/48	0.60	0.60	1.54	1.54
Disturbance x Fertilization	2/48	<b>6.85**</b>	<b>6.85**</b>	0.18	0.18
Disturbance x Sown	2/48	0.25	0.25	<b>3.53*</b>	<b>3.53*</b>



**Fig. 4.21:** Mean relative cover (%) of species with spherical or cylindrical shaped diaspores in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the means of the species with spherical diaspores and between the means of the species with cylindrical diaspores.

There was a significant disturbance x sown interaction for the relative number of species with spherical or cylindrical diaspores in February 1994 (Table 4.18). High soil disturbance decreased the relative number of species with spherical diaspores and increased species with cylindrical diaspores only in sown plots (Fig. 4.22). Fertilization did not significantly affect the relative number of species with spherical or cylindrical diaspores in February 1994. However, fertilization significantly increased the relative number of species with spherical diaspores and decreased species with cylindrical diaspores in March 1993 and November 1993 (Appendix 7).



**Fig. 4.22:** Mean relative number (%) of species with spherical or cylindrical shaped diaspores in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of the diaspore shape categories.

#### 4.3.16 Diaspore Dispersal Morphology

Fertilization significantly increased the relative cover of species without diaspore dispersal appendages in February 1994 (Table 4.19; Fig. 4.23). The effect of fertilization was greater in summer than in spring (Appendix 7). Soil disturbance did not significantly affect the relative cover of species without diaspore dispersal appendages in February 1994, but did increase their cover in November 1993. Sowing did not significantly affect the relative cover of species without diaspore dispersal appendages in February 1994, but did increase cover in spring.

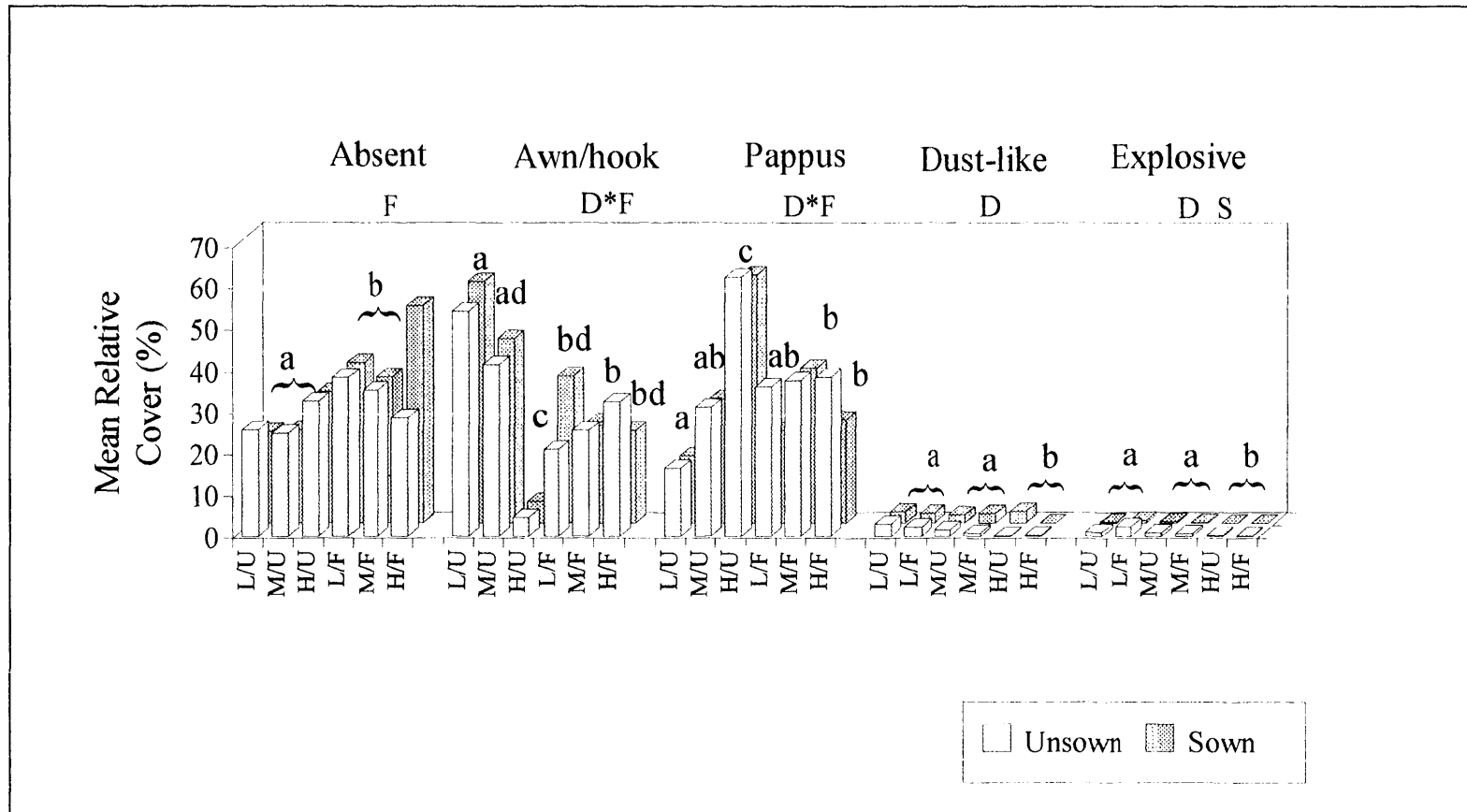
**Table 4.19:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species in the diaspore dispersal morphology categories with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown, fertilization x sown and disturbance x fertilization x sown interactions were not significant. Disturbance x fertilization interaction was not significant for relative number of species.  $\uparrow$  - increased;  $\downarrow$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Absent	Awn/hook	Pappus	Dust-like	Explosive
<b>Relative Cover (%)</b>						
Disturbance	2/48	0.75	24.75***	20.74***	$\downarrow$ 12.60***	$\downarrow$ 9.58***
Fertilization	1/48	$\uparrow$ 8.66**	6.32*	0.90	2.85	0.57
Sown	1/48	0.81	0.41	3.38	3.03	$\downarrow$ 8.93**
Disturbance x Fert.	2/48	0.38	25.09***	19.60***	0.87	2.54
<b>Relative Number (%)</b>						
Disturbance	2/48	$\uparrow$ 9.56***	$\downarrow$ 3.72*	3.09	2.06	$\downarrow$ 12.62***
Fertilization	1/48	1.00	2.66	$\uparrow$ 6.51*	$\downarrow$ 9.42**	$\downarrow$ 4.49*
Sown	1/48	$\uparrow$ 11.75**	0.62	$\downarrow$ 9.19**	1.41	1.01

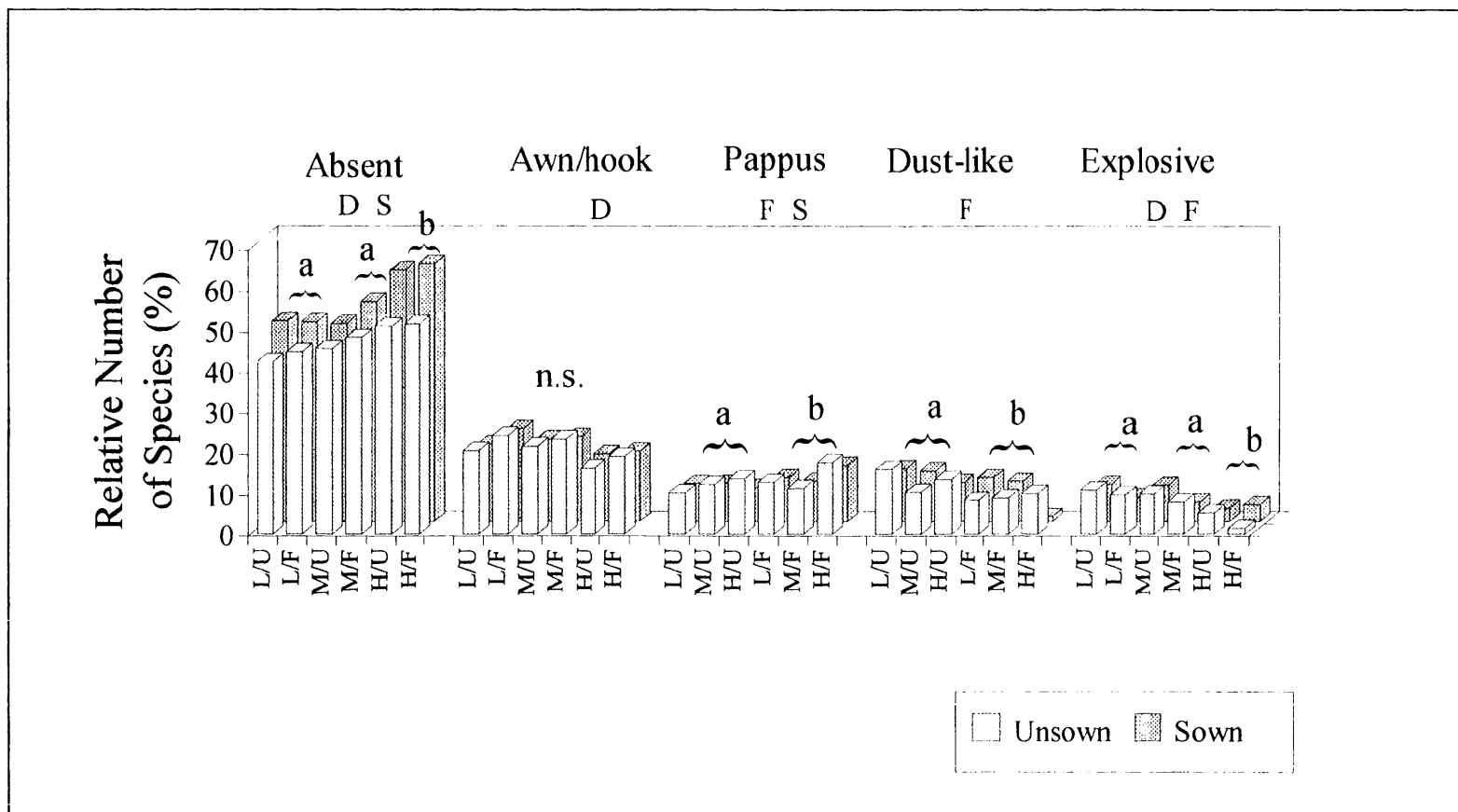
Anova detected a significant disturbance x fertilization interaction for the relative cover of species with awns/hooks or pappus on their diaspores (Table 4.19). Fertilization decreased the relative cover of species with awns/hooks on their diaspores in low and moderately disturbed plots, but increased their cover in highly disturbed plots (Fig. 4.23). High disturbance increased the relative cover of species with pappus on their diaspores only in unfertilized plots. The effect of the disturbance x fertilization interaction on the cover of species with awns/hooks or pappus increased linearly over time (Appendix 7). High soil disturbance decreased the relative cover of species with dust-like or explosive diaspores in February 1994). Fertilization significantly increased the relative cover of species with dust-like diaspores in March 1993 only. Fertilization did not significantly affect the relative cover of species with explosive diaspores at any time during the study. The relative cover of species with explosive diaspores was significantly decreased by sowing in February 1994 (1,48 df;  $p < 0.01$ , Bonferroni test). Sowing did not significantly affect the relative cover of species with awns/hooks or pappus on their diaspores or dust-like diaspores at any time during the study.

High soil disturbance increased the relative number of species without diaspore dispersal appendages in February 1994 (Fig. 4.24; Table 4.19). Sowing increased the relative number of species without diaspore dispersal appendages (1,48 df;  $p < 0.01$ , Bonferroni test). Fertilization did not significantly affect the relative number of species without diaspore dispersal appendages or with awns/hooks at any time during the study (Appendix 7). Although anova revealed that disturbance significantly affected the relative number of species with awns/hooks in February 1994, Bonferroni pairwise comparisons found no significant differences between the treatment means.

Fertilization significantly increased the relative number of species with pappus on their diaspores and decreased species with dust-like diaspores in February 1994 (Fig. 4.24; Table 4.19). The effect of fertilization on species with pappus and species with dust-like diaspores increased linearly over time (Appendix 7). Soil disturbance significantly increased the relative number of species with pappus on their diaspores only in spring. The relative number of species with dust-like diaspores was not significantly affected by soil disturbance at any time during the study. Sowing decreased the relative number of species with pappus on their diaspores in February 1994 (1,48 df;  $p < 0.01$ , Bonferroni test). High soil disturbance significantly decreased the relative number of species with explosive diaspores. The effect of disturbance on species with explosive diaspores increased linearly over time. The relative number of species with explosive diaspores was decreased by fertilization (1,48 df;  $p < 0.05$ , Bonferroni test). Sowing did not significantly affect the relative number of species with awns/hooks, dust-like or explosive diaspores at any time during the study.



**Fig. 4.23:** Mean relative cover (%) of species with awn/hook, pappus, dust-like or explosive diaspores in each of the twelve treatments in February 1994. Note the change in order of treatments for species with dust-like or explosive diaspores. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each diaspore dispersal morphology category.



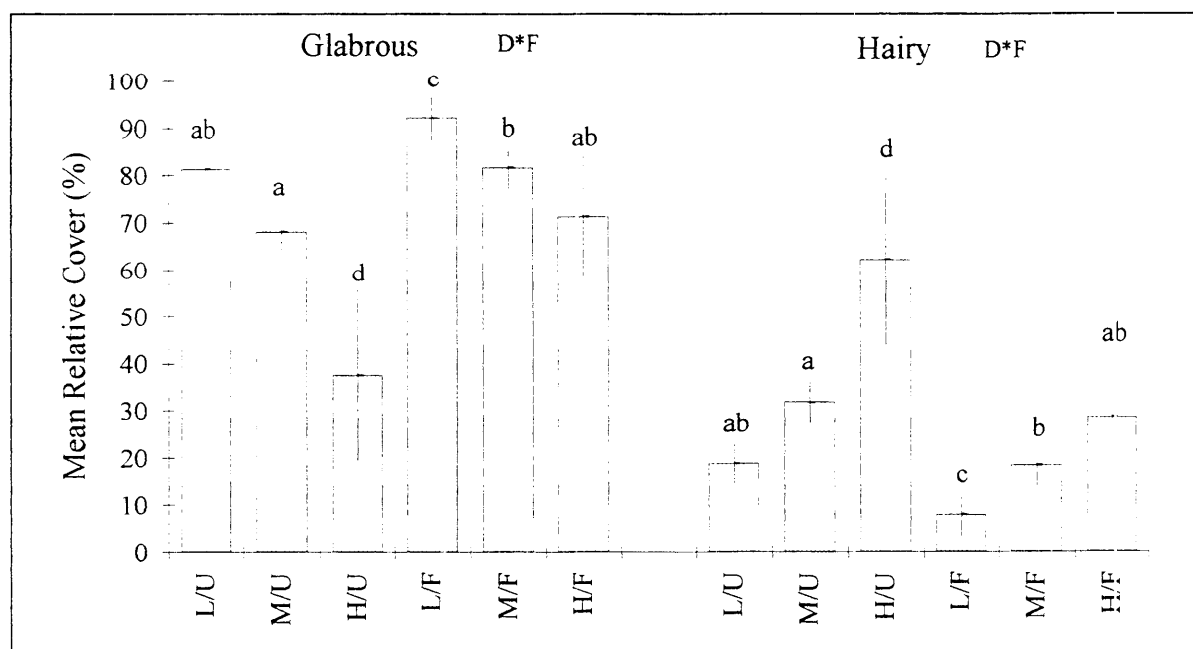
**Fig. 4.24:** Mean relative number (%) of species with awns/hooks, pappus, dust-like or explosive diaspores in each of the twelve treatments in February 1994. Note the change in order of treatments for species with pappus on their diaspores and dust-like diaspores. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each diaspore dispersal morphology category.

### 4.3.17 Leaf Hairiness

Anova revealed a significant disturbance x fertilization interaction for the relative cover of species with glabrous or hairy leaves in February 1994 (Table 4.20). The increase in the relative cover of species with glabrous leaves and the decrease in species with hairy leaves with fertilization increased with increasing soil disturbance (Fig. 4.25). Sowing did not significantly affect the cover of species with glabrous or hairy leaves at any time during the study (Appendix 7).

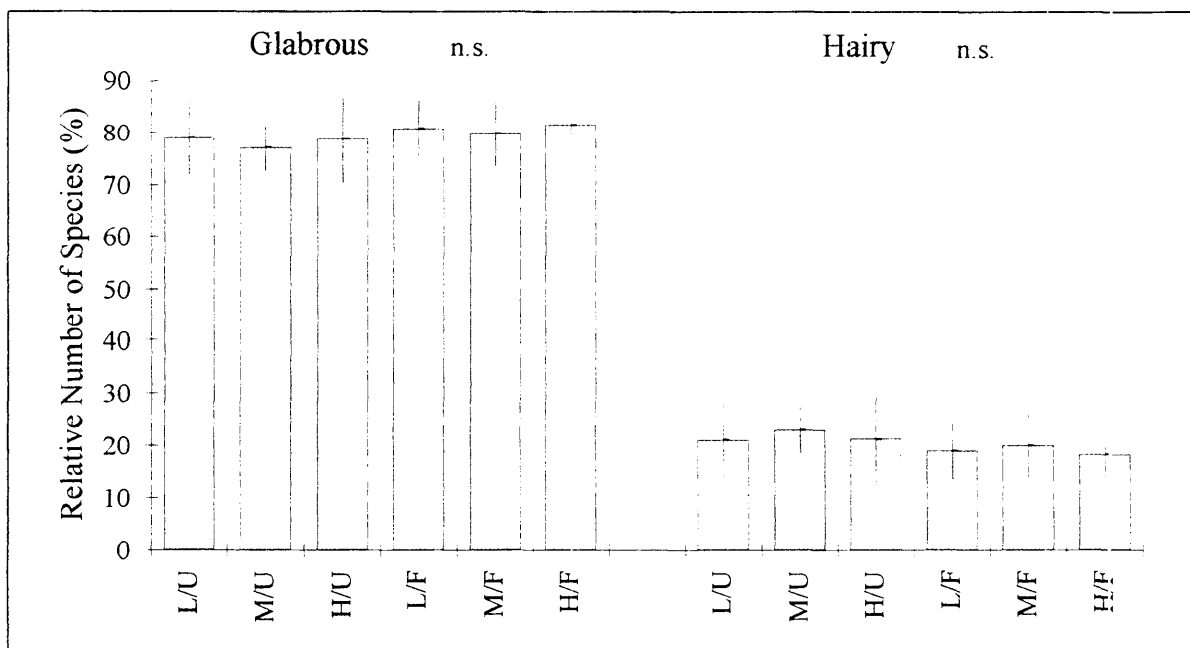
**Table 4.20:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species with glabrous or hairy leaves with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown, fertilization x sown and disturbance x fertilization x sown interactions were not significant. ↑ - increased; ↓ - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Relative Cover (%)		Relative Number of Species (%)	
		Glabrous	Hairy	Glabrous	Hairy
Disturbance	2/48	56.09***	56.09***	0.43	0.43
Fertilization	1/48	62.74***	62.74***	2.64	2.64
Sown	1/48	1.72	1.72	0.21	0.21
Disturbance x Fertilization	2/48	5.19**	5.19**	0.03	0.03



**Fig. 4.25:** Mean relative cover (%) of species with glabrous or hairy leaves in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the means of the species with glabrous leaves and between the means of the species with hairy leaves.

The relative number of species with glabrous or hairy leaves was not significantly affected by soil disturbance and sowing in February 1994 (Table 4.20; Fig. 4.26), nor at any other time during the study (Appendix 7). Fertilization increased the relative number of species with glabrous leaves and decreased species with hairy leaves in November 1993 only.



**Fig. 4.26:** Mean relative number (%) of species with glabrous or hairy leaves in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard error. Different letters denote significant differences ( $p < 0.05$  level) between the means of the species with glabrous leaves and between the means of the species with hairy leaves.

#### 4.3.18 Diaspore Surface Texture

Anova revealed a significant disturbance  $\times$  fertilization interaction for the relative cover of species with smooth or rugose/striate diaspores in February 1994 (Table 4.21). Fertilization decreased the relative cover of species with smooth diaspores in low disturbance plots, but increased their cover in highly disturbed plots (Fig. 4.27). Fertilization increased the relative cover of species with rugose/striate diaspores in low disturbance plots only. The effect of the disturbance  $\times$  fertilization interaction increased linearly over time (Appendix 7). Sowing significantly increased the relative cover of species with smooth diaspores (1,48 df;  $p < 0.01$ ) and decreased species with rugose/striate diaspores (1,48 df;  $p < 0.05$ ) in February 1994.

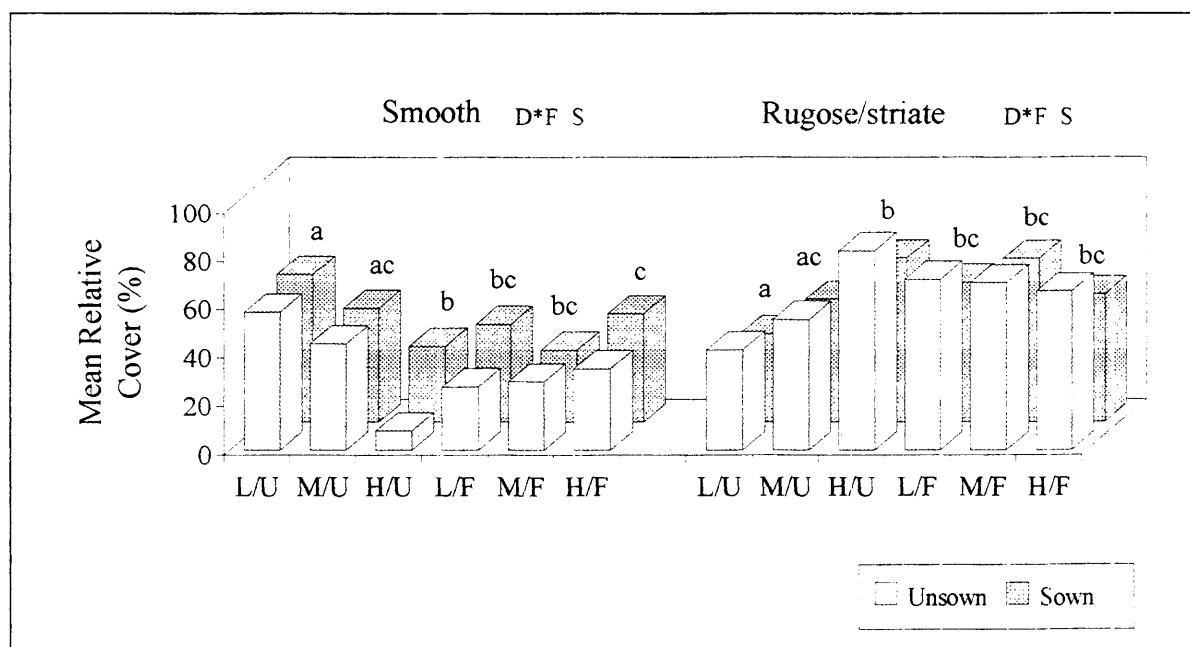
There was a significant disturbance  $\times$  sown interaction for the relative number of species with smooth or rugose/striate diaspores in February 1994 (Table 4.21). High soil



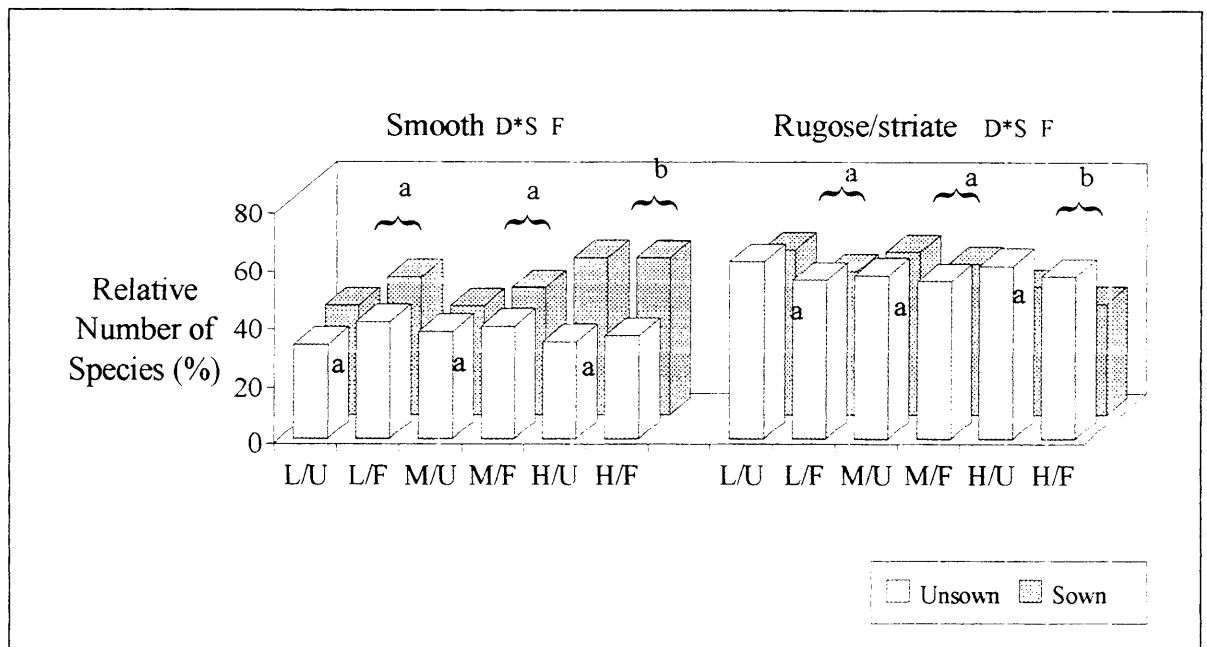
disturbance significantly increased the relative number of species with smooth diaspores and decreased species with rugose/striate diaspores in sown plots only (Fig. 4.28). Fertilization increased the relative number of species with smooth diaspores (1,48 df;  $p < 0.01$ ) and decreased species with rugose/striate diaspores (1,48 df;  $p < 0.01$ ) in February 1994.

**Table 4.21:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of the diaspore surface texture categories with disturbance, fertilization & sown as factors for February 1994. Fertilization x sown and disturbance x fertilization x sown interactions were not significant. Disturbance x sown interaction was not significant for relative cover and disturbance x fertilization interaction was not significant for relative number of species.  $\uparrow$  - increased;  $\downarrow$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Smooth	Rugose/striate
<b>Relative Cover (%)</b>			
Disturbance	2/48	8.39**	6.07**
Fertilization	1/48	5.23*	5.29*
Sown	1/48	$\uparrow$ 8.77**	$\downarrow$ 4.81*
Disturbance x Fertilization	2/48	17.11***	11.57***
<b>Relative Number of Species (%)</b>			
Disturbance	2/48	3.89*	4.38*
Fertilization	1/48	$\uparrow$ 7.97**	$\downarrow$ 7.55**
Sown	1/48	27.95***	21.83***
Disturbance x Sown	2/48	9.52***	6.80**



**Fig. 4.27:** Mean relative cover (%) of species with smooth or rugose/striate diaspores in each of the treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the means of the species with smooth diaspores and between the species with rugose/striate diaspores.



**Fig. 4.28:** Mean relative number (%) of species with smooth or rugose/striate diaspores in each of the treatments for February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the means of the species with smooth diaspores and between the species with rugose/striate diaspores.

#### 4.3.19 Root:Shoot Ratio and Allometric Constant of Seedlings

The canopy cover of species was negatively correlated with their root:shoot ratio in highly disturbed fertilized plots in November 1993 (Table 4.22). In February 1994, the negative correlation remained significant in highly disturbed fertilized plots, while a significant positive correlation occurred on the control (i.e. unfertilized, low disturbance) plots. Correlations between the allometric constant of a species and their canopy cover were not significant in any of the treatments.

**Table 4.22:** Spearman Rank correlation coefficients between the root:shoot ratio or the allometric constant of species and their absolute cover (%) in each treatment in November 1993 and February 1994. Significant correlations are marked in bold. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. \* -  $p < 0.05$ ; \*\* -  $p < 0.01$ ; \*\*\* -  $p < 0.001$ .

Plant Attribute		n	L/U	M/U	H/U	L/F	M/F	H/F
Root:Shoot ratio	Nov. 1993	16	0.274	0.131	-0.173	-0.107	-0.191	-0.360*
	Feb. 1994	16	<b>0.321*</b>	0.207	-0.059	-0.125	-0.246	-0.365*
Allometric constant	Nov. 1993	14	-0.001	-0.094	-0.215	0.050	-0.211	-0.242
	Feb. 1994	14	0.131	0.040	0.006	-0.033	-0.208	-0.203

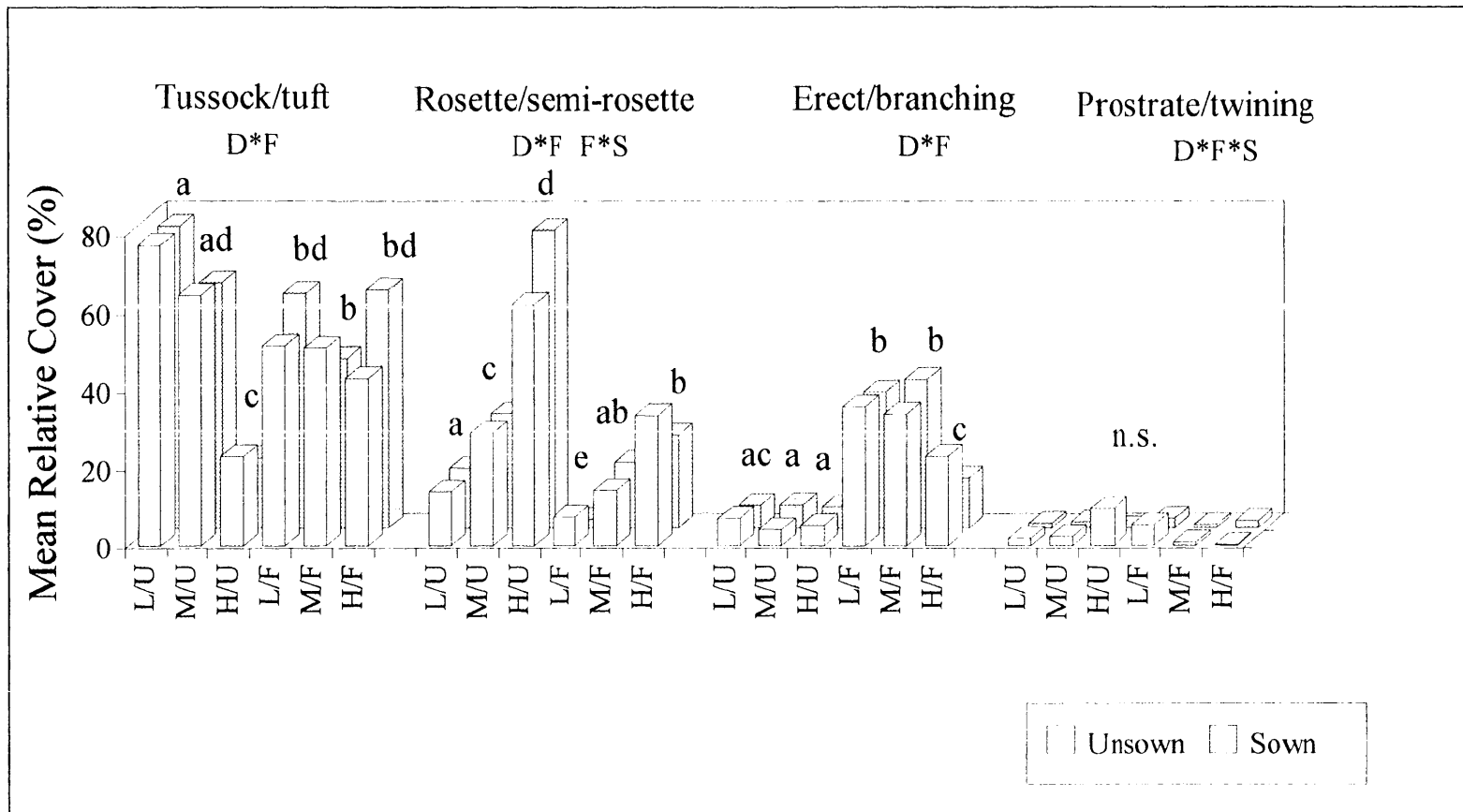
#### 4.3.20 Stem Structure

Anova detected a significant disturbance x fertilization interaction for the relative cover of species with tussock/tuft, rosette/semi-rosette or erect/branching stem structures in February 1994 (Table 4.23). Fertilization decreased the relative cover of tussock/tuft species in low and moderately disturbed plots, but increased their cover in highly disturbed plots (Fig. 4.29). Moderate and high soil disturbance increased the relative cover of rosette/semi-rosette species to a greater extent in unfertilized plots. High soil disturbance decreased the relative cover of erect/branching species in fertilized plots only. The effect of these disturbance x fertilization interactions increased linearly over time (Appendix 7).

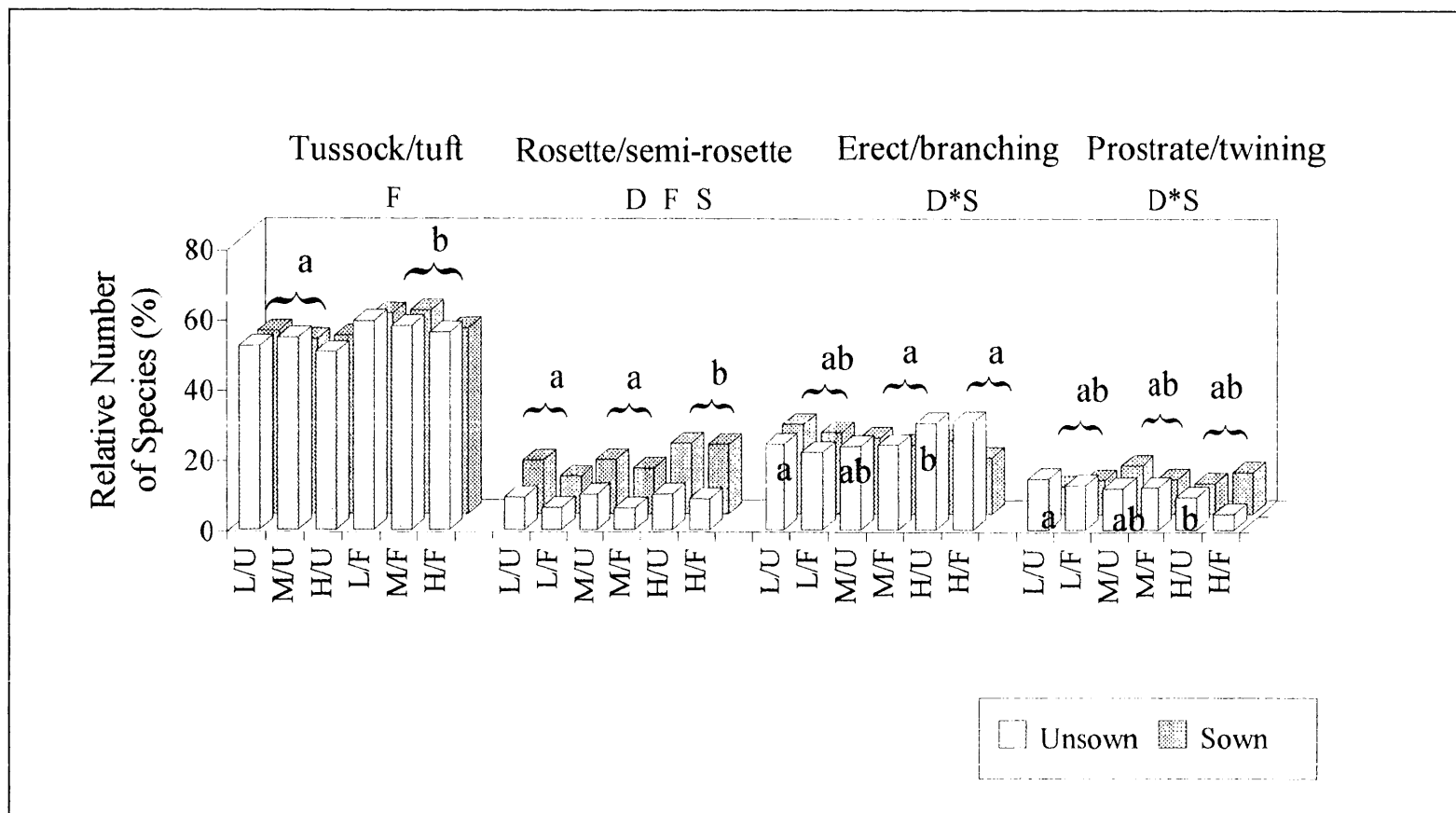
There was a significant fertilization x sown interaction for the relative cover of rosette/semi-rosette species (Table 4.23). Fertilization decreased the relative cover of rosette/semi-rosette species to a greater extent in sown than unsown plots (1,48 df;  $p < 0.001$ , Bonferroni tests). Sowing did not significantly affect the relative cover of tussock/tuft or erect/branching species in February 1994, but there was a significant disturbance x fertilization x sown interaction in March 1993 (Appendix 7). Although anova revealed a significant disturbance x fertilization x sown interaction for the relative cover of prostrate/twining species in February 1994, Bonferroni pairwise comparisons found no significant difference between the treatment means.

**Table 4.23:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species of the stem structure categories with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown interaction was not significant for relative cover. Disturbance x fertilization, fertilization x sown and disturbance x fertilization x sown interactions were not significant for relative number of species.  $\hat{\uparrow}$  - increased;  $\hat{\downarrow}$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Tussock/tuft	Rosette/ semi-rosette	Erect/ branching	Prostrate/ twining
<b>Relative Cover (%)</b>					
Disturbance	2/48	39.90***	84.95***	6.57**	1.40
Fertilization	1/48	0.28	76.77***	109.88***	0.09
Sown	1/48	0.66	0.07	0.32	3.97
Disturbance x Fertilization	2/48	<b>36.28***</b>	<b>8.14**</b>	<b>4.75*</b>	2.02
Fertilization x Sown	1/48	2.28	<b>4.48*</b>	0.32	3.23
Disturbance x Fertilization x Sown	2/48	2.05	2.06	0.83	<b>3.75*</b>
<b>Relative Number of Species (%)</b>					
Disturbance	2/48	1.02	$\hat{\uparrow}$ <b>6.76**</b>	0.88	3.49*
Fertilization	1/48	$\hat{\uparrow}$ <b>10.03**</b>	$\hat{\downarrow}$ <b>7.40**</b>	1.80	0.67
Sown	1/48	1.23	$\hat{\uparrow}$ <b>52.94***</b>	12.54**	0.04
Disturbance x Sown	2/48	0.05	1.70	<b>8.22**</b>	<b>5.60**</b>



**Fig. 4.29:** Mean relative cover (%) of tussock/tuft, rosette/semi-rosette, erect/branching and prostrate/twining species in each of the treatments in February 1994. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each stem structure category.



**Fig. 4.30:** Mean relative number (%) of tussock/tuft, rosette/semi-rosette, erect/branching and prostrate/twining species in each of the treatments in February 1994. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Note the change in the order of treatments for tussock/tuft species. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each stem structure category.

Fertilization significantly increased the relative number of tussock/tuft species in February 1994 (Fig. 4.30; Table 4.23). Disturbance did not significantly affect the relative number of tussock/tuft species at any time during the study (Appendix 7). Sowing did not significantly affect the relative number of tussock/tuft species in February 1994, but there was a significant fertilization x sown interaction in November 1993. High soil disturbance increased the relative number of rosette/semi-rosette species in February 1994, but the effect had diminished over time. The relative number of rosette/semi-rosette species was significantly decreased by fertilization (1,48 df;  $p < 0.01$ , Bonferroni test) and was significantly increased by sowing (1,48 df;  $p < 0.001$ , Bonferroni test).

Anova revealed a significant disturbance x sown interaction for the relative number of species with erect/branching or prostrate/twining stem structures in February 1994 (Table 4.23). The relative number of erect/branching in highly disturbed unsown plots was greater than in low disturbance unsown plots and moderately or highly disturbed sown plots (Fig. 4.30). The relative number of prostrate/twining species in highly disturbed unsown plots was lower than in low disturbance unsown plots. Fertilization did not significantly effect the relative number of species with erect/branching or prostrate/twining stem structures at any time during the study (Appendix 7).

#### **4.3.21 Leaf Shape**

Anova detected a significant disturbance x sown interaction for species with circular/obovate or elliptic leaves in February 1994 (Table 4.24). The relative cover of species with circular/obovate leaves in highly disturbed sown plots was greater than in all of the other treatments (Fig. 4.31). Sowing increased the relative cover of species with elliptic leaves only in highly disturbed plots. The effect of the disturbance x sown interaction on the cover of species with circular/obovate leaves increased linearly over time. There was a significant disturbance x fertilization interaction for the relative cover of species with circular/obovate leaves. The relative cover of species with circular/obovate leaves in highly disturbed unfertilized plots was greater than in low and moderately disturbed plots (2,48 df;  $p < 0.01$ , Bonferroni test) and highly disturbed fertilized plots (2,48 df;  $p < 0.01$ , Bonferroni test). Fertilization did not significantly affect the relative cover of species with elliptic leaves in February 1994, but did significantly increase their cover in March 1993 (Appendix 7).

There was a significant disturbance x fertilization interaction for the relative cover of species with linear/filiform leaves in February (Table 4.24); high soil disturbance decreased cover to a greater extent in unfertilized than fertilized plots (Fig. 4.31). Sowing did not significantly affect the relative cover of species with linear/filiform leaves at any time during the study (Appendix 7). Both moderate and high soil disturbance significantly increased the relative cover of species with lanceolate/oblanceolate leaves in February 1994. The effect of soil disturbance on species with lanceolate/oblanceolate leaves had diminished over time.

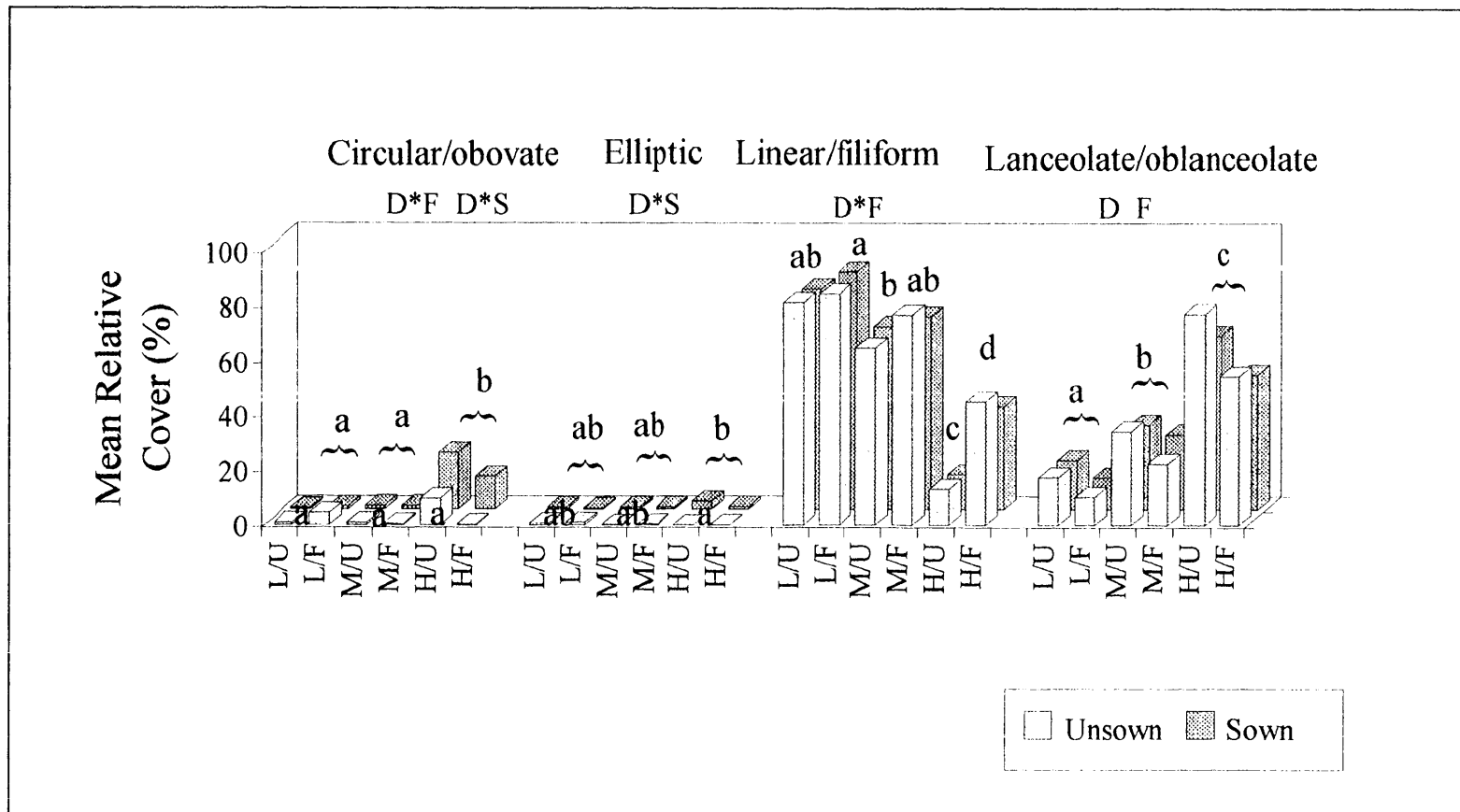
Fertilization decreased the relative cover of species with lanceolate/oblanceolate leaves (1,48 df;  $p < 0.01$ , Bonferroni test). The effect of fertilization on species with lanceolate/oblanceolate leaves had increased linearly over time. Sowing did not significantly affect the relative cover of species with lanceolate/oblanceolate leaves in February 1994, but did significantly decrease their cover in November 1993.

**Table 4.24:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species in the leaf shape categories with disturbance, fertilization & sown as factors for February 1994. Fertilization x sown and disturbance x fertilization x sown interactions were not significant for relative cover. Disturbance x fertilization interaction was not significant for relative number of species.  $\hat{\uparrow}$  - increased;  $\hat{\downarrow}$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Circular	Elliptic	Linear/filiform	Lanceolate
<b>Relative Cover (%)</b>					
Disturbance	2/48	22.70***	0.24	104.64***	$\hat{\uparrow}$ 58.82***
Fertilization	1/48	1.50	0.01	20.82***	$\hat{\downarrow}$ 11.70**
Sown	1/48	14.95***	9.33**	0.13	0.82
Disturbance x Fertilization	2/48	7.40**	0.54	4.88*	0.68
Disturbance x Sown	2/48	16.11***	3.25*	0.27	1.01
<b>Relative Number of Species (%)</b>					
Disturbance	2/48	2.48	2.88	$\hat{\downarrow}$ 5.02*	0.86
Fertilization	1/48	0.10	0.10	3.21	4.53*
Sown	1/48	70.54***	1.58	$\hat{\downarrow}$ 15.45***	1.91
Disturbance x Sown	2/48	10.96***	0.24	2.66	0.14
Fertilization x Sown	1/48	1.56	0.79	2.05	4.87*
Disturbance x Fertilization x Sown	2/48	4.13*	0.62	0.62	0.83

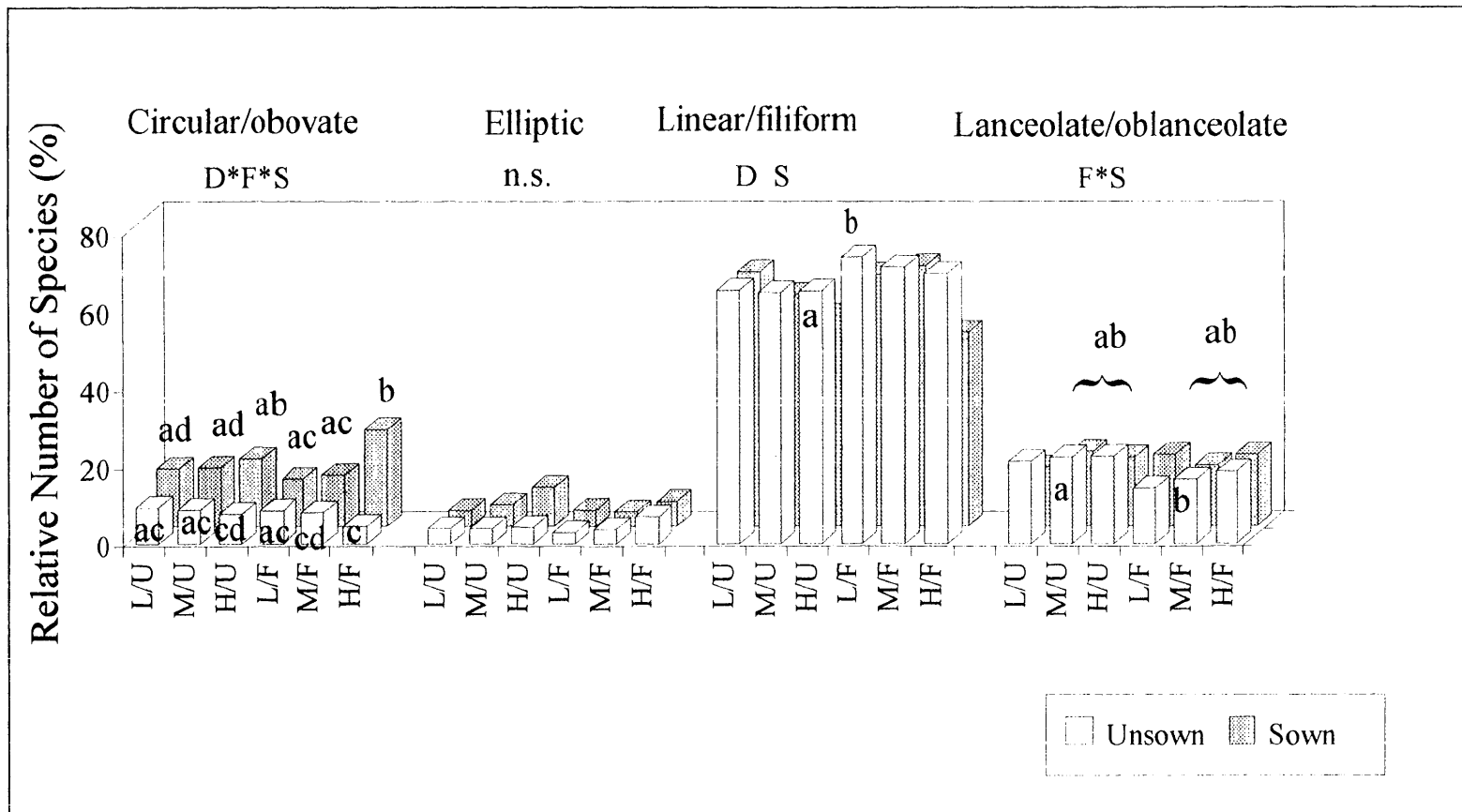
Anova revealed a significant disturbance x fertilization x sown interaction for the relative number of species with circular/obovate leaves in February 1994 (Table 4.24). The relative number of species with circular/obovate leaves in the highly disturbed fertilized sown plot was greater than in all other treatments except the highly disturbed unfertilized sown plots (Fig. 4.32). The relative number of species with circular/obovate leaves in moderately and highly disturbed fertilized unsown plots was lower than in highly disturbed sown plots. Disturbance and sowing did not affect the relative number of species with elliptic leaves at any time during the study (Appendix 7). Fertilization significantly decreased the relative number of species with elliptic leaves in November 1993 only.

Sowing significantly decreased the relative number of species with linear/filiform leaves in February 1994 (Fig. 4.32; Table 4.24). The relative number of species with linear/filiform leaves in highly disturbed plots was lower than in low disturbance plots (2,48 df;  $p < 0.05$ , Bonferroni test). Fertilization did not significantly affect the relative number of species with linear/filiform leaves at any time during the study. There was a significant fertilization x sown interaction for the relative number of species with lanceolate/oblanceolate leaves in February 1994. Fertilization decreased the relative number of species with lanceolate/oblanceolate leaves in unsown plots, but had no effect in sown plots. Disturbance had no significant effect on the relative number of species with lanceolate/oblanceolate leaves at any time during the study.



**Fig. 4.31:** Mean relative cover (%) of species with circular/obovate, elliptic, linear/filiform or lanceolate/oblanceolate leaves in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each leaf shape category.





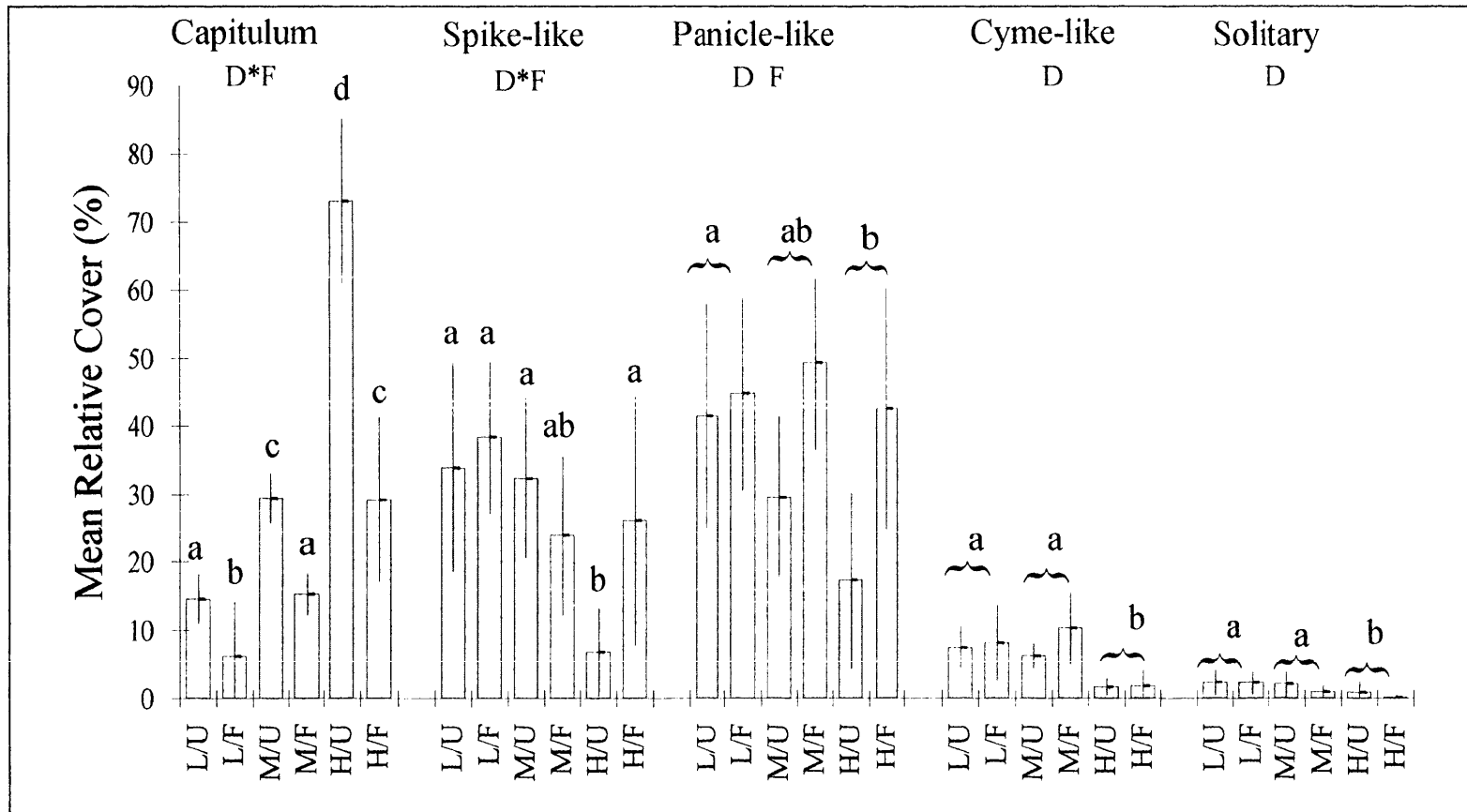
**Fig. 4.32:** Mean relative number (%) of species with circular/obovate, elliptic, linear/filiform or lanceolate/oblanceolate leaves in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each leaf shape category.

### 4.3.22 Inflorescence Form

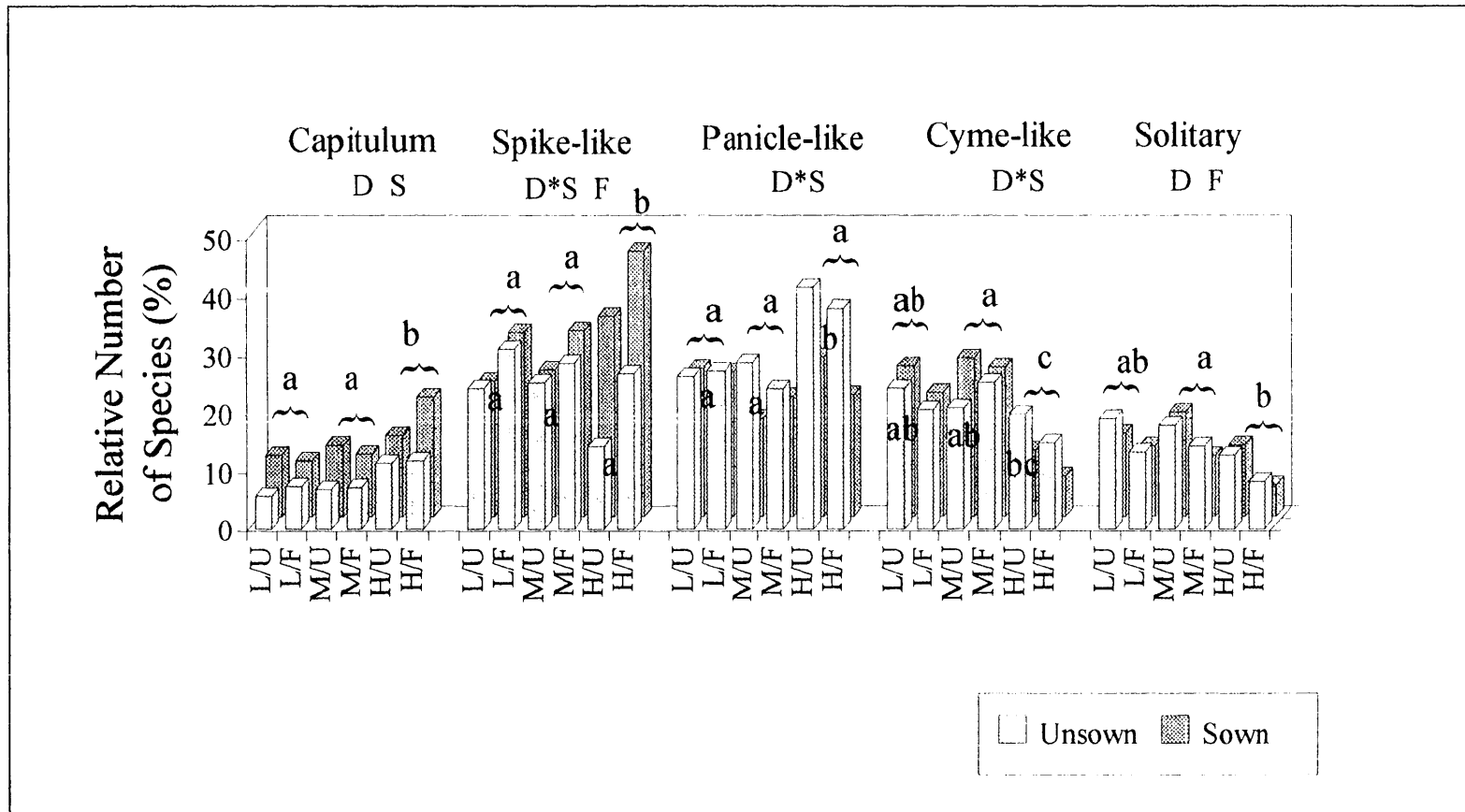
There was a significant disturbance x fertilization interaction for the relative cover of species with capitulum or spike-like inflorescences in February 1994 (Table 4.25). Moderate and high soil disturbance increased the relative cover of species with capitulum inflorescences to a greater extent in unfertilized than fertilized plots (Fig. 4.33). High soil disturbance decreased the relative cover of species with spike-like inflorescences in unfertilized plots, but had no effect in fertilized plots. The effect of the disturbance x fertilization interaction on species with spike-like inflorescences was greater in spring than in summer (Appendix 7). High soil disturbance significantly decreased the relative cover of species with panicle-like, cyme-like or solitary inflorescences. The effect of disturbance species with cyme-like or solitary inflorescences was greater in spring than in summer. Fertilization significantly increased the relative cover of species with panicle-like inflorescences (1,48 df;  $p < 0.001$ , Bonferroni test). Fertilization did not significantly affect the relative cover of species with solitary or cyme-like inflorescences in February 1994. However, fertilization increased the relative cover of species with solitary inflorescences in March 1993. Sowing did not significantly affect the relative cover of species with capitulum, spike-like, panicle-like, cyme-like or solitary inflorescences at any time during the study.

**Table 4.25:** Analysis of variance (F values) of the relative cover (%) and relative number (%) of species in the inflorescence form categories with disturbance, fertilization & sown as factors for February 1994. Fertilization x sown and disturbance x fertilization x sown interactions were not significant. Disturbance x sown interaction was not significant for relative cover and disturbance x fertilization interaction was not significant for relative number of species.  $\hat{\uparrow}$  - increased;  $\hat{\downarrow}$  - decreased. \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

	df	Capitulum	Spike-like	Panicle-like	Cyme-like	Solitary
<b>Relative Cover (%)</b>						
Disturbance	2/48	119.65***	11.84***	$\hat{\downarrow}$ 4.30*	$\hat{\downarrow}$ 20.30***	$\hat{\downarrow}$ 11.57***
Fertilization	1/48	106.02***	2.32	$\hat{\uparrow}$ 18.03***	3.02	1.24
Sown	1/48	1.47	0.21	0	0.01	0.47
Disturbance x Fert	2/48	13.83***	5.82**	3.03	1.73	0.60
<b>Relative Number (%)</b>						
Disturbance	2/48	$\hat{\uparrow}$ 16.97***	0.98	7.26**	22.28***	$\hat{\downarrow}$ 4.09*
Fertilization	1/48	0.95	$\hat{\uparrow}$ 21.83***	0.65	2.59	$\hat{\downarrow}$ 8.43**
Sown	1/48	$\hat{\uparrow}$ 27.92***	16.11***	16.69***	0.53	1.56
Disturbance x Sown	2/48	0.14	12.93***	3.61*	5.37**	0.06



**Fig. 4.33:** Mean relative cover (%) of species with capitulum, spike-like, panicle-like, cyme-like or solitary inflorescences in each of the six treatments in February 1994. The sown treatment was not significant and therefore is not shown. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Bars represent  $\pm 1$  standard errors. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each inflorescence form category.



**Fig. 4.34:** Mean relative number (%) of species with capitulum, spike-like, panicle-like, cyme-like or solitary inflorescences in each of the treatments in February 1994. H = high soil disturbance; M = moderate soil disturbance; L = low soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ( $p < 0.05$  level) between the treatment means of each inflorescence category.

High soil disturbance significantly increased the relative number of species with capitulum inflorescences in February 1994 (Fig. 4.34; Table 4.25). Fertilization did not significantly affect the relative of species with capitulum inflorescences in February 1994, but did increase their relative number in November 1993 (Appendix 7). The sown treatment significantly increased the relative number of species with capitulum inflorescences (1,48 df;  $p < 0.001$ , Bonferroni test). The relative number of species with solitary inflorescences in highly disturbed plots was lower than in moderately disturbed plots. Fertilization decreased the relative number of species with solitary inflorescences (1,48 df;  $p < 0.01$ , Bonferroni test). The effect of disturbance and fertilization on species with solitary inflorescences increased linearly over time. The sown treatment did not significantly affect the relative number of species with solitary inflorescences at any time during the study.

There was a significant disturbance x sown interaction for the relative number of species with spike-like, panicle-like or cyme-like inflorescences in February 1994 (Table 4.25). Sowing significantly increased the relative number of species with spike-like inflorescences and decreased species with panicle-like inflorescences only in highly disturbed plots (Fig. 4.34). High soil disturbance decreased the relative number of species with cyme-like inflorescences only in sown plots. The relative number of species with cyme-like inflorescences in highly disturbed unsown plots was lower than in moderately disturbed sown plots. The effect of the disturbance x sown interaction on the relative number of species with spike-like or panicle-like inflorescences increased linearly over time (Appendix 7).

Fertilization increased the relative number of species with spike-like inflorescences (1,48 df;  $p < 0.001$ , Bonferroni test). The effect of fertilization on species with spike-like inflorescences had increased linearly over time. Fertilization did not significantly affect the relative number of species with panicle-like or cyme-like inflorescences in February 1994. However, there was a significant disturbance x fertilization interaction for species with panicle-like inflorescences and a significant disturbance x fertilization x sown interaction for the relative number of species with cyme-like inflorescences in November 1993 (Appendix 7).

## 4.4 DISCUSSION

Both relative cover and relative number were used as response variables to examine whether soil disturbance, fertilization or sowing affects the abundance of species with particular plant attributes. Other studies have used a variety of response variables including cover (e.g. Fernández Alés *et al.* 1993; Wilson & Tilman 1991), biomass (e.g. Gomez Sal *et al.* 1986; Hobbs & Atkin 1988) and number of species (e.g. Floret *et al.* 1990; Montalvo *et al.* 1991; McIntyre *et al.* 1995). Baker (1972) acknowledged that the number of species with a particular attribute does not distinguish between abundant and rare taxa and suggested that an abundant taxon is probably better adapted to prevailing conditions than a rare one. However, whether a dominant species can be regarded as more successful than a subordinate species, in terms of persisting at a site, is unknown. Mueller-Dombois and Ellenberg (1974) suggested that composition of plant attributes in a community (i.e. number of species) gives information on community response to a particular environmental factor, while cover values give information on the use of space. A large number of species with a particular attribute in a particular environment suggests that a number of species have independently found the same solution to the environmental problem. A large cover of species with a particular attribute in a particular environment suggests that one or more species have not only found a solution to the environmental problem, but successfully dominate space.

The problem with species cover is that the abundance of a particular attribute may be due to the success of one dominant species and thus the attribute is less likely to represent a general adaptation to the environment. On the other hand, the subordinate species have little influence on the results, despite their ability to coexist successfully with the dominants. On the highly disturbed plots in this study, the presence or absence of one species can have a large effect on the response of the relative number and cover of species with a particular plant attribute because so few species survive on these plots that one species can make a relatively large contribution. The only way to avoid this problem is to have a less severe or less frequent soil disturbance.

### 4.4.1 Species Origin

The response of the relative number of native and exotic species to fertilization depended not only on the level of soil disturbance, but also on whether the plots were sown. The results were due to all of the sown species being exotic and being most successful under highly disturbed conditions (e.g. fertilized: *Lolium perenne* and *Dactylis glomerata*, unfertilized: *Sanguisorba minor*). The weak positive correlation between the absolute number of exotic species and native species within a plot was in contrast to the negative correlations found by Fox and Fox (1986) and McIntyre *et al.* (1988). High soil disturbance strongly

influenced the result because the severity of the treatment meant that few species survived regardless of whether they were native or exotic. Thus, where the severity of soil disturbance is high, exotic species probably have little influence on native species richness.

The response of the relative cover of native and exotic species to fertilization depended on the level of soil disturbance. Fertilization decreased the relative cover of natives and increased exotics in low and moderately disturbed plots, but had no effect in highly disturbed plots. For native species cover this interaction occurred because few natives survived high soil disturbance to respond to fertilization. Two other Australian studies found that native species richness decreases with soil disturbance (McIntyre *et al.* 1988; McIntyre & Lavorel 1994a). Hobbs and Huenneke (1992) suggested that the lack of natives found under severely disturbed conditions may be due to few native species being adapted to these habitats because of the short history of agriculture in Australia. On the low and moderately disturbed plots, fertilization probably decreased native cover through the indirect effects of increased biomass and decreased light penetration to the soil surface. Native species are adapted to growing under nutrient-poor conditions because Australian soils are naturally low in nitrogen and phosphorus (Amor & Piggitt 1977).

For exotic species, the interaction between soil disturbance and fertilization suggests that the exotic species that increased in cover with fertilization (e.g. *Aira cupaniana* and *Briza minor*) could not tolerate high soil disturbance, while exotic species that could tolerate high soil disturbance (e.g. *Hypochaeris radicata*) did not respond to fertilization. Although the cover of exotics was enhanced under conditions of high fertility, the number of exotic species was not, probably because dominance by a few exotic species suppressed other exotic species. Thus contrary to popular belief (e.g. Amor & Piggitt 1977) not all exotic species are favoured by fertilization. Hobbs and Atkins (1988) found that the combination of fertilization and soil disturbance increased the biomass of exotics to a greater extent than that produced by fertilization or soil disturbance alone. A similar synergistic effect of fertilization and moderate soil disturbance on exotic cover was found at Newholme, but did not occur when fertilization was combined with high soil disturbance.

McIntyre and Lavorel (1994a) identified three broad groups in relation to the tolerance of species on the Northern Tablelands to exogenous disturbance: intolerant of disturbance, tolerant of disturbance and disturbance specialists. Most species in the present study in the 'intolerant of disturbance' category were native and contributed greatly to species richness, in agreement with their findings. McIntyre and Lavorel (1994a) suggested that the 'tolerant of disturbance' category consists of both native and exotic species. However, in this study species 'tolerant of high soil disturbance' were exotic, but species 'tolerant of moderate soil disturbance' were either exotic or native. Therefore, the balance of exotic and native species in the 'tolerant' category depends on the intensity of disturbance.

For exotic species on the Northern Tablelands, species 'tolerant of disturbance' had similar frequencies (usually non-dominant, < 10% cover) at sites of low and high richness and 'disturbance specialists' had high frequencies (usually dominant) at sites of low richness

(McIntyre 1993). On the basis of this study, the exotic species *Lolium perenne* and *Dactylis glomerata* could be put into McIntyre's 'disturbance specialist' group only when fertilized and were found in plots of low species richness. *Sanguisorba minor* could be put into McIntyre's 'disturbance specialist' group only when unfertilized and was found in plots of low species richness. *Hypochaeris radicata* could be put in the 'tolerant of disturbance' category and was found in plots of low and high species richness, consistent with McIntyre's classification of this species. *Vulpia* spp., *Aira cupaniana* and *Acetosella vulgaris* could be put in McIntyre's 'tolerant of disturbance' category only when fertilized and were found in plots of low and high species richness. In contrast, McIntyre and Laval (1994a) classified *Vulpia* spp. as a 'disturbance specialist'. The exotic annual, *Briza minor*, could be put in the 'intolerant of disturbance' category and was found in plots of high richness. The results were consistent with the comment by McIntyre (1993) that dominant exotic plants were not associated with high native richness, except in the case of annual grasses.

#### 4.4.2 Life Cycle

The response of the number of annual species to soil disturbance depended on whether the plots were sown, while the response of perennial species depended on whether the plots were fertilized or sown. High soil disturbance increased the relative number of annuals, but was only significant in sown plots because the biennial sown species, *Plantago lanceolata*, was included in with the annuals and was most successful in highly disturbed plots. Other Australian studies have found that annual species richness increases with soil disturbance (Hobbs & Atkins 1988; McIntyre *et al.* 1995). The results were consistent with annuals exploiting environments intermittently favourable for plant growth (Grime 1979). Fertilization increased the relative number of annuals in spring 1993 suggesting that a short life cycle is advantageous in nutrient-rich habitats. Annual species richness increased with fertilization in a number of Western Australian plant communities (Hobbs & Atkins 1988). Fertilization decreased the relative number of perennials only in highly disturbed, sown plots. Since most of the sown species in the highly disturbed fertilized plots were perennial (e.g. *Lolium perenne* and *Dactylis glomerata*), the results suggest that they had a competitive effect on other perennial species in these plots.

Fertilization increased the relative cover of annuals and decreased the cover of perennials, suggesting that a short life cycle not only allows species to persist in nutrient-rich habitats, but also to dominate space. The results for perennial cover are consistent with the proposal by Grime (1979) that plants adapted to nutrient-poor habitats are comparatively long-lived. Other studies have found that the cover of annuals increases with fertilization (Wilson & Tilman 1991; Hobbs & Atkins 1988). Tilman (1987a) found that the increase in annual cover and decrease in perennial cover with fertilization is often transient (2 or 3 years). He suggested that as perennials reach a biomass that inhibits the germination of



annuals, the ability of annuals to rapidly pre-empt available space diminishes. Thus the high cover of annuals in low and moderately disturbed, fertilized plots in this study may be transitory; a longer study would establish whether their cover diminishes over time. One of the common annuals at Newholme, *Vulpia* spp., would not have remained abundant under conditions of high biomass if the study had continued because its seedling recruitment is severely inhibited by the presence of standing pasture over autumn and winter (Jones & Whalley 1993).

The relative cover of annual and perennial species was unresponsive to soil disturbance in summer. Other studies have found that disturbance increased annual cover and decreased perennial cover (Trémont 1994; Wilson & Tilman 1991; Inouye *et al.* 1987). Soil disturbance probably did not enhance the cover of the annuals here because the timing of disturbance in August each year occurred shortly after the germination period of the common winter annuals (e.g. *Aira cupaniana*, *Briza minor* and *Vulpia* spp.) and probably killed the recently germinated seedlings. A lack of opportunity for germination or establishment due to dry weather conditions was not a likely explanation because the cover of annuals in low disturbance plots was high in spring.

The results suggest that although a number of species had adopted a typically 'ruderal' (*sensu* Grime 1979) solution to successfully maintain a presence in highly disturbed plots, these species do not dominate the space made available by the disturbance. Ruderal species regenerate either by seasonal regeneration in gaps, small wind-dispersed seeds or by persistent seed banks (Grime 1979). The seedbank of *Vulpia* species, a common annual in this study, is large because it is constantly being replenished because seedling recruitment (and therefore reproduction) occurs over an extended period (Jones & Whalley 1993). However, *Vulpia* spp. does not possess the type of persistent seed bank described by Grime (1979) because its seed bank is relatively short-lived (Dillon & Forcella 1984; Peart & Foin 1985). Annuals can be successful without a large reservoir of seeds if their germination is timed to coincide with annual openings in the vegetation caused by a regular disturbance imposed by climate (Grime 1978). The seasonal climate at Newholme may have selected for annual species able to germinate in openings created when vegetation becomes dormant in winter as a result of low temperatures and low rainfall, as opposed to openings created by soil disturbance. Consistent with this idea the death of two common annual grasses, *A. cupaniana* and *B. minor*, on the fertilized plots in summer created a dense mat of litter which may have functioned to keep the space free for them to germinate next autumn. This early germination would allow the annuals to pre-empt the available space.

#### 4.4.3 Growth Form

Soil disturbance decreased the relative number of forb species in spring, but a number of forbs were adapted to recover from the damage because the effect had diminished by summer. Fertilization decreased the relative number of forb species. The susceptibility of forbs to fertilization was probably due to the low light levels associated with fertilized plots (Section 2.3.4), because the forbs tended to be low-growing or of small width. The response of the relative cover of forbs to soil disturbance depended on the level of fertilization; the increase in forb cover with high soil disturbance was greater in unfertilized than fertilized plots. Other studies have found that forb cover increases with severe soil disturbance (Ruthven *et al.* 1993) and a lack of disturbance decreases forb cover (Willems 1983; Inouye *et al.* 1987; McIntyre *et al.* 1993). The results suggest that the forbs dominating the highly disturbed plots were not favoured by fertilization (e.g. *Hypochaeris radicata* and *Sanguisorba minor*). The forbs dominating the highly disturbed plots were well anchored against soil disturbance by their taproots and their low-growing rosettes were competitive in bare ground but were susceptible to shading under fertilized conditions.

Sowing initially increased the relative number of forb species (November 1992) and decreased the relative number of sedge/rush species (November 1992 and March 1993), but the effect diminished over time. The increase in the relative number of forbs with sowing was due to three of the sown species being forbs (i.e. *S.minor*, *Plantago lanceolata* and *Capsella bursa-pastoris*) and the decrease in the number of sedges/rushes declined with sowing because none of the sown species were sedge/rush species. The effect of sowing declined over time because some of the sown species failed to persist in some plots (e.g. *C.bursa-pastoris*).

The response of the relative number of grass species to soil disturbance depended on the level of fertilization or sowing and the response of grass cover to soil disturbance depended on the level of fertilization. The decrease in grass cover with high soil disturbance was greater in unfertilized than fertilized plots. Thus, the grass species that dominated the highly disturbed plots were favoured by fertilization (e.g. *Lolium perenne*, *Dactylis glomerata* and *Vulpia* spp.). The native grass species were neither adapted to high soil disturbance or nutrient-rich conditions because they have evolved on nutrient-poor soils and mechanical soil disturbance has been a rare event at the study site. The exotic grasses were adapted to both soil disturbance and fertilization and therefore succeeded where the natives failed. Grass cover is often high under nutrient-rich conditions (Duffy *et al.* 1974; Inouye *et al.* 1987). However, fertilization only increased grass cover here when it was combined with high soil disturbance.

High soil disturbance decreased the relative number and cover of sedge/rush species, while fertilization increased their number and cover. Inouye *et al.* (1987) found that the cover of sedges increased with field nitrogen. The sedges and rushes in the present study tended to be slow-growing with fibrous long-lived leaves (Section 3.3.3), so their slow rate of recovery from damage and biomass loss make them particularly susceptible to severe soil disturbance.

#### 4.4.4 Raunkiaer Life Form

The response of the relative number of hemicryptophyte species to soil disturbance depended on the level of fertilization; high soil disturbance decreased hemicryptophytes only in combination with fertilization. The hemicryptophytes not favoured by high soil disturbance were also not favoured by nutrient-rich conditions (e.g. *Aristida ramosa*, *A. warburgii* and *Richardia stellaris*). Another study on the Northern Tablelands found that the number of hemicryptophytes decreases with increasing soil disturbance (McIntyre *et al.* 1995). The intolerance of hemicryptophytes to soil disturbance may relate to their perennating buds not being protected under the soil surface.

Fertilization increased the relative cover of amphiphyte species and decreased the cover of hemicryptophytes. The presence of perennating buds both above and in the soil surface in amphiphyte species, together with the possession of rhizomes, may allow them to actively forage for nutrients and dominate space in nutrient-rich environments. It is unclear why hemicryptophyte species (e.g. *Aristida ramosa*, *A. warburgii* and *Hypochaeris radicata*), with their perennating buds located just in the soil surface, are intolerant of fertilization. Perhaps the morphology of hemicryptophyte species, where growth originates from ground level, is such that the placement of the leaf canopy in response to changing light conditions is inflexible or costly? Alternatively, the dominant hemicryptophytes are adapted to nutrient-poor soils because they have evolved under these conditions and the function of the hemicryptophytic habit is unrelated to fertility (i.e. protects the perennating buds against frosts, moisture stress or fire). High soil disturbance increased the relative cover of amphiphytes and decreased the cover of hemicryptophytes. The amphiphytes were not only able to tolerate high soil disturbance, but were able to dominate space.

High soil disturbance increased the relative number of amphiphyte species. The amphiphyte species would not be expected to be favoured by soil disturbance because the location of their perennating buds both above and in the soil surface provides little protection against soil disturbance. However the possession of rhizomes (Section 3.3.3) may have afforded these two amphiphyte species greater resistance to soil disturbance. Other studies on the Northern Tablelands found no species behaving as both chamaephytes and hemicryptophytes, but they found that the number of chamaephyte species decreased with grazing and soil disturbance (Trémont 1994; McIntyre *et al.* 1995).

Disturbance did not affect the relative number of therophyte species in February 1994, but high soil disturbance decreased their relative number in March 1993 and increased their number in November 1993. The number of therophytes increased with increasing soil disturbance (McIntyre *et al.* 1995) and grazing (Trémont 1994) on the Northern Tablelands. Disturbance did not affect the relative cover of therophytes in February 1994, but high soil disturbance decreased their cover in November 1992, March 1993 and November 1993. Fertilization increased the relative number of therophytes in February 1994. The increase in hemicryptophytes and decrease in therophytes with sowing was due to most of the sown

species being hemicryptophytes (e.g. *Dactylis glomerata*, *Lolium perenne*, *Plantago lanceolata* and *Sanguisorba minor*), but the effect diminished over time because some of the sown species failed to persist in some plots. The response of the therophytes (annuals) to soil disturbance and fertilization has been discussed previously (Section 4.4.2) in more detail.

The decrease in the relative number and cover of geophyte species with high soil disturbance was only observed in spring because they died back to underground tubers, and were no longer visible, in summer. The geophyte species (number and cover) could tolerate a moderate level of soil disturbance. McIntyre *et al.* (1995) found that the number of geophytes on the Northern Tablelands was unaffected by soil disturbance (less severe than in this study) and grazing. Further, Trémont (1994) found a greater proportion of geophytes in grazed plots than in plots protected from grazing for 16 years. Thus, geophytes can tolerate grazing and moderate soil disturbance, but cannot tolerate long-term protection from grazing (i.e. biomass accumulation) or severe soil disturbance. The geophytes in this study (e.g. *Drosera peltata* and *Microtis unifolia*) locate their perennating buds at depth underground in the form of stem tubers (Section 3.3.3), which provides protection against moderate soil disturbance. However, severe soil disturbance probably buried their stem tubers at an inappropriate depth. Some geophytes have the capacity to regulate the depth of their stem tubers in the soil (Raunkiaer 1934), suggesting that the position of the stem tubers influences survival. When stem tubers are buried deep in the soil their stored resources may be exhausted before the shoots reach the surface, while shallow burial could lead to desiccation. The geophyte species (number and cover) were generally unaffected by fertilization and thus are able to tolerate nutrient-rich soils. By virtue of their phenology, geophytes may be able to avoid periods of low light intensity associated with the lower levels of bare ground in summer. However, the decrease in the relative number of geophytes with fertilization had strengthened by the second spring of the study (but remained non-significant). The predominantly rosette/semi rosette habit of the geophytes means that they may be susceptible to shading if litter accumulation is high.

#### **4.4.5 Height, Width and Height:Width Ratio**

Species of short vegetative stature were more common than species of tall vegetative stature in fertilized, highly disturbed plots in spring. This is consistent with species of persistently disturbed habitats (i.e. 'ruderal' species) being characteristically small (Grime 1979). Other studies have found that the cover of short-statured species increased and the cover of tall species decreased with soil disturbance, grazing and mowing (Belsky 1992; Díaz *et al.* 1992; Odgers & Rogers 1993). Light levels were high in the severely disturbed plots (Section 2.3.4), so competition for light was low and the benefit of greater height would not outweigh its cost of construction. Species of tall vegetative stature were more common than species of short vegetative stature in fertilized, low disturbance plots in summer. This is consistent with species of productive, undisturbed habitats (i.e. 'competitive' species) being

characteristically tall (Grime 1979). Other studies have found that undisturbed, nutrient-rich habitats are characterised by tall species while nutrient-poor habitats are characterised by small species (Beadle 1966; Elberse & Berendse 1993; Fernández Alés *et al.* 1993). Light levels were low in the fertilized, low disturbance environments (Section 2.3.4), so competition for light was high and the benefit of greater height in accessing light would outweigh its cost of construction.

Narrow species were more common than wide species in unfertilized, low disturbance plots and the moderately disturbed plots in spring. 'Stress-tolerant' species (i.e. species of unproductive undisturbed habitats) have a wide range of growth forms (Grime 1979), but the results here suggest that the lateral spread of spring 'stress-tolerators' (e.g. *Drosera peltata*) was limited, while summer 'stress-tolerators' (e.g. *Aristida ramosa*) have a wider range of lateral spread. Narrow species may have avoided the higher biomass levels of summer by having its growth period early in the season. Tall, narrow species were more common than short, wide species in low and moderately disturbed plots. Light and bare ground are limited in low and moderately disturbed plots (Section 2.3.4), so the benefits of investing in height rather than width enable greater access to light. Although investment in greater width would increase the area over which light can be intercepted, the benefits would not outweigh the costs because competition with neighbouring foliage in these plots would be high. Similarly, Díaz *et al.* (1992) found that growth forms became more vertical with decreasing grazing pressure, while Gomez Sal *et al.* (1986) found that vertically growing species increased with succession for up to 8 years. Thus, in this study, plant size was not only related to productivity, as found by Fernández Alés *et al.* (1993), but was also related to soil disturbance and season.

#### 4.4.6 Leaf Texture

High soil disturbance decreased the relative number of species with fibrous leaves and increased the number of species with soft leaves. The results contrast with Beadle's (1966) suggestion that leaf texture is not correlated with habitat factors. Lower investment in lignin and other structural compounds (i.e. soft leaves) means that leaves can be produced rapidly to pre-empt available space and the cost of a disturbance event is minimised because soft leaves are inexpensive to replace. Although increased cell wall material in a leaf has been suggested to increase resistance to trampling (Lambers & Poorter 1992), the results suggest that increased structural leaf strength was not advantageous in soil disturbed habitats.

Fertilization did not significantly affect the relative number of species with fibrous or soft leaves at any time during the study. The response of the relative cover of species with fibrous or soft leaves to soil disturbance depended on the level of fertilization. Fertilization decreased the relative cover of species with fibrous leaves and increased the cover of soft-leaved species in low and moderately disturbed plots, but had no effect in highly disturbed

plots. Fertilization enabled some species with soft leaves to dominate low and moderately disturbed plots (e.g. *Briza minor* and *Sporobolus creber*). The rate of nutrient cycling between the plant and the soil is high in species with soft short-lived leaves, increasing the risk of nutrient loss (Grime 1977; Chabot & Hicks 1982). The increased risk of nutrient loss may be affordable in nutrient-rich habitats. Species investing in leaves high in lignin and other structural compounds could not tolerate nutrient-rich conditions in combination with low and moderately soil disturbance. Sowing decreased the relative number of fibrous-leaved species and increased the number of soft-leaved species because most sown species had soft leaves (e.g. *Dactylis glomerata*, *Lolium perenne*, *Plantago lanceolata* and *Sanguisorba minor*).

#### 4.4.7 Persistent Litter

The response of the relative number of species without persistent litter to soil disturbance depended on the level of fertilization. Species without persistent litter could not tolerate soil disturbance unless plots were nutrient-rich. A lack of persistent litter is associated with rapid leaf decomposition and a high risk of nutrient loss (Chabot & Hicks 1982), thus this risk may not be affordable in soil disturbed conditions unless fertility was high. Disturbance initially (November 1992, March 1993 and November 1993) decreased the relative cover of species without persistent litter, but the effect had diminished by February 1994. Fertilization increased the relative cover of species without persistent litter. Thus fertilization enabled some species without persistent litter to dominate (e.g. *Aira cupaniana* and *Briza minor*). There appears to be two groups of species that do not accumulate persistent litter. The first group, geophytes that occur in unfertilized, low and moderately disturbed plots, are consistent with species characteristic of undisturbed, unproductive environments (i.e. 'stress-tolerant' species) having sparse rarely persistent litter (Grime 1979). The second group occurs in fertilized plots and consists mainly of annual species.

The relative number of species with persistent litter up to 5 cm in depth was increased by high soil disturbance and was decreased by fertilization. The response of the relative cover of species with persistent litter up to 5 cm to soil disturbance depended on the level of fertilization. The increase in the relative cover of species with persistent litter up to 5 cm in depth with high soil disturbance was reduced when combined with fertilization. The decrease in the relative cover of species with persistent litter greater 5 cm deep with high soil disturbance was exacerbated when combined with fertilization. Although anova revealed that disturbance, fertilization and sowing had an effect on the relative number of species with litter greater than 5 cm, pairwise comparisons provided no evidence as to which treatment means.

The response of the relative cover of species with persistent litter greater than 5 cm in depth to fertilization depended on the level of soil disturbance. Fertilization decreased the relative cover of species with persistent litter greater 5 cm deep in low and moderately

disturbed plots, but had no effect on highly disturbed plots because few species with deep litter survived. Species accumulating deep litter tended to have fibrous/thick leaves which were medium to long-lived (Section 3.3.3). Thus their slow leaf turnover would be a disadvantage in disturbed and fertilized habitats because leaf replacement after disturbance would be expensive and slow leaf turnover makes them poor competitors with species able to respond to fertilization. Alternatively, deep litter may be a disadvantage in fertilized plots possibly because it may hinder photosynthesis by contributing to low light conditions. The results contrast with species of undisturbed, productive environments (i.e. 'competitive' species) having copious amounts of litter which enables them to compete with neighbours (Grime 1979).

#### 4.4.8 Underground Storage Organs

Soil disturbance, fertilization and sowing did not affect the relative number of species without underground storage organs at any time during the study. The response of the relative cover of species without underground storage organs to soil disturbance depended on the level of fertilization. High soil disturbance only decreased the relative cover of species without underground storage organs in unfertilized plots. The dominant species without underground storage organs which could tolerate high soil disturbance were also favoured by fertilization. This suggests that some species without underground storage organs rely on high soil nutrients to recover from mechanical damage (e.g. *Dactylis glomerata* and *Lolium perenne*) or germinate and colonize (e.g. *Aira cupaniana* and *Vulpia* spp.) after soil disturbance.

High soil disturbance increased the relative number of species with stolons. Stolons are advantageous in soil disturbed habitats because they play an anchorage, reproductive and dispersal function (Grace 1993). Rhizomes are more costly to produce than stolons because the former are perennial and perform a storage function, while the latter are usually short-lived (Fitter 1986). Thus, species with stolons may be favoured over species with rhizomes in severely disturbed habitats (see below) because the cost of a disturbance event may be reduced by producing stolons which still achieve anchorage, but are less expensive than rhizomes to replace. Fertilization did not affect the relative number of species with stolons at any time during the study. The relative cover of species with stolons was not affected by soil disturbance or fertilization at any time during the study.

The response of the relative number and cover of species with short rhizomes to soil disturbance depended on the level of fertilization. Fertilization increased the relative number of species with short rhizomes only in low disturbance plots. The relative cover of species with short rhizomes was decreased by high soil disturbance only in fertilized plots. This suggests that species with short rhizomes were able to dominate in low disturbance, nutrient-rich plots by actively foraging for nutrients and light by vegetative expansion but were unable

to tolerate mechanical damage. Species capable of vegetative reproduction are often successful where establishment from seed is precluded by dense biomass (Grime 1979).

The relative cover of species with long rhizomes was not affected by soil disturbance at any time during the study. Fertilization increased the relative cover of species with long rhizomes suggesting that long rhizomes enabled some species to dominate space in nutrient-rich habitats (e.g. *Acetosella vulgaris* and *Sporobolus creber*). The relative number of species with long rhizomes was decreased by fertilization. Rhizomes possess anchorage, storage, reproductive and dispersal functions (Grace 1993), but there is no evidence from this study that they enabled species to resist uprooting, recover from mechanical damage using stored resources or pre-empt available space created by soil disturbance.

The response of the relative number of species with long rhizomes or taproots to soil disturbance depended on the level of sowing. Sowing decreased the relative number of species with long rhizomes only in highly disturbed plots because the sown species were most successful in highly disturbed plots, but none of them had long rhizomes. Sowing increased the relative number of species with taproots in moderately and highly disturbed plots because two of the sown species had taproots (e.g. *Plantago lanceolata* and *Sanguisorba minor*) and were most successful in these plots. The response of the relative cover of species with taproots to soil disturbance depended on the level of fertilization. Both moderate and high soil disturbance increased the relative cover of species with taproots to a greater extent in unfertilized than fertilized plots. The dominant species with taproots which could tolerate high soil disturbance were not favoured by fertilization (e.g. *Hypochaeris radicata* and *S.minor*). Fertilization did not affect the relative number of species with taproots at any time during the study. Taproots enabled some species in the present study to resist uprooting, recover from mechanical damage or burial using stored resources and pre-empt the available space (Grace 1993).

The decline in the number and cover of species with stem tubers with high soil disturbance was only observed in spring because, by summer, they had died back to their underground tubers and were no longer visible. Species with stem tubers are probably sensitive to mechanical damage because production of aerial shoots is dependent on the photosynthate produced during the previous year and stored in the tuber. Even without damage, burial of stem tubers at inappropriate depths may reduce survival (Section 4.4.4). However, cover of species with stem tubers benefited from the reduction in neighbour biomass produced by moderate soil disturbance. The response of the relative cover of species with root tubers to soil disturbance depended on the level of fertilization. The relative cover of species with root tubers was decreased by high soil disturbance only in fertilized plots. Fertilization did not affect the relative number of species with root tubers at any time during the study. High soil disturbance decreased the number of species with root tubers, consistent with plants with large tubers being associated with productive stable habitats where the neighbours are large (Grace 1993).



#### 4.4.9 Diaspore Number and Mass

Species with high diaspore number per plant were more common than species with low diaspore number in highly disturbed plots in spring. These results agree with Grime's (1979) prediction that species of persistently disturbed habitats (i.e. 'ruderal' species) devote a large proportion of their annual production to seeds. Higher reproductive allocation has often been found in disturbed habitats (Kay 1987) and declines during succession (Gleeson & Tilman 1990). High diaspore number per plant may be advantageous in soil disturbed habitats because the chance of survival of a germinating individual is unpredictable in soil disturbed habitats, thus provision of a large number of potential individuals (i.e. seed) increases the chance that some will survive. There was no significant relationship between the diaspore mass of a species and its cover. Similarly, Gleeson and Tilman (1994) found no trend between seed size and the successional status of a species. Leishman *et al.* (1995) suggested that seed size is more strongly associated with other plant attributes than with the environmental conditions for establishment. However, other studies have found that species of favourable environments produce few large seeds, while species of adverse or disturbed environments produce numerous smaller ones (Baker 1972; Southwood 1988; Fernández Alés *et al.* 1993).

#### 4.4.10 Commencement of Flowering

Soil disturbance did not affect the relative number or cover of early (August - October) and mid-flowering (November - December) species at any time during the study. Fertilization did not affect the relative number of early or mid-flowering species, but fertilization increased their relative cover of species that commenced flowering early and mid-season. The possession of rhizomes or stolons may have enabled some early and mid flowering species to dominate (e.g. *Acetosella vulgaris*) in nutrient-rich conditions. Soil disturbance did not affect the relative cover of early and mid-season flowering species at any time during the study. Trémont (1994) found that the proportion of species flowering early in the season was greater in grazed plots than in ungrazed plots, but concluded that this was due to a greater proportion of exotic, annual species in the grazed plots. There was no evidence in this study to suggest that early flowering species tended to be exotic or annual (Section 3.3.3).

The response of the relative number of late flowering (January - February) species to soil disturbance depended on the level of fertilization; late flowering species could not tolerate the combination of high soil disturbance and fertilization. High soil disturbance decreased the relative cover of late flowering species. Trémont (1994) found that the proportion of species flowering late in the season was greater in ungrazed plots than in grazed plots, and concluded this was due to a greater proportion of native, perennial species in the ungrazed plots. Similarly, the dominant late-flowering species that could not tolerate high soil

disturbance in this study (e.g. *Aristida ramosa* and *A.warburgii*) were native perennials. Sowing decreased the relative number of early and late flowering species and increased the number of mid-flowering species because most of the sown species were mid-season flowering species (e.g. *Dactylis glomerata*, *Lolium perenne*, *Plantago lanceolata* and *Sanguisorba minor*).

#### 4.4.11 Flowering Period Duration

On the unfertilized plots in summer, species with a long flowering period duration were more common than species with a short flowering period. Species with long flowering period also had long-lived leaves and produced a small number of large diaspores (Section 3.3.3). Thus, they may be favoured in nutrient-poor habitats because they possess attributes associated with the conservative use of nutrients. Soil disturbance did not affect the abundance of species with long or short flowering periods. However, Odgers and Rogers (1993) found that species characteristic of road banks and mown habitats had longer flowering periods than species characteristic of forest species.

#### 4.4.12 Leaf Life Span

Species with short-lived leaves (e.g. *Aira cupaniana* and *Vulpia* spp.) were more common than species with long-lived leaves in highly disturbed, fertilized plots. The same was true on the moderately disturbed fertilized plots, but only in spring. Species with short-lived leaves were favoured by the combination of soil disturbance and fertilization because fertilization enabled them to rapidly complete their life cycle, despite a high risk of nutrient loss, and their minimal investment in biomass ensured that biomass loss by disturbance events was small. Other studies confirm that species with shorter leaf life spans are prevalent in fertilized habitats (Diemer *et al.* 1992).

Species with long-lived leaves (e.g. *Aristida ramosa* and *A.warburgii*) were more common than species with short-lived leaves in low disturbance, unfertilized plots. Species with long-lived leaves were favoured under nutrient-poor, low disturbance conditions because the benefits of investing in structurally tough and well defended leaves only outweighs its cost if it persists for a long time (i.e. not removed by disturbance). The results are consistent with long leaf life spans being favoured in nutrient-poor habitats because of more efficient use of nutrients (Chabot & Hicks 1982). Reich *et al.* (1992) found that species with short-lived leaves tend to be common early in succession and species with long-lived leaves tend to be common late in succession. The results are consistent with plants of unproductive, undisturbed habitats ('stress-tolerators') having long-lived leaves and plants of productive, undisturbed ('competitive') and productive, disturbed habitats ('ruderal') having relatively

short-lived leaves (Grime 1979). Species in this study with long-lived leaves tended to be more abundant in summer than in spring, which is consistent with species adapted to temporal microhabitats having short-lived leaves (Reich *et al.* 1992).

#### 4.4.13 Leaf Size

The response of the relative number of species with leptophyll (< 25 mm<sup>2</sup>) sized leaves to soil disturbance depended on the level of fertilization; high soil disturbance decreased species with leptophyll leaves only in fertilized plots. Thus, a number of species with small leaves could not tolerate the combination of high soil disturbance and fertilization. Disturbance did not affect the relative cover of species with leptophyll leaves at any time during the study. Fertilization enabled some species with relatively small leaves to dominate nutrient-rich plots (e.g. *A.cupaniana* and *Oxalis exilis*). These results are inconsistent with other studies suggesting that species from high light environments tend to have small leaves (Givnish & Vermeij 1976; Olff *et al.* 1990). The increase in the cover of species with leptophyll leaves with fertilization was greater in spring than in summer, suggesting that the dominant spring-growing species which responded to fertilization tended to have small-leaves (e.g. *A.cupaniana*). Although both grazing and soil disturbance create open space, the leaf sizes favoured in grazed habitats differ from those favoured in soil disturbed habitats; under high grazing pressure reduced leaf size enables species to evade herbivory (Díaz *et al.* 1992).

High soil disturbance decreased the relative number and cover of species with nanophyll (25 - 225 mm<sup>2</sup>) sized leaves and increased number and cover of species with microphyll (225 - 2025 mm<sup>2</sup>) sized leaves. Species with relatively large leaves were favoured in highly disturbed plots because the benefits of rapidly pre-empting and dominating the available space outweigh the costs of constructing large leaves (e.g. *Hypochaeris radicata*, *Acetosella vulgaris* and *Dactylis glomerata*). The response of the relative number of species with nanophyll or microphyll leaves to fertilization depended on the level of sowing. Fertilization decreased the relative number of species with nanophyll leaves and increased species with microphyll leaves only in sown plots because most sown species that were favoured by fertilization (e.g. *D.glomerata*, *Lolium perenne* and *Plantago lanceolata*) had microphyll leaves and the sown species not favoured by fertilization (*Sanguisorba minor*) had nanophyll leaves. Fertilization did not affect the relative cover of species with nanophyll leaves at any time during the study and decreased the cover of species with microphyll leaves in November 1993 only. The results on the sown plots were consistent with the observation that leaf size tends to increase with soil fertility (Beadle 1966; Givnish & Vermeij 1976).

#### 4.4.14 Diaspore Hairiness

High soil disturbance decreased the relative number of species with glabrous diaspores and increased species with hairy diaspores. The results are not consistent with other studies that have found that the advantage of antrorse hairs in aiding the radicle to penetrate the soil and anchoring the diaspore is less influential in disturbed habitats where burial can be achieved passively (Peart 1979; Rogers & Whalley 1989). Hairs may be of benefit in soil disturbed habitats because a reduction in the rate of water loss by evaporation may be advantageous in exposed conditions (Peart 1979). Fertilization significantly increased the relative number of species with glabrous diaspores and decreased species with hairy diaspores in November 1992, but the effect had diminished by February 1994. The response of the relative cover of species with glabrous or hairy diaspores to soil disturbance depended on the level of fertilization. Fertilization increased the relative cover of species with glabrous diaspores and decreased species with hairy diaspores in low and moderately disturbed plots, but not in highly disturbed plots. Fertilization enabled some species with glabrous diaspores (e.g. *Briza minor* and *Sporobolus creber*) to dominate the low and moderately disturbed plots.

#### 4.4.15 Diaspore Shape

The response of the relative number of species with spherical or cylindrical diaspores to soil disturbance depended on the level of sowing. High soil disturbance decreased the relative number of species with spherical diaspores and increased species with cylindrical diaspores only in sown plots because the two sown species with cylindrical diaspores (e.g. *Dactylis glomerata* and *Lolium perenne*) were most successful in highly disturbed plots and the two sown species with spherical diaspores (e.g. *Plantago lanceolata* and *Sanguisorba minor*) were present in low and moderately disturbed plots. Fertilization increased the relative number of species with spherical diaspores and decreased the number of species with cylindrical diaspores in March 1993 and November 1993, but the effect had diminished by February 1994.

The response of the relative cover of species with spherical or cylindrical diaspores in to soil disturbance depended on the level of fertilization. The increase in the relative cover of spherical diaspores and the decrease in the cover of species with cylindrical diaspores with fertilization diminished with increasing soil disturbance. Fertilization enabled some species with spherical seeds (e.g. *Sporobolus creber*) to dominate, but soil disturbance reduced this effect. Species with cylindrical diaspores (e.g. *Aristida ramosa* and *A. warburgii*) dominated the unfertilized plots. Spherical seeds are more easily passively buried and incorporated into the seed bank than cylindrical seeds (Peart 1979). Perhaps the dominant species of the low and moderately disturbed fertilized plots have spherical seeds because being incorporated into the seed bank is advantageous in conditions where there is a lack of opportunity for

establishment. In contrast, greater bare ground in unfertilized or highly disturbed habitats may increase opportunities for establishment and therefore delayed germination enforced by burial is not advantageous.

#### 4.4.16 Diaspore Dispersal Morphology

High soil disturbance increased the relative number of species without diaspore dispersal appendages. In contrast, McIntyre *et al.* (1995) found that soil disturbance decreased the number of species on the Northern Tablelands with an undefined dispersal mechanism. Peart (1984) found that grasses with unawned diaspores rely on passive burial as a result of soil movement and the activity of small mammals and insects. Therefore, diaspores which lack appendages may be advantageous in soil-disturbed habitats because they are easily buried. Fertilization did not significantly affect the relative number of species without diaspore dispersal appendages, but did increase their relative cover. Thus, some species without diaspore appendages dominated the fertilized plots (e.g. *Sporobolus creber*, *Carex breviculmis* and *Schoenus apogon*). Soil disturbance increased the relative cover of species without diaspore dispersal appendages in November 1993, but the effect diminished by February 1994.

Fertilization did not significantly affect the relative number of species with awns/hooks at any time during the study. Although anova revealed that disturbance significantly affected the relative number of species with awns/hooks, Bonferroni pairwise comparisons found no significant differences between the treatment means. The response of the relative cover of species with awns/hooks on their diaspores to soil disturbance depended on the level of fertilization; high soil disturbance decreased cover only in unfertilized plots. Species with awns are less prevalent in mown habitats (Odgers & Rogers 1993) and on the frequently perturbed, high organic matter soils of sheep camps (Rogers & Whalley 1989). Peart (1979, 1981) showed experimentally that hygroscopic awns move the diaspore across the ground causing it to lodge in a suitable micro-site (e.g. soil crack), while rigid awns orientate the diaspore so that its callused end becomes embedded in the soil surface. Awns increase the chance of successful establishment in less disturbed habitats because they position the diaspore so that it is anchored in the soil, while passive burial is more likely in soil disturbed habitats. However, this was only the case in unfertilized plots.

The relative number of species with pappus on their diaspores was increased by fertilization and soil disturbance in spring. Similarly, soil disturbance increased the proportion of wind-dispersed species on the Northern Tablelands (McIntyre *et al.* 1995). The results are consistent with regeneration involving numerous wind-dispersed diaspores being adapted to exploit forms of disturbance which are spatially unpredictable (Grime 1979). The increase in the relative number of species with pappus on their diaspores with fertilization was consistent with species of productive, undisturbed habitats (i.e. 'competitive' species)

producing wind-dispersed diaspores to facilitate colonization of new habitat where seedling establishment is not restricted by high biomass (Grime 1979). The response of the relative cover of species with pappus on their diaspores to soil disturbance depended on the level of fertilization; high soil disturbance only increased cover in the unfertilized plots.

Soil disturbance did not affect the relative number of species with dust-like ( $\leq 0.03$  mg) diaspores at any time during the study, but their cover was decreased. Fertilization decreased the relative number of species with dust-like diaspores probably because their small resources would not maintain them through the long establishment phase typical of high biomass environments. Further, dust-like diaspores may be advantageous in nutrient-poor habitats because their high dispersal efficiency may be a mechanism to increase the chance of contact between the seed and mycorrhiza (Grime 1979). McIntyre *et al.* (1995) also found that soil disturbance decreased the number of species with dust-like diaspores on the Northern Tablelands. The proposal that small-seeded species are favoured in soil-disturbed habitats (Harper *et al.* 1970) did not hold for species with dust-like seeds ( $\leq 0.03$  mg) because their burial is probably lethal due to insufficient resources for shoots to reach the soil surface.

High soil disturbance significantly decreased the relative number and cover of species with explosive diaspores. Fertilization decreased the relative number of species with explosive diaspores, but their cover remained unaffected. Sowing increased the relative number of species without diaspore appendages and decreased the number of species with pappus and the relative cover of species with explosive diaspores because most of the sown species were without diaspore appendages (e.g. *Dactylis glomerata*, *Lolium perenne*, *Plantago lanceolata* and *Sanguisorba minor*).

#### 4.4.17 Leaf Hairiness

High soil disturbance decreased the relative number of species with glabrous leaves and increased species with hairy leaves. Leaf hairs decrease transpiration and increase water use efficiency (Lambers & Poorter 1992). Thus, species with hairy leaves may be favoured in open, soil-disturbed habitats where transpiration is high. Fertilization increased the relative number of species with glabrous leaves and decreased species with hairy leaves in November 1992, but the effect had diminished by February 1994. Species that invest in leaf hairs may be favoured in nutrient-poor habitats because hairs reduce herbivory (Lambers & Poorter 1992) and herbivory affects the nutrient use efficiency of a plant (Chabot & Hicks 1982). Some types of leaf pubescence reduces water contact with the leaves, thereby reducing the loss of nutrients by leaching (Chapin 1980). The response of the relative cover of species with glabrous or hairy leaves to soil disturbance depended on the level of fertilization. High soil disturbance decreased the relative cover of species with glabrous leaves and increased the cover of species with hairy leaves to a greater extent in unfertilized than fertilized plots. Some

species with glabrous leaves dominate the fertilized low and moderately disturbed plots, and species with hairy leaves dominate the unfertilized highly disturbed plots.

#### **4.4.18 Diaspore Surface Texture**

The response of the relative number of species with smooth or rugose/striate diaspores to soil disturbance depended on the level of sowing. High soil disturbance increased the relative number of species with smooth diaspores and decreased species with rugose/striate diaspores only in sown plots because most of the sown species had smooth diaspores (e.g. *D.glomerata*, *L.perenne* and *P.lanceolata*). Fertilization increased the relative number of species with smooth diaspores and decreased species with rugose/striate diaspores. The response of the relative cover of species with smooth or rugose/striate diaspores to soil disturbance depended on the level of fertilization. High soil disturbance decreased the relative cover of species with smooth diaspores and increased species with rugose/striate diaspores in unfertilized plots, but had no effect in fertilized plots. Species with smooth diaspores may be favoured in soil disturbed habitats, where evapotranspiration is high, because the seed-water contact and water uptake of seed is increased by a smooth surface texture (Harper *et al.* 1970). Water loss may be less of a problem in fertilized plots because the vegetation would reduce evaporation. Sowing increased the relative cover of species with smooth diaspores and decreased species with rugose/striate diaspores because most of the sown species had smooth diaspores.

#### **4.4.19 Root:Shoot Ratio and Allometric Constant of Seedlings**

Species whose seedlings allocated more biomass to the shoots than the roots were more common in fertilized, highly disturbed plots than species that allocated more biomass to roots than shoots. In summer, species whose seedlings allocated more biomass to roots than shoots were more common in low disturbance, unfertilized plots (i.e. control plots). These results are consistent with species from infertile or dry habitats investing a higher proportion of biomass in roots and species from nutrient-rich habitats investing a higher proportion of biomass in shoots (Chapin 1980; Lambers & Dijkstra 1987). Tilman (1988) suggested that species allocating more biomass to above-ground structures are favoured in undisturbed, nutrient-rich environments because they are light-poor environments and species allocating more biomass to below-ground structures are favoured in nutrient-poor environments because they are light-rich. However, light availability is not the only factor involved because species allocating more biomass to above-ground structures were favoured in nutrient-rich plots when they were light-rich (i.e. highly disturbed). The results found here suggest that greater allocation to the shoots may be advantageous in soil disturbed habitats by allowing rapid pre-

emption of available space or completion of reproduction before the next disturbance event. Gleeson and Tilman (1994) found that late successional species allocated more biomass to the roots than early successional species in the field, but the opposite was true for seedlings in the greenhouse. Thus, in the allocation patterns demonstrated at the seedling stage in the glasshouse in this study may not have continued through to adulthood.

#### 4.4.20 Stem Structure

The relative number of tussock/tuft species was increased by fertilization, but was not affected by soil disturbance at any time during the study. Tussock/tuft species may be favoured in high biomass conditions of nutrient-rich plots because their erect linear leaves achieve the greatest height advantage for a given amount of biomass, enabling greater access to light. The capacity of tussock grasses to resist canopy closure and to produce shade enables them to persist under intense competition for light (Díaz *et al.* 1992). The response of the relative cover of tussock/tuft species to soil disturbance depended on the level of fertilization. Fertilization decreased the relative cover of tussock/tuft species in low and moderately disturbed plots, but increased their cover in highly disturbed plots. Some tussock/tuft species dominated the fertilized highly disturbed plots (e.g. *Vulpia* spp. and *Lolium perenne*). The decline in some tussock/tuft species with fertilization, in low and moderately disturbed plots, may be due to the dominant tussock species (e.g. *Aristida* spp.) having a poor capacity to resist canopy closure or to produce shade because, although their tussocks were large, their foliage was sparse. Other studies have found that the proportion of tussock or tufted species is greater in ungrazed plots than grazed plots (Trémont 1994) and in undisturbed forest than on road banks or mown areas (Odgers & Rogers 1993). Here, high soil disturbance only decreased the relative cover of tussock/tuft species in unfertilized plots.

High soil disturbance increased the relative number of rosette/semi-rosette species. The response of the relative cover of rosette/semi-rosette species to soil disturbance depended on the level of fertilization; moderate and high soil disturbance increased cover to a greater extent in unfertilized than fertilized plots. Some rosette/semi-rosette species dominated the highly disturbed nutrient-poor plots to a greater extent than nutrient-rich plots (e.g. *Hypochaeris radicata* and *Sanguisorba minor*). Other studies on the Northern Tablelands have found that the proportion of rosette species increases with soil disturbance (McIntyre *et al.* 1995) and grazing (Trémont 1994). Flat/versatile rosette growth form may be efficient for light interception and space pre-emption on the open ground of disturbed habitats (McIntyre *et al.* 1995). The relative number of rosette/semi-rosette species was decreased by fertilization. The low leaf height of the rosette/semi-rosette stem structure may be a disadvantage under the low light conditions associated with the fertilized plots. Díaz *et al.* (1992) found that rosettes with below-ground reserve organs are associated with high light conditions and cannot compete under a dense canopy. The increase in the relative number of



rosette/semi-rosette species with sowing was due to two of the sown species having a rosette/semi-rosette habit (e.g. *Plantago lanceolata* and *S.minor*). The response of the relative cover of rosette/semi-rosette species to fertilization depended on the level of sowing. Fertilization decreased the cover of rosette/semi-rosette species to a greater extent in sown than unsown plots because the sown species, *S.minor*, had rosette/semi-rosette stem structure and was not favoured by fertilization.

The response of the relative number of species with erect/branching or prostrate/twining stem structures to soil disturbance depended on the level of sowing. The relative number of erect/branching in highly disturbed unsown plots was greater than in low disturbance unsown plots and moderately or highly disturbed sown plots because the sown species were successful in moderately and highly disturbed plots, but none had erect/branching habits. The response of the relative cover of species with erect/branching habits to fertilization depended on the level of soil disturbance; fertilization increased cover to a greater extent in low and moderately disturbed plots than highly disturbed plots. Fertilization enabled some erect/branching species to dominate low and moderately disturbed plots probably because they were able to penetrate the high levels of biomass on these plots or their elevated, dispersed growing points allow them to re-adjust their leaf canopy in response to changing light conditions. High soil disturbance decreased the relative number of prostrate/twining species but only in unsown plots. Another study on the Northern Tablelands found that the proportion of trailer forb species was lower in grazed plots than in ungrazed plots (Trémont 1994). Fertilization did not effect the relative number of species with erect/branching or prostrate/twining stem structures at any time during the study. Although anova revealed a significant disturbance x fertilization x sown interaction for the relative cover of prostrate/twining species in February 1994, Bonferroni pairwise comparisons found no significant difference between the treatment means.

#### **4.4.21 Leaf Shape**

The response of the relative number of species with circular/obovate leaves to soil disturbance depended on the level of fertilization and sowing. The relative number of species with circular/obovate leaves in the highly disturbed fertilized sown plot was greater than in all other treatments except the highly disturbed unfertilized sown plots because one of the sown species, *Sanguisorba minor*, had circular leaves and was most successful in highly disturbed plots. The response of the relative cover of species with circular/obovate leaves to soil disturbance depended on the level of sowing because *S.minor* had circular leaves and dominated in highly disturbed plots. Round leaves are effectively the largest for a given investment of leaf tissue (Givinish & Vermeij 1976). Thus *S.minor* may dominate soil disturbed habitats because its effectively larger leaves allows pre-emption of the available space. The response of the relative cover of species with circular/obovate leaves to soil

disturbance depended on the level of fertilization; cover in highly disturbed unfertilized plots was greater than in all of the other treatments.

Disturbance did not affect the relative number of species with elliptic leaves at any time during the study. Fertilization significantly decreased the relative number of species with elliptic leaves only in November 1993. Sowing increased the relative cover of species with elliptic leaves only in highly disturbed plots because one of the sown species had elliptic leaves (e.g. *Plantago lanceolata*) and was most successful under conditions of high soil disturbance. Fertilization increased the relative cover of species with elliptic leaves in March 1993 only.

Since two of the sown species had linear/filiform leaves (e.g. *Dactylis glomerata* and *Lolium perenne*), the decrease in the relative number of species with linear/filiform leaves with sowing was probably due to a competitive effect by the sown species on resident species with linear/filiform leaves. High soil disturbance decreased the relative number of species with linear/filiform leaves. Fertilization did not affect the relative number of species with linear/filiform leaves at any time during the study. The response of the relative cover of species with linear/filiform leaves to soil disturbance depended on the level of fertilization; high soil disturbance decreased cover to a greater extent in unfertilized than fertilized plots. According to the predictions of Givnish (1982), linear/filiform leaves would experience low levels of self-shading and therefore may be advantageous under the conditions of high biomass and low light associated with the low and moderately disturbed plots.

The response of the relative number of species with lanceolate/oblanceolate leaves to fertilization depended on the level of sowing. Fertilization decreased the relative number of species with lanceolate/oblanceolate leaves only in unsown plots. Since none of the sown species had lanceolate/oblanceolate leaves, no explanation for the interaction is apparent. Moderate and high soil disturbance had no effect on the relative number of species with lanceolate/oblanceolate leaves, but did increase their relative cover. The high degree of self-shading in species with lanceolate/oblanceolate leaves (Givnish 1982) was not a disadvantage in the high light environment of soil disturbed habitats and may have been an advantage by reducing evapotranspiration (e.g. *Acetosella vulgaris* and *Hypochaeris radicata*). Fertilization decreased the relative cover of species with lanceolate/oblanceolate leaves. The high degree of self-shading in species with lanceolate/oblanceolate leaves is probably a disadvantage under high biomass conditions and low light. Sowing decreased the relative cover of species with lanceolate/oblanceolate leaves in November 1993 only. Since none of the sown species themselves had lanceolate/oblanceolate leaves, the results suggest the sown species may have had a competitive effect on some species with lanceolate/oblanceolate leaves.

#### 4.4.22 Inflorescence Form

The response of the relative cover of species with capitulum or spike-like inflorescences to soil disturbance depended on the level of fertilization. Moderate and high soil disturbance increased the relative cover of species with capitulum inflorescences to a greater extent in unfertilized than fertilized plots. Some dominant species with capitulum inflorescences (e.g. *H. radicata*) were favoured by disturbed nutrient-poor conditions. High soil disturbance increased the relative number of species with capitulum inflorescences. Fertilization increased the relative number of species with capitulum inflorescences in November 1993 only. All of the species with capitulum inflorescences also belonged to the Asteraceae, had low growing habits (rosettes or prostrate) and were exotic (Section 3.3.3). The response of species with capitulum inflorescences may relate to their geographical origin because exotic species tend to be favoured by high soil disturbance and fertilization (Section 4.4.1). The sown treatment increased the relative number of species with capitulum inflorescences because one of the sown species, *Sanguisorba minor*, had capitulum inflorescences.

High soil disturbance decreased the relative cover of species with spike-like inflorescences only in unfertilized plots. Dominant species with spike-like inflorescences (e.g. *Aristida ramosa*) that could not tolerate high soil disturbance, were also not favoured by fertilization. The response of the relative number of species with spike-like inflorescences to soil disturbance depended on the level of sowing. Sowing significantly increased the relative number of species with spike-like inflorescences in highly disturbed plots because three of the sown species had spike-like inflorescences (e.g. *Dactylis glomerata*, *Lolium perenne* and *Plantago lanceolata*) and were favoured by high soil disturbance. Fertilization increased the relative number of species with spike-like inflorescences. The vertical flower arrangement in species with spike-like inflorescences may increase the chance of pollinators encountering the inflorescence in densely vegetated habitats and ensures that seed dispersal is not hindered by neighbouring foliage. The clustering of a number of flowers in a spike-like arrangement (as opposed to greater distance between solitary flowers) may increase the number of flowers that a pollinator encounters in dense biomass.

High soil disturbance decreased the relative cover of species with panicle-like (e.g. *Aristida warburgii*), cyme-like (e.g. *Hypericum gramineum*) or solitary (e.g. *Drosera peltata*) inflorescences. Some species with panicle-like (e.g. *Aira cupaniana* and *Briza minor*) and solitary (e.g. *Oxalis exilis*) inflorescences dominated space in the fertilized plots. Fertilization did not affect the relative cover of species with cyme-like inflorescences. The response of the relative number of species with panicle-like and cyme-like inflorescences to soil disturbance depended on the level of sowing. High soil disturbance decreased the number of species with cyme-like inflorescences and increased species with panicle-like inflorescences only in unsown plots because none of the sown species had cyme-like or panicle-like inflorescences.

Fertilization increased the relative cover of species with solitary inflorescences in March 1993 only. The relative number of species with solitary inflorescences in highly disturbed plots was lower than in moderately disturbed plots, but not significantly different to the low disturbance plots. Moderate soil disturbance may favour species with solitary inflorescences because access to pollinators and seed dispersal may be enhanced when biomass is moderate. The risk of loss of seed production, in severely disturbed habitats, may be high for species with solitary inflorescences because the reproductive structures are invested in only a few location. Fertilization decreased the relative number of species with solitary inflorescences, possibly because high biomass may reduce the chance of pollinators encountering the few dispersed flowers.