# CHAPTER FIVE

# AN EXPERIMENTAL TEST OF THE C-S-R MODEL

## 5.1 INTRODUCTION

The C-S-R model (Fig. 1.1) proposed by Grime (1979) is a predictive framework of vegetation pattern based on the relationship between plant attributes and the environment (Section 1.1.2). The model consists of an equilateral triangle, the corners of which are associated with the evolution of three primary strategies: competitors (C), ruderals (R) and stress-tolerators (S). Grime (1974) suggested that a practical method allowing the ordination of species or vegetation within the framework of the triangular model, would require measurable plant attributes which vary in accordance with any two of the three sets of contours of the relative importance of competition, stress and disturbance.

The first attempt by Grime (1974) to find such a method was based on the hypothesis that the primary strategies correspond to three permutations between maximum relative growth rate (Rmax) and morphology: rapidly growing and large (competitors), rapidly growing and small (ruderals), and slow growing and small (stress-tolerators). Grime (1974) proposed an additive Morphology Index based on attributes believed to confer a competitive advantage to the species that possess them (i.e. height, lateral spread and litter depth). This Morphology Index reflects the maximum size attained by a plant species under favourable conditions. Vegetation samples from a wide variety of habitats could then be ordinated with respect to a C-S-R strategy by the Rmax and Morphology Index of each species, weighted according to their relative frequency in the sample (Grime 1979).

A more sophisticated method of assigning a C-S-R strategy to a species was developed by Grime *et al.* (1988) using a preliminary dichotomous key based upon characteristics of plant life-history, morphology and phenology (Fig. 5.1). The key allowed a number of 'marker species' to be assigned to one of the seven established plant strategies (i.e. competitor, stress-tolerator, ruderal, competitive ruderal, stress-tolerant ruderal, stress-tolerant competitor or C-S-R strategist). Grime *et al.* (1988) emphasised that the key was a provisional classification, which could only be applied with confidence to a restricted number of species.

The literature review (Section 1.1.2) demonstrated that the ability of C-S-R model to predict vegetation response and pattern has rarely been adequately studied. Attempts to test the C-S-R model (or plant strategy theory) have used varied approaches. Shipley and Peters (1990a) suggested that deductive models can be tested by either addressing the hypotheses, or the predictive outcomes of the model. Agreement between the predicted and observed patterns does not necessarily mean that the initial hypotheses of a model are correct, because several models may account for the same pattern. They suggest that tests of the hypotheses on which a model is based are powerful because they are directed at the heart of the model. Both approaches were used here to test Grime's (1979) C-S-R and the results are reported in this chapter. First, two underlying hypotheses of the model were tested: (i) that maximum relative growth rate (Rmax) and (ii) the Morphology Index of species are associated with the relative importance of stress and disturbance (Table 5.5A).

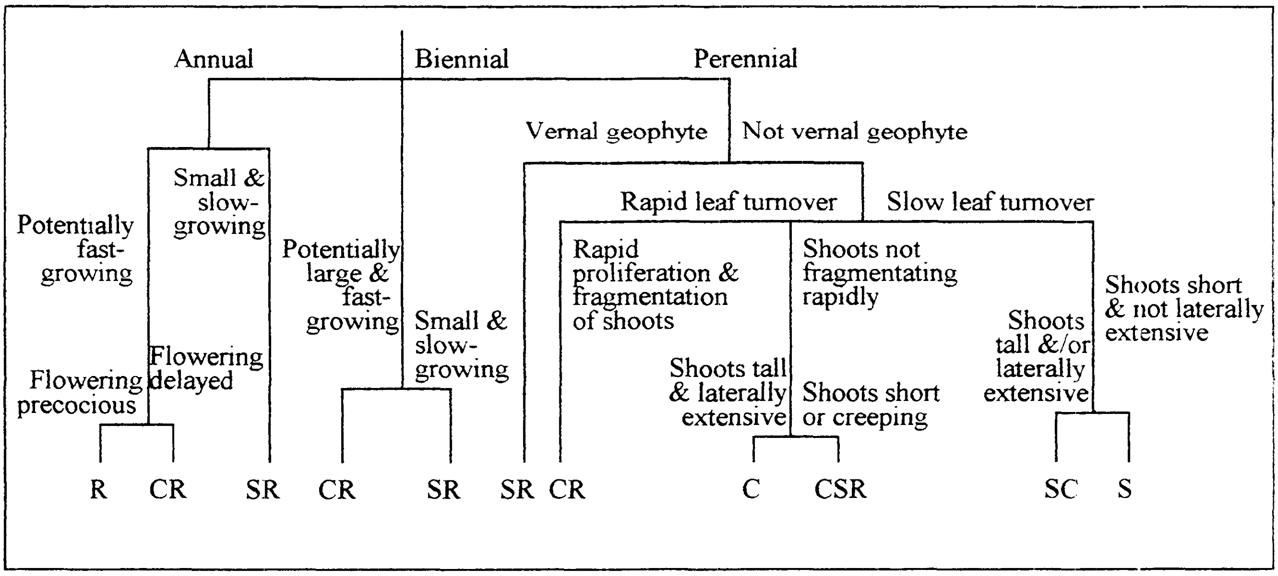


**Fig: 5.1:** The dichotomous key to C-S-R strategies in herbaceous plants proposed by Grime *et al.* (1988). C = competitor; S = stress-tolerator; R = ruderal; CR = competitive-ruderal; SR = stress-tolerant ruderal; CS = stress-tolerant competitor; CSR = CSR strategist.

Second, the outcomes of the experiment were compared to those predicted by the model using two methods. The dichotomous key (Grime *et al.* 1988) was used to assign a C-S-R strategy to the species in the field experiment and the response of species of particular strategies to soil disturbance and fertilization was compared to that predicted by the model (Table 5.5B). Although the reservation of Grime *et al.* (1988) that the key is only preliminary should be kept in mind, the use of the key was worthwhile given the absence of other ways of objectively assigning a strategy to each species. The second method was to examine whether the ordination of vegetation samples from the different soil disturbance and fertilization treatments by the mean Rmax and the mean Morphology Index of its component species were consistent with the predictions of the model (Table 5.5C).

The C-S-R model makes predictions about species response over a wide range of habitats. Thus to test the model adequately it was necessary to ensure that a wide range of species attributes were available for examination. As the pre-treatment condition of the site was one of low fertility and moderate disturbance (i.e. grazing), the possibility existed that the majority of species would possess 'stress-tolerant' (*sensu* Grime 1979) characteristics. The sown treatment, which supplied seed of competitive and ruderal species to the plots, eliminated the question of whether certain strategies failed to establish because they were not present at the site and their dispersal at that particular time or place was limiting.

The aim of this chapter is to evaluate the C-S-R model by addressing the following questions:

1. Is the maximum relative growth rate of each species positively correlated with its abundance on the disturbed plots and negatively correlated with its abundance on the low disturbance plots?
2. Is the maximum relative growth rate of each species positively correlated with its abundance on the fertilized plots and negatively correlated with its abundance on the unfertilized plots?
3. Is the Morphology Index (Grime 1979) of each species positively correlated with its abundance on the fertilized, low disturbance plots and negatively correlated with its abundance on the unfertilized and disturbed plots?
4. Do the C-S-R strategies, as determined by the dichotomous key of Grime *et al.* (1988), respond to soil disturbance and fertilization as predicted by the C-S-R model?
5. Does the ordination of the vegetation samples of the different treatments, by the mean Rmax and mean Morphology Index of its component species, correspond to the predictions of the C-S-R model?

## 5.2 METHODS

The mean maximum seedling relative growth rate (Rmax) of the 22 Newholme species was determined as described in Section 3.2.2a. The additive Morphology Index (MI) proposed by Grime (1974) was determined for each species using the attributes previously determined in the field (Section 3.2.1) and was calculated as:

$$MI = (a + b + c)/2 \qquad (5.1)$$

where

a - the maximum vegetative height (1, < 12 cm; 2, 12 - 25 cm; 3, 25 - 37 cm; 4, 37 - 50 cm; 5, 50 - 62 cm; 6, 62 - 75 cm; 7, 75- 87 cm; 8, 87 - 100 cm; 9, 100 - 112 cm; 10, > 112 cm).

b - lateral spread (0, small therophytes; 1, robust therophytes; 2, perennials with compact unbranched rhizome or forming small (< 10 cm diameter) tussock; 3, perennials with rhizomatous system or tussock attaining diameter 10 - 25 cm; 4, perennials attaining diameter 26 - 100 cm; 5, perennials attaining diameter > 100 cm).

c - estimated maximum accumulation of persistent litter (including dead attached) (0, none; 1, thin discontinuous cover; 2, thin continuous cover; 3, up to 1 cm in depth; 4, up to 5 cm in depth; 5, > 5 cm in depth).

Since Grime (1979) described the Morphology Index as reflecting the maximum size attained by a plant under favourable conditions, the Morphology Index was calculated from measurements of plants from the fertilized plots (for species that responded to fertilization).

The Rmax and Morphology Index of each species were correlated with their mean absolute cover in each treatment using SYSTAT (Wilkinson *et al.* 1992). As the correlations were within each treatment rather than between treatments, absolute cover values were 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 in case there were seasonal differences in the abundance of species with certain Rmax and Morphology Index values.

The dichotomous key developed by Grime *et al.* (1988) was used to classify the herbaceous species at Newholme with respect to C-S-R strategy (Fig. 5.1). As no thresholds to define the general terms in the key were given, the median values for the attributes of the species at Newholme were used. 'Slow' leaf life span was defined by the median as $\geq$ 98.5 days and 'rapid' as $<$ 98.5 days. 'Tall' shoots were defined by the median as $\geq$ 13.5 cm and 'short' shoots $<$ 13.5 cm. 'Fast-growing' was defined as $\geq$ 1.0 g per g per week and 'slow-growing' as $<$ 1.0 g per g per week. Species that commenced flowering before or in mid-November were regarded as 'flowering precociously'. Only those species for which the necessary information had been obtained were assigned a strategy. For this reason, *Vulpia bromoides* and *V.myuros* were omitted from analysis because the two species were not identified separately in the field and the Rmax of the two species differed.

The response of the strategies assigned by the key to soil disturbance, fertilization and sowing was determined by analysis of variance (anova) of the relative cover and relative number of species of a particular strategy. The relative cover of species with a particular strategy was determined by summing together the canopy cover of each species in the plot with the strategy and expressing it as a percentage of the total canopy cover in the plot. The relative number of species with a particular strategy was determined by summing together the number of species in the plot with the strategy and expressing it as a percentage of the total number of species in the plot. Relative cover and relative number of species were used because absolute values would merely reflect the low levels of vegetation cover and species richness in highly disturbed plots. In other words, high soil disturbance would *always* produce a significant decrease in the absolute cover or number of *all* of the strategies examined, because few species survived high soil disturbance.

The fully factorial anova of the relative cover and relative number of species with each strategy was carried out for each of the four sampling times 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. There were five replicates for each treatment. Pairwise comparisons of the means were made using Bonferroni tests. Estimates of canopy 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). Further details as to the rationale of data analysis used here is given in Section 2.2.5.

Ordination of each of the sixty (1m$^2$) vegetation samples along the axes of mean relative growth rate and mean Morphology Index was carried out following the approach of Grime (1979). The five replicates of the twelve treatments (i.e. 3 levels of soil disturbance x 2 levels of fertilization x 2 levels of sowing) were treated separately. The mean values for each plot were calculated by weighting the Rmax of each species (as determined above) by its canopy cover in that plot. The same procedure was carried out for the Morphology Index.

## 5.3 RESULTS

### 5.3.1 Effects of Fertilization and Soil Disturbance on Maximum Relative Growth Rate of Seedlings

The canopy cover of species was negatively correlated with their maximum seedling relative growth rate on the unfertilized, low disturbance plots (Table 5.1). This negative correlation was also found on the moderately disturbed, unfertilized plots but only in unsown plots in summer (February 1994). The canopy cover of species was positively correlated with its Rmax on the highly disturbed plots, but only in sown plots.

**Table 5.1**: Spearman Rank Correlation Coefficients (n = 16) between the logarithm of the maximum seedling relative growth rate of a species and its transformed (arcsine) canopy 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. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

| Maximum relative growth rate | | L/U | M/U | H/U | L/F | M/F | H/F |
|---|---|---|---|---|---|---|---|
| November 1993 | Unsown | **-0.444**** | -0.201 | 0.232 | -0.112 | -0.107 | 0.104 |
| | Sown | **-0.353*** | -0.227 | **0.691***** | 0.028 | 0.297 | **0.735***** |
| February 1994 | Unsown | **- 0.514**** | **- 0.360*** | 0.368 | - 0.218 | - 0.085 | 0.155 |
| | Sown | **- 0.543**** | - 0.305 | **0.508**** | - 0.131 | 0.209 | **0.721***** |

The contribution each of the ten most common species (descending in order of importance) made to the correlation between Rmax and canopy cover in each treatment is shown in Fig. 5.2. Soil disturbance increased the canopy cover of species with high Rmax and decreased the canopy cover of species with low Rmax (compare Fig. 5.2a with c and e). Further, species with high Rmax tended to increase in abundance with fertilization (compare Fig. 5.2a with b, Fig. 5.2c with d and Fig. 5.2e with f).

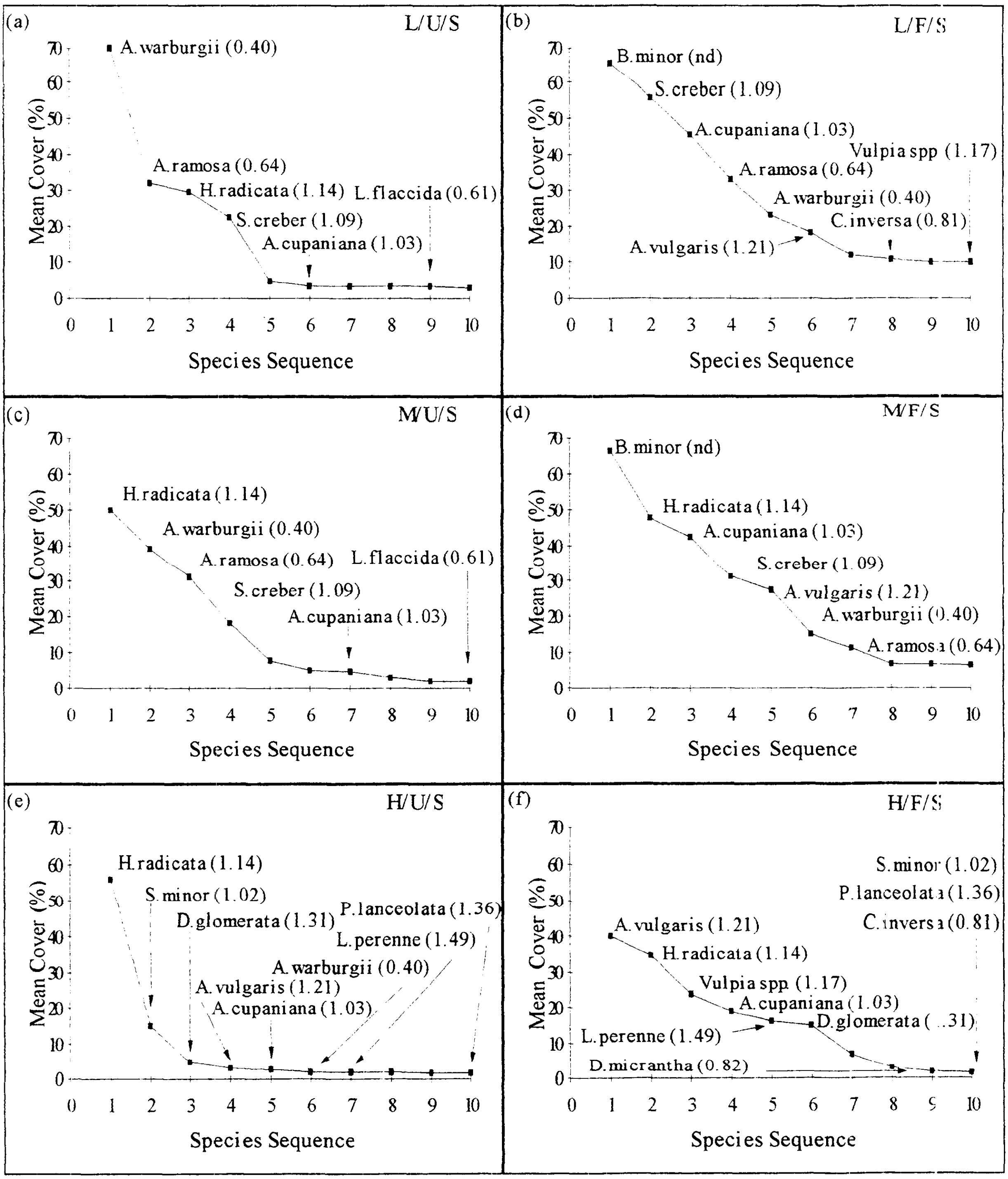


Fig. 5.2: Sequence of species in descending order of mean canopy cover (%) in February 1994 and their maximum seedling relative growth rate (in parentheses) in (a) L/U/S - low disturbance, unfertilized and sown (b) L/F/S - low disturbance, fertilized and sown (c) M/U/S - moderate disturbance, unfertilized and sown (d) M/F/S - moderate disturbance, fertilized and sown (e) H/U/S - high disturbance, unfertilized and sown (f) H/F/S - high disturbance, fertilized and sown treatments. See Appendix 1D for full specific names. nd = maximum seedling relative growth rate not determined.

## 5.3.2 Effects of Fertilization and Soil Disturbance on Morphology Index

The canopy cover of a species was not correlated with its Morphology Index in spring (Table 5.2). However in summer, the canopy cover of species was positively correlated with morphology index in low and moderately disturbed, unfertilized plots. Further, the correlations tended to be more positive in summer than spring, suggesting that the percentage cover of species with high morphology index values was greater in summer.

**Table 5.2**: Spearman Rank Correlation Coefficients between the logarithm of the Morphology Index of a species and its transformed (arcsine) canopy 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. ¹ - See Section 5.2 for a description of the Morphology Index proposed by Grime (1974). * $p < 0.05$.

| Morphology Index¹ | | | L/U | M/U | H/U | L/F | M/F | H/F |
|---|---|---|---|---|---|---|---|---|
| November 1993 | 51 | Unsown | -0.013 | 0.033 | 0.020 | 0.042 | -0.029 | -0.049 |
| | 51 | Sown | -0.074 | -0.202 | 0.136 | 0.034 | 0.069 | -0.094 |
| February 1994 | 50 | Unsown | **0.260*** | **0.310*** | 0.147 | 0.186 | 0.206 | 0.044 |
| | 50 | Sown | 0.153 | 0.065 | 0.220 | 0.191 | 0.140 | 0.032 |

## 5.3.3 Effects of Fertilization and Soil Disturbance on C-S-R Strategy

### (a) C-S-R Strategy Derived From the Dichotomous Key

Nine of the 30 species (Table 5.3) were designated as stress-tolerant competitors (SC) by the dichotomous key of Grime *et al.* (1988); six were stress-tolerators (S), six were CSR strategists, three were competitive-ruderal/ruderal (CR/R), three were stress-tolerant ruderals (SR), two were competitors (C) and one was competitive ruderal (CR).

**Table 5.3:** The C-S-R strategy assigned to the Newholme species using the dichotomous key of Grime *et al.* (1988). SC, stress-tolerant competitors; S, stress-tolerators; CSR, CSR strategists; C, competitors; CR, competitive ruderals; CR/R, competitive-ruderal/ruderal; SR, stress-tolerant ruderals.

| Species | Strategy | Species | Strategy |
|---|---|---|---|
| *Acetosella vulgaris* | CSR | *Hypericum gramineum* | SC |
| *Aira cupaniana* | CR/R | *Hypochaeris radicata* | CSR |
| *Aristida ramosa* | SC | *Lolium perenne* | CSR |
| *Aristida warburgii* | SC | *Luzula flaccida* | CSR |
| *Briza minor* | CR/R | *Microtis unifolia* | SR |
| *Carex breviculmis* | SC | *Oxalis exilis* | S |
| *Carex inversa* | SC | *Panicum effusum* | C |
| *Cymbopogon refractus* | SC | *Plantago lanceolata* | CR |
| *Dactylis glomerata* | C | *Richardia stellaris* | S |
| *Dichelachne micrantha* | CSR | *Sanguisorba minor* | S |
| *Drosera peltata* | SR | *Sporobolus creber* | SC |
| *Elymus scaber* | S | *Tricoryne elatior* | CSR |
| *Eragrostis leptostachya* | SC | *Vulpia bromoides* | SR |
| *Eragrostis 'red'* | SC | *Vulpia myuros* | CR/R |
| *Fimbristylis dichotoma* | S | *Wahlenbergia planiflora* | S |

*Relative Number of Species*

Disturbance did not significantly affect the relative number of competitor (C) or stress-tolerator (S) species in February 1994 (Table 5.4), nor at any other time during the study (Appendix 7). Anova revealed a significant fertilization x sown interaction for the relative number of C species; fertilization increased C species only in sown plots (Fig. 5.3). Fertilization increased the relative number of competitive-ruderal/ruderal (CR/R) species. The relative number of CR/R species was greater 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 number of CR/R or S species at any time during the study (Appendix 7).

**Table 5.4**: Analysis of variance (F values) of the relative number (%) and relative cover (%) of the species in the C-S-R strategy categories with disturbance, fertilization & sown as factors for February 1994. Disturbance x sown interaction for relative number was not significant. C - competitive; CR/R - competitive-ruderal/ruderal; CSR - competitive/stress-tolerant/ruderal; S - stress-tolerators; SC - stress-tolerant/competitive species ⇧ - increased; ⇩ - decreased. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

| | df | C | CR/R | CSR | S | SC |
|---|---|---|---|---|---|---|
| **Relative Number (%)** | | | | | | |
| Disturbance | 2/48 | 1.63 | ⇧ **21.50***** | 2.18 | 0.30 | ⇩ **17.92***** |
| Fertilization | 1/48 | 4.01 | ⇧ **28.61***** | 4.27* | ⇩ **7.96**** | ⇩ **8.38**** |
| Sown | 1/48 | 12.29** | 1.05 | 0.39 | 0.55 | ⇩ **13.53**** |
| Dist. x Fertilization | 2/48 | 2.97 | 0.60 | 5.59** | 0.40 | 2.10 |
| Fertilization x Sown | 1/48 | **4.87*** | 0.02 | 3.00 | 1.58 | 2.42 |
| Dist. x Fert. x Sown | 2/48 | 0.03 | 0.87 | **3.25*** | 0.35 | 1.20 |
| **Relative Cover (%)** | | | | | | |
| Disturbance | 2/48 | 6.30** | 1.51 | ⇧ **113.88***** | 0.21 | 333.46*** |
| Fertilization | 1/48 | ⇧ **4.67*** | 140.08*** | ⇩ **6.71*** | 2.65 | 104.79*** |
| Sown | 1/48 | 24.65*** | 0.53 | 0.49 | 2.68 | 1.61 |
| Dist. x Fertilization | 2/48 | 0.90 | **4.45*** | 0.37 | 9.19*** | **11.75***** |
| Disturbance x Sown | 2/48 | **18.88***** | 0.82 | 1.20 | 8.24** | 0.21 |
| Fertilization x Sown | 1/48 | 3.15 | 0.14 | 3.13 | 20.05*** | 1.22 |
| Dist.. x Fert. x Sown | 2/48 | 1.15 | 0.35 | 2.57 | **13.88***** | 0.71 |

Anova detected a significant disturbance x fertilization x sown interaction for the relative number of competitive/stress-tolerant/ruderals (CSR) species in February 1994 (Table 5.4). The relative number of CSR species in highly disturbed fertilized sown plots was greater than low disturbance fertilized unsown and highly disturbed unfertilized sown plots (Fig. 5.3). Fertilization decreased the relative number of stress-tolerant (S) and stress-tolerant/competitor (SC) species. The relative number of SC 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; $p < 0.01$, Bonferroni test). The relative number of SC species was lower in sown plots than unsown plots (1,48 df; $p < 0.01$, Bonferroni test).

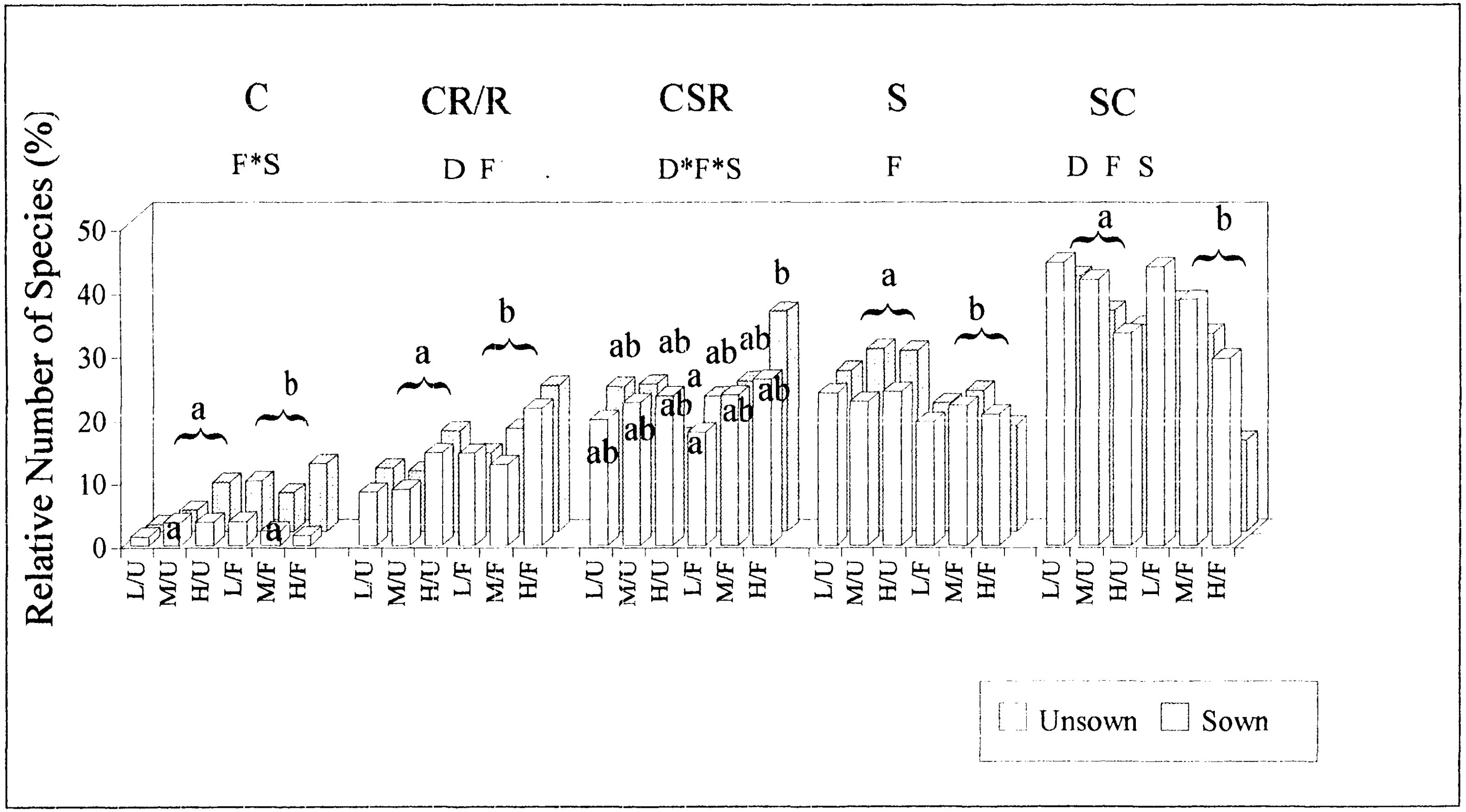


**Fig. 5.3**: Mean relative number (%) of competitive (C), competitive-ruderal/ruderal (CR/R), competitive/stress-tolerant/ruderal (CSR), stress-tolerators (S) or stress-tolerant/competitor (SC) species in each of the twelve treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ($p < 0.05$ level) between the treatment means of each C-S-R strategy.

Due to a large number of zero scores, the data for the relative number of stress-tolerant/ruderal (SR) species in February 1994 was not normally distributed and therefore was not analysed. However in November 1992, March 1993 and November 1993, high soil disturbance significantly decreased the relative number of SR species (Appendix 7). Fertilization did not significantly affect the relative number of SR species at any time during the study.

### *Relative Cover of Species*

Anova revealed a significant disturbance x sown interaction for the relative cover of competitive (C) species in February 1994; high soil disturbance increased cover only in sown plots (Fig. 5.4). The relative cover of C species was greater in fertilized plots than unfertilized plots (1,48 df; $p < 0.05$, Bonferroni test) in February 1994, but this effect had diminished over time (Appendix 7). There was a significant disturbance x fertilization interaction for the relative cover of CR/R species; the increase in cover with fertilization diminished with increasing soil disturbance. Both moderate and high soil disturbance significantly increased the relative cover of competitive/stress-tolerant/ruderals (CSR) species. The relative cover of CSR species was lower in fertilized plots than unfertilized plots (1,48 df; $p < 0.05$, Bonferroni test).

There was a significant disturbance x fertilization x sown interaction for the relative cover of stress-tolerant (S) species in February 1994 (Table 5.4). The relative cover of S species was greater in the highly disturbed unfertilized sown plots than all of the other treatments (Fig. 5.4). Anova detected a significant disturbance x fertilization interaction for the relative cover of stress-tolerant/competitive (SC) species. Fertilization decreased the relative cover of SC species on the low and moderately disturbed plots, but had no effect on the highly disturbed plots. The sown treatment did not significantly affect the relative cover of CR/R, CSR or SC species at any time during the study (Appendix 7). The relative cover of stress-tolerant/ruderal (SR) species was zero in March 1993 and February 1994 and therefore these sampling dates were not analysed. However in both November 1992 and 1993, high soil disturbance significantly decreased the relative cover of SR species. Fertilization and sowing did not significantly affect the relative cover of SR species at any time during the study.

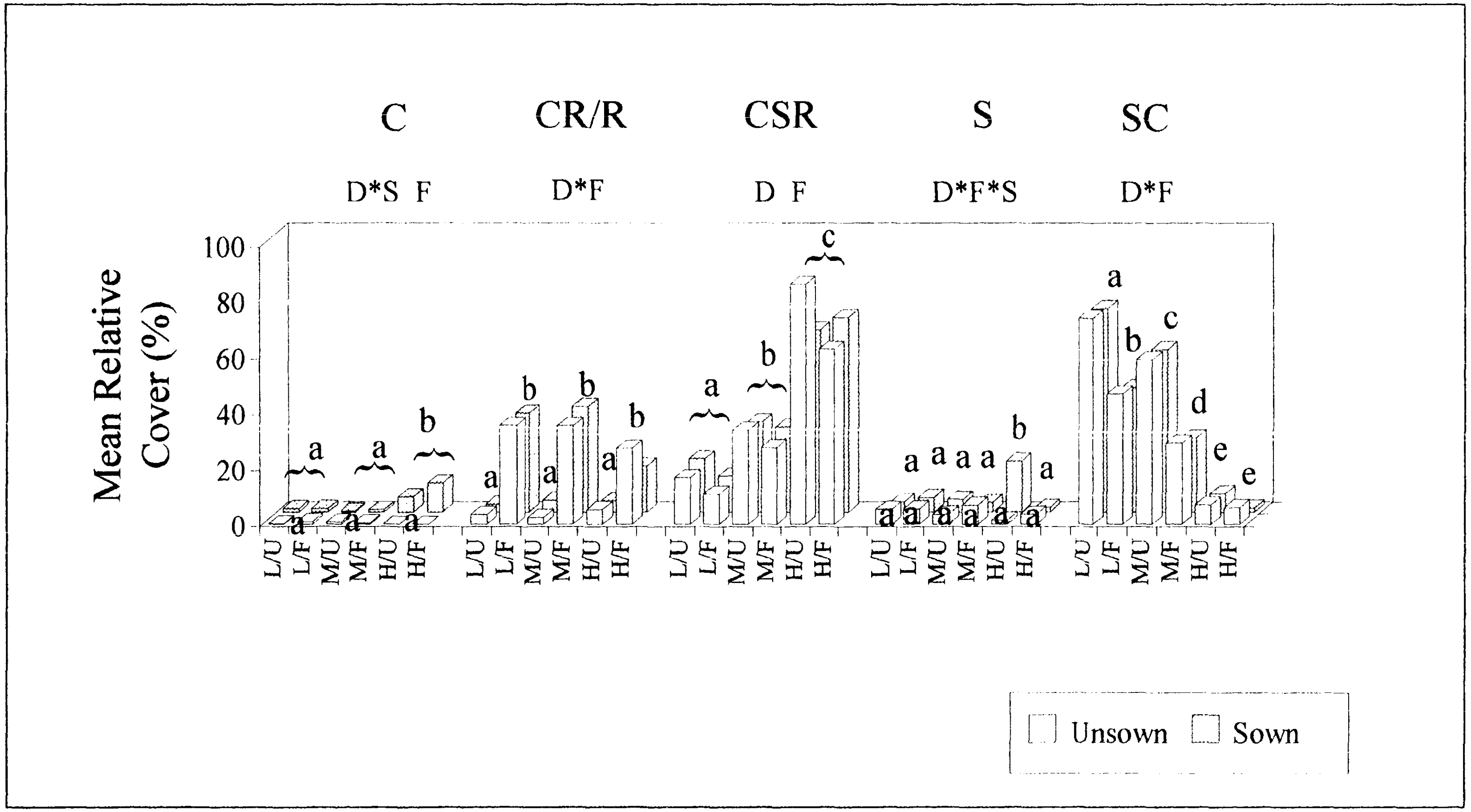


**Fig. 5.4**: Mean relative cover (%) of competitive (C), competitive-ruderal/ruderal (CR/R), competitive/stress-tolerant/ruderal (CSR), stress-tolerators (S) or stress-tolerant/competitors (SC) species in each of the treatments in February 1994. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized. Different letters denote significant differences ($p < 0.05$ level) between the treatment means of each C-S-R strategies.

## (b) Ordination of the Newholme Species and Vegetation Samples by Mean Rmax and Mean Morphology Index

The ordination of the Newholme species by their mean Rmax and Morphology Index (MI) showed that annuals (*Vulpia bromoides, V.myuros, Aira cupaniana* and *Juncus bufonius*) occupied the bottom of the ordination and had moderate Rmax and low MI values (Fig. 5.5). The top left-hand corner of the ordination is occupied by the native, perennial, tussock grasses (*Aristida ramosa, A.warburgii* and *Cymbopogon refractus*) and perennial sedges (*Carex inversa* and *Luzula flaccida*) which had low Rmax and high MI values. The top right-hand corner of the ordination is occupied by the exotic, sown species (*Dactylis glomerata, Lolium perenne* and *Plantago lanceolata*) which had high Rmax and moderate to high MI values.

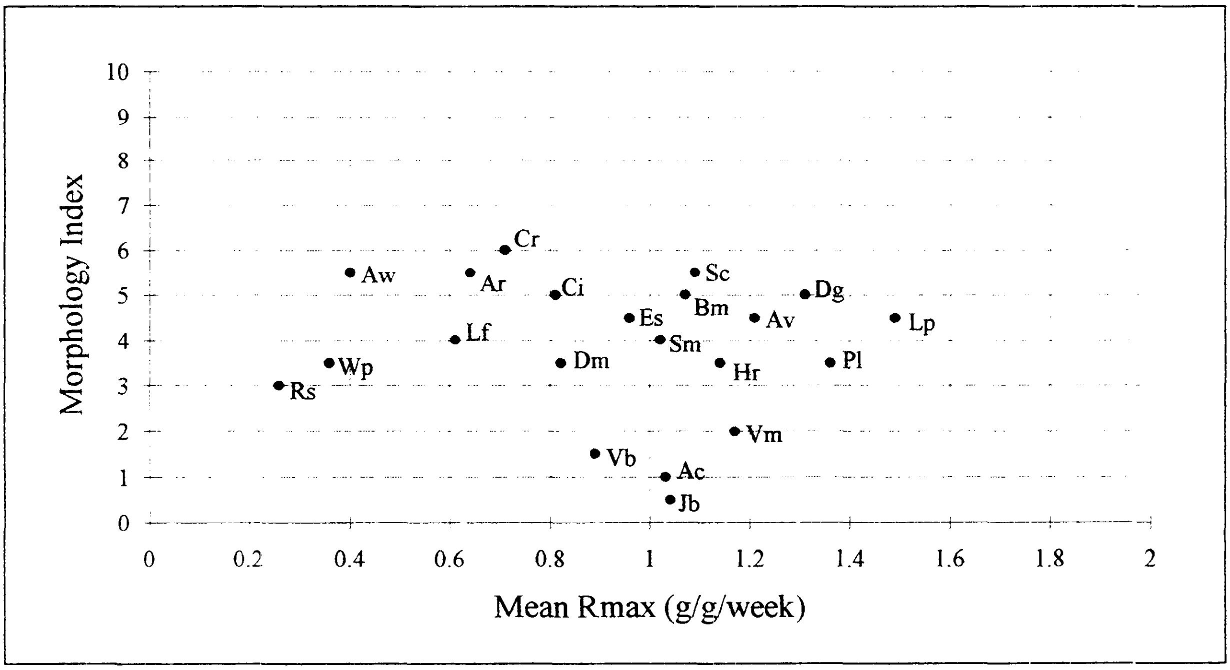


**Fig. 5.5:** Ordination of Newholme herbaceous species by their mean Rmax (g/g/week) and Morphology Index. Av, *Acetosella vulgaris*; Aw, *Aristida warburgii*; Ac, *Aira cupaniana*; Ar, *Aristida ramosa*; Bm, *Bothriochloa macra*; Ci, *Carex breviculmis*; Cr, *Cymbopogon refractus*; Dm, *Dichelachne micrantha*; Dg, *Dactylis glomerata*; Es, *Elymus scaber*; Hr, *Hypochaeris radicata*; Jb, *Juncus bufonius*; Lp, *Lolium perenne*; Lf, *Luzula flaccida*; Pl, *Plantago lanceolata*; Rs, *Richardia stellaris*; Sc, *Sporobolus creber*; Sm, *Sanguisorba minor*; Vb, *Vulpia bromoides*; Vm, *Vulpia myuros*; Wp, *Wahlenbergia planiflora*.

Grime (1974) found a wider range of Rmax (0.5 - 2.7) and Morphology Index (0 - 8) values in the Sheffield flora than found here for the Newholme species. The range of values found by Grime can be arbitrarily divided into low Rmax (< 1.2 g/g/week), moderate Rmax (1.21 - 1.9 g/g/week), high Rmax (> 1.9 g/g/week), low Morphology Index (< 2.7), moderate Morphology Index (2.7 - 5.3) and high Morphology Index (> 5.3) to test Grime's predictions. The ordination of the February 1994 vegetation samples (i.e. sixty 1 $m^2$ plots), along the axes of the mean maximum relative growth rate (Rmax) and mean Morphology Index revealed that most of the vegetation samples had low Rmax and moderate Morphology Index values relative to those found by Grime (1974) (Fig. 5.6). The exceptions were that vegetation samples from the fertilized low and moderately disturbed plots had low Rmax and low to moderate Morphology Index values and the highly disturbed, fertilized plots had low to moderate Rmax and moderate Morphology Index values. The vegetation samples were located in the area predicted by the triangular model (Grime 1979) to be intermediate between C-S-R strategists and stress-tolerant competitor (SC).

A closer look at the distribution of the vegetation samples for each treatment in November 1993 reveals that, relative to the other treatments, the low disturbance, unfertilized plots tended to have the lowest mean Rmax and the highest mean Morphological Index values. Samples from the moderately disturbed, unfertilized treatment tended to have a higher mean Rmax than the control (i.e. low disturbance, unfertilized) plots, but similar mean Morphological Index (Fig. 5.6). Samples from the high disturbance, unfertilized treatment tended to have higher mean Rmax and lower mean Morphological Index values than the control plots. They were located further towards the CSR strategists area of the ordination. Samples from the fertilized, low disturbance treatments tended to have higher mean Rmax and lower mean Morphological Index than the control plots. They were located towards the CSR strategist area of the ordination. Samples from the fertilized, moderately disturbed treatments tended to have the higher mean Rmax and lower mean Morphological Index values than the control plots. They were located towards the stress-tolerant (S) and CSR strategist area of the ordination. Samples from the fertilized, highly disturbed treatment tended to have the highest mean Rmax and lower mean Morphological Index values than the control plots. They were located further towards the CSR strategist area of the ordination. The distributions of corresponding sown and unsown plots were similar, except on the highly disturbed, fertilized treatments where the sown plots had higher mean Rmax and higher mean Morphology Index values.

The vegetation samples in November 1993 tended to have higher mean Rmax values and slightly lower mean Morphology Index values than in February 1994 (Fig. 5.7). The distribution of the vegetation samples for each treatment in February reveals that vegetation samples from all of the treatments had low mean Rmax and moderate mean Morphological Index values, except on the highly disturbed, fertilized plots which had low to moderate Rmax values. Most of the samples were located in the stress-tolerant competitors (SC) area of the ordination. The distributions of corresponding sown and unsown plots were similar, except for the highly disturbed, fertilized treatments where the sown plots had higher mean Rmax and higher mean Morphology Index.

When the mean Morphology Index values were calculated using plant attribute measurements from the unfertilized areas, the resulting ordinations for both November 1993 and February 1994 (Appendix 7) were similar to those where measurements had been taken from the fertilized plots (Fig. 5.6; Fig. 5.7). The exception was that the mean Morphology Index values were generally lower and thus the samples were located further towards the stress-tolerant and ruderal corners of the ordination.

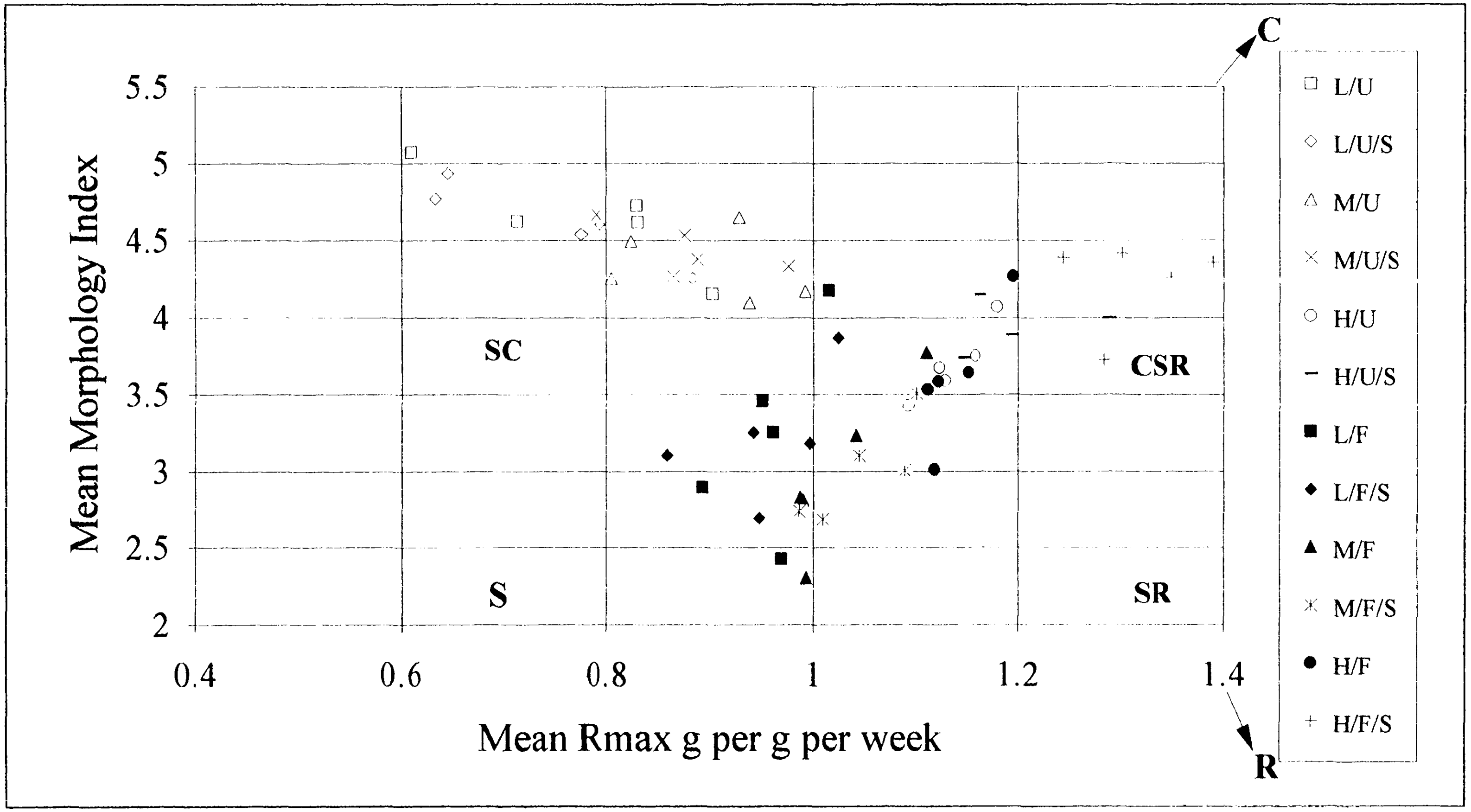


**Fig. 5.6:** Ordination of the mean maximum relative growth rate (Rmax) and the mean Morphology Index of the vegetation in each treatment (n = 5 replicates per treatment) in November 1993. Mean Morphology Index was calculated from measurements taken from the fertilized plots. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized; S = sown. The associations of the competitive (C), stress-tolerant (S) and ruderal (R) strategies with the two axes, as proposed by Grime (1974), are also shown.

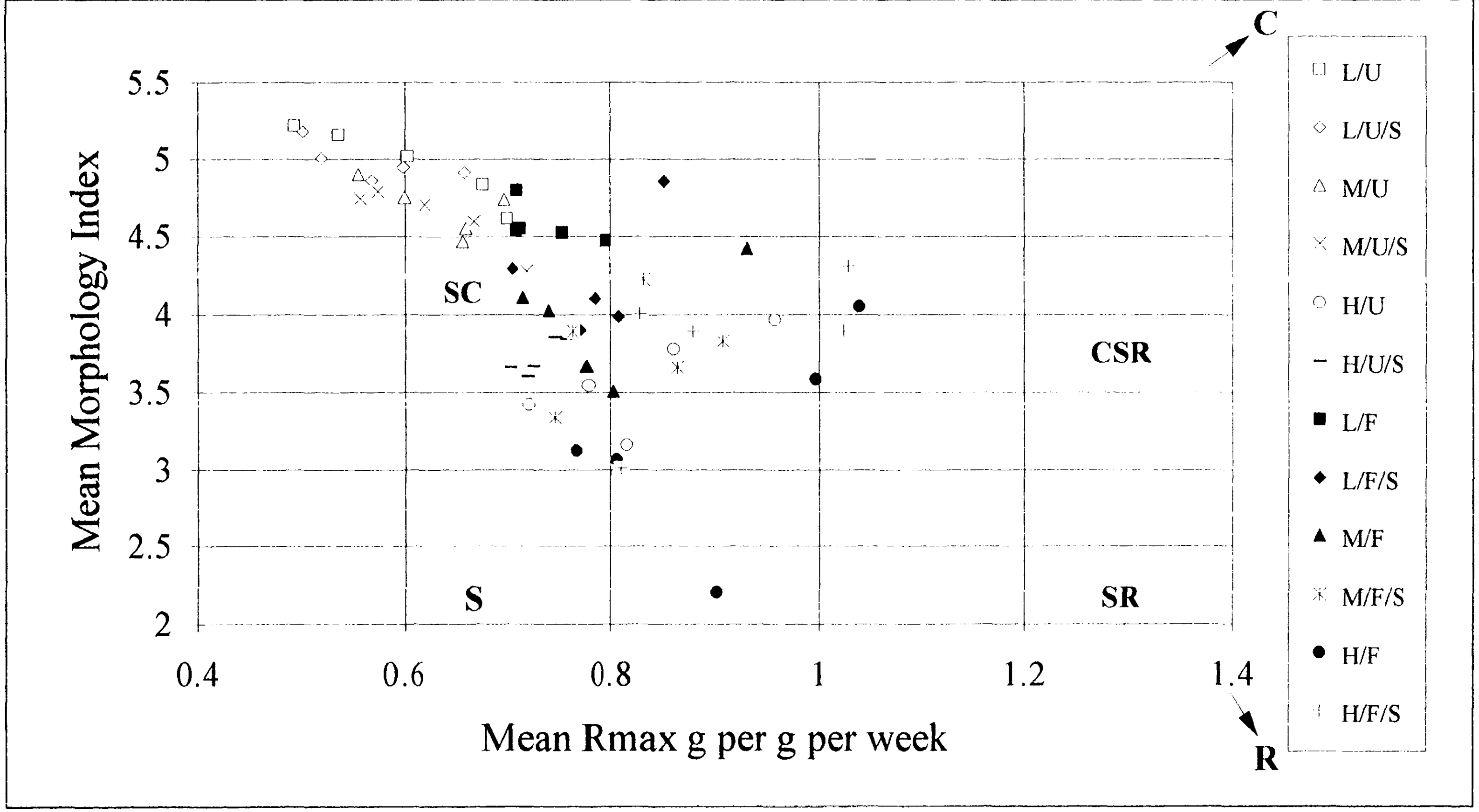


**Fig. 5.7:** Ordination of the mean maximum relative growth rate (Rmax) and the mean Morphology Index of the vegetation in each treatment (n = 5 replicates per treatment) in February 1994. Mean Morphology Index was calculated from measurements taken from the fertilized plots. L = low soil disturbance; M = moderate soil disturbance; H = high soil disturbance; U = unfertilized; F = fertilized; S = sown. The associations of the competitive (C), stress-tolerant (S) and ruderal (R) strategies with the two axes, as proposed by Grime (1974), are also shown.

## 5.4 DISCUSSION

### Maximum Relative Growth Rate of Seedlings

The results were consistent with the prediction that the maximum relative growth rate (Rmax) of each species is positively correlated with its abundance in disturbed plots and negatively correlated with abundance in low disturbance plots (Table 5.5A). Species with low Rmax were more common than species with high Rmax in the low disturbance, unfertilized (i.e. control) plots. Species of unproductive, low disturbance habitats (i.e. stress-tolerant species) have slow maximum potential growth rates (Grime 1979). Berendse and Elberse (1990) suggested that a low potential growth rate may not have any advantage in itself, but may just be a consequence of features that enable the plant to survive in nutrient poor-environs. Similarly, Lambers and Poorter (1992) concluded that a low relative growth rate *per se* does not confer ecological advantage in an unfavourable environment, but one of the components linked with relative growth rate (i.e. leaf area ratio or net assimilation rate) is the target of selection. Whether leaf area ratio (LAR) is more useful than relative growth rate was not assessed in this study because the LAR data set was small and biased towards the larger-leaved species. Further, they suggest that trade-offs in leaf function (i.e. photosynthesis, defence, competition, storage and structural requirements) determine the value of specific leaf area and its relationship with photosynthesis and in that way influence the relative growth rate of the plant. In support of this suggestion, species in this study with slow-growing seedling also tended to accumulated persistent litter and had fibrous, long-lived leaves (Section 3.3.3). These attributes are indicative of a nutrient-conserving strategy and may be traded for low Rmax.

On the highly disturbed plots, species with high Rmax were more common than species with low Rmax. Similarly, Gleeson and Tilman (1994) found that late successional species (i.e. undisturbed habitats) have a lower Rmax than early successional species (i.e. recently disturbed habitats). Species of persistently disturbed habitats (i.e. ruderal species) have rapid maximum potential growth rates (Grime 1979). High growth rates enable a species to rapidly occupy a large amount of space or complete their life-cycle rapidly which is an advantage in disturbed habitats because they are often temporary (Grime 1979; Lambers & Poorter 1992). Species with slow growth rates are not favoured in soil disturbed habitats because recovery after disturbance is slow and loss of leaf tissue that is expensive to replace (i.e. long-lived and defended against herbivores) is particularly damaging (Wisheu & Keddy 1994).

**Table 5.5:** Summary of predictions tested in this chapter and whether the results (for February 1994) supported, rejected or were inconsistent with the predictions. A - predictions testing the underlying hypotheses of the C-S-R model; B - predictions testing the dichotomous key for the C-S-R strategies; C - predictions testing the ordination of vegetation samples by the mean maximum relative growth rate (Rmax) and the mean Morphology Index (MI) of the component species.

| | | **Prediction** | **Upheld** | **Rejected** | **Inconsistent** | **Reference** |
|---|---|---|---|---|---|---|
| A | 1 | Rmax positively correlated with abundance in disturbed plots | ✓ | | | Grime (1974) |
| | 2 | Rmax negatively correlated with abundance in low disturbance plots | ✓ | | | |
| | 3 | Rmax positively correlated with abundance in fertilized plots | | | ✓ | |
| | 4 | Rmax negatively correlated with abundance in unfertilized plots | | | ✓ | |
| | 5 | MI positively correlated with abundance in fertilized, low disturbance plots | | ✓ | | |
| | 6 | MI negatively correlated with abundance in unfertilized and disturbed plots | | ✓ | | |
| B | 7 | The number of S species decrease with soil disturbance | | ✓ | | Grime *et al.* (1988) |
| | 8 | The number of S species decrease with fertilization | ✓ | | | |
| | 9 | The number of C species decrease with soil disturbance | | ✓ | | |
| | 10 | The number of C species increase with fertilization | | | ✓ | |
| | 11 | The number of CR/R species increase with soil disturbance | ✓ | | | |
| | 12 | The number of CR/R species increase with fertilization | ✓ | | | |
| | 13 | The number of SC decrease with soil disturbance | ✓ | | | |
| C | 14 | Low disturbance, unfertilized plots ordinated in S area (low Rmax, low MI) | | | ✓ | Grime (1974) |
| | 15 | Low disturbance, fertilized plots ordinated in C area (high Rmax, high MI) | | ✓ | | |
| | 16 | Moderate disturbance, unfertilized plots ordinated in SR to CSR area (moderate Rmax, low MI) | | ✓ | | |
| | 17 | Moderate disturbance, fertilized plots ordinated in CR to CSR area (high Rmax, moderate MI) | | | ✓ | |
| | 18 | High disturbance, fertilized plots ordinated in R area (high Rmax, low MI) | | ✓ | | |

The results were inconsistent with the prediction that maximum relative growth rate of each species is positively correlated with its abundance in fertilized plots and negatively correlated with abundance in unfertilized plots (Table 5.5A). The correlations between Rmax and abundance in fertilized and unfertilized plots depended on the level of soil disturbance. Species with low Rmax were more common than species with high Rmax in unfertilized plots only in combination with low or moderately soil disturbance. The results suggest that species with low Rmax adapted to nutrient-poor conditions could not tolerate high soil disturbance. Species with high Rmax adapted to nutrient-rich conditions could not tolerate low or moderate soil disturbance. In contrast, other studies have found that fast growth rates are characteristic of plants from nutrient-rich environments and slow growth rates are characteristic of plants from adverse environments (Lambers & Dijkstra 1987; Grime & Hunt 1975; Atkin & Day 1990). Species with high Rmax were more common than species with low Rmax in fertilized plots, only in combination with high soil disturbance. The results are inconsistent with species of productive, low disturbance habitats (i.e. competitive species) having high potential growth rates (Grime 1979).

Neither slow-growing nor fast-growing species were more prevalent in fertilized, low and moderately disturbed plots. The coexistence of slow-growing and fast-growing species may be a transient phase and if the study had continued the fast-growing species may eventually out-compete the slow-growing species because they can attain a large size, pre-empt available space and re-adjust their leaf canopy to changing light conditions in nutrient-rich environs. If the result is not transient, then it may be that species survive the low light conditions created by the fast-growing species forming the canopy by investing in expensive long-lived leaves and low growth rates.

Species with low Rmax were more common than species with high Rmax in unfertilized, moderately disturbed plots (in summer) and species with high Rmax were more common than species with low Rmax in unfertilized, highly disturbed plots. Grime (1979) made no prediction for the Rmax of species of unproductive, disturbed habitats. The results suggest that species of unproductive, moderately disturbed habitats are similar to stress-tolerators in that they have slow potential growth rates, while species of unproductive, highly disturbed plots are similar to ruderals in that they have rapid growth rates. Species of highly soil disturbed habitats are capable of high growth rates even when nutrients are limited. They may achieve this by avoiding stress through a short life cycle (e.g. *Aira cupaniana*) or possessing storage organs (e.g. *Hypochaeris radicata* and *Sanguisorba minor*).

A model by Aerts and van der Peijl (1993) demonstrated how highly productive species dominate nutrient-poor environments early in succession and are replaced by nutrient-conserving species later in succession (Fig. 5.8). In nutrient-poor environments low productive, nutrient-conserving species attain a higher equilibrium biomass than highly productive species (that have high nutrient loss rates), but the highly productive species attain their equilibrium biomass at a faster rate than the low productive species. Thus fast-growing species may be abundant initially, but due to their liberal use and high loss of nutrients the slower-growing nutrient-conserving species will become dominant over time. The results in this study are consistent with this model because fast-growing species were common in highly disturbed, unfertilized plots and slow-growing nutrient-conserving species were common in low disturbance, unfertilized plots. Species with fast-growing seedlings cannot dominate low disturbance, nutrient-poor habitats because their nutrient exploitive strategy (soft, short-lived leaves and the lack of persistent litter) cannot be supported. However, the results suggest that fast-growing species may not lose dominance (or are slow to lose dominance) in low and moderately disturbed plots when fertilized, because their liberal use and high loss of nutrients can be supported in nutrient-rich environments.

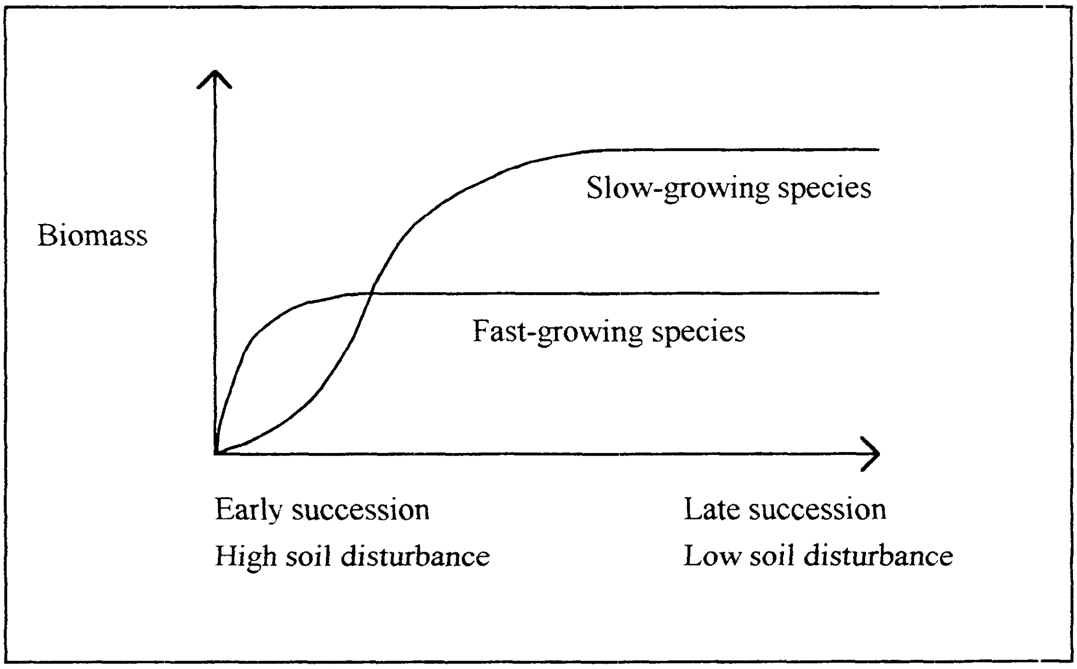


**Fig. 5.8:** Hypothesized long-term biomass dynamics of slow-growing nutrient-conserving species and fast-growing nutrient-exploiting species growing under nutrient-poor conditions (after Aerts & van der Peijl 1993).

In conclusion, two of the four hypotheses relating to the relationship between Rmax and the level of disturbance and productivity in a habitat were upheld. The Rmax of species can be predictably related to the level of soil disturbance in a habitat, but the relationship between Rmax and the level of fertility depends on the level of soil disturbance. These results were obtained despite the range of Rmax values encountered being small, some values possibly be being under-estimates and the chosen species being biased towards species with high germination rates. Without the presence of the sown species the positive correlation between the Rmax of each species and its abundance in highly disturbed plots was not demonstrated. This suggests that few resident species present were adapted to high soil disturbance and had high relative growth rates. Thus the addition of propagules of a number of species (i.e. sown treatment) was a necessary part of the experimental design, as it ensured that a wider range of plant attributes was available to test the underlying hypotheses of the triangular model.

## Morphology Index

The results did not support the prediction that the Morphology Index (MI) of each species is positively correlated with its abundance in fertilized, low disturbance plots and negatively correlated with abundance in unfertilized and disturbed plots (Table 5.5A). In summer, species with high MI values were more common than species with low MI values in low and moderately disturbed, unfertilized plots. In contrast Grime (1974) found that species with low Morphology Index values are prevalent in disturbed vegetation (e.g. paths, fallow, arable and demolition sites), while species with high values are common in relatively undisturbed vegetation (e.g. enclosed pastures, road verges and hedge bottoms) or in fertile habitats (e.g. manure heap). The results were not consistent with species of unproductive, undisturbed habitats (i.e. stress-tolerators) having a wide range of stature and spread (Grime 1979). In summer, dominance in the low and moderately disturbed unfertilized plots was achieved by species of large stature or width rather than numerous individuals of small statured species. However, in the highly disturbed and fertilized plots in summer and all the treatments in spring, species with low and high MI coexisted. The spring species, with low MI values (mainly winter annuals), evidently succeeded in the temporal microhabitat created by the later growth of the summer growing species and since this microhabitat was only temporary they were favoured if they completed their life cycle rapidly.

The lack of agreement with the predictions of Grime (1979) may be due to the Newholme species having a limited range of Morphology Index values; consequently, any relationships were not fully tested. However, few of the species investigated by Grime (1974) had MI values greater than those measured in the present study. C-S-R theory proposes that species competitive ability varies predictably with disturbance and productivity, but the Morphology Index used here may not reflect the competitive ability of a species. A competition experiment by Harradine (1976) confirmed the poor interspecific competitive ability of *Aristida ramosa*, yet it had one of the highest MI values in the present study. Grime (1979) suggested that competitive ability is a function of the activity and the distribution through space and time of the plant surfaces through which resources are absorbed. The Morphology Index fails to take the latter attributes into account (e.g. foliage density or life span of leaves, stems and roots). Both *A.ramosa* and *Dactylis glomerata* were given the same MI, despite *A.ramosa* having a sparse distribution of narrow, fibrous long-lived leaves and *D.glomerata* having a dense distribution of wide, soft, short-lived leaves. Short-lived leaves may be advantageous in competitive situations because the plant has the capacity to adjust the placement of its leaves in response to spatial and temporal changes in light levels. Species of nutrient-poor environments can afford to invest in large size (height and width) if they minimise their investment by having sparse, long-lived foliage that is unpalatable to herbivores (e.g. *A.ramosa*).

Wilson and Keddy (1986a) found that species on exposed, nutrient-poor shores had low competitive abilities, while those growing on sheltered, nutrient-rich shores had high competitive abilities. They concluded that the competitive abilities of plant species vary predictably, so that superior 'competitors' are frequently found in habitats where stress and disturbance (*sensu* Grime 1979) are minimal and diffuse competition is intense. Competitive ability in their study was determined not by plant attributes but by competition experiments. At present, there is insufficient knowledge as to which plant attributes infer competitive ability, so competition experiments carried out in the field (e.g. Wilson & Keddy 1986a) remain the most useful method of determining the competitive ability of a species.

## C-S-R Strategy

Most of the species at Newholme were designated as stress-tolerant competitors (SC) by the dichotomous key of Grime *et al.* (1988), followed by stress-tolerators (S), CSR strategists, competitive-ruderal/ruderals (CR/R), stress-tolerant ruderals (SR), competitors (C) and competitive ruderals (CR). The only C-S-R strategy not represented was the ruderal strategy, which is consistent with the site being nutrient-poor and severe disturbance being a rare event at the site. The dominant species were designated as SC species, while all of the S species were subordinate species and most of the annuals were CR/R species.

Four of the seven predicted responses of the C-S-R- strategies (determined by the dichotomous key of Grime *et al.* 1988) to soil disturbance and fertilization were upheld (Table 5.5B). Grime (1979) proposed that S species are adapted to low disturbance, but the results here were inconsistent with the prediction that the number of stress-tolerant species would decrease with increasing soil disturbance. The relative cover of S species was greatest in highly disturbed, unfertilized, sown plots because one of the sown species (i.e. *Sanguisorba minor*) was designated a S species by Grime *et al.* (1988) and was most successful in these plots. This result suggests that either the species designated as a stress-tolerator in Britain was not necessarily a S species on the Northern Tablelands, or that a longer study is required to determine whether *S.minor* is favoured by high soil disturbance in the long-term. Grime (1979) acknowledged that intra-specific variation with respect to strategy may occur, but the degree to which this phenomenon effects the ecological amplitude of a species is not yet known. The results were consistent with the prediction that the number of stress-tolerant species would decrease with fertilization. Stress-tolerant species are adapted to nutrient-poor conditions by maintaining dry matter production at low levels (Grime 1979).

According to Grime (1979), competitive (C) species are adapted to low levels of disturbance. However, the relative number of C species was unaffected by soil disturbance in the present study and so was inconsistent with the prediction that the number of C species decreases with soil disturbance. In fact the opposite was true for the relative cover of C species, which increased with high soil disturbance. Grime (1979) proposed that competitive (C) species are adapted to capturing above and below-ground resources in nutrient-rich habitats and maximising dry matter production. However, the prediction that the number of C species increases with fertilization was only upheld in the sown plots. The contradiction between the results of the sown and the unsown plots was due to one of the sown species (i.e. *Dactylis glomerata*) being designated a C species by Grime *et al.* (1988) and being most successful in fertilized plots. On the other hand, the results for relative cover were consistent with the prediction as fertilization increased the relative cover of C species.

The results were consistent with the prediction that the number of competitive-ruderal/ruderal (CR/R) species increased with soil disturbance. Grime (1979) proposed that CR and ruderal (R) species are adapted to soil disturbance by facilitating rapid completion of life-cycle through high rates of dry matter production. Grime (1979) suggested that habitats colonized by CR species experience a smaller effect of disturbance than those populated exclusively by 'ruderals' (e.g. damage which is sufficient to check the vigour of 'competitors' but not to eliminate them). The results were consistent with the prediction that the number of CR/R species increased with fertilization. However, the response of the relative cover of CR/R species to fertilization depended on the level of soil disturbance. The increase in the relative cover of CR/R species with fertilization was reduced by high soil disturbance.

The results were consistent with the prediction that the number of stress-tolerant/competitor (SC) species decreased with soil disturbance. These results confirm that SC species are adapted to low levels of disturbance (Grime 1979). On the other hand, the response of the relative cover of SC species to soil disturbance depended on the level of fertility. The decrease in the relative cover of SC species with soil disturbance was greater in unfertilized than fertilized plots. Stress-tolerant/competitors species are adapted to moderate levels of productivity and low disturbance, but this prediction could not be tested as there were only two levels of fertility in the present study (Grime 1979). Fertilization decreased the number and cover of SC species, especially in combination with low or moderate disturbance.

According to Grime (1979), CSR species are adapted to moderate levels of disturbance and fertility and thus could not be tested in the present study. The relative number of competitive/stress-tolerant/ruderal (CSR) species was greater in highly disturbed, fertilized sown plots than in low disturbance, fertilized unsown and highly disturbed, unfertilized sown plots because one of the sown species (i.e. *Lolium perenne*) was designated as a CSR strategist by Grime *et al.* (1988) and was most successful in highly disturbed, fertilized plots. The relative cover of CSR species was increased by moderate and high soil disturbance and decreased by fertilization.

The number of stress-tolerant/ruderal (SR) species was decreased by high soil disturbance. This result is consistent with the prediction by Grime (1979) that SR species are adapted to moderate levels of disturbance, but in this study they could also tolerate low disturbance. The effect of disturbance on the SR species in the present study was greater in spring than in summer because most of the SR species were geophytes and remained dormant below-ground during summer. The number of SR species was unaffected by fertilization and so was inconsistent with the prediction by Grime (1979) that SR species are adapted to low levels of productivity.

## Ordination of Newholme Species and Vegetation Samples

The distribution of the mean maximum relative growth rates (Rmax) of the Newholme species was skewed towards low Rmax values in comparison with the species of Sheffield, but the range of Morphology Index (MI) values were similar (cf. Grime 1974). The annuals (*Vulpia bromoides*, *V.myuros*, *Aira cupaniana* and *Juncus bufonius*) were grouped together in the ordination and had moderate Rmax and low MI values. The native, perennial, tussock grasses (*Aristida ramosa, A.warburgii* and *Cymbopogon refractus*) and perennial sedges (*Carex inversa* and *Luzula flaccida*) were grouped together and had low Rmax and high MI values. The exotic, sown species (*Dactylis glomerata, Lolium perenne* and *Plantago lanceolata*) were grouped together and had high Rmax and moderate to high MI. *Sporobolus creber* and *Bothriochloa macra* lie in close proximity to each other on the ordination; they had moderate Rmax and high MI values and have similar distributions on the Northern Tablelands (Lodge & Whalley 1989).

The range of mean maximum relative growth rate (Rmax) and Morphology Index (MI) values found for the vegetation samples at Newholme was narrow compared to that found by Grime (1974) in Sheffield. This difference in ecological amplitude is probably due to differences in sampling since the Newholme sample consisted of 21 species from an area of 1500 $m^2$ compared to a sample of 100 species from a wide variety of habitats in the Sheffield region. Comparison of the mean Rmax and mean MI at Newholme to those from Sheffield indicated that most of vegetation samples at Newholme had low Rmax and moderate MI values. Thus, despite the addition of the sown species the full range of the triangular ordination was not tested. Ordination of the vegetation samples, along the axes of mean Rmax and mean MI values, revealed that the vegetation samples were located in the area predicted by the C-S-R model (Grime 1979) to be intermediate between SC and CSR strategists. Grime (1979) remarked that in many unfertilized pastures in temperate regions, where nutrient 'stress' and moderate defoliation by grazing are more or less constant features of the habitat, species with characteristics of the CSR strategy are most common. The results are consistent with this comment since the site is of low fertility and moderately grazed by sheep. Similarly, Thompson *et al.* (1996) found that species of an infertile limestone grassland community in Derbyshire were strategically uniform and, with a few exceptions, were confined to a small part of the range of strategies found for the British flora.

The results did not support three of the five predictions testing the ordination of vegetation samples by their mean Rmax and MI values (Table 5.5C). Vegetation samples from low disturbance, fertilized plots were not ordinated in the area predicted as competitive (C) by the model because they did not have high Rmax and high MI, rather they had low

Rmax and low to moderate MI and were ordinated as stress-tolerant competitors (SC) to stress-tolerators (S). Vegetation samples from moderately disturbed, unfertilized plots were not ordinated in the stress-tolerant ruderals (SR) to CSR strategist area as predicted because they did not have moderate Rmax and low MI, rather they had low Rmax and moderate MI and were ordinated as stress-tolerant competitors. Vegetation samples from highly disturbed, fertilized plots were not ordinated in the ruderal (R) area as predicted because they did not have high Rmax and low MI, rather they had low to moderate Rmax and moderate MI and were ordinated as SC to CSR. The results for the two other predictions (Table 5.5C) were inconsistent. Vegetation samples from low disturbance, unfertilized plots were not ordinated in the S area as predicted because they had moderate rather than low MI and were ordinated as SC. However, consistent with the two predictions these samples had low Rmax values. Vegetation samples from moderately disturbed, fertilized plots were not ordinated in the CR to CSR area as predicted because they had low rather than high Rmax and were ordinated as SC to S. However, consistent with the predictions these samples had low to moderate MI values.

Comparison of the Newholme vegetation samples from the different treatments, relative to each other, showed that the low disturbance, unfertilized plots had the lowest mean Rmax and highest mean Morphological Index values. These results are consistent with the 'biomass-storer' plant strategy proposed by Kautsky (1988) for aquatic macrophytes. Biomass-storers are associated with habitats of low disturbance and high stress and characteristically are of large spread and slow growth rates (Kautsky 1988). Plant strategy theory predicts that highly disturbed, unproductive habitats are not viable habitats (Grime 1979). However, samples from the highly disturbed, unfertilized treatment had higher mean Rmax and lower mean MI values than the control (i.e. low disturbance, unfertilized) plots and were located towards the CSR strategist area of the ordination. Thus, species of highly disturbed nutrient-poor habitats had reduced stature and spread and a higher capacity to recover from soil disturbance or complete their life-cycle rapidly. These species are not disadvantaged by minimising in above-ground biomass because competition for light and space is low in highly disturbed nutrient-poor habitats, but they require a growth rate that will allow rapid recovery of photosynthetic activity. Kautsky's (1988) 'stunted' strategy, which is associated with highly disturbed unproductive habitats, characteristically has low Rmax and is of small stature, in contrast to the results found here.

Samples from the fertilized, low disturbance treatments had higher mean Rmax and lower mean MI values than the control plots and were located towards the stress-tolerant (S) area of the ordination. This result is inconsistent with the prediction by Grime (1979) that species of productive, low disturbance habitats (competitors) have high MI. Samples from the fertilized, moderately disturbed treatments had higher mean Rmax and lower mean MI values than the control plots and were located towards the S and CSR strategist area of the ordination. Samples from the fertilized, highly disturbed treatment had the highest mean Rmax and lower mean MI values than the control plots and were located towards the CSR area of the ordination. This result is consistent with the prediction by Grime (1979) that species of productive, highly disturbed habitats (ruderals) have high Rmax and low MI. When highly disturbed and fertilized, the sown plots tended to have higher mean Rmax and higher mean MI values and were located further towards the CSR area of the ordination than the unsown plots. This result was due to the sown species having relatively high Rmax and high MI values and attaining their largest size in highly disturbed, fertilized plots. The results suggest that the sown species were more ruderal than the resident species of the site.

The vegetation samples in spring had higher mean Rmax and slightly lower mean MI values and were located further towards the CSR area of the ordination than the vegetation samples in summer. The results suggest that the spring-growing species were more ruderal than the summer-growing species. The higher Rmax and lower mean MI for the fertilized, low disturbance plots in spring was due to the prevalence of winter annuals on these plots. Consistent with this result, Grime (1979) remarked that seasonal regeneration in vegetative gaps is particularly associated with SR and CR species adapted to moderate, seasonally predictable disturbances. Grime (1988) predicted that C-S-R strategies found within a plant community would change spatially and temporally because habitats change seasonally and on a successional time scale.

Several studies have found that S and R species coexist in the same habitat; an arctic environment (Grulke & Bliss 1988), under the same flooding regime (Menges & Waller 1983), in response to fire and drought (reviewed by Menges & Waller 1983) and in infertile moderately grazed grassland (this study). Even the simulation model of Colasanti and Grime (1993), based on the rules of plant strategy theory, confirmed that both R and S strategies may occur at conditions of low to medium resource supply when combined with low to medium disturbance intensity. The simulation model suggested that the success of R species was conditional upon the presence of unexploited resources, which may occur not only in disturbed, resource-rich habitats, but also briefly in habitats where the low resource supply is too spatially discontinuous to allow rapid colonization by S species. The latter finding was inconsistent with C-S-R theory. In the present study, the unexploited resource which enabled S and CR/R species to coexist appeared to be the spatially discontinuous gaps associated with the seasonal climate.

Stress tolerant and ruderal species may be able to coexist in the same habitats because there is more than one evolutionary response to a particular environmental challenge (Southwood 1988). For example, Southwood (1988) described how xerophytic species that remains in one location perceive the desert habitat as very adverse with long unfavourable periods (i.e. stress), while ephemeral species perceive the habitat as a temporally or spatially discontinuous patch of a favourable habitat (i.e. disturbance). Thus, whether a environmental factor (e.g. water availability) is a stress or a disturbance depends on the attributes that the plant species possess (Grubb 1976; Southwood 1988). In contrast, Grime (1978) believed that whether a factor is a stress (e.g. low rainfall climate) or a disturbance (e.g. drought) relates to the constancy of their occurrence.

# CHAPTER SIX

# ORDINATION OF TREATMENT GROUPS USING FLORISTIC AND PLANT ATTRIBUTE DATA

## 6.1 INTRODUCTION

The literature review (Section 1.1.1) demonstrated that joint consideration of a number of attributes (using multivariate techniques) provides stronger conclusions than interpreting each attribute separately because plant attributes are often correlated with each other. Chapter 4 examined separately the response of each plant attribute to fertilization and soil disturbance. Using multivariate techniques, these responses can be summarized and those attributes showing the strongest relationship with soil disturbance and fertilization identified.

Studies using multivariate techniques to examine the relationship between a number of plant attributes and the environment can be divided into two groups. The first group includes studies that use multivariate techniques to group species with similar plant attributes together and then examine the relative abundance of these groups at different sites or under different experimental conditions. This approach will obtain homogeneous groups of species with similar characteristics, but are less likely to vary predictably with the environment. For example, Fernández Alés *et al.* (1993) classified species into groups with similar characteristics using plant attributes with high loadings in principal component analysis (PCA) as a basis of classification. They then compared the relative cover of these groups in ploughed, unploughed, grazed and ungrazed (unreplicated) sites. The second group includes studies that use multivariate techniques to relate plant attributes (without prior grouping) directly to the environment and then use techniques to form functional groups. This approach is more likely to obtain groups of species that vary predictably with the environment, but are heterogenous with respect to the characteristics they possess. For example, Díaz *et al.* (1991) used detrended correspondence analysis to examine how the morphological traits of species differed with grazing intensity and then used clustering techniques to delimit groups of morphologically similar species.

Without experimentation, multivariate analytical methods (e.g. ordination and classification) are primarily descriptive in nature and can only suggest roles, processes and causes of vegetation pattern (James & McCulloch 1990). Ordination describes the pattern of relationships among objects (individuals, quadrats, taxa) by reducing a matrix of distances or similarities among the objects to one or more dimensions (James & McCulloch 1990). In ordination the objects are usually displayed in a graphic space in which the axes are gradients of combinations of the attributes (e.g. linear discriminant function analysis). Cluster analysis also describes the pattern of relationships among objects (individuals, quadrats, taxa) by classifying the objects into hierarchical categories on the basis of a matrix of inter-object similarities (James & McCulloch 1990). Cluster analysis creates groups on the basis of similarity or dissimilarity of attributes and is suitable when there is no prior knowledge of groups existing in the data set. Cluster analysis produces clusters, regardless of whether natural groupings exist, and the results depend on both the similarity measure chosen and the algorithm used for clustering (James & McCulloch 1990).

When the objects of study fall into two or more groups, defined *a priori*, differences among the groups based on a set of attributes can be tested using multivariate analysis of variance (James & McCulloch 1990). Further, linear discriminant function analysis can be used to describe which of these attributes contribute most to the differences between the groups. In ecology, linear discriminant function analysis is most often used as an exploratory ordination procedure, but can also be used to summarise the results of an experiment, reduce multi-group data to fewer dimensions, or to assign new objects to previously separated groups (James & McCulloch 1990).

The present study has a distinct advantage over non-experimental studies, in that *a priori* groups were defined by the application of the twelve experimental treatments. Linear discriminant function analysis is suitable to examine the response of a number of plant attributes to fertilization and soil disturbance and as a basis to define functional groups. The approach of using cluster analysis to form functional groups and then examine the abundance of these groups in each treatment by analysis of variance could be used here. However, cluster analysis would fail to take advantage of the present study's completely randomized experimental design, the groups formed may not be "natural groupings" and they may not bear any relationship to the environment. Most of the studies to date have had to rely on clustering techniques because they had no pre-defined groups and often used a large number of species from widely differing, but undefined, habitats.

The aim of this chapter, then, is to ask:

1. Can group membership of a variety of habitats (differing in levels of soil disturbance and fertilization) be predicted from plant attributes?
2. Which plant attributes maximize the differences among these groups?
3. Do the observed relationships between plant attributes and treatment groups agree with any previously described models?

## 6.2 METHODS

Discriminant function analysis finds the best combination of predictor variables that maximize differences among groups defined *a priori*. The first discriminant function maximally separates groups, then a second dimension, orthogonal to the first, is found that best separates groups on the basis of information not accounted for by the first discriminant function (Tabachnick & Fidell 1983). Direct (standard) discriminant function analysis, where the functions are solved simultaneously on the basis of all predictor variables (Tabachnick & Fidell 1983), was carried out in this study using SYSTAT (Wilkinson *et al.* 1992).

Direct discriminant function analysis was used to predict group membership on the basis of two types of predictor variables. The first type of predictor variable was the relative cover of plant species (Section 2.2.3) in each treatment in February 1994 (the final sampling time). The winter annuals that had died but were still rooted in the ground in February 1994 were included in the data. Thus, the data reflected the spring and summer samples combined, but with the winter annuals likely to be under-represented. The second type of predictor variable, the relative cover of species with a particular plant attribute, was produced by combining the species cover x plot matrix with the species x attribute matrix to obtain the attribute cover x plot matrix (Section 4.2). The groups were those created by the experimental treatments. For the discriminant function analysis using relative cover of plant species as the predictor variable, full analysis with all twelve treatments (3 levels of disturbance x 2 levels of fertility x 2 levels of sowing) was carried out, as well as analysis with the sown and unsown plots pooled to form six groups (3 levels of disturbance x 2 levels of fertility). Although the sown species (*Lolium perenne, Dactylis glomerata, Sanguisorba minor* and *Plantago lanceolata*) could not be used as predictor variables because they were absent from the unsown plots, their contribution to the vegetation cover (and thus their influence on the relative cover of the resident species) was not removed from the data. If *L.perenne, D.glomerata, S.minor* and *P.lanceolata* were good predictor variables in the sown plots, their removal from the analysis meant that the next best predictor variables were chosen.

For the direct discriminant function analysis using the relative cover of plant attributes as the predictor variable, full analysis with all twelve treatments (3 levels of disturbance x 2 levels of fertilization x 2 levels of sowing) was carried out. However, the full analysis was uninformative because the experiment was designed with the sown species all being exotic, and thus the sown treatment had a greater cover of exotic species and attributes associated with being exotic (i.e. soft leaves and no litter). For this reason, the sown and unsown data were pooled and analysis was carried out on the six treatments (3 levels of disturbance x 2 levels of fertilization). Being exotic may not be regarded as a functional attribute because it does not directly influence plant regeneration or establishment. Therefore, the analysis was carried out with and without the exotic attribute. The presence of the exotic attribute in the analysis did not affect the order of importance of the other attributes. Thus, only the results of the analysis including the exotic attribute are presented from which the results of the analysis excluding the exotic attribute may be extrapolated.

Linear discriminant function analysis does not formally require any assumptions but is most efficient under conditions similar to those for multi-analysis of variance (James & McCulloch 1990; Tabachnick & Fidell 1983). Since the groups in this study were defined by the experimental design, unequal sample size was not a problem. Discriminant function analysis is inefficient for non-linear data or data that are not multivariate normal (e.g. categorical data). Since estimates of percentage cover from samples are not distributed normally about their mean, the data were arcsine transformed to improve the efficiency of analysis. After multi-analysis of variance the residuals were examined for outliers and those predictor variables which possessed outliers were removed before continuing with discriminant function analysis (Tabachnick & Fidell 1989).

Discriminant function analysis assumes a linear relationship among all predictor variables within each group, but the violation of this assumption is not serious and simply leads to reduced power (Tabachnick & Fidell 1983). When correlations among the predictor variables are high or one variable is a near-linear combination of other variables, the variable provides information that is redundant. Multicollinearity and singularity may result if the number of cases does not notably exceed the number of variables or if highly redundant discriminating variables are included (Tabachnick & Fidell 1989). As SYSTAT does not protect against multicollinearity and singularity (it does provide warning messages), variables known to be redundant from previous analysis (Chapter 3 and 4) were removed. Some predictor variables were directly correlated because species had been assigned to one of two plant attribute categories (e.g. exotic vs native) and thus only one of the categories was retained. Maximum relative growth rate of seedlings was removed from the analysis because it was highly correlated with leaf lifespan, which is the easier of the two to measure and was measured for fewer species. Plant attributes originally measured as continuous data (e.g. height) were converted to a number of categories (e.g. tall, moderate height and short) so that the relative cover of plants with a particular attribute could be determined. After removing predictor variables which possessed outliers or were redundant, 23 plant species variables and 44 plant attribute variables remained.

Only the first two dimensions identified by discriminate function analysis are presented because they reliably discriminant among groups (Tabachnick & Fidell 1983). The loading matrices, which are correlations between predictor variables and one of the linear combinations constructed by the analysis (James & McCulloch 1990), are presented. They suggest how well a single variable could substitute for the linear combination if one had to make do with that single variable. The loadings are useful in naming and interpreting the discriminant functions, but do not necessarily indicate which variables contribute most heavily to discrimination among groups (Tabachnick & Fidell 1983). Univariate F values, which represent the ability of each predictor variable by itself to predict group membership, are also presented. However, by themselves, univariate F values can be misleading because they neither take into account correlations between predictor variables nor compensate for increased Type I errors with multiple testing (Tabachnick & Fidell 1983). For those predictor variables shown to discriminate among groups, comparisons of group means show how groups differ on those variables (Tabachnick & Fidell 1983). Scatter plots of the first two discriminant functions, which may be used in the interpretation of results as well as for classification purposes, are also presented.

## 6.3 RESULTS

### 6.3.1 Ordination of Treatment Groups by Species

The direct discriminant function analysis performed using the relative cover of 23 plant species as predictors of membership of the twelve treatments and the six treatments were similar. Therefore, only the results for the discriminant function analysis performed on the six treatments (i.e. sown and unsown pooled) are presented. The first discriminant function maximally separated the low soil disturbance treatments (A and B in Fig. 6.1) from the high soil disturbance treatments (E and F). The moderate soil disturbance treatments (C and D) fell between the low and the high disturbance treatments, but were closer to the low disturbance treatments. The second discriminant function separated the unfertilized treatments (A, C and E) from the fertilized treatments (B, D and F). However, this separation was small for the high soil disturbance treatments (E and F).

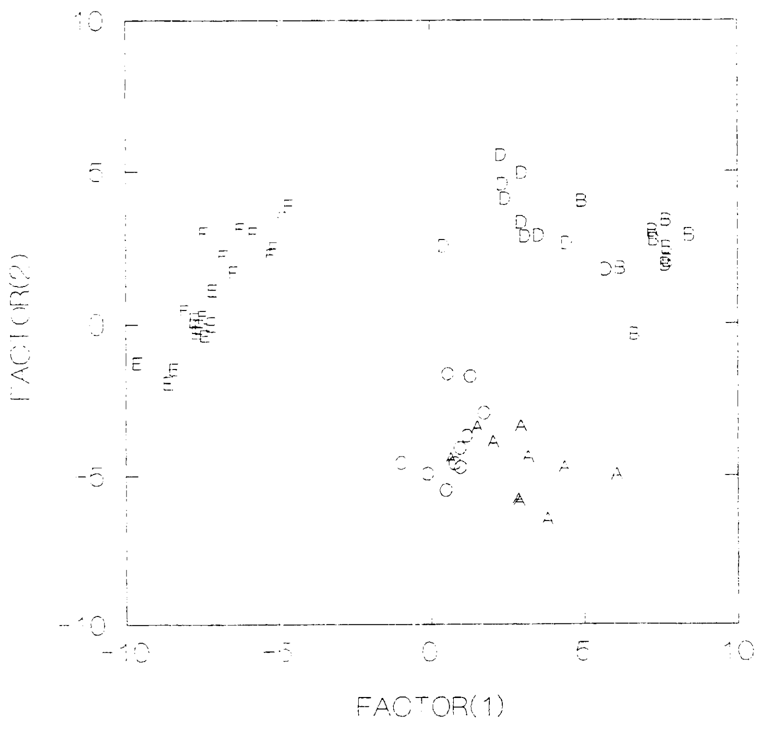


**Fig. 6.1:** Plot of the six treatments (n=10) on two discriminant functions derived from the abundance of 23 plant species. A = low disturbance, unfertilized; B = low disturbance, fertilized; C = moderate disturbance, unfertilized; D = moderate disturbance, fertilized; E = high disturbance, unfertilized; F = high disturbance, fertilized.

The canonical loading matrix of the correlations between the predictor variables and the discriminant functions indicated that the primary variable distinguishing between low and high soil disturbance treatments (i.e. the first function, Factor 1) was the relative cover of *Aristida ramosa* (Table 6.1). The low disturbance plots had a greater cover of *A.ramosa* than the highly disturbed plots (Appendix 8). Also contributing to the discrimination between these groups was the relative cover of *Sporobolus creber, Briza minor* and *Hypochaeris radicata.* The low disturbance plot had a greater cover of *S.creber* and *B.minor* than on the highly disturbed plots. On the other hand, the low disturbance plots had a lower cover of *H.radicata* than the high disturbance plots.

**Table 6.1:** Results of discriminant function analysis of the abundance of 23 plant species for the six treatments (i.e. unsown and sown plots together). Predictor variables are listed in descending order of univariate F values. The four highest canonical loading are marked in bold. Note: *B.minor* and *A.cupaniana* individuals were dead, but remained rooted in plots in February 1994.

| Predictor Variable | Canonical Loadings | | Univariate | Probability |
|---|---|---|---|---|
| | Factor 1 | Factor 2 | F (5, 54) | |
| *Briza minor* | **0.280** | **0.480** | 54.22 | 0.000 |
| *Aristida ramosa* | **0.324** | **-0.291** | 45.55 | 0.000 |
| *Sporobolus creber* | **0.310** | 0.124 | 34.83 | 0.000 |
| *Hypochaeris radicata* | **-0.171** | -0.018 | 15.28 | 0.000 |
| *Aira cupaniana* | 0.060 | **0.310** | 12.66 | 0.000 |
| *Tricoryne elatior* | 0.170 | 0.120 | 12.23 | 0.000 |
| *Aristida warburgii* | 0.117 | **-0.239** | 11.78 | 0.000 |
| *Carex inversa* | 0.102 | 0.201 | 9.60 | 0.000 |
| *Oxalis exilis* | 0.116 | 0.065 | 6.62 | 0.000 |
| *Luzula flaccida* | 0.101 | 0.006 | 6.16 | 0.000 |
| *Fimbristylis dichotoma* | 0.110 | 0.098 | 5.79 | 0.000 |
| *Schoenus apogon* | 0.104 | 0.049 | 5.32 | 0.000 |
| *Vulpia* species | -0.031 | 0.145 | 4.99 | 0.001 |
| *Richardia stellaris* | 0.067 | -0.106 | 4.39 | 0.002 |
| *Hypericum gramineum* | 0.104 | -0.048 | 4.26 | 0.002 |
| *Carex breviculmis* | 0.098 | -0.025 | 3.60 | 0.007 |
| *Acetosella vulgaris* | -0.048 | 0.133 | 3.25 | 0.012 |
| *Panicum effusum* | 0.088 | 0.003 | 2.94 | 0.020 |
| *Eragrostis 'red'* | 0.043 | -0.063 | 1.71 | 0.149 |
| *Haloragis heterophylla* | 0.015 | -0.018 | 1.50 | 0.206 |
| *Dichelachne micrantha* | 0.020 | 0.026 | 1.02 | 0.415 |
| *Wahlenbergia planiflora* | 0.029 | -0.046 | 0.92 | 0.473 |
| *Eragrostis leptostachya* | 0.008 | -0.063 | 0.74 | 0.599 |

The primary variable distinguishing between unfertilized and fertilized treatments (i.e. the second function, Factor 2) was the relative cover of *Briza minor* (Table 6.1). The fertilized plots had a greater cover of *B.minor* than the unfertilized plots (Appendix 8). Also contributing to discrimination between these two groups was the relative cover of *Aira cupaniana, Aristida ramosa* and *A.warburgii.* The fertilized plots had a greater cover of *A.cupaniana* than unfertilized plots. The fertilized plots had a lower cover of *A.ramosa* and *A.warburgii* than unfertilized plots.

### 6.3.2 Ordination of Treatment Groups by Plant Attributes

A direct discriminant function analysis was performed using the abundance of 44 plant attribute variables as predictors of membership in the six groups defined by the experimental treatments (3 levels of disturbance x 2 levels of fertility). The discriminant function analysis using abundance of species with a particular plant attribute as the predictor variable (Fig. 6.2) produced tighter and better separated groups than analysis using plant species as the predictor variable (Fig. 6.1). The first discriminant function maximally separated the low and moderate soil disturbance treatments (A, B, C and D in Fig. 6.2) from the high soil disturbance treatments (E and F). The unfertilized, moderate disturbance treatment (C) was close to the unfertilized low disturbance treatment (A), while the fertilized, moderate disturbance treatment (D) was close to the fertilized low disturbance treatment (B). The fertilized high disturbance treatment (F) fell between the low and moderately disturbed treatments and the unfertilized highly disturbed treatment (E). The second discriminant function separated the unfertilized from the fertilized treatments, but only on the highly disturbed plots (E and F). The second discriminant function also separated the low soil disturbance treatment from the moderately disturbed treatment, but only when fertilized (B and D).

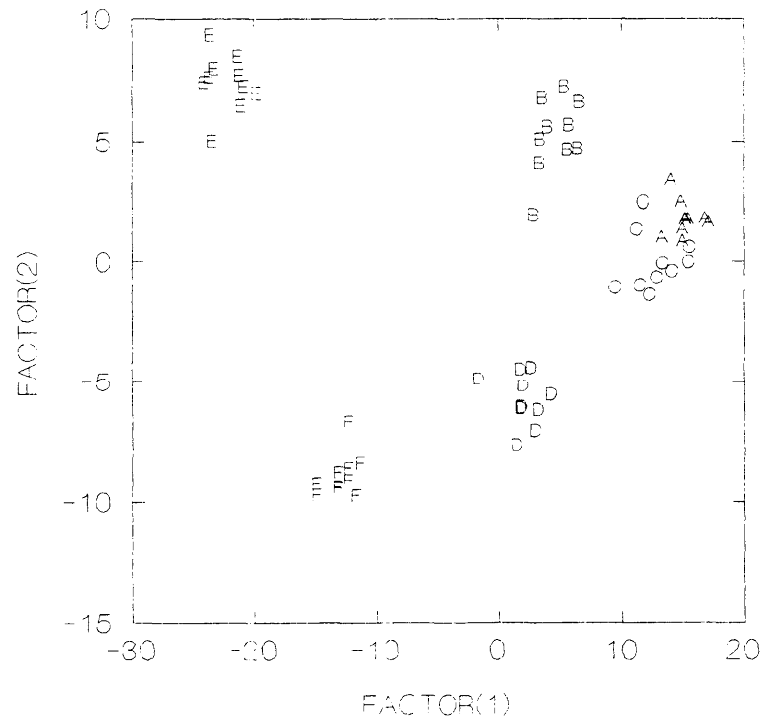


**Fig. 6.2:** Plot of the six treatments (n=10) on two discriminant functions derived from the abundance of 44 plant attribute variables. A = low disturbance, unfertilized; B = low disturbance, fertilized; C = moderate disturbance, unfertilized; D = moderate disturbance, fertilized; E = high disturbance, unfertilized; F = high disturbance, fertilized.

The canonical loadings indicate that the primary variable distinguishing between the high soil disturbance treatments and the low and moderate disturbance treatment (i.e. the first function, Factor 1) was the relative cover of exotics (Table 6.2). The highly disturbed plots had a greater cover of exotics than the low and moderately disturbed plots (Appendix 8). The relative cover of exotics was greater in fertilized than unfertilized plots, but only in low and moderately disturbed plots. Also contributing to discrimination between these groups was the relative cover of plants with fibrous leaves, plants with deep litter and tall plants. The low and moderately disturbed plots had a greater cover of plants with fibrous leaves, deep litter and tall plants than the highly disturbed plots. The relative cover of plants with fibrous leaves, plants with deep litter and tall plants was greater in unfertilized than fertilized plots, but only in low and moderately disturbed plots.

The canonical loading indicated that the primary variable distinguishing between the unfertilized and fertilized plots when highly disturbed, and between the low and moderately disturbed when fertilized (i.e. the second function, Factor 2) was also the relative cover of exotics (Table 6.2). When highly disturbed (E and F), the fertilized plots had a higher cover of exotics than the unfertilized treatments (Appendix 8). Also contributing to discrimination between these groups was the relative cover of hemicryptophytes, plants without litter and therophytes. When highly disturbed, the fertilized plots had a lower cover of hemicryptophytes than the unfertilized plots. When highly disturbed, the fertilized plots had a greater cover of plants without litter and therophytes than the unfertilized plots. When fertilized, the moderately disturbed plots had greater cover of exotics, therophytes and plants with no litter than the low disturbance plots (D and B). When fertilized, the moderately disturbed plots had lower cover of hemicryptophytes than the low disturbance plots.

The higher canonical loadings (Table 6.2) of the established phase attributes indicated that the relative cover of established phase attributes (e.g. exotic, leaf life span, height, leaf texture) were more useful in distinguishing between the treatment groups than regenerative attributes (e.g. seed mass, seed number, underground storage organs). If any of the established phase and regenerative attributes were correlated, potentially useful regenerative attributes may have been obscured by the established phase attributes. It would be beneficial not only to understand the mechanisms by which plant attributes enhance the chances of remaining established in a particular habitat, but also to understand which attributes enhance regeneration in particular habitats, especially disturbed ones. Therefore, the established phase and regenerative attributes were subsequently analysed separately.

**Table 6.2:** Results of discriminant function analysis of 44 plant attributes for the six treatments (i.e. unsown and sown plots pooled). Predictor variables are listed in descending order of univariate F values. The four highest canonical loading are marked in bold.

| Predictor Variable | Canonical Loadings | | Univariate | Probability |
|---|---|---|---|---|
| | Factor 1 | Factor 2 | F (5, 54) | |
| Exotic | **-0.289** | **-0.202** | 204.39 | 0.000 |
| Fibrous leaves | **0.224** | 0.092 | 120.30 | 0.000 |
| Deep litter | **0.187** | 0.096 | 83.26 | 0.000 |
| Tall (vegetative) | **0.171** | -0.005 | 67.23 | 0.000 |
| Rosette/semi-rosette | -0.105 | 0.078 | 48.88 | 0.000 |
| Taproot | -0.102 | 0.090 | 45.60 | 0.000 |
| Forb | -0.124 | 0.039 | 44.64 | 0.000 |
| Moderate litter | -0.121 | 0.049 | 42.99 | 0.000 |
| Hemicryptophyte | 0.060 | **0.174** | 40.91 | 0.000 |
| Short (vegetative) | -0.093 | 0.097 | 40.77 | 0.000 |
| Hairy leaves | -0.086 | 0.073 | 36.73 | 0.000 |
| Grass | 0.114 | -0.052 | 36.32 | 0.000 |
| No litter | -0.008 | **-0.141** | 33.59 | 0.000 |
| Short flowering period | -0.016 | -0.131 | 32.51 | 0.000 |
| Therophyte | -0.014 | **-0.136** | 31.15 | 0.000 |
| High seed number | -0.026 | -0.127 | 29.08 | 0.000 |
| Tussock/tuft | 0.101 | -0.068 | 28.57 | 0.000 |
| Erect/branching | 0.007 | -0.080 | 27.28 | 0.000 |
| Low seed mass | 0.095 | 0.080 | 26.15 | 0.000 |
| Awns/hooks | 0.095 | -0.057 | 24.48 | 0.000 |
| No underground storage | 0.090 | -0.084 | 23.72 | 0.000 |
| Nanophyll leaves | 0.097 | 0.044 | 22.74 | 0.000 |
| Moderate height (vegetative) | -0.038 | -0.112 | 21.53 | 0.000 |
| Short leaf life span | -0.091 | -0.039 | 21.0 | 0.000 |
| Moderate seed number | 0.002 | 0.090 | 19.90 | 0.000 |
| Microphyll leaves | -0.085 | -0.005 | 19.02 | 0.000 |
| Low seed number | 0.070 | 0.112 | 18.40 | 0.000 |
| Moderate seed mass | -0.080 | -0.029 | 16.68 | 0.000 |
| Pappus | -0.069 | 0.060 | 15.88 | 0.000 |
| Cylindrical seeds | -0.010 | 0.003 | 14.56 | 0.000 |
| Moderate leaf life span | 0.070 | 0.021 | 13.04 | 0.000 |
| Long flowering period | -0.042 | 0.083 | 11.10 | 0.000 |
| Sedge/rush | 0.051 | -0.003 | 10.32 | 0.000 |
| Long leaf life span | 0.056 | 0.053 | 10.09 | 0.000 |
| Short rhizomes | 0.041 | 0.032 | 9.18 | 0.000 |
| Moderate flowering period | 0.053 | 0.022 | 8.74 | 0.000 |
| Leptophyll leaves | -0.007 | -0.073 | 6.38 | 0.000 |
| Dust-like seeds | 0.040 | 0.062 | 5.57 | 0.002 |
| Explosive seeds | 0.031 | 0.045 | 4.48 | 0.000 |
| Amphiphyte | -0.039 | -0.047 | 4.47 | 0.002 |
| High seed mass | -0.007 | -0.045 | 3.20 | 0.013 |
| Long rhizomes | 0.003 | -0.036 | 2.27 | 0.000 |
| No dispersal mechanism | -0.017 | -0.021 | 2.17 | 0.071 |
| Prostrate/winding | 0.008 | 0.042 | 1.18 | 0.331 |

The direct discriminant function analysis performed using the abundance of 28 established phase attributes as predictors of membership of the six groups defined by the experimental treatments (sown and sown plots pooled) was not as well separated as that using both established phase and regenerative attributes together. In particular, the low disturbance, fertilized and the moderately disturbed fertilized treatments (B and D in Fig. 6.3) were not well distinguished. The variables distinguishing between the high soil disturbance treatments and the low and moderate disturbance treatment in this analysis (Table 6.3) were the same as for the analysis using both established phase and regenerative attributes (i.e. relative cover of exotics, plants with fibrous leaves, plants with deep litter and tall plants).

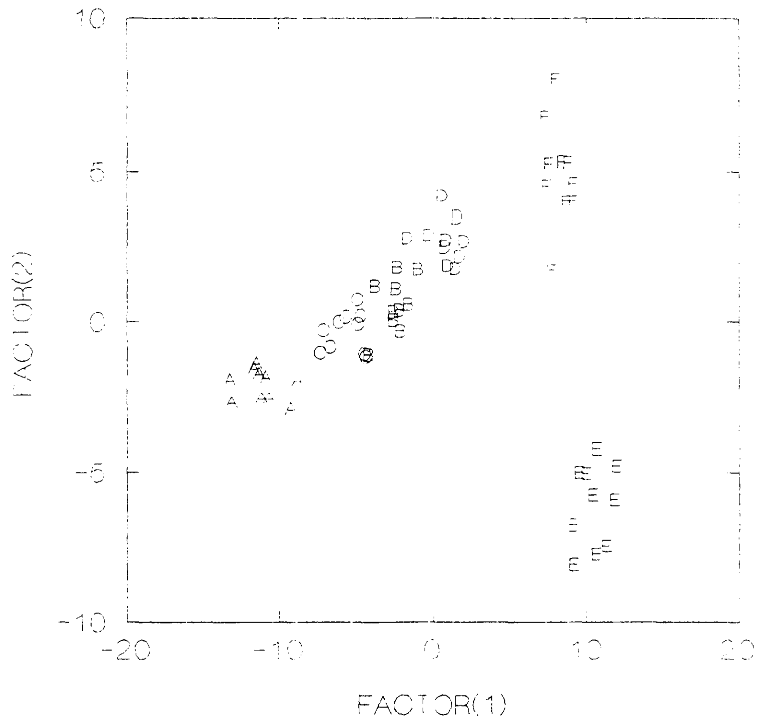


Fig. 6.3: Plot of the six treatments (n=10) on two discriminant functions derived from the abundance of 28 established phase plant attribute variables. A = low disturbance, unfertilized; B = low disturbance, fertilized; C = moderate disturbance, unfertilized; D = moderate disturbance, fertilized; E = high disturbance, unfertilized; F = high disturbance, fertilized.

The main difference between the analysis using established phase attributes alone and the analysis using established phase and regenerative attributes together was that the relative cover of exotics was no longer the primary variable for the second function distinguishing between the unfertilized and fertilized plots, when highly disturbed (Table 6.3). The relative cover of hemicryptophytes became most important, while the relative cover of plants without litter, therophytes and plants flowering for a short period continued to contribute to the discrimination. The fertilized plots had a lower cover of hemicryptophytes and higher cover of therophytes, plants without litter and plants flowering for a short duration than the unfertilized plots, especially in highly disturbed plots (Appendix 8).

**Table 6.3:** Results of discriminant function analysis of 28 established phase plant attributes for the six treatments (i.e. unsown and sown plots pooled). Predictor variables are listed in descending order of univariate F values. The four highest canonical loading are marked in bold.

| Predictor Variable | Canonical Loadings | | Univariate | Probability |
|---|---|---|---|---|
| | Factor 1 | Factor 2 | F (5, 54) | |
| Exotic | **0.537** | 0.172 | 204.39 | 0.000 |
| Fibrous leaves | **-0.416** | -0.074 | 120.30 | 0.000 |
| Deep litter | **-0.347** | -0.065 | 83.26 | 0.000 |
| Tall (vegetative) | **-0.308** | 0.108 | 67.23 | 0.000 |
| Rosette/semi-rosette | 0.175 | -0.328 | 48.88 | 0.000 |
| Forb | 0.213 | -0.228 | 44.64 | 0.000 |
| Moderate litter | 0.207 | -0.241 | 42.99 | 0.000 |
| Hemicryptophyte | -0.128 | **-0.370** | 40.91 | 0.000 |
| Short (vegetative) | 0.153 | -0.333 | 40.77 | 0.000 |
| Hairy leaves | 0.143 | -0.295 | 36.73 | 0.000 |
| Grass | -0.196 | 0.220 | 36.32 | 0.000 |
| No litter | 0.041 | **0.361** | 33.59 | 0.000 |
| Short flowering period | 0.054 | **0.340** | 32.51 | 0.000 |
| Therophyte | 0.049 | **0.342** | 31.15 | 0.000 |
| Tussock/tuft | -0.180 | 0.157 | 28.57 | 0.000 |
| Erect/branching | 0.008 | 0.261 | 27.28 | 0.000 |
| Nanophyll leaves | -0.176 | 0.010 | 22.74 | 0.000 |
| Moderate height (vegetative) | 0.087 | 0.259 | 21.53 | 0.000 |
| Short leaf life span | 0.172 | 0.034 | 21.00 | 0.000 |
| Microphyll leaves | 0.151 | -0.083 | 19.02 | 0.000 |
| Moderate leaf life span | -0.133 | -0.026 | 13.04 | 0.000 |
| Long flowering period | 0.065 | -0.205 | 11.10 | 0.000 |
| Sedge/rush | -0.081 | 0.088 | 10.32 | 0.000 |
| Long leaf life span | -0.100 | 0.002 | 10.09 | 0.000 |
| Moderate flowering period | -0.102 | -0.049 | 8.74 | 0.000 |
| Leptophyll leaves | 0.020 | 0.157 | 6.38 | 0.000 |
| Amphiphyte | 0.074 | 0.057 | 4.47 | 0.002 |
| Prostrate/winding | -0.015 | -0.032 | 1.18 | 0.331 |

A direct discriminant function analysis was performed using the abundance of 16 regenerative plant attribute variables as predictors of membership of the six groups defined by the experimental treatments (i.e. sown and sown plots pooled). The groups were not as tight or as well separated as the analysis using the established phase plant attributes either alone or in combination with the regenerative attributes. In particular, the low and moderately disturbed plots (A, B, C and D in Fig. 6.4) were not clearly distinguished from each other. The canonical loadings indicated that the primary variable distinguishing between the high soil disturbance treatments and the low and moderately disturbed treatment (i.e. the first function) was the relative cover of plants with taproots (Table 6.4). The highly disturbed plots had a higher cover of plants with taproots than the low and moderately disturbed plots (Appendix 8). Also contributing to the discrimination between these groups was the relative cover of plants with large seed mass, with awns or hooks on their seeds and with low seed number. The low and moderately disturbed plots had a greater cover of plants with large seed mass, with awns or hooks on their seeds and low seed number than the highly disturbed plots.

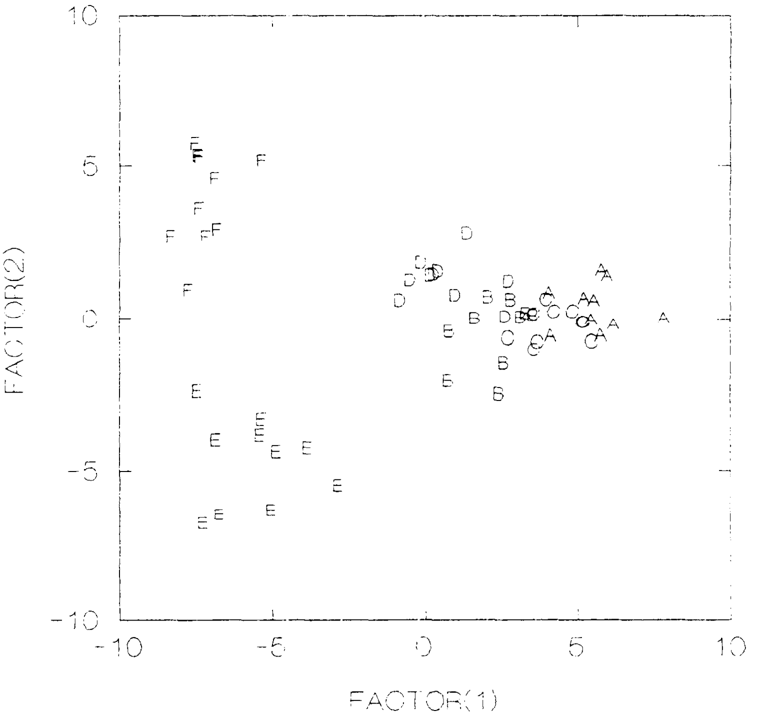


**Fig. 6.4:** Plot of the six treatments (n=10) on two discriminant functions derived from the abundance of 16 regenerative plant attribute variables. A = low disturbance, unfertilized; B = low disturbance, fertilized; C = moderate disturbance, unfertilized; D = moderate disturbance, fertilized; E = high disturbance, unfertilized; F = high disturbance, fertilized.

The canonical loadings indicated that the primary variable distinguishing between the unfertilized and fertilized plots when highly disturbed (i.e. the second function) was also the relative cover of plants with taproots (Table 6.4). When highly disturbed, the unfertilized plots had a higher cover of plants with taproots than the fertilized plots (Appendix 8). Also contributing to discrimination between these groups was the relative cover of plants with high seed number, plants without underground storage organs and plants with pappus on their seeds. When highly disturbed, the unfertilized plots had a lower cover of plants with high seed number and without underground storage organs and greater cover of plants with pappus on their seeds than the fertilized plots.

**Table 6.4:** Results of discriminant function analysis of the abundance of 16 regenerative plant attributes for the six treatments (i.e. unsown and sown plots pooled). Predictor variables are listed in descending order of univariate F values. The four highest canonical loading are marked in bold.

| Predictor Variable | Canonical Loadings | | Univariate | Probability |
|---|---|---|---|---|
| | Factor 1 | Factor 2 | F (5, 54) | |
| Taproot | **-0.248** | **-0.438** | 45.60 | 0.000 |
| High seed number | -0.101 | **0.291** | 29.08 | 0.000 |
| Large seed mass | **0.278** | -0.049 | 26.15 | 0.000 |
| Awns/hooks | **0.232** | 0.275 | 24.48 | 0.000 |
| No underground storage | 0.218 | **0.338** | 23.72 | 0.000 |
| Moderate seed number | 0.025 | -0.240 | 19.90 | 0.000 |
| Low seed number | **0.232** | -0.138 | 18.40 | 0.000 |
| Moderate seed mass | -0.221 | -0.054 | 16.68 | 0.000 |
| Pappus | -0.158 | **-0.280** | 15.88 | 0.000 |
| Cylindrical seeds | -0.038 | -0.058 | 14.56 | 0.000 |
| Short rhizomes | 0.129 | -0.003 | 9.18 | 0.000 |
| Dust-like seeds | 0.131 | -0.073 | 5.57 | 0.000 |
| Explosive | 0.095 | -0.015 | 4.48 | 0.002 |
| Small seed mass | -0.028 | 0.103 | 3.20 | 0.013 |
| Long rhizomes | -0.005 | 0.107 | 2.27 | 0.060 |
| No dispersal mechanism | -0.052 | 0.044 | 2.17 | 0.071 |

## 6.4 DISCUSSION

The discriminant function analysis showed that membership of a plot to one of the treatment groups could be successfully predicted by the relative cover of plant species. The relative cover of *Aristida ramosa, Sporobolus creber* and *Briza minor* was greater on low disturbance plots than on highly disturbed plots (Table 6.5). The relative cover of *Hypochaeris radicata* was greater on highly disturbed plots than on low disturbance plots. The relative cover of *A.ramosa* and *A.warburgii* was greater on unfertilized than fertilized plots, while the relative cover of *Aira cupaniana* and *B.minor* was greater on fertilized than unfertilized plots. The low and moderately disturbed plots were closer together on the ordination than the unfertilized and fertilized treatments, the ordination indicating that fertilization changed species composition to a greater extent than moderate soil disturbance. Differences in species composition between the unfertilized and fertilized plots was greater at low and moderate levels of soil disturbance than at a high level of disturbance. At low and moderate levels of soil disturbance, fertilization markedly changed species composition, but at high levels of soil disturbance species composition in fertilized and unfertilized plots were fairly similar. This suggests that species that could tolerate severe soil disturbance could tolerate a wide range of soil fertility. It appears that altered light conditions had a greater affect on species composition than the direct affect of fertilization.

Discriminant function analysis showed that membership of plots to the six treatment groups could be successfully predicted by the relative cover of plants with particular plant attributes. The relative cover of exotics, plants with fibrous leaves, deep litter and tall stature discriminated between the highly disturbed plots and the low and moderately disturbed plots. These same attributes also discriminated between the unfertilized and fertilized plots, subject to low and moderate soil disturbance. Exotic species dominated the highly disturbed plots and plants with fibrous leaves, deep litter and tall stature dominated the low and moderately disturbed plots (Table 6.5). On the low and moderately disturbed plots, fertilization increased the relative cover of exotics and decreased the cover of plants with fibrous leaves, deep litter and tall stature. Thus, both fertilization and soil disturbance promoted exotic species and reduced plants with attributes related to the conservation of nutrients (e.g. fibrous leaves and deep litter). This is consistent with Grime's (1979) proposal that attributes concerned with a conservative use of nutrients are typical of the stress-tolerant plant strategy.

**Table 6.5:** Plant species and plant attributes that discriminated between plants from the low and moderately disturbed unfertilized plots, the low and moderately disturbed fertilized plots, the highly disturbed unfertilized plots and the highly disturbed fertilized plots. See text for full specific names.

| | Low and Moderately Disturbed, Unfertilized | Low and Moderately Disturbed, Fertilized | Highly Disturbed, Unfertilized | Highly Disturbed, Fertilized |
|---|---|---|---|---|
| Species | ***A.ramosa & A.warburgii*** | ***S.creber & B.minor*** | ***H.radicata*** | ***H.radicata & A.cupaniana*** |
| Origin | **native** | **native & exotic** (more exotic for moderately disturbed) | **exotic** | **exotic** |
| Raunkiaer Life Form | **hemicryptophytes & therophytes** | **therophytes & hemicryptophytes** (more therophytes for moderately disturbed) | **hemi-cryptophytes** | **therophytes** |
| Leaf Texture | **fibrous** | **fibrous & soft** | **soft** | **soft** |
| Persistent Litter | **deep litter** | **deep & no litter** (more no litter for moderately disturbed) | **no litter & deep** | **no litter** |
| Height | **tall** | **tall & short** | **short** | **short** |
| Flowering Period | **long & short flowering** | **short & long flowering** (more short for moderately disturbed) | **long flowering** | **short flowering** |
| Underground Storage Organs | **no storage** | **no storage** | **taproot** | **taproot & no storage** |
| Diaspore Mass | **large** | **large** | **small** | **small** |
| Diaspore Number | **low** | **low** | **high** | **highest** |
| Diaspore Dispersal Appendages | **awns/hooks** | **awns/hooks** | **pappus & unawned/no hooks** | **unawned/no hooks** |

The relative cover of exotics, hemicryptophytes, therophytes, plants without litter and plants flowering for a short duration discriminated between low and moderately disturbed plots, but only when fertilized. These same attributes also discriminated between the unfertilized and fertilized plots, but only when highly disturbed. Thus, fertilization promoted exotic species and plants with attributes associated with an exploitive use of nutrients (e.g. therophytes and no litter) and reduced hemicryptophytes, but only in combination with high soil disturbance. This is consistent with Grime's (1979) proposal that attributes which are not concerned with the conservation of nutrients are typical of the ruderal plant strategy (e.g. short lifespan and flowering, absence of litter). When fertilized, moderate soil disturbance promoted the relative cover of exotics, therophytes and plants with no litter and reduced hemicryptophytes.

Similar to the effects of soil disturbance in this study, Díaz *et al.* (1991) found that plant height, persistence, leaf size and verticality decreased with increasing grazing intensity. Some commonalities exist between these two types of disturbances, in that both grazing and soil disturbance promote shorter, less persistent (annual) plants. Fernández Alés *et al.* (1993) found that in the absence of grazing, species with short life cycles declined while tall species increased. The low and moderately disturbed, fertilized treatment, which had the highest species richness, also had the greatest richness of plant attributes (Table 6.5). Similarly, Montalvo *et al.* (1991) found that grasslands with numerous morphological traits have high species diversity.

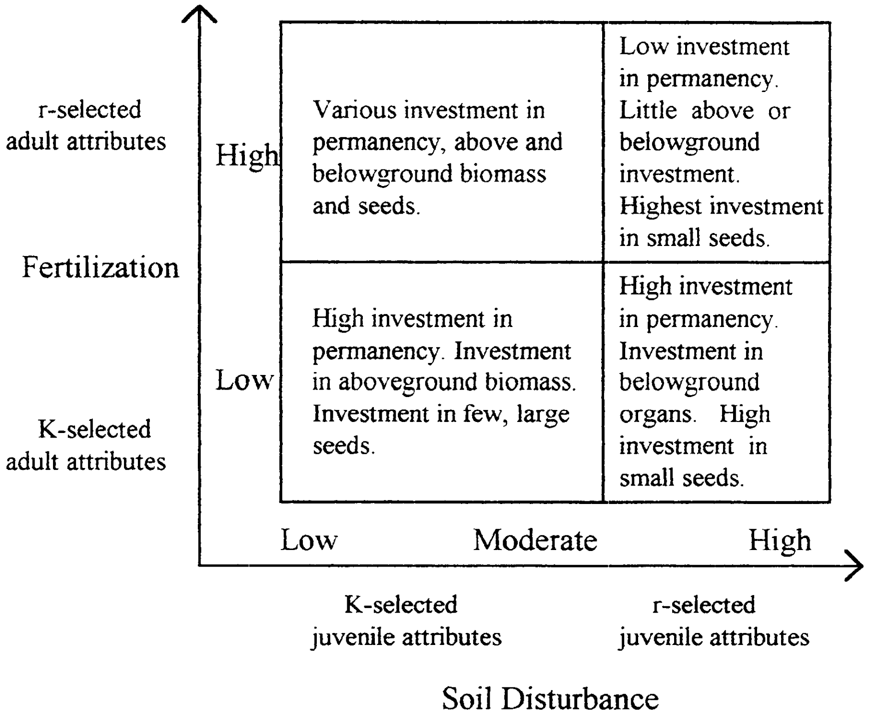
The difference between the cover of plants with particular attributes in the unfertilized and the fertilized plots increased with increasing soil disturbance. The reverse trend occurred when the analysis was based upon species composition. Thus, although fertilization markedly changed species composition at low and moderate levels of soil disturbance, the attributes possessed by these species changed little. Meanwhile on the highly disturbed plots, fertilization changed species composition very little while the attributes possessed by these species on the unfertilized plots were markedly different from those on the fertilized plots. The latter result probably reflects the smaller number of species in highly disturbed plots, and thus small changes in species composition may have made a large contribution to the effect on attribute composition.

Discriminant function analysis showed that membership of a plot to the six treatment groups could also be predicted by the relative cover of particular regenerative plant attributes. Groups based on regenerative attributes were not as distinct as those based on established phase attributes, explaining why the regenerative attributes had low loadings when analysed together with the established phase attributes. Soil disturbance promoted the relative cover of plants with taproots and reduced the cover of plants with large seeds, low seed number and awns/hooks on their seeds (Table 6.5). Fertilization reduced the relative cover of plants with taproots and with pappus on their seeds and promoted the cover of plants with high seed number and plants without underground storage organs, but only in combination with high soil disturbance. When fertilized, moderate soil disturbance reduced the relative cover of plants with taproots and pappus on their seeds and promoted the cover of plants with high seed number and no underground storage organs. Similar to the effects of soil disturbance in the fertilized plots in this study, Fernández Alés *et al.* (1993) found that species with small seeds and short life cycles dominate ploughed plots, while species with larger seeds and longer life cycles are more abundant in unploughed plots. Fernández Alés *et al.* (1993) concluded that plant size is predictably related to stress, with larger plants dominating productive habitats and smaller in unproductive habitats. Plant size was related to soil disturbance in this study. However, most of the species in the study by Fernandez Alés *et al.* (1993) were annual, the fertility of their study areas was not measured and the presence of grazing was acknowledged for one site but not clear for the other two. Nor did the study examine interactions between productivity and disturbance. As the present work demonstrates, different combinations of disturbance and fertility levels result in the promotion of different attributes and therefore they cannot be interpreted in isolation. For example, the recovery of vegetation cover after high soil disturbance was faster on the fertilized plots than the unfertilized plots. For this reason, we would expect that the attributes of species from nutrient-poor, disturbed plots would differ from those of nutrient-rich, disturbed plots to allow them to cope with, or contribute to, the more rapid canopy closure.

Although membership of a plot to the six treatment groups was successfully predicted by both species identity and plant attributes, group membership based on the relative cover of species with a particular plant attribute was tighter and better separated along both discriminant functions. Similarly, Díaz *et al.* (1991) found stronger differences between sites subject to different intensities of grazing when the ordination was based on morphological attributes than that based on floristic composition. However, Montalvo *et al.* (1991) found that altitudinal trends were better defined by floristic data than morphological attributes. They found that species composition facilitated better differentiation between grasslands from different localities, while non-taxonomic composition expressed the influence of environmental variability in a more gradual form. Montalvo *et al.* (1991) found that annuals and species with low biomass density, soft leaves and high seed production increased with decreasing altitude. Thus, attributes found to be important in relation to altitude were similar to those strongly related to soil disturbance and fertilization in this study.

In summary, four groups of species were distinguished (Fig. 6.5): three of the groups had distinct attributes while the fourth had a mixture of attributes (Table 6.5). On nutrient-poor plots experiencing low and moderate levels of soil disturbance, plants tended to invest in attributes which favour permanency (e.g. fibrous leaves and long flowering periods). These plants tended to invest in above-ground biomass (e.g. tall stature and deep litter), but did not invest in underground storage organs. The idea of leaves being involved in storage has received little investigation. However, Chapin (1980) suggested that leaves appear to be at least as important as roots or stems as sites of nutrient accumulation and storage in evergreen species. These plants also invested in a small number of large seeds. The attributes common to the species in this treatment (Fig. 6.5) suggest that a conservative use of resources over a long period enables survival in low fertility environments subject to low or moderate levels of soil disturbance.

The second group of species (Fig. 6.5), on nutrient-poor plots experiencing high levels of soil disturbance also invested in attributes related to permanency. They tended to be hemicryptophytes (which by definition are also perennial), had long flowering periods and possessed taproots. In contrast to the first group, these plants invested in below-ground (e.g. taproots) rather than in above-ground biomass (e.g. soft leaves, no litter and a short stature). These plants also invested in a large number of small seeds (Table 6.5). The attributes common to the species in this treatment suggested greater investment below and above-ground, and in organs resistant to soil disturbance (e.g. taproot), over a long period facilitates survival in a low fertility, highly disturbed environment.



| | | |
|---|---|---|
| High | Various investment in permanency, above and belowground biomass and seeds. | Low investment in permanency. Little above or belowground investment. Highest investment in small seeds. |
| Low | High investment in permanency. Investment in aboveground biomass. Investment in few, large seeds. | High investment in permanency. Investment in belowground organs. High investment in small seeds. |

**Fig. 6.5:** Summary model describing attributes of plants subjected to different levels of fertilization and soil disturbance in the Newholme field experiment.

Kautsky (1988) proposed a modified version of Grime's (1979) strategies, with two types of stress-tolerant strategies (stunted and biomass storer) as well as the ruderal and competitor strategies. Plants belonging to their biomass storer strategy were of tall stature and were long-lived, similar to the group of species found here in unfertilized low and moderately disturbed plots. Plants of their stunted strategy were of small stature and were long-lived, consistent with the group of species in unfertilized, highly disturbed plots. Three of the four groups identified here (Table 6.5) correspond to the three clusters identified by Grime *et al.* (1988) based on established phase plant attributes: annuals (ruderals), perennials of low vegetative spread and low canopy height (stress-tolerators), and perennials of high vegetative spread and high canopy height (competitors). However, the correspondence did not extend to the habitats believed to be associated with these ruderal, stress-tolerant and competitive strategies (Grime 1979).

The third group of species (Fig. 6.5) in nutrient-rich plots experiencing high levels of soil disturbance, tended to invest in attributes related to a lack of permanency (e.g. annual, short flowering period and no underground storage organs). These plants invested little in above or below-ground biomass (e.g. annual, no underground storage organs, soft leaves and no litter) and made a large investment in sexual reproduction by producing a large number of small seeds. The attributes common to the species in this treatment suggested that exploitive use of resources over a short period, to rapidly produce a large number of seeds, ensures survival in a high fertility environment subject to high levels of soil disturbance. The fourth group of species, found in nutrient-rich plots experiencing low and moderate levels of soil disturbance, possessed attributes indicative of various degrees of investment in permanency, underground storage organs, leaves and seeds (Fig. 6.5; Table 6.5). The attributes of the species in these treatments were intermediate between the other treatments. The range of strategies included annuals with high investment in reproduction (e.g. *Briza minor*), perennials with investment in above-ground biomass (e.g. *Sporobolus creber*) and perennials with investment in below-ground organs rather than above-ground biomass (e.g. *Hypochaeris radicata*).

Both this and previous studies have consistently found that persistence is strongly related to the environment. Montalvo *et al.* (1991) concluded that their altitudinal gradient corresponded to a change from low persistence ecosystems with a temporal, short duration structure (semi-arid Mediterranean grasslands) to more persistent types (high mountain Mediterranean grasslands). Díaz *et al.* (1992) found that a capacity for sustained occupation of above-ground space was important for herbaceous plants subject to different levels of grazing. Persistence also often separates functional groups of plants which are defined solely on the basis of attributes and independent of environmental factors (e.g. Grime *et al.* 1988; Boutin & Keddy 1993). Similar to this study, Thompson *et al.* (1996) found that species of infertile limestone grassland possessed attributes associated with the use and conservation of nutrients (e.g. tissue nutrient concentration, tissue turnover and litter decomposition rate).

Overlaying the templet shown in Fig. 6.5 is the effect of the change of the seasons (which could be regarded as a predictable disturbance). This phenological niche (*sensu* Grubb 1986) is available to species with attributes enabling seasonal regeneration (i.e. winter annuals). Grubb (1986) described the phenological niche as one where coexisting species capture resources at different times of the year. The perennial later-growing species do not eliminate the earlier-growing species because the supplies of resources are renewed by next spring and the early-growing species are able to grow above the litter of the previous year's late-growing plants (Grubb 1986). The seasonal opening of vegetation cover in habitats subject to low and moderate soil disturbance (Section 2.3.4) enables these plants to coexist with plants of perennial life histories (Table 6.5). This group of species is somewhat similar to the guild of spring-active herbs identified by Menges and Waller (1983), which experience the same flooding frequency but are displaced phenologically from the other groups of species.

Similar to the ruderal plant strategy proposed by Grime (1979), the plants in the highly disturbed, fertilized plots tended to have short life spans, produced a large number of seeds, confined storage to seeds and lacked persistent litter (Table 6.5). The plants in the low and moderately disturbed, unfertilized plots were similar to Grime's stress-tolerant species in that they had fibrous leaves and possessed persistent litter. However, unlike Grime's predictions for stress-tolerators, both annuals and perennials were present, storage did not occur in the roots and they tended to be tall. The plants in the low and moderately disturbed, fertilized plots were not similar to any of Grime's plant strategies, while sets of attributes characteristic of his competitive plant strategy were not observed at all. It is likely that a great deal of fertilizer would have to be applied for many years before the nutrient-poor Newholme soils could support Grime's competitive species.

Grime (1979) suggested that the combination of high disturbance and stress would prevent the establishment of plants and thus the C-S-R model makes no predictions for this type of habitat. However, in agreement with Grubb (1985) the combination of low productivity and disturbance at levels found in this study were viable plant habitats. Southwood (1988) included an unproductive, highly disturbed habitat in his templet model of plant strategies. His fourth strategy predicts that plants will invest in defence, a moderate life span and a moderate number of large and highly mobile offspring. These attributes do not correspond to the characteristics of species found in the nutrient-poor habitats highly disturbed plots here (Table 6.5).

Menges and Waller (1983) examined changes in the plant attributes of floodplain herbs with flooding frequency and found that ruderals avoid flooding by completing their life cycle before the next flood, while perennial graminoids tolerate the flooding with physiological and morphological adaptations. Thus they suggest that a flood can be either a stress (*sensu* Grime 1979) or a disturbance, depending on whether the affected species has evolved a physiological-morphological or a life-history solution. If a similar view is taken of the response of species to soil disturbance here, plants subject to high soil disturbance in combination with low fertility have attributes characteristic of tolerating both soil disturbance and low fertility (Fig. 6.5; Table 6.5). In contrast, plants subject to high soil disturbance in combination with high fertility have attributes characteristic of avoiding soil disturbance. Thus, whether a plant adopts the strategy of tolerating or avoiding a disturbance may depend on other habitat characteristics (e.g. fertility, climate). A plant is more likely to successfully avoid soil disturbance if it has soil nutrients available to complete its life cycle rapidly.

Other studies have demonstrated a lack of consistent association between attributes of the established and regenerative phases (Grime *et al.* 1988; Leishman & Westoby 1992). Shipley *et al.* (1989) showed that there is no association between juvenile and adult traits, which is an important assumption of r-K selection. Species having r-selected juvenile traits can have either r-selected or K-selected traits as adults and *vice versa*. Shipley *et al.* (1989) proposed a model using the four combinations of r-selected adults, r-selected juveniles, K-selected adults and K-selected juveniles. Various permutations of r-selected and K-selected adult and juvenile traits appear to correspond to the groups identified in this study (Fig. 6.5), with the exception of the low and moderately disturbed, fertilized treatment. On the low and moderately disturbed unfertilized treatments, K-selected juvenile attributes (e.g. few large seeds) and K-selected adult attributes (e.g. high investment in permanency) are favoured. On the highly disturbed fertilized treatment, r-selected juvenile attributes (e.g. numerous small seeds) and r-selected adult attributes (e.g. low investment in permanency and biomass) are favoured. On the highly disturbed unfertilized treatment, r-selected juvenile attributes (e.g. numerous small seeds) and K-selected adult attributes (e.g. high investment in permanency) are favoured. However, the low and moderately disturbed, fertilized treatment does not favour K-selected juvenile attributes and r-selected adult attributes, as Fig. 6.5 would predict. Instead, various combinations of different attributes were found.

The model in Fig. 6.5 makes ecological sense because in environments where large gaps and nutrients are limited (low and moderately disturbed, unfertilized plots), K-selected juvenile attributes are more likely to allow regeneration in the presence of vegetation cover and K-selected adult attributes may enable a conservative use of the limited resources over a long period. In environments where large gaps are present but nutrients are low (highly disturbed, unfertilized plots), r-selected juvenile attributes are more likely to enable the seed to reach the gap and establish in the absence of vegetation cover and K-selected adult attributes may enable a conservative use of the limited resources over a long period. In environments where large gaps are present and nutrients are high (highly disturbed, fertilized plots), r-selected juvenile attributes may enable the seed to reach the gap and establish in the absence of vegetation cover and r-selected adult attributes may enable a rapid completion of the life cycle before the vegetation cover re-establishes or disturbance reoccurs. It is possible that not enough time has elapsed on the low and moderately disturbed fertilized treatment, for biomass to increase to a level where K-selected juvenile attributes and r-selected adult attributes are explicitly favoured over other attributes. Compared to a site with a long history of fertilization and exclusion of grazers, the fertilized treatment in this study may only be of moderate fertility and the low soil disturbance treatment may really be moderately disturbed. Thus, Fig. 6.5 may only represent part of a broader picture, if habitats left undisturbed and fertilized for a longer period were included.

Figure 6.5 suggests that when plots of similar fertility are compared, juvenile attributes may be important in distinguishing between different levels of soil disturbance. When plots subject to similar levels of soil disturbance are compared, adult attributes may be important in distinguishing between different levels of soil fertility. Interestingly, McIntyre *et al.* (1995) found that traits related to regeneration were relevant to soil disturbance, but not to grazing or water addition. It may therefore be more effective to bias the chosen attributes towards juvenile or adult traits, depending on the environmental variables being examined. However, Fig. 6.5 also indicates that disturbance and fertility should not be examined in isolation.

# CHAPTER SEVEN

# CONCLUDING DISCUSSION

## 7.1 The Effects of Soil Disturbance and Fertilization

Soil disturbance changed the physical environment of the plant community (Section 2.3.4) by decreasing above-ground biomass, increasing bare ground, increasing light penetration to the soil surface and providing a pulse of available nitrogen. On the other hand, fertilization increased above-ground biomass, decreased bare ground, decreased light penetration to the soil surface and increased soil pH, phosphorus, sulphur and available nitrogen. Bare ground decreased in the control (i.e. low disturbance, unfertilized) plots over time as a result of the exclusion of livestock. The effect of soil disturbance on biomass and light penetration was independent of the level of fertilization (and vice versa). However, the effect of soil disturbance on bare ground depended on the level of fertility, with the increase in bare ground with disturbance being greater in unfertilized than fertilized plots.

Initial colonization after severe soil disturbance occurred primarily through sprouting vegetative fragments (e.g. *Hypochaeris radicata*, *Acetosella vulgaris* and *Sanguisorba minor*), contrary to theories emphasising regeneration by seed in disturbed habitats. The greater contribution made by vegetative regeneration was due to the timing of soil disturbance, which occurred shortly after the germination period of the winter annuals and killed their recently germinated seedlings. Annuals with an extended germination period (e.g. *Vulpia* spp.) were able to tolerate high soil disturbance because they were more likely to have seedlings germinating after soil disturbance. The small contribution made by seed regeneration in the severely soil disturbed plots may also have been related to the below-average rainfall during the study period. The results suggest that species capable of tolerating high soil disturbance either resprout from taproots or rhizomes, have an extended germination period, or have a germination period occurring after the soil disturbance (Section 2.4).

Most of the resident species could not tolerate high soil disturbance, but could tolerate moderate soil disturbance. Only one native perennial grass (*A.ramosa*) and moss species. were sensitive to moderate soil disturbance, while two exotic perennial forbs were favoured by high soil disturbance. Severe mechanical soil disturbance would have been a rare event at the site and thus the species were not adapted to survive such conditions. Two-thirds of the resident species responded positively to fertilization, but for some of them the effect was only transitory. Some species increased immediately with fertilization (e.g. *A.vulgaris* and *Vulpia* spp.), while others showed a transient increase which changed to a decrease with further fertilization (e.g. *Hypochaeris radicata, Hypericum gramineum* and *Drosera peltata*). The latter species, probably decreased as a result of increased biomass and decreased light penetration, rather than to a direct intolerance of high nutrient levels.

Interactions between the effect of soil disturbance and fertilization on species cover occurred often (Section 2.4). The most common type of interaction was where the positive or negative effect of fertilization on species cover decreased with increasing soil disturbance (e.g. *Sporobolus creber, Aristida ramosa, A.warburgii, Oxalis exilis, Briza minor* and *Aira cupaniana*). This interaction occurred because few individuals survived high soil disturbance to respond to the increase in nutrients. Another type of interaction was where the combination of fertilization and soil disturbance had a greater effect than soil disturbance and fertilization alone (i.e. a synergistic effect). For example, the increase in the abundance of some species with soil disturbance (e.g. *Vulpia* spp. and *Lolium perenne*) was enhanced further by fertilization.

The sown species were most abundant in highly disturbed, fertilized plots, except for *Sanguisorba minor* which was most abundant in highly disturbed, unfertilized plots. The pattern of abundance of the sown species in the different treatments reflected the effect of fertilization and soil disturbance on both emergence and seedling survival. The lower emergence and suppressed growth of the sown species in low and moderately disturbed plots, emphasises the important role disturbance plays in plant establishment. The seedlings of all of the sown species could not compete well with the established vegetation because the size difference (i.e. seedling - adult competition) overshadowed any species-specific effects (e.g. the competitive ability of the respective species).

Most of the resident species were eliminated from the highly disturbed plots, where the sown species were dominant, and thus they were rarely in competition with the sown species. However, sowing did have a negative effect on six resident species, usually in highly disturbed or fertilized plots. Under these conditions the sown species grew to a mature size, suggesting that most competitive effects relate to characteristics of mature plants. Surprisingly, sowing had a positive effect on seven resident species (Section 2.4). Since these positive effects occurred under conditions of low disturbance, and were often more pronounced for the first spring after the sown treatment was applied, the effect was probably due to the small disturbance created by the method of sowing rather than from any mutualism between the resident and sown species.

### 7.1.1 Species Richness

Species richness was influenced by (i) the level of soil disturbance and fertilization, (ii) species characteristics and (iii) site history. Species richness was generally greatest under conditions of moderate soil disturbance, providing support for the intermediate disturbance hypothesis. However, the difference between species richness in low and moderately disturbed habitats was not significant (Section 2.3.2). The results support the view that the relationship between disturbance and species richness is a bell-shaped curve (Fig. 1.2), and as a result, the direction of change in species richness with soil disturbance depends on the range of disturbance under investigation. Species richness may increase or decrease in response to increasing disturbance depending on whether the range of disturbance under investigation is less than or greater than the level of disturbance that produces maximum species richness in the community.

The intermediate-disturbance hypothesis relies on the species-pool hypothesis (Section 1.1.3), which predicts that high species richness occurs when the existing species pool is large and low species richness occurs when the existing species pool is small (Eriksson 1993). Studies in grassland (Goldberg & Gross 1988; Panetta & Wardle 1992; Hook *et al.* 1994) have found that small gaps (e.g. moderate disturbance) are more common than large gaps (e.g. severe disturbance) and an absence of gaps (e.g. undisturbed). If moderately disturbed grasslands are more common than undisturbed or severely disturbed grasslands, perhaps the number of species that have evolved in moderately disturbed habitats is larger (i.e. large species-pool) than in undisturbed or severely disturbed habitats (i.e. small species-pool). Thus, species number may be higher in moderately disturbed habitats because these habitats have a larger species-pool and, according to the species pool hypothesis, high species richness is expected when the species-pool is large.

There was a transient increase in species richness with fertilization that diminished with further fertilization. The results suggest that if the study had continued, species richness may have decreased as biomass accumulated with further fertilization. Initially the effect of soil disturbance on species richness was independent of fertilization, but by February 1994 the combination of fertilization and high soil disturbance decreased species richness to a greater extent than high soil disturbance alone. Although the effect of sowing on species richness was not significant, the sown plots were primarily responsible for this disturbance x fertilization interaction. On the unsown plots, disturbance had a similar effect on species richness irrespective of the level of fertility (and vice-versa). The combination of high soil disturbance and fertilization was particularly detrimental to species richness when the sown species were present. This reduction of species richness with sowing, on the highly disturbed fertilized plots, was not due to an increase in biomass or a decrease in bare ground. In fact sowing increased the percentage of bare ground in the highly disturbed plots. Thus, low species richness on the sown, highly disturbed, fertilized plots was due to the presence of particular species (i.e. sown species) or characteristics associated with particular species (e.g. tall leafy growth form, large leaves, hemicryptophyte life form and high growth rate). Species richness may differ markedly in habitats of similar biomass if they have been subject to differing levels of fertility and soil disturbance (Section 2.4). Other factors besides biomass influenced plant species richness and biomass alone is not a good predictor of species richness in habitats with different levels of disturbance and fertility.

Denslow (1985) concluded that species richness is likely to be maximized when the disturbance pattern resembles that which is historically characteristic of the community. This study supports this view because low species richness occurred in the low and highly disturbed plots. The pool of species suitable for these types of habitat would be small because ungrazed, unburnt or highly soil-disturbed conditions have been rare at the site. This idea can also be extended to other forms of anthropogenic changes, such as fertilization and the introduction of exotic propagules, since the lowest species richness occurred here when high soil disturbance, fertilization and sowing were combined. Thus, species richness after a novel change in environmental conditions (a disturbance or fertilizer regime different to past regimes) may be limited, in the short term, by the local pool of species adapted to the new conditions. Tilman (1993) came to a similar conclusion about the response of species richness to fertilization in an unburnt grassland in Minnesota, which had historically been unproductive and subjected to burning. Although species adapted to highly disturbed conditions (unsealed road) were located nearby they did not colonize the highly disturbed plots probably because dispersal was limited or conditions were not suitable for their germination. Perhaps these species of highly disturbed unfertilized conditions do not have 'weedy' characteristics typical of highly disturbed, fertile habitats.

### 7.1.2 Relevance to Management and Conservation

Denslow (1985) suggested that under disturbance regimes only slightly different from the historic one there may only be a shift in the relative abundance of species rather than a loss of species. This was the case here, where historically the study site had been subjected to a moderate level of soil disturbance created by trampling of livestock, but mechanical soil disturbance had been rare. As a result, most species could not tolerate severe soil disturbance and species richness declined, while only a few species were sensitive to moderate soil disturbance and only species abundance was altered. The results suggest that most species were favoured by maintaining anthropogenic soil disturbance at a level similar to the historic regime. The combination of fertilization and high soil disturbance was particularly detrimental to species richness suggesting that it should be avoided on similar sites of high conservation value. The importance of maintaining existing disturbance regimes for conservation has recently been emphasized by McIntyre *et al.* (1996).

One way of managing for maximum species richness in modified variegated landscapes is to stratify land-use (McIntyre *et al.* 1996). This approach increases richness, unless the land-use is far removed from the historical experience. For example, Tilman (1993) found that contrary to predictions, an increase in the spatial heterogeneity of nitrogen supply decreased species richness, probably because species that do well under fertile conditions were rare on the infertile soils of the study area.

The accumulation of biomass and litter with low disturbance and the recovery of vegetation cover after high soil disturbance, was faster on the fertilized plots than on the unfertilized plots. Thus, species loss with fertilization is likely to be greater under low disturbance conditions due to rapid growth of dominant species. Meanwhile, the slow recovery of biomass on infertile sites after severe soil disturbance increases the risk of erosion. Susceptibility of an area to rapid invasion by exotics, after severe soil disturbance, is likely to be greater on nutrient-rich sites and therefore these sites require a speedy response to minimise the impact of disturbance (and exotics) on native species by land managers involved in conservation. Burke and Grime (1996) also concluded that attempts to predict invasion by species should take site productivity into account as well as disturbance regime.

## 7.2 Plant Attributes

The untreated vegetation of the study site was described in terms of the presence of particular plant attributes (Section 3.4). The predominant plant attributes of the species were a reflection of (i) the vegetation type, (ii) the grazing history, (iii) the natural infertility, (iv) the climate of the site and (v) the immigration of exotic species. Plant size and the size of photosynthetic and reproductive structures are generally positively correlated (Raunkiaer 1934; Baker 1972). Therefore, the prevalence of species with relatively small leaves and seeds found here reflects the predominance of the herbaceous habit and the absence of shrubs and trees. The tendency for species to be wider than taller may be a constraint of the herbaceous habit because herbaceous plants lack structural support provided by wood. The predominance of species with spike-like inflorescences suggests that species with tall, narrow inflorescences may be favoured in relatively short vegetation such as grassland, perhaps by enhancing pollination and seed dispersal.

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). The change in the fire regime from irregular burning in summer by aborigines to periodic (often annual) late-winter burning by pastoralists (Norton 1971), meant the timing of the opening of vegetation was no longer suited to the establishment of summer annuals, but favoured cool-season annuals. As a result, most exotic annuals and the three native annual grasses presently at Newholme were adapted to spring growth, i.e. cool-season (Section 3.4.1a). 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). The recent exclusion of fire from the site probably did not change the timing of the opening of the vegetation because the seasonal climate means that the vegetation is open in spring as a result of frosts and winter dormancy. But exclusion of fire may have limited the annuals present at the site today to those which regenerate through seasonal regeneration, and excluded those annuals regenerating by a persistent seed bank which responds to fire (Section 4.4.2). Thus, the seed bank and germination traits of the species at the study site play an important role in determining vegetation pattern (Section 2.4 & Section 4.4.2). The paucity of information about the germination characteristics of the species in the present study requires attention if the dynamics are going to be better understood.

The introduction of grazing and regular burning on the Northern Tablelands in the nineteenth century had a significant impact on vegetation composition (Whalley *et al.* 1978). The resident species possibly survived regular burning by protecting their renewal buds in the soil surface (i.e. hemicryptophyte habit), from which the plants sprouted after fire (Section 3.4.1a). For species with underground storage organs, the prevalence of rhizomes reflects the long history (130 years) of sheep and cattle grazing at the site because rhizomes protect the plant's meristems and reduce the chance of close defoliation (Section 3.4.1d). Hemicryptophytes (i.e. renewal buds situated in soil surface) may also be common at Newholme because the protection of their buds in the soil or litter during the cold winter increases their survival, while 'pure' chamaephytes (i.e. renewal buds borne on shoots very close to ground) are uncommon because their buds remain unprotected from frosts (Section 3.4.1a). Field observations also suggested that the hemicryptophyte habit may protect the buds of *Hypericum gramineum, Wahlenbergia planiflora* and *Haloragis heterophylla* from desiccation at times of severe water stress.

Most of the species were perennial, consistent with infertile habitats being dominated by perennial rather than annual species (Grime & Hunt 1975). Maximum seedling growth rates of species (Section 3.4.2) were low in comparison to those of other habitats (cf. Grime & Hunt 1975), consistent with species of unproductive habitats having slow maximum potential growth rates (Grime 1979). The herring-bone root systems of some of the common perennial species (e.g. *Hypochaeris radicata, Aristida ramosa* and *Sporobolus creber*) reflects the low fertility and moisture availability of the study site. Herring-bone root systems are favoured on dry or nutrient-poor soils because they explore and exploit the soil most efficiently (Fitter 1987). The greater root number in the deeper soil layers of some of the common perennial species (e.g. *A.ramosa, Acetosella vulgaris* and *H.radicata*) reflects their ability to access subsoil water when rainfall is low.

### 7.2.1 Relationships Between Plant Attributes and Soil Disturbance and Fertilization

Fertilization probably favoured some annual species because they tend to lack underground storage organs and only have a short time available to accumulate resources necessary for reproduction (Section 4.2.2). The resident annual and perennial species were unresponsive to soil disturbance probably because the timing of the disturbance killed recently germinated seedlings of the annual species. The forbs tended to be low-growing or of small width and were susceptible to the low light conditions associated with the fertilized plots (Section 4.2.3). 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. 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. In contrast, the exotic grasses were adapted to both soil disturbance and fertilization. The sedges and rushes tended to be slow-growing with fibrous long-lived leaves, so the cost of leaf-replacement after disturbance would be high and their rate of recovery would be slow, making them particularly susceptible to severe soil disturbance.

Rosette or semi-rosette species may be able to tolerate soil disturbance because they also possessed stem-tubers or taproots which anchored them and enabled them to regenerate after the loss of photosynthetic tissues (Section 4.4.20). Alternatively, the rosette habit enables efficient light interception and space pre-emption on the open ground of disturbed habitats (McIntyre *et al.* 1995). The rosette/semi-rosette habit was not favoured by fertilization because low leaf height would be a disadvantage in low light conditions. Thus there was no evidence to suggest that underground storage organs function to sustain rosette/semi-rosette species during prolonged periods of low light. The susceptibility of tussock or tufted species to soil disturbance in unfertilized plots may be due to poor anchorage and a limited ability to recover from damage when nutrient levels are low because they also lacked underground storage organs. Tussock/tuft species were favoured in high biomass conditions of nutrient-rich plots possibly because their erect linear leaves achieve the greatest height advantage for a given amount of biomass, enabling greater access to light. Some erect/branching species were favoured in fertilized, low and moderately disturbed plots possibly because their elevated, dispersed growing points and an ability to expand vegetatively (i.e. rhizomes) enable them to successfully forage for light in nutrient-rich habitats.

Hemicryptophytes were intolerant of fertilization possibly because their growing-points are located at ground level and therefore adjustment of the leaf canopy in response to changing light conditions may be inflexible or costly (Section 4.4.4). The ability of amphiphytes to not only tolerate high soil disturbance, but dominate space, was probably due to their possession of rhizomes. The presence of perennating buds both above and in the soil surface, together with the possession of rhizomes, enabled the amphiphytes to forage for light and dominate space in nutrient-rich environments. The geophytes locate their perennating buds at depth underground in the form of stem tubers, which provides protection and non-photosynthetic resources to recover from moderate soil disturbance. However, severe soil disturbance may bury their stem tubers at an inappropriate depth; too deep and their stored resources may be exhausted before the shoots reach the surface, while shallow burial could lead to desiccation. Most of the geophytes had a rosette/semi rosette habit and thus they are susceptible to shading if litter accumulation is high.

Species with soft leaves were favoured in severely disturbed plots because a low investment in structural compounds means that leaves can be produced rapidly to pre-empt available space, while the cost of a disturbance event is minimised because soft leaves are inexpensive to replace. The risk of nutrient loss during nutrient cycling is greater in species with soft leaves than in species with fibrous leaves (Section 4.4.6). Thus, species with soft leaves may dominate fertilized, low and moderately disturbed plots because a high risk of nutrient loss may be affordable in nutrient-rich habitats. Inexpensive, short-lived leaves may also enable the plants of the fertilized, low and moderately disturbed plots to re-adjust their leaf canopy in response to the changing light conditions associated with the accumulation of biomass on these plots. In contrast, species with long-lived, fibrous leaves that accumulate deep litter were not favoured in disturbed and fertilized habitats because leaf replacement after disturbance would be expensive and slow leaf turnover makes these species poor competitors (Section 4.4.7). Species with long-lived leaves were favoured under nutrient-poor, low disturbance conditions (Section 4.4.12) 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 suggest that some species without underground storage organs rely on high soil nutrients to recover from mechanical damage, or germinate and colonize, after soil disturbance (Section 4.4.8). Species with short rhizomes were unable to tolerate mechanical soil disturbance, but they enabled some species to dominate the low disturbance, nutrient-rich plots by actively foraging for nutrients and light. Long rhizomes also enabled some species to dominate space in nutrient-rich habitats. However, there was little evidence to suggest that rhizomes enabled species to resist uprooting, recover from mechanical damage using stored resources or pre-empt available space created by soil disturbance. Stolons may be favoured over species with rhizomes in severely disturbed habitats 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. Taproots enabled some species to resist uprooting, recover from damage using stored resources and pre-empt the available space. Species with taproots were not favoured by fertilization probably because common species with taproots were also low growing forbs and were susceptible to shading under fertilized conditions.

### 7.2.2 Utility of the C-S-R Model

The results supported two of the six predictions that test the underlying hypotheses (Table 5.5A) of the C-S-R model proposed by Grime (1979). Maximum relative growth rate (Rmax) of each species was positively correlated with its abundance in disturbed plots and negatively correlated with abundance in low disturbance plots. Species with high Rmax were favoured in severely soil disturbed plots because they can rapidly pre-empt available space or complete their life cycle before the next disturbance. Species with low Rmax were not favoured in severely disturbed plots because their recovery after disturbance is slow and their leaf tissue is expensive to replace because they are high in structural and defence compounds (Section 5.4).

The results were inconsistent with the two predictions that the Rmax of each species is positively correlated with its abundance in fertilized plots and negatively correlated with abundance in unfertilized plots (Table 5.5A). The relationship between Rmax and fertilization depended on the level of soil disturbance. The Rmax of each species was positively correlated with its abundance in fertilized plots, only in combination with high soil disturbance. Species with high growth rates were dominant in fertilized highly disturbed plots, but coexisted with species with low growth rates in fertilized, low and moderately disturbed plots. Rmax was negatively correlated with abundance in unfertilized plots, only in combination with low and moderate soil disturbance. Species with low growth rates were favoured in nutrient-poor low and moderately disturbed plots because they use resources conservatively, but were not favoured in highly disturbed plots because the replacement cost of their leaves is high. Species with low Rmax were more common than species with high Rmax in unfertilized, moderately disturbed plots (in summer) and species with high Rmax were more common than species with low Rmax in unfertilized, highly disturbed plots. Thus species with low growth rates and a conservative use of nutrients could tolerate the small leaf replacement cost associated with moderate soil disturbance. Species of highly disturbed habitats were capable of high growth rates even when nutrients are limited because they avoid stress by having a short life cycle or investing in below-ground storage organs.

The results did not support the two remaining predictions that the Morphology Index (MI) of each species is positively correlated with its abundance in fertilized, low disturbance plots and negatively correlated with abundance in unfertilized and disturbed plots (Table 5.5A). In summer, dominance in the low and moderately disturbed, unfertilized plots was achieved by species of large height or width rather than by numerous individuals of species of small stature. However, in spring, species with low and high MI coexisted. The temporal microhabitat created by the delayed growth of the summer growing species enabled the spring growing species to succeed, despite their low MI values. C-S-R theory proposes that species competitive ability varies predictably with disturbance and productivity. Although the Morphology Index reflects the maximum size attained by a plant under favourable conditions (Grime 1979), the results here suggest that it does not reflect the competitive ability of a species (Section 5.4).

Most of the species at Newholme were designated as stress-tolerant competitors (SC) by the dichotomous key (Fig. 5.1) of Grime *et al.* (1988), followed by stress-tolerators (S), CSR strategists, competitive-ruderal/ruderals (CR/R), stress-tolerant ruderals (SR), competitors (C) and competitive ruderals (CR). The dominant species were designated as SC species, all of the S species were subordinate and most of the annuals were CR/R species (Section 5.4). The results supported four of the seven predictions (Table 5.5A) based on the dichotomous key which classifies herbaceous species with respect to C-S-R strategy. In agreement with the predictions, the number of S species decreased with fertilization, the number of CR/R species increased with soil disturbance and fertilization, and the number of SC species decreased with soil disturbance. Stress-tolerators decrease with fertilization because they are overgrown by competitors in nutrient-rich habitats (Grime 1979). The results did not support the prediction that the number of S and C species would decrease with soil disturbance. The results were inconsistent with the prediction that the number of C species would increase with fertilization: the prediction was only upheld in the sown plots.

The results suggest that keys such as that developed by Grime *et al.* (1988) may, with modification, be suitable for flora in locations other than Sheffield. It was expected that the predominant species of the infertile study site would be stress-tolerators (S), but the tall stature of the dominant Newholme species meant they were designated as stress-tolerant competitors. The stress-tolerant strategy may need to include species of large and small stature or a separate strategy created. Alternatively, height may be better replaced with biomass or foliage density because the dominant species, although of large stature, had sparse foliage. The species were designated as S species on the basis of being perennial, but would have been better designated as stress-tolerant ruderal (SR) because they were not diminished by soil disturbance (Section 5.4). Thus the SR strategy may need to include perennial species other than vernal geophytes. The quantities used here to define the terms in the key (e.g. 'slow', 'fast', 'small' and 'tall') were based on the Newholme species and therefore were characteristic of infertile, moderately grazed grassland (Section 4.2). If future definitions of the key are based on species from a wider range of habitats, the fit between the predicted and the actual response of the C-S-R strategies may be improved.

Compared to the mean Rmax and mean MI of the vegetation samples from Sheffield (Grime 1979), most of the vegetation samples at Newholme had low Rmax and moderate MI values (Section 5.4). For this reason the results did not support any of the five predictions testing the ordination of vegetation samples by the mean Rmax and mean MI of its component species (Table 5.5C). Most of the vegetation samples were ordinated in the area predicted by the model to be intermediate between stress-tolerant competitors (SC) and CSR strategists.

Comparison of the ordination of Newholme vegetation samples relative to each other, revealed that the low disturbance, unfertilized plots had the lowest mean Rmax and the highest MI values. These results are consistent with Kautsky's (1988) biomass-storer strategy which had large spread and slow growth rates and was associated with habitats of low disturbance and high stress. The C-S-R model (Grime 1979) does not propose a plant strategy for highly disturbed, unproductive habitats, but the results here show that samples from the highly soil disturbed, unfertilized plots had higher mean Rmax and lower mean MI values than samples from the control (i.e. low disturbance, unfertilized) plots. Thus, species of highly disturbed nutrient-poor habitats had reduced stature and spread, and a greater capacity to recover from soil disturbance or complete their life cycle rapidly.

Grime (1974) suggested that to derive a practical method of ordination for the triangular model, the minimum requirement would be to find measurable plant attributes which vary in accordance with any two of the three sets of contours of the relative importance of competition, stress and disturbance. Plant attributes other than maximum relative growth rate and the Morphology Index may be more useful to the model (Section 5.4). Lambers and Poorter (1992) believed that one of the components of relative growth rate (i.e. leaf area ratio or net assimilation rate) is the target of selection rather than relative growth rate itself. Attributes such as leaf area ratio, plant defence, longevity of plant parts or withdrawal of nutrients from senescent plant parts may be more useful than relative growth rate. The Morphology Index (MI) was often responsible for inconsistencies between the results and the model. Contrary to model predictions, the slow growing perennials which dominated the unfertilized plots were large in size, while small fast growing annuals dominated the fertilized plots. Species of nutrient-poor environments can afford to invest in large size (height and width) if they minimise the long-term cost with sparse, long-lived foliage that is unpalatable to herbivores (e.g. *Aristida ramosa*). Measures such as leaf longevity, above-ground biomass (Shipley *et al.* 1989) or the amount of shade cast (Díaz *et al.* 1991), which have been suggested to reflect competitive ability, may improve the Morphology Index.

The vegetation samples had higher mean Rmax and slightly lower mean Morphology Index values in spring than in summer. Thus, the ordination of the vegetation samples changed seasonally because spring-growing species were more ruderal than the summer-growing species. Although Grime (1988) acknowledged that the prevalence of C-S-R strategies may change according to season, this has not been formally included into the C-S-R model. Since the influence of season on the plant strategies is potentially large, the model would be improved if seasonal changes could be incorporated. Although plant strategy theory (Grime 1979) does not predict that stress-tolerant (S) and ruderal (R) species cannot coexist in the same habitat, the way in which the model is represented does not allow the strategies that can coexist in the same habitat to be predicted. The unexploited resource which enabled S and CR/R species in this study to coexist appeared to be the spatially discontinuous gaps associated with the seasonal climate (Section 5.4). Further study is needed to determine whether ruderal species can be divided into those that regenerate through seasonally predictable climatic disturbances (e.g. the phenological niche associated with seasonal environmental factors) and those that regenerate through more infrequent physical disturbance.

In conclusion, the greatest support for the C-S-R model was found using the key (4 predictions upheld, 1 inconsistent and 2 rejected). Support for the model was also found by testing its underlying hypotheses (2 predictions upheld, 2 inconsistent and 2 rejected), while the ordination of vegetation samples by the mean Rmax and MI of its component species was unsuccessful (0 predictions upheld, 2 inconsistent and 3 rejected).

### 7.2.3 Utility of the Plant Attribute Approach

Group membership in a variety of habitats (differing in the level of soil disturbance and fertilization) was successfully predicted using the relative cover of plant species and also using the relative cover of species with particular plant attributes (Section 6.4). Plant attributes were slightly better than plant species in predicting group membership of different treatments. The regenerative plant attributes did not predict treatment group membership as well as the established phase attributes. However, separate analysis of the regenerative attributes showed relationships obscured by the established phase attributes when they were analysed together. These relationships, although less powerful by themselves, may be of practical use when used in combination with the established phase attributes because the suite of attributes important for regeneration may be independent of the suite of attributes important for persistence at a site. Of the few studies that have examined relationships between a number of plant attributes and environmental influences (including the present study), most have found that attributes related to species persistence are important. Further, the established phase attributes that were strongly related to fertilization and soil disturbance in this study, were typically associated with conservative versus liberal use of resources (e.g. leaf texture, litter depth, height, Raunkiaer life form, life cycle and length of flowering period). The regenerative attributes most strongly related to soil disturbance and fertilization were underground storage organs, diaspore mass, diaspore number and diaspore dispersal appendages.

Four groups of species were distinguished, three of which had distinctive plant attributes associated with the degree of persistence, and the investment and use of resources (Fig. 6.5). Three of the four groups also correspond to permutations of r-selected and K-selected adult and juvenile attributes. This is consistent with Grime's (1979) suggestion that uncoupling the juvenile and adult phases of the life-cycle may resolve inconsistencies apparent when the suite of characters attributed to r and K organisms are applied. In environments where large gaps and nutrients were limited (unfertilized, low and moderately disturbed plots), K-selected juvenile attributes (large diaspores) enabled regeneration in the presence of vegetation cover and K-selected adult attributes (tall stature, fibrous leaves and deep litter) enabled persistence and a conservative use of resources. In environments where large gaps were present but nutrients were low (unfertilized, highly disturbed plots), r-selected juvenile attributes (numerous small diaspores) enabled gaps to be reached (spatial or temporal dispersal), while K-selected adult attributes (perennial and taproot) enabled persistence and conservative use of resources. In environments where large gaps were present and nutrients were high (fertilized, highly disturbed plots), r-selected juvenile attributes (numerous small diaspores) may have enabled gaps to be reached, while r-selected adult attributes (annual, soft leaves, no storage organs and short stature) may have enabled rapid completion of life cycle before the vegetation cover re-established or disturbance reoccurred. Disturbance tends to favour short-lived species when fertility is high and long-lived species when fertility is low. Thus, annuals may require a certain level of nutrients before they can take advantage of disturbed habitats. Alternatively, rapid completion of life cycle is less advantageous in nutrient-poor, highly disturbed sites because the re-establishment of vegetation on these sites is slow.

On the fertilized, low and moderately disturbed plots, the plant species possessed attributes related to varying strategies of investment in persistence, below-ground storage organs, above-ground biomass and reproduction. The range of strategies included annuals with high investment in reproduction, perennials with investment in above-ground biomass and perennials with investment in below-ground organs (Section 6.4). Overlying the relationships described for the four groups, was the influence of a phenological niche (*sensu* Grubb 1986) where the seasonal opening in vegetation cover allowed species with seasonal regeneration attributes (i.e. the winter annuals) to coexist with perennial plants. If the study had continued, the phenological niche may have been over-ridden by the effects of fertilization as the perennials reached a biomass that inhibited the germination of annuals.

In summary, a conservative use of resources over a long period favours survival in nutrient-poor environments subject to low and moderate levels of soil disturbance. Storage of resources in an underground organ which is also resistant to soil disturbance (e.g. taproot), over a long period, favours survival in nutrient-poor, highly disturbed environments. A liberal use of resources over a short period, to produce a large number of small diaspores, favours survival in nutrient-rich environments subject to high levels of soil disturbance.

Keddy (1989) believed that plant ecologists over-emphasise consumptive competition of resources and that resource conservation might be an overlooked aspect of plant competition in low nutrient conditions. The results here confirm that resource conservation is an important mechanism involved in vegetation pattern and response. The results are also consistent with there being a trade-off between features that are favourable in nutrient-rich habitats and those favourable in nutrient-poor habitats (Grime 1979; Berendse & Elberse 1989; Lambers & Poorter 1992; Thompson *et al.* 1996). One such trade-off may be between growth rate and nutrient loss. High investment in leaf area and photosynthetic apparatus, rather than in structural and defence compounds, leads to higher growth rates but has negative consequences for the nutrient economy of the plant through high nutrient loss. This nutrient loss is due to higher rates of herbivory and a reduction in nutrient re-cycling because of rapid leaf senescence and decomposition (Chapin 1980). On the other hand, plant features that diminish nutrient loss (e.g. long-lived, well-defended leaves) and contribute to a plant's success in nutrient-limited habitats, may lead to low growth rates.

Variation in plant attributes between species is associated both with phylogeny (e.g. family membership) and with ecology (Leishman *et al.* 1995). For example, in this study most grasses had linear leaves (Section 3.4.1c) and were favoured under conditions of low or moderate soil disturbance (Section 4.2.3). The question is whether this relationship is due to linear leaves being an advantage under low light conditions (Section 4.4.21) or due to the evolution of grasses being constrained by their genetic inheritance of linear leaves. Leishman *et al.* (1995) believe that the wide divergence found for seed mass within lineages refutes the hypothesis that the genetic inheritance of smaller-seeded taxa constrains the evolution of larger seeds. Rather, Leishman *et al.* (1995) believe that lineages have particular constellations of attributes which are successful in particular niches and thus their descendants continue to have the same attributes and occupy the same niches (i.e. phylogenetic niche conservatism). If phylogenetic constraint had an over-riding influence on the relationship between plant attributes and the environment, then we would expect that taxonomically defined attributes such as 'grass' or 'sedge/rush' would have had the highest loadings in the direct discriminant function analysis (Section 6.3.2). This was not the case. However it is acknowledged that when the plant attributes were ordinated by the fertilization and soil disturbance treatments (Section 6.3.2), phylogeny may have contributed to the patterns being less clear.

### 7.2.4 Relevance to Management and Conservation

The potential of the plant attribute approach for management and conservation has been proposed by a number of investigators (Grime *et al.* 1988; Hodgson 1986; Wisheu & Keddy 1994; Trémont & McIntyre 1994). However, this potential has only been demonstrated by a small number of studies. Using plant attributes, Gomez Sal *et al.* (1986) demonstrated that the traditional practice of intermittent shift ploughing, to increase the area available to livestock in semi-natural Mediterranean pasture, was not justified because it actually decreased the biomass of the most palatable species. Hodgson (1990) used plant attributes and C-S-R strategies to examine why some species used in habitat reconstruction succeeded or failed in establishing from seed or transplantation. Hodgson (1986) found that in Central England, the greater levels of fertility and disturbance associated with modern land use is resulting in the replacement of communities of stress-tolerant species by those with competitive or ruderal strategies. The present study suggests that managing the site for animal production (i.e. fertilization and the sowing of pasture species) would push the plant community further towards the competitive corner of Grime's C-S-R model (Section 5.3.3b), which would have the effect of decreasing species richness.

#### *Exotic Species*

For the plant attribute approach to be successfully used for management, the attributes must be selected to specifically address management problems. Species origin is an attribute relevant to vegetation management because the control of exotic species and enhancement of native species is often a conservation or management goal. The response of the relative cover of exotic and native species to fertilization in this study depended on the level of soil disturbance (Section 4.4.1). Fertilization increased the cover of exotics and decreased the cover of natives in low and moderately disturbed plots, but had no effect in highly disturbed plots. 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*) were not favoured by fertilization. Fertilization should be avoided if the conservation of native species on nutrient-poor sites is a management goal. 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. The increase in exotic cover with increasing soil disturbance supports the hypothesis by Fox and Fox (1986) that the degree of invasion and the degree of disturbance is related. Severe soil disturbance promotes exotic species, regardless of the level of fertility of the site. The paucity of native species under highly disturbed conditions was due to their intolerance of severe soil disturbance rather than competition from the exotic species which were favoured by disturbed conditions. Thus, where the severity of soil disturbance is high, exotic species probably have little influence on native species richness.

### *Species Coexistence*

Grubb (1977) reviewed the mechanisms that may contribute to the maintenance of species richness in plant communities. He proposed four kinds of niche differentiation: habitat niche, phenological niche, regeneration niche and life form niche. The habitat niche was demonstrated in this study by the differential response of the species to fertilization and soil disturbance (Section 2.4). There also appeared to be a phenological separation between some of the species in this study. That is, species coexisting as a result of capturing light, water and mineral nutrients at different times of the year (Section 6.4). The study also suggests that the interplay of rainfall, disturbance regime and the regeneration niche gives species the opportunity to enter into the matrix of established stress tolerators, competitors and ruderals (Section 2.4). Differences in life form amongst the herbaceous species at the site was also seen, for example low growing forbs coexisting with tall grasses (Section 3.4.1). The results here suggest that if there is a difference between the way in which groups of species use their resources. That is, two species may coexist as a result of using light, water and mineral nutrients in different ways (Section 6.4): a conservative use of resources (slow growth, storage and long-lived structures) versus an exploitative use of resources (rapid growth and short-lived structures). Thus, the life form niche recognised by Grubb (1977) could be expanded to include plant 'function' as well as 'form'. Alternatively, a fifth niche could be recognised as the 'resource niche' or 'function niche'.

## 7.3 Limitations of the Present Study

The results were limited by the range of attributes encountered in the Newholme species which was presumably a consequence of the history of the site. On a community scale, the influence of historical factors on vegetation response was not removed by the plant attribute approach, although it was somewhat reduced. Thus, the relationships found using the plant attribute approach were of intermediate generality and are applicable to sites with a similar history (i.e. low fertility, moderately grazed temperate grassland subject to recent fertilization and severe mechanical soil disturbance).

The study was also limited by the nature of the rainfall during the study period. The response of the plant community to fertilization and soil disturbance would have been influenced by the low rainfall during the study period. Species response, especially that of the sown species, may have been quite different had the study occurred during a wet period. For example, a greater response of "competitors" to fertilization and regeneration from the seed bank may have been observed. Limitations due to inter-annual variability of climate may only be overcome by doing longer-term studies.

The results suggested that the response of some species to fertilization and soil disturbance may be transitory, especially the response to fertilization (Section 2.4). Thus, the interpretation of results would have been improved if the study was longer-term (say five years) because transient features and the long-term establishment of the sown species would have been revealed. Belsky (1992) suggested that even three years may be inadequate for all species in perennial herbaceous communities to respond to the manipulation of disturbance.

The present study illustrated how caution must be observed in attributing adaptive significance to plant attributes. Some plant attributes may not be adaptive, but may be correlated with another attribute that is. For example, the response of species with capitulum inflorescences to soil disturbance and fertilization was more likely a consequence of characteristics associated with being exotic or belonging to the Asteraceae, rather than any direct advantage of possessing or not possessing capitulum inflorescences (Section 4.4.22). Correlations among attributes may be an advantage in some cases because attributes which are time consuming to measure may be replaced with simpler measures. For example, maximum seedling relative growth rate, measured in the glasshouse, was correlated with adult leaf life span, measured in the field (Section 3.3.3). Thus a considerable time saving could have been achieved if leaf life span was substituted for maximum relative growth rate. Considering the difficulty in obtaining below-ground information about plants, correlations established among below-ground and above-ground attributes would be particularly useful.

There was some overlap between the categories of some of the plant attributes due to an overlap in definitions (e.g. Raunkiaer life form and underground storage organs) (Section 3.4.1a). Some attributes were related to each other as a result of the physical constraints of the plant and the environment (e.g. commencement of flowering and flowering period duration).

Species which begin flowering late in the season had fewer months available to them for flowering, compared to species which begin flowering early (Section 3.4.1b). It is advisable to have no more than four categories within each plant attribute for community studies, otherwise small sample sizes may necessitate combining categories in ways later revealed to be unsuitable (e.g. erect with branching and prostrate with twining habits). Plant attributes which were not predictably related to soil disturbance or fertilization in this study, such as stem structure and leaf shape (Section 4.4.19 and 4.4.20), may be useful in other vegetation types, at larger scales, or in response to other environmental variables. This is because the history of a site limits the range of attributes encountered, and for some attributes there is a predominance of species in one particular category that lessens its discriminatory power.

Although soil disturbance and fertilization provided a wide range of habitats to test Grime's (1979) C-S-R model, the relatively fine-grained scale of this study meant that the results did not completely fit the coarse-grained scale of the C-S-R model. This problem illustrates the difficulty of testing general models because of their large scale. Discrepancies with the predictions of the C-S-R model (Table 5.5) will occur (at least in the short term) when vegetation is subjected to a level of disturbance or fertility that is novel to that habitat because the availability of suitable species is limited by the local species pool which is pre-adapted to a different disturbance and fertility regime. For example, competitive species associated with productive, low disturbance habitats were lacking (Section 5.4) because a great deal of fertilizer would have to be applied for many years before the nutrient-poor Newholme soils could support Grime's competitive species. In cases where experimentation is chosen to test the C-S-R model, the introduction of propagules may have the potential to solve the problem of the pre-adaptation of the local species pool. The sown treatment provided species with higher growth rates than the resident species and was responsible for the relationship between Rmax and soil disturbance (Section 5.4). To ensure that all strategies are represented in the experiment, a large number of species with a wide range of plant strategies must be sown so that the establishment of a particular strategy is not reliant on a few species which may fail to establish. The experiment must be long-term to ensure that the pattern of occurrence of the sown species reflects successful establishment because the C-S-R model was developed for plants of the established phase.

The results also raised the question of whether the level of productivity in the fertilized plots was high enough to test the C-S-R model adequately. C-S-R theory (Grime 1979) bases its predictions on the relative importance of productivity, disturbance and competition. Perhaps the prevalence of species or vegetation types found in the middle of the triangular C-S-R model in British studies (Grime 1974; Grime *et al.* 1988; Hodgson 1990) is due to most of the natural habits examined so far being of moderate productivity and few of high productivity? Productivity in Sheffield may be limited by the seasonally cold climate. In this study, fertilization was used to achieve 'high productivity', but moisture stress and the seasonally cold climate at Newholme may have limited productivity in the fertilized plots to a moderate level. Perhaps high productivity environments only exist in naturally fertile or fertilized sites in humid tropical climates? For the C-S-R model to be tested adequately, it must be tested at a scale equivalent to the one for which it was intended. This means that experiments need to be longer-term or comparisons made among sites where the current conditions have existed for a long period. Further, a wide range of sites where radiation, temperature and nutrient and water supply are not constrained are needed.

In conclusion, the plant attribute approach is worthy of further study because:-

i) Plant attributes can discriminate between habitats as well as, or better than, floristic data.
ii) The responses identified may be applicable to sites with a different species composition, but with a similar fertilizer and disturbance history.
iii) Insights into the possible mechanisms influencing vegetation pattern were provided by the plant attribute approach and areas worthy of more detailed study were revealed. As there is a natural tendency to explain species response in terms of the attributes possessed by a plant (Section 2.4), measuring them objectively can only enhance interpretation.
iv) Since herbaceous plant communities generally include a large number of sparse species, the plant attribute approach enables them to be included in analyses (Section 2.4) because of the increase in sample size.
v) The plant attribute approach complements the species-based approach, it does not necessarily have to replace it (Díaz *et al.* 1992).

Some of the limitations of using plants attributes were:-

i) Many plant attributes were inter-correlated, therefore a large number of them should be examined simultaneously and the correlations among them examined.
ii) The mechanism responsible for the response of a species with a particular plant attribute may be due to an entirely different (but correlated) plant attribute, which may or may not have been examined.
iii) For a small number of attributes, the response of species possessing these attributes was complex and difficult to interpret, possibly as a result of not being directly related to the environment.

## 7.4 Approach for Further Study

Factors such as disturbance and fertility should not be examined in isolation because interaction between them is common (Section 2.4). Grubb (1985) suggested that although it is inevitable to emphasise single environmental factors when working out the key characters of plants growing in various conditions, these factors often do not act independently. Thus, where generalisations are made in relation to disturbance for management purposes it must be remembered that disturbance interacts with other factors to generate exceptions.

Further study is required to find plant attributes most useful for the prediction of vegetation pattern and response and to find different ways of measuring attributes, particularly underground plant features. The results support the view that the best approach for studying plant attributes is to screen a large number of species for a number of traits simultaneously (Grime *et al.* 1993; Keddy 1992) because of the numerous correlations among plant traits. Depending on the purpose of the study, plant attributes should be chosen by either selecting a wide range of attributes or selecting attributes relevant to management purposes (as encouraged by Friedel *et al.* 1988). There is a need for studies which demonstrate the usefulness of the plant attribute approach for management purposes. As more studies are carried out over time, it will become clearer which plant attributes are redundant. For attributes known to be correlated with each other, the one more easily measured or recognisable in the field should be chosen (Friedel *et al.* 1988). Grime *et al.* (1993) advocated replacing data collected from the field with more objective data gained under standard glasshouse conditions. However, there was no evidence here to suggest that attributes measured under standardized glasshouse conditions were better predictors of habitat than those measured in the field.

As Keddy (1989) suggested, the chosen attributes should focus on resource conservation as well as resource competition and consumption. Attributes relating to plant persistence, biomass partitioning (leaves, reproduction, storage), conservative versus liberal use of resources, life span of individual plant organs, time available for reproduction and attributes suggestive of whether resource intake is coupled or uncoupled from growth may be particularly useful (Section 6.4). However, attributes relating to critical driving forces in the environment should not be ignored (e.g. fluctuating water levels, drought etc.). The morphological attributes in this study were more strongly related to the environment if they had a physiological basis (e.g. litter depth). Evidence suggesting whether species of fertile, low disturbance habitats can be successfully linked to a particular suite of plant attributes in the longer-term or whether they remain highly variable, as found here (Section 6.4), is needed.

Day *et al.* (1988) believed that there is a need for summary models which lie between catalogues of site-specific vegetation response and broad general models that might not apply to specific communities or at small scales. They suggested that different viewpoints along this continuum may reveal principles that would be missed by insisting upon either specific detail or broad generality alone. This study provided a summary model for a low fertility, moderately grazed, temperate grassland (Fig. 6.5) and showed how models may be viewed as a starting point for research and refinement rather than something that must be either wholly accepted or rejected. Much can be learnt through the process of model refinement, which involves cycles of testing by experimentation or monitoring, refinement and further testing (Grime *et al.* 1988).