AN INVESTIGATION OF THE INFLUENCE OF DROUGHT AND OTHER SOIL FACTORS ON THE STRUCTURE OF A CALCAREOUS GRASSLAND

by

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To my mother and in memory of my father

بسم الله الرحمن الرحيم

وترى الارض هامدة فاذا انزلنا عليها الماء اهتزت وربت
وانبتت من كل زوج بهيج

قرآن كريم

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SUMMARY

Previous experimental investigations (Grime & Curtis 1976; Hillier 1984), and long term climatic monitoring (Rorison *et al* 1986a,b) have revealed the frequent occurrence of drought during the summer period in calcareous grassland on the south-facing slopes of limestone dales in the Peak District of North Derbyshire, Northern England. The main objective of the studies in this thesis was to examine the role of drought as a determinant of the characteristics of one selected calcareous grassland system at Tongue End in Millersdale. Particular attention has been given to the interaction of drought with soil heterogeneity and mineral nutrient stress. Efforts have been made to differentiate between mechanisms of drought tolerance and drought avoidance, and this has allowed some assessment of the contribution of diversity in morphology, life history and physiology to the maintenance of species-richness in the vegetation at the site.

Three complementary methods of investigation were adopted; (1) analysis of spatial patterns by grid sampling of the field site. (2) comparative study of 17 component species in standardized environments. (3) synthesis of plant communities in turf microcosms simulating certain aspects of the Tongue End habitats. In the final chapter (Chapter 8) an attempt is made to integrate results from the observations and experiments described in previous chapters.

Evidence from the investigation suggests that on the south-facing slope at Tongue End, floristic diversity is maintained by naturally occurring phenomena, in which drought and low nutrient status interact with soil depth and rock exposure. These factors are responsible for high seedling mortality, gap creation and spatial heterogeneity. The hypothesis is formulated that (1) the species -rich community established on the south-facing slope at Tongue End contains an assemblage of plants most of which are attuned to both regular predictable disturbance and chronic nutrient-deficiency. (2) drought interacts with the mosaic in soil depth and rock exposure within the studied site; species with the potential to develop deep root-systems are locally prominent in circumstances where there is access to continuously moist subsoil.

ACKNOWLEDGEMENTS

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My many colleagues in the NERC Unit of Comparative Plant Ecology have contributed their skill, advice and encouragement in the course of work described in this thesis. I would like to thank all of them most warmly for their generous helps.

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CONTENTS

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Chapter 1

'General introduction'

1.1:

Calcareous grassland has been recognized as a resource of great ecological interest and value for nature conservation (Ratcliffe 1977). Variation in the floristic composition of calcareous grassland is often striking, with each geological formation or geographical area tending to have its own assemblage of characteristic plant species (Ratcliffe 1977). This can be illustrated by the fact that about 700 plant species, in Europe, including some 200 bryophytes and lichens, occur in this community. Roughly one third of this number is restricted to this habitat (Willems 1982).

Calcareous grassland comprises an intimate mixture of grasses, forbs, sedges, and mosses, which may exceed fifty species per metre square (Rorison 1990). It is well known that high species density (richness) is usually positively correlated with high genetic diversity within the constituent species (Duyvendax and Leusink 1979). On this assumption calcareous grassland can be considered a valuable genetic resource. Duyvendak, Leusink and Vos (1981) have advocated the preservation of species-rich grassland for modern agricultural plant breeding purposes.

In attempting to understand and retain this diversity, calcareous grasslands have long attracted the attention of scientists particularly plant community ecologists. The initial descriptive phase (e.g. Hope-Simpson 1938; and Tansley 1939), during which broad, distinctive features of calcareous grassland were recognized, has been followed by the application of plant physiology, soil science and climatology (Rorison 1990). Therefore these communities have regularly been the focus of a great variety of field observations and experimental investigations (e.g. Balme 1953; Watt 1962; wells 1971; Grubb 1976; Grime and Curtis 1976; Smith 1980; Sydes 1980; Hillier 1984; Grime, Shacklock and Band 1985; Rorison, Sutton, and Hunt 1986b; Mahdi and Law 1987). This has led to hypotheses which attempt to explain how plants of very different habit and growth potential can co-exist. Although the descriptive phase of our understanding of calcareous grassland is well advanced, we still know remarkably little about the functional aspects (Rorison 1990).

1.2: The reasons for high diversity:

Species-richness in calcareous grassland coincides with mineral nutrient stress (Rorison 1960; Park, Rawes & Allen 1962; Grime 1963a,b; Lloyd & Pigott 1967; Smith, Elston & Bunting 1971; Jeffrey 1971; Willis & Yemm 1961; Willis 1963; Grime & Curtis 1976) and with grazing (Wells 1971; Brown 1982), and often also with small-scale spatial and temporal variation in the turf environment (Grubb 1977; Sydes & Grime 1984; Silvertown 1983; Grime, Shacklock & Band 1985), Mycorrhizal connections between species (Grime *et al* 1987), and periodical summer drought (McClean 1935; Grime & Curtis 1976; Sydes 1980; Hillier 1984) are additional features of many of the more diverse calcareous grassland.

This thesis is mainly concerned with the contribution of drought to the processes controlling the structure, species composition and species-richness of calcareous grassland. Numerous studies have already implicated moisture stress in the evolution of species-rich calcareous vegetation. On global scales, Margalef (1968), Stebbins (1952, 1972), and Bartholomew, Eaton and Raven (1973) have recognized a linkage between aridity, calcicoly and speciation. According to these authors it would appear that the majority of calcicoles evolved in semi-arid conditions at lower latitudes. Here the effect of a low precipitation:evaporation ratio was to maintain a high base status at the soil surface and to create both a high degree of vegetation disturbance by drought and a general tendency for high rates of population turnover and accelerated speciation.

In the narrower context of the British Isles the phytosociological data of the National Vegetation Classification suggest that the incidence of moisture stress is an important determinant of the distribution of the species of calcareous grassland (Rodwell 1990). From 3500 samples of calcareous grasslands giving a good geographical coverage of the country (data from McVean & Ratcliffe 1962; Shimwell 1968; Wells 1975; Willems 1978; Birse 1980, 1984), 14 communities have been characterized. Variations in climate, particularly differences in precipitation and temperature, correspond closely with variations in the floristics of the communities. Rodwell (1990) suggested that climate controls plant distribution through both direct effects on the plants themselves and also through the process of soil development. Among these 14 communities some, e.g. *Festuca ovina-Avenula pratensis* and *Festuca-Thymus-Hieracium*, are widespread throughout the warm and dry south-east. Towards the north and west, these vegetation types become increasingly confined to south-facing slopes (Perring 1960; Rodwell 1990). These communities are always associated with shallow seasonally-droughted soils and their openness is due partly to extreme nutrient poverty and partly to some kind of disturbance; e.g. drought, frost-heaving, grazing (Lloyd 1964; Lloyd and Pigott 1967; Wells *et al* 1976; King 1977; Smith 1980; Hillier 1984).

The main objective in this thesis is, to examine the role of drought as a determinant of the characteristics of one selected calcareous grassland system in North Derbyshire (England). Particular attention has been given to the interaction of drought with mineral nutrient stress. Efforts have been made to differentiate between mechanisms of drought tolerance and drought avoidance, and this has allowed some assessment of the contributions of diversity in morphology, life-history and physiology to the maintenance of species-richness.

The reasons for selection of this site are first, it supports species-rich vegetation and has been the subject of numerous previous studies (Davison 1964; Grime & Curtis 1976; Thompson 1977; Thompson & Grime 1979; Hillier 1984) which yielded information relevant to this work. Second, experimental investigations (Grime & Curtis 1976; Hillier

1984), and long term climatic monitoring (Rorison *et al* 1986) have revealed the occurrence of drought in this site during the summer period. More detailed information about this site can be found in Chapter 2 (Field study).

1.3: drought tolerance and drought avoidance:

A wide range of morphological, physiological, and biochemical attributes influence the ability of plants to exploit droughted habitats. As a result, resistance to drought is difficult to define and to measure (Levitt 1980). According to plant strategy theory (Grime 1974, 1979), effects of water shortage can be classified into two catagories; (1) stress in which plant growth is restricted, (2) disturbance in which the plant is partially or totally killed. In this thesis different durations and intensities of drought are created and two important ecological criteria are measured; growth (biomass production), and survivorship. In an experiment which is discussed in Chapter 3, plants experienced long-term water-stress from an intermittent watering regime. The species are ranked on the basis of their ability to tolerate the induced water-stress. The criterion for ranking is the plant biomass production (growth) in the drought treatment, in comparison to control. In an other experiment (Chapter 6), the plants experienced a continuous drought period without any watering for three weeks. In this experiment, species were presented with opportunity to avoid the drought by penetrating deep, moist 'crevices'. Therefore in the context of the present study the two following criteria are used;

DROUGHT TOLERANCE:

The most commonly used measure of drought-tolerance has been biomass (yield) under conditions of drought. Tolerance is a combination of many things since biomass depends not only on the ability to survive the drought, but also on ability to grow, in comparison to control conditions.

DROUGHT AVOIDANCE:

In contrast to tolerance, drought avoidance is morphological-anatomical in nature. As these plants have a longer root system, they are able to penetrate deeper into the soil, therefore avoiding the drought.

It is difficult, if not impossible, to devise ways of distinguishing drought tolerance from avoidance under a single set of environmental conditions. In this study, biomass and survival are employed as criteria of tolerance and avoidance in the experiments described in Chapter 3 and 6 respectively. It must be stressed, however, that the reason for the use of these criteria are purely pragmatic; their use in this way does not imply that tolerance or avoidance can be defined in such terms.

1.4: Investigation methods:

Most investigations of floristic diversity have involved studies of natural vegetation but in practice, field observations and measurements can do no more than indicate possibilities (Ford 1990), since some potentially important factors are not amenable to precise field measurement or manipulation. Therefore this thesis adopts three complementary methods of investigation (Fig 1.1); (1) collection of data by field survey. (2) the comparative study in standardized environments of 17 species selected from the study site in a species-rich calcareous grassland at Tongue End, Millers Dale. (3) manipulation of soil fertility and water supply in a turf microcosm experiment. The turf microcosm experiment is an alternative research strategy introduced by Grime *et al* (1987). Here communities were allowed to develop in turf microcosms providing factorial combinations of soil heterogeneity, drought, and nutrient treatments, all of which are suspected to have a role in promoting diversity in this particular type of grassland.

In the first stage of the project, a field study was conducted to examine the spatial relationship of each individual species with other species and with edaphic factors. The drought tolerance of each species was measured experimentally in Chapter 3, and in Chapter 4 the interaction of drought and nutrient-stress was examined in

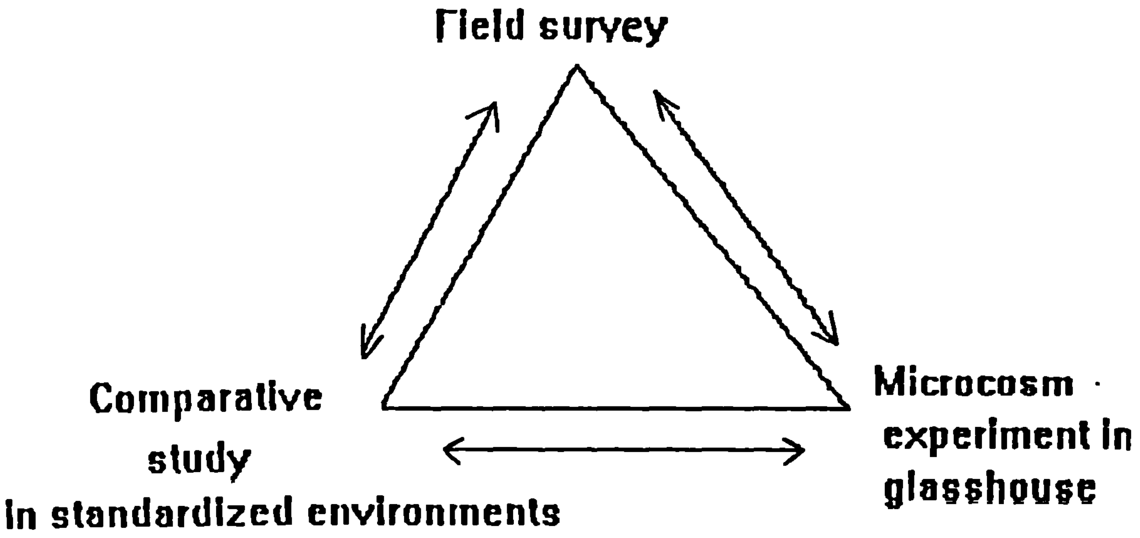

Figure 1.1: Complementary methods of investigation used in this thesis.

two contrasted species. In Chapter 5, the potential for drought avoidance was assessed in an experiment measuring the depth of root penetration in continuously moist and droughted conditions. The study reported in Chapter 6 is concerned with the survivorship and dominance of species in response to drought disturbance in connection with other nutritional and soil depth treatments, in communities which were allowed to develop in turf microcosms (the microcosm approach is fully discussed in the introduction to Chapter 6). In another microcosm experiment (Chap. 7), the effect of varying species composition on drought survivorship and dominance was studied. The final chapter (General Discussion) uses information from the whole project to draw some conclusions.

Chapter 2

'Analysis of spatial patterns in the field site'

2.1. INTRODUCTION:

Ashby (1948) was among the first to suggest that soil heterogeneity was a possible factor controlling local plant distribution and species diversity, but since then little experimental evidence has been published concerning the influence of this factor on the micro-distribution of species.

The probability has been recognized that species co-existence in some calcareous grasslands may be related to small-scale spatial variation in the turf environment (Grubb 1977; Grime 1978; Sydes & Grime 1984; Silvertown 1983). This phenomenon is particularly obvious on rock outcrops over fissured limestone; here it is not uncommon to find robust perennial herbs occurring above deep crevices in close proximity to succulents or small winter annuals situated on crusts of shallow organic soil (Grime 1990). It is the purpose of this field-study to examine the contribution of soil-heterogeneity, and in particular soil depth, to the pattern of vascular plant distribution within a calcareous grassland community.

2.2. SITE CHARACTERISTICS:

The site chosen for the investigation was an area of steeply-sloping south-facing grassland at Tongue End near Litton Mills in Millers Dale (Nat.Grid Ref. SK155732, altitude 213 m) on the Carboniferous Limestone in North

Derbyshire, England. Climatic data are not available for Millers Dale, but measurements made on north- and south-facing slopes over a period of years in neighbouring Lathkill Dale (Nat.Grid Ref. SK177656) (Rorison & Sutton 1975; Rorison *et al* 1986a,b) show the general pattern of weather which may be experienced by slopes of such different aspect in Derbyshire (Hillier 1984). As a result of a combination of the above general and particular causes, predicted annual mean inputs of total solar radiation to the north- and south-facing slopes, respectively, amount to 4.89 and 6.80 MJ m^{-2} d^{-1}. Overall the two slopes differ by 2.4°C in mean soil temperature and 2.9°C in mean air temperature. The largest differential between the two slopes is daily maximum summer temperature (6°C for soil, 7°C for air). In winter, no differential exceeds 2°C. Differences in temperature between slopes are less marked at night (<2°C) but may approach 11°C in air and 7°C in soil during the day. Annual variations between seasons occur in the temperature integral (maximum-minimum) for the south slope soil are almost three times those of the north slope air (Rorison *et al* 1986a,b). For other detailed information see Appendices 2.1.2-2.1.5.

Rainfall data collected at Chatsworth (12.9 km from Litton Mills) are included in Appendix2.1. Water stress, in general, is relatively infrequent in the Derbyshire climate (Rorison & Sutton 1975). On a local scale, however, severe water stress does occur in exposed places (Sydes 1980) (Appendix 2.1.1). Some physical and chemical characteristics of the soil at the experimental site are presented in Appendix 2.1.

Beside climatic conditions, a combination of other factors, such as steeper slope, thinner soil and more exposed bed rock (Plate 2.1) had led some investigators (Davison 1964; Grime & Curtis 1978; Hillier 1984) to recognize an important role for drought in structuring the vegetation on this particular south-facing slope.

2.3. MATERIALS & METHODS:

In August 1989, an area of 25 square metres (5m x 5m) was selected. This area was divided into twenty five, 1 m^2 plots. In each plot,four points were sampled (Figure 2.1). In total, 100 circular samples each of diameter 50 mm and evenly distributed on a grid were collected.

At each sample site, soil depth, pH, and angle of slope were measured. Living and dead plant material and top soil (0-3 cm) were collected. Collected materials were stored in a 5°C cold room. Living material of the vascular plants was separated into species, in the case of the bryophytes all living material regardless of species was separated as one component. Litter consisted of all above-ground dead plant materials. All separated living and dead plants were oven-dried at 80°C and then weighed. Soil pH was measured in each sample after adding sufficient deionized water to create a stiff paste.

DATA ANALYSIS:

Although today plant ecology has at last achieved a level of

Plates 2.1: (a) General view of the grassland at Tongue End, Millersdale
(b) A local area of turf within the sampled area.

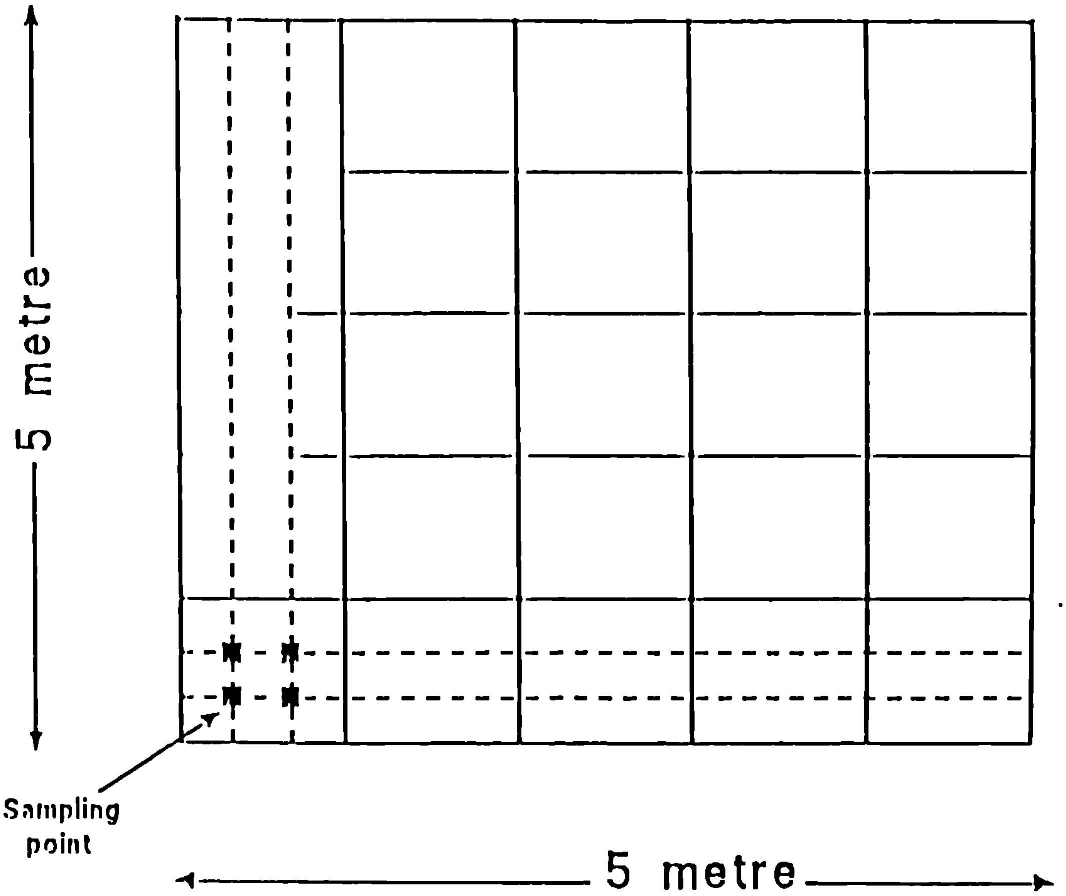

Figure 2.1: The distribution of samples within a 5m x 5m area of calcareous grassland at Tongue End Millersdale.

numerical sufficiency with DECORANA, TWINSPAN, etc. providing extremely powerful and effective methods of organizing large data sets (Kershaw & Looney 1985), we have to bear in mind that despite these methods, interpretation of the underlying vegetation mechanisms remains subjective. In order to assist pattern recognition and to aid interpretation, it was considered desirable to use several different methods of data analysis. Accordingly, Indicator Species Analysis (TWINSPAN) (Hill 1979a), Detrended Correspondence Analysis (DECORANA) (Hill 1979b), and Canonical Correspondence Analysis (CCA) (Ter Braak 1986) were employed to investigate the relationships between species and between individual species and particular environmental factors.

2.3. RESULTS:

2.3.1 Correlations between species distributions and site characteristics:

Soil depth, pH and slope measurements are shown in Figure 2.2. Eleven percent of the samples coincided with exposed rock. Soil depth ranged from 0-200 mm, with nearly 50% of the samples occupying areas with between 0 and 60 mm of soil (Figure 2.2). Lowest and highest pH values were 5.9 and 7.3 respectively. Sixty four percent of the soil samples occurred in the pH range 6.3-6.8. The mean angle of slope was 30^0 with variation over the range $0-40^0$.

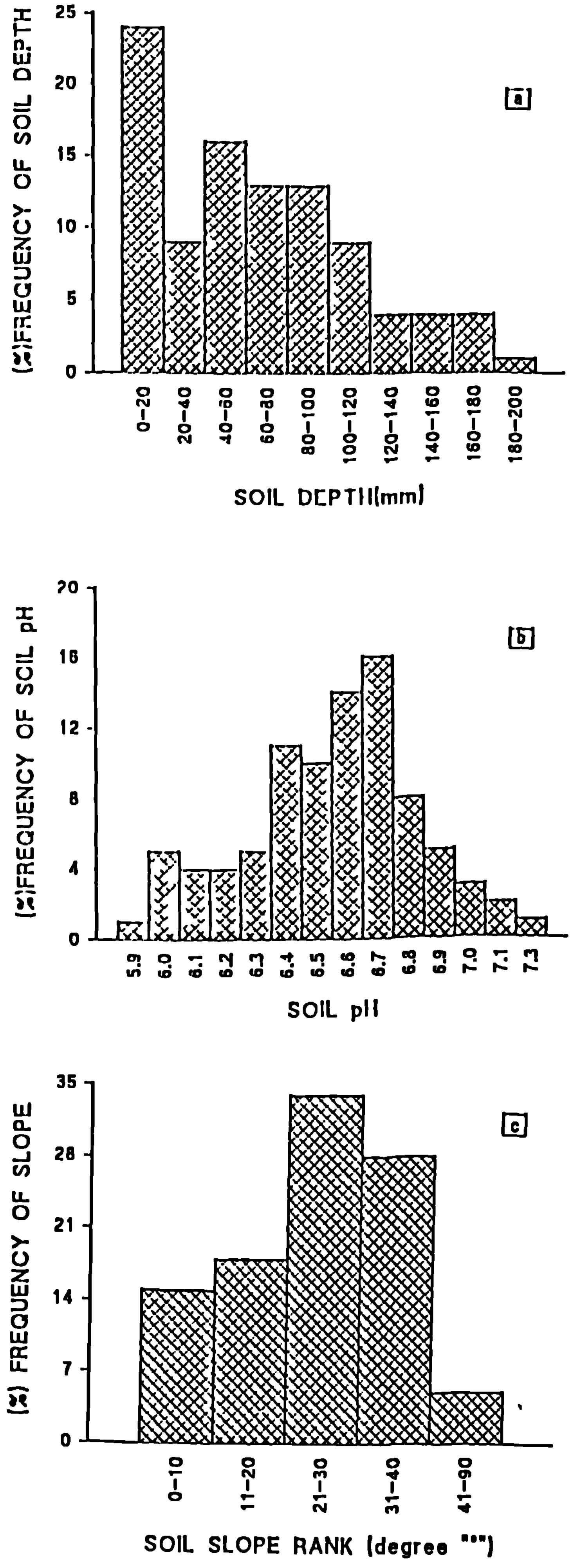

Figure 2.2: Distribution of (a) soil depth, (b) pH, and (c) angle of slope on the studied site.

Species composition of the sampled site is described in terms of percentage occurrence of established plants in the hundred samples in Table 2.1. Twenty five species of vascular plants were recorded. Mean species number per sample was 6.3, and the maximum and minimum were 12 and 1 respectively. Species classified as stress-tolerant (Grime, Hodgson & Hunt 1988) were abundant in the system, and the most frequent species were; *Festuca ovina, Thymus praecox, Briza media,* and *Avenula pratensis.*

A correlation matrix including some vegetation characteristics and environmental factors recorded at the site is presented in Table 2.2. Only significant ($P<0.05$) correlations are shown. Soil depth and soil pH were negatively correlated (Figure 2.3). Both total shoot biomass and dry weight of litter increased with soil depth, and decreased at higher values of soil pH (Table 2.2).

Minimum and maximum total biomass + litter were 67.07 and 3473.70 mg per sample respectively. Fifty-nine percent of samples contained fewer species than the mean (6.3 species per sample), and 63 percent of samples fell below the mean total biomass (1262 mg per sample).

Species-richness was associated positively with total shoot biomass ($P<0.001$), and dry weight of living bryophyte ($P<0.05$). A relationship consistent with the humped-back model (Grime 1973) was obtained (Figure 2.4), when the number of species recorded in each biomass class was plotted against the total shoot biomass + litter. A correlation matrix relating variation in the total shoot

Table 2.1: The percentage frequency of species in the studied site (south-facing slope of Millers Dale, Derbyshire).

SPECIES	(%) FREQUENCY	Established Strategy *
Festuca ovina	90	S
Thymus praecox	79	S
Briza media	67	S
Avenula pratensis	62	S/S-C
Hieracium pilosella	46	S/C-S-R
Carex flacca	38	S
Helianthemum nummularium	34	S
Pimpinella saxifraga	26	S
Koeleria macrantha	22	S
Campanula rotundifolia	22	S
Centaurea scabiosa	18	S/C-S-R
Leontodon hispidus	17	S
Lotus corniculatus	17	S/C-S-R
Polygala vulgaris	17	S
Viola hirta	12	S
Brachypodium sylvaticum	8	S/S-C
Sanguisorba minor	8	S
Solidago virgaurea	8	S
Plantago lanceolata	7	C-S-R
Linum catharticum	4	S-R
Viola riviniana	2	S
Origanum vulgare	1	C-S-R/S-C
Centaurea nigra	1	C-S-R/S
Scabiosa columbaria	1	S/S-R
Silene nutans	1	S

* From Grime *et al* (1988)
S; stress-tolerant, C-S-R; intermediate strategy,
S-R; stress-tolerant ruderal, S-C; stress-tolerant competitor

Table 2.2: A Correlation matrix relating some environmental factors and vegetation characteristics sampled within a 5m x 5m area of calcareous grassland at Tongue End, Millersdale.
Only significant correlations are shown.
* P<0.05, ** P<0.01, *** P<0.001

SPECIES	Soil depth	Soil pH	Slope	Species number	Bryophyte dry wt	Litter dry wt.	total shoot biomass dry wt.
Soil depth	XXXXXX						
Soil pH	-0.43***	XXXXXX					
Slope			XXXXX				
Species number				XXXXXXX			
Bryophyte dry wt.				0.20*	XXXXXXXXX		
Litter dry wt.	0.22 *	-0.29**				XXXXXXX	
Total shoot biomass dry wt				0.48***		0.20 *	XXXXXXX
Total shoot biomass+litter	0.26 **	-0.27**			0.56 ***	0.81***	0.47***

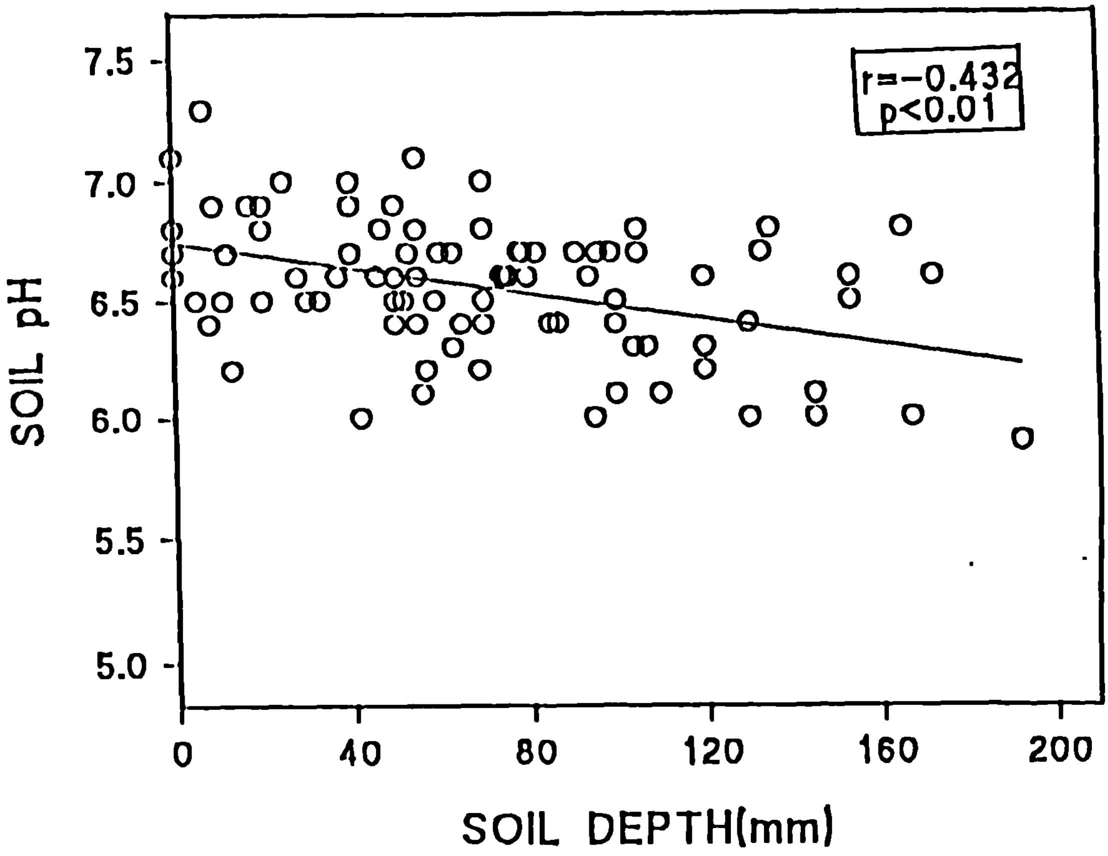

Figure 2.3: Relationship between soil depth and soil pH (0-3 cm) within a 5m x5m area of calcareous grassland at Tongue End in Millersdale.

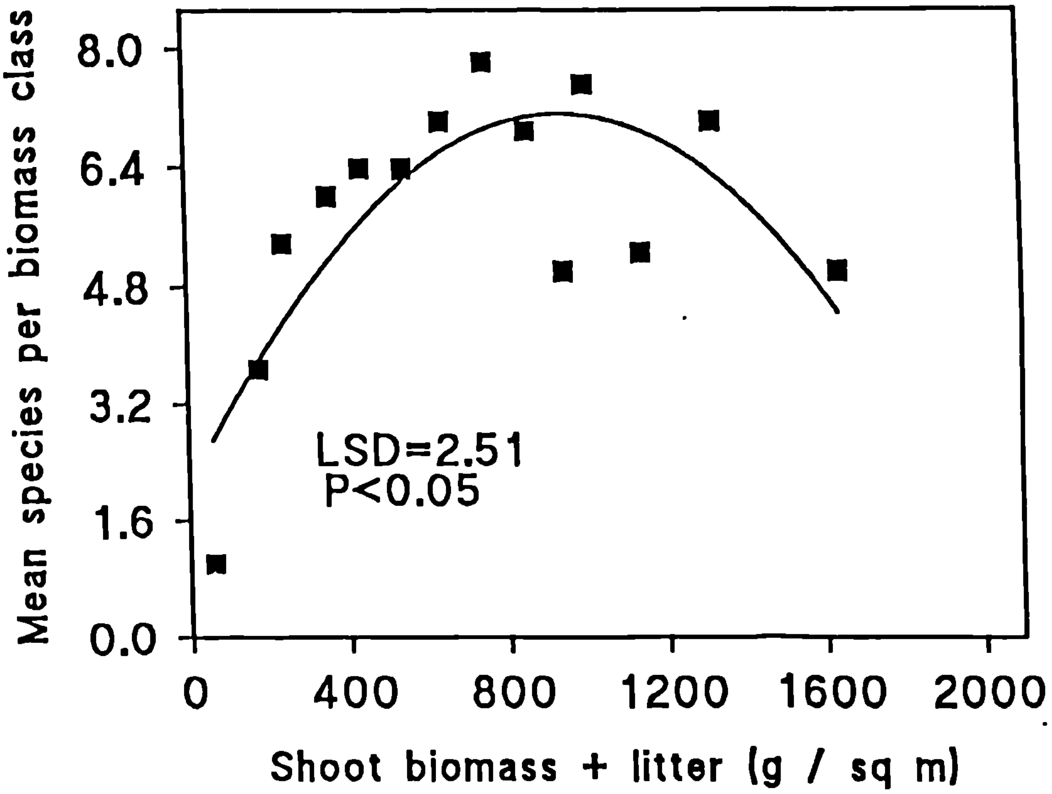

Figure 2.4: The relationship between mean species number per sample and total shoot biomass + litter in samples removed from a 5m x 5m grid in calcareous grassland at Tongue End in Millersdale, North Derbyshire.

biomass (vascular plants + bryos.) to variation in environmental factors and vegetation characteristics is presented in Table 2.3. *Avenula pratensis* (positive) and *Thymus praecox* (negative) exhibited significant correlations with soil depth. The mean total shoot dry weight of each species was calculated for each soil depth class (soil depth class based on 20 mm intervals), and a curve fitting procedure was applied by 2nd. order polynomial regression analysis. The results illustrated in Figure 2.5b show that *Thymus praecox* and *A. pratensis* occupy opposite extremities of the range in soil depth. However the distributions of certain other common species (e.g. *F. ovina, Briza media)* appear to be independent of soil depth. In other cases e.g. *Plantago lanceolata* the low frequency of occurrence yielded insufficient information for useful analysis.

The shoot biomass of *Avenula pratensis, F. ovina* (negatively) and *T. praecox* (positively) correlated with soil pH (Table 2.3). *Centaurea scabiosa* and *Leontodon hispidus* occurred in species-rich, and *T. praecox* in species-poor samples. *Carex flacca* was the only species to exhibit a significant correlation (positive) with the dry mass of bryophyte.

Avenula pratensis, *F. ovina*, and *C. scabiosa* were positively and *Hieracium pilosella* and *T. praecox* negatively associated with litter. *Thymus praecox* showed a negative correlation with the total shoot biomass of vascular plants, and a positive correlation was detected for *C. scabiosa, C. flacca* and *A. pratensis.*

Table 2.3: Correlation coefficients relating variation in the shoot biomass of individual species with various vegetation characteristics and environmental factors within a 5m x 5m sampled area of calcareous grassland at Tongue End, Millersdale.
Only significant correlations are shown.
* P<0.05, ** P<0.01, *** P<0.001

SPECIES	Soil depth	Soil pH	Slope	Species number	Bryophyte (dry wt)	Litter	Plant living dry wt.	Total biomass +litter
A. pratensis	0.37 **	-0.22				0.32**		0.28**
B. media								
B. sylvaticum			-0.2*					
C. rotundifolia								
C. flacca					0.35 ***			0.24 *
C. scabiosa				0.24*		0.26**	0.22 *	0.32 **
F. ovina		-0.23*				0.20 *	-0.24*	
H. pilosella						-0.22*		
H. nummularium								
K. macrantha								
L. hispidus				0.33**				
L. corniculatus								
P. vulgaris								
P. lanceolata								
P. saxifraga								
S. minor				-0.21*			0.21*	
S. virgaurea								
T. praecox	-0.24 *	0.24*		-0.25*		-0.30**		-0.27**
V. hirta								

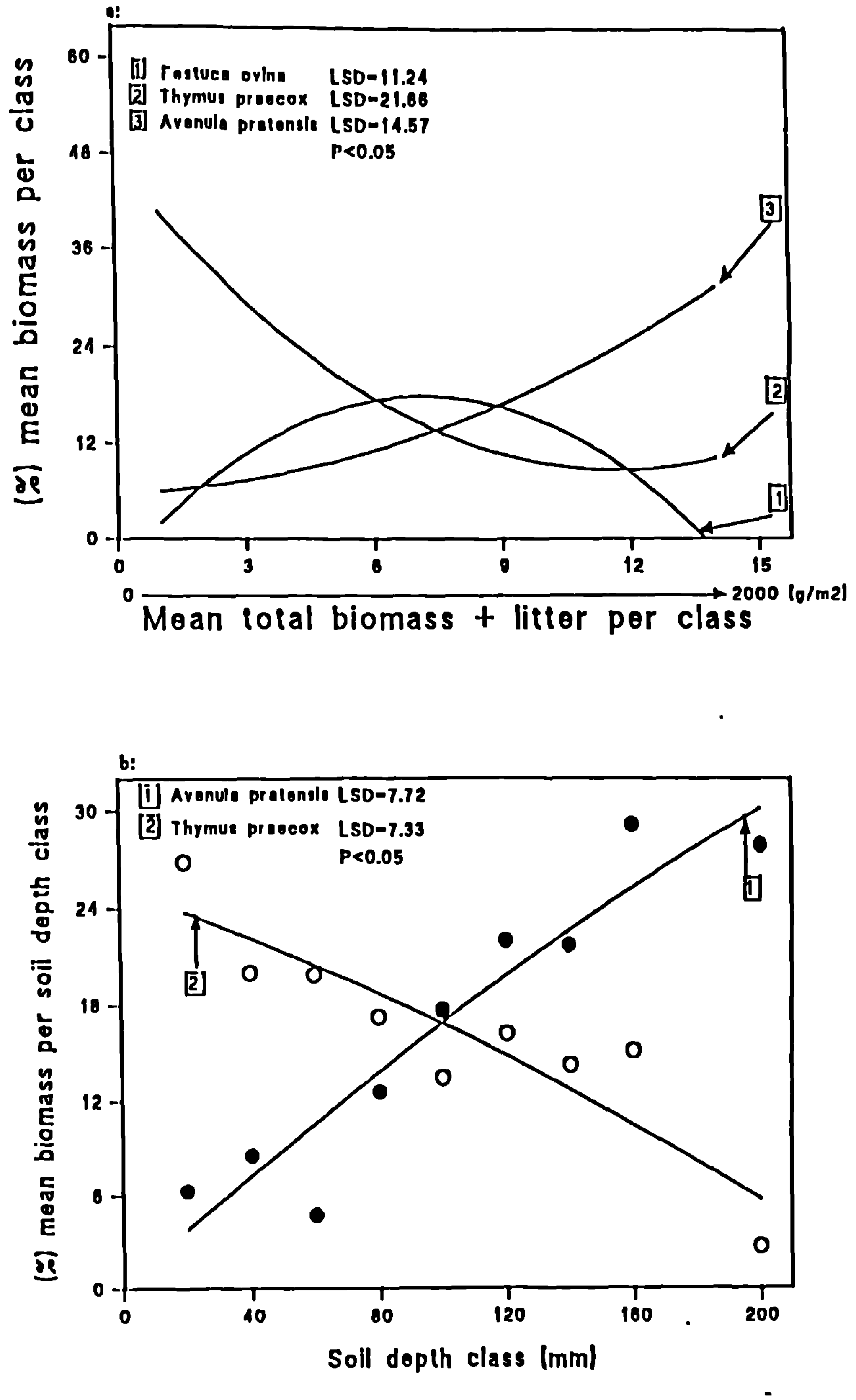

Figure 2.5: a; The mean shoot dry weight (%) of *T. praecox*, *A. pratensis* and *F. ovina* plotted against the mean total biomass class.
b; The mean shoot dry weight (%) of *T. praecox* and *A. pratensis* were plotted against soil depth class (each class based on 20 mm). Data sampled within a 5m x 5m area of calcareous grassland at Tongue End in Millersdale, Derbyshire.

When the mean contributions of T. praecox, A. pratensis and *F.ovina* to various classes of total shoot biomass for all vascular plant components were examined (Figure 2.5a) interesting contrasts appeared. *Festuca ovina* displayed a log normal distribution with increasing total shoot biomass+litter, whilst the percentage contribution of *A.pratensis* and *T.praecox* increased or decreased respectively with increasing total shoot biomass+litter.

2.3.2 Analysis using TWINSPAN

The result of the analysis of the data set using TWINSPAN is given in Table 2.4 in the form of the actual computer print-out. At the first division a separation occurred between samples containing *Helianthemum nummularium* (Group I) and those characterised by the presence of *Carex flacca, Centaurea scabiosa,* and *Pimpinella saxifraga* (Group II) (Table 2.5a). In an attempt to interpret this dichotomy, associated differences in environmental factors were examined. Mean species-richness, total shoot biomass, litter and biomass of bryophyte were lower in Group I than Group II (Table 2.5b). The second dichotomy in the TWINSPAN analysis involved *A. pratensis, Campanula rotundifolia* and *Lotus corniculatus* as indicator species of Group III and *T. praecox* , *H. nummularium, H. pilosella* and *Briza media* of Group IV. Table 2.5c reveals that groups III and IV differed consistently in soil depth,litter,and total shoot biomass. Group III (+ *A.pratensis*) was characterised by deeper soil,

Table 2.4: The analysis of the data set sampled within a 5m x 5m area of calcareous grassland at Tongue End in Millersdale using 'TWINSPAN' (Hill 1979) is given in the form of actual computer-print out. Samples are columns, and species are rows. Entries in the table are the pseudospecies levels not quantitative values.

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                  34156699 35 3 12254873334445161225681491 1245468 37 18291 233468899 78682355 6779467778825 57217996
                  6744367394878207688167179289198645953754883137470636415735102500690634144200259095622382795 35321121

15 Sang mino  -13------------2--1-------2---------1---------2----------------1-----------------------------  000
18 Viol hirt  4444----------4-4------1----1------------3-------------2--------------1-----------2--------------  000
 4 Care flac  -4-2-444444----44443244-4-4442 4444444442------3-------4----44--------------------------432------.  0010
10 Leon hisp  3------------4-444444-42----------2-33-------2---------------2-------2-------------------3--------  0010
12 Pimp saxi  34-44-1---444-22----2-2-4-22-----------313-21--------114------------4-----------4--1--------------  0010
13 Plan lanc  -------4-----44-3-----2--------------------------------------------------3--------4---------------  0010
14 Poly vulg  34--------3-24------22---2--------------------3-----432--------3---------------2-------2------44---  0011
 5 Cent scap  ---------------------------3--------------44444-----4444444-----------------------4---------------  01
 9 Koel macr  ---------------------33------------4-32---342344----343443 4-----------2---2-----------------4-----  01
19 Hier pilo  ---------------4---44444---4444-4---44444-243444------------------3---2----4---4444-3444444444--334--------  1000
 1 Brac sylv  -3-------------2-------2-------------------------4---------3-----------4-------------------2-2------  1001
 2 Briz medi  --2-24---3421434 4323344---44332-244--44--3244--344443333----2----4344444441--4444443-4-----4-4-334-4--------  1001
 8 Aven prat  4244444-3----1-4444----------------443-344344---444442442444444444444444-41-------442-------2-------3----4-444  1001
17 Thym prae  4-44 2-----------4----32444-----3444----4444-44-24---434423444--44-4444-42-44-1----434443444-44444442 4444 2-44------  1001
 6 Fest ovin  2334344444424-1421424444--34--24-332214-34--44-444---3-344342434234434344 1444---434-243444134424244-----  101
11 Lotu corn  ---34-------------------333--------1-2----------4--------------------1-----444----3--------4-------3-4--  101
 3 Camp rotu  ----------2---------311111-----------1-------------------------------23-------------221-231-3412-2  11
 7 Hell numm  -4-3----------------------------2-------44444------------444-----444----44-4---24-444444------------------4444444443-----  11
16 Soli virg  --------1------4--------------------------------21-----------------2--------------------------1-44---------  11

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                        000110000000111111111111100111111       00000011 00011111100000000011111000001111100000000011
                                  00111111000111111111  000111  011111        00010111111111111110001 1      01111000000011
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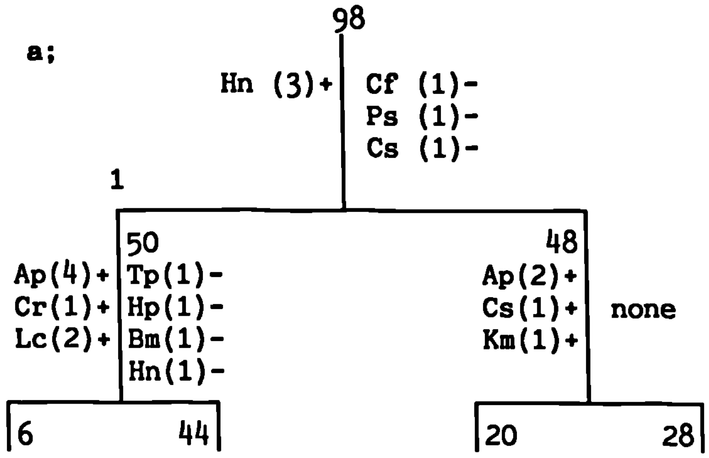
Table 2.5: a; Inverse indicator species analysis (TWINSPAN) of the quantitative data collected within a 5m x 5m area at Tongue End, Millers Dale.
b; Comparison between two sides of first division.
c; Comparison between two sides of second division.

a;



b;

Factors	Hn+ *	Cf,Cs,Ps- *	P<
Bryophyte	193.8	341.6	0.01
Species number	5.1	7.3	0.001
Total biomass	11123.0	1413.0	0.01

c;

Factors	Ap,Cr,Lc+	Tp,Hp,HN,Bm-	P<
Soil depth(mm)	85.5	70.0	0.05
Litter	875.2	592.9	0.05
Total biomass	1382.6	1119.6	0.02

* mg/sample, species number/sample

Key to species; *Avenula pratensis* (Ap), *Briza media* (Bm) *Campanula rotundifolia* (Cr), *Centaurea scabiosa* (Cs), *Carex flacca* (Cf), *Helianthemum nummularium* (Hn) *Hieracium pilosella* (Hp), *Lotus corniculatus* (Lc), *Koeleria macrantha* (Km), *Thymus praecox* (Tp).

and high densities of litter and total shoot biomass.

2.3.3 Analysis using DECORANA

The first axis emerging from the DECORANA analysis (Table 2.6) is difficult to interpret; litter is the only discriminating feature. The second axis is more informative in that there are associated differences in several environmental factors. Soil depth, litter and total shoot biomass + litter are negatively and soil pH positively correlated with the second axis.

Avenula pratensis, *C. rotundifolia*, *L. corniculatus*, *P. saxifraga*, and *P. lanceolata* are negatively and *T. praecox*, *H. nummularium*, and *S. virgaurea* positively associated with the second axis.

2.3.4 CCA (Canonical Correspondence Analysis)

The results of the Canonical Correspondence Analysis (CCA) are displayed in an ordination diagram with species represented by points and environmental variables represented by arrows (Fig 2.6). The species points and arrows of the environmental variables jointly reflect the species distributions along each of the environmental variables. The figure reveals that there is a strong positive association between soil depth, litter accumulation and dry weight of *A. pratensis*. The analysis also reveals that the creeping shrub *T. praecox* is negatively associated

Table 2.6: Loadings of species on, and correlation coefficients of environmental factors with first and second axis of Detrended Correspondence Analysis (DECORANA) of data sampled within a 5m x 5m area at Tongue End, Millersdale. Only significant ($P<0.05$) environmental correlations and species whose loadings exceed 0.20 in absolute values are shown. *; $P<0.05$ **; $P<0.01$

ENVIRONMENTAL FACTORS	**AXIS I**	**AXIS II**
Soil depth		-0.33 **
Soil pH		0.22 *
Total biomass (+ litter)		-0.37 **
Litter	-0.25 *	-0.36 **
SPECIES		
Avenula pratensis	-0.33	-0.62
Campanula rotundifolia		-0.28
Carex flacca	0.43	
Centaurea scabiosa	-0.44	
Hieracium pilosella	0.32	
Helianthemum nummularium	-0.37	0.38
Koeleria macrantha	-0.22	
Leontodon hispidus	0.30	
Lotus corniculatus		-0.21
Pimpinella saxifraga	0.32	-0.26
Plantago lanceolata	0.35	-0.20
Solidago virgaurea	0.27	0.37
Thymus praecox	-0.30	0.41
Viola hirta	0.25	

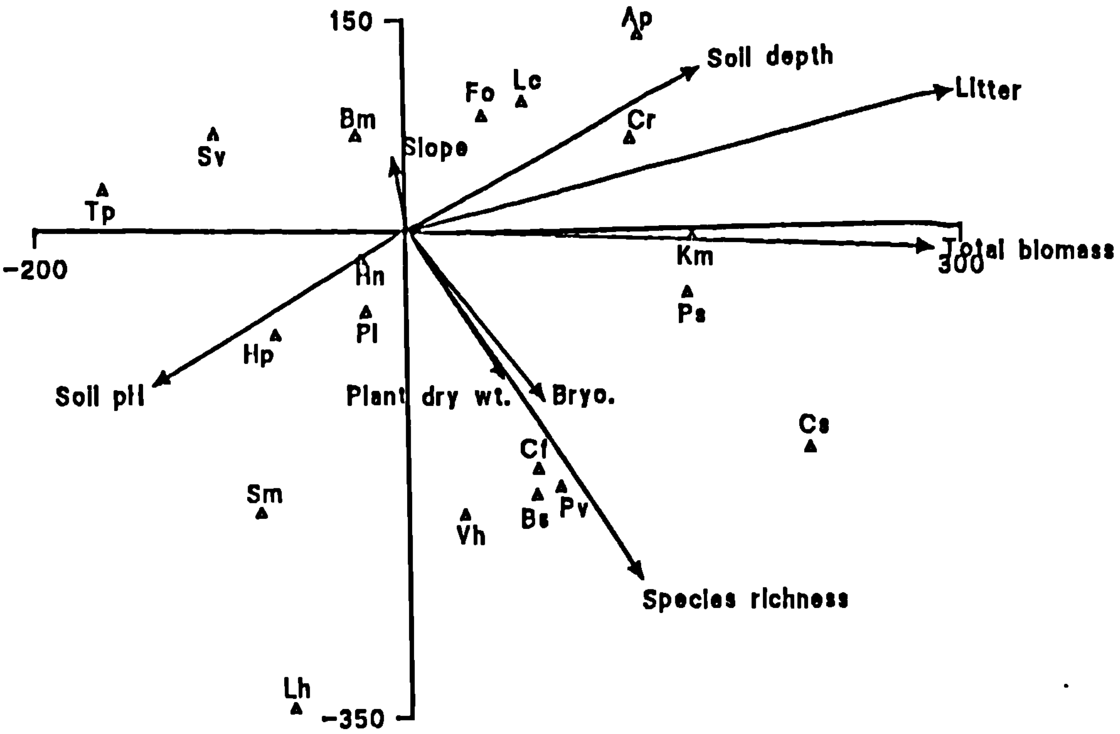


Figure 2.6: Canonical correspondence analysis ordination diagram with vascular plant species (Δ), vegetation characteristics (arrowed) and environmental variables (arrowed). The first axis is horizontal, the second vertical. Key to species:

Ap. Avenula pratensis; Bm. *Briza media*; Cf. *Carex flacca*; Cr. Campanula rotundifolia; Cs. *Centaurea scabiosa*; Fo. *Festuca ovina*; Hn. *Helianthemum nummularium*; Hp. *Hieracium pilosella*; Km. Koeleria macrantha; Lc. *Lotus corniculatus*; Lh. *Leontondon hispidus*; Pl. *Plantago lanceolata*; Ps. *Pimpinella saxifraga*; Pv. *Polygala vulgaris*; Sm. *Sanguisorba minor*; Tp. *Thymus praecox*; Vh. Viola hirta.

The analysis is based upon 100 circular samples each of diameter 50 mm evenly distributed on a grid within a 5 m x 5 m area of limestone grassland on a south-facing slope in Millersdale, North Derbyshire, England.

with *A.pratensis*, and tends to occur on locally shallow soil of high pH.

It is evident that a majority of the other vascular plants present within the site reach maximum abundance in circumstances intermediate between those exploited by *A. pratensis*, and *T. praecox*; here the vegetation occupies locally species-rich microsites.

2.4. DISCUSSION:

Table 2.1 illustrates the high frequency of stress-tolerant (*sensu* Grime 1979) grasses such as *Festuca ovina* and the presence of xeromorphic species, e.g. *Thymus praecox* and *Helianthemum nummularium* (Davison 1964; Sydes 1980; Hillier 1984) in the grassland at Tongue End. A consistent feature of the site was the occurrence of areas of shallow soil. There were many unvegetated gaps with bare soil and uncovered bed rock.

The results reveal the existence of a local mosaic in soil depth and its association with other environmental factors, plant production, litter, and species distributions. Pockets of deeper soil appeared to provide opportunities for some species to avoid drought during summer and the distribution of shoot biomass and litter suggests that the microsites provided better conditions for plant growth and litter accumulation. Soil pH at the surface of the profile varied inversely with soil depth; the basis of this variation is well known in that shallower areas are under a more direct influence of the underlying limestone bedrock whereas in deeper parts, the loss of calcium carbonate by leaching lowers the pH of the surface soil (Balme 1953).

It is interesting to consider to what extent diversity at the Millers Dale site is determined by the variation in soil depth. It seems quite likely that the resulting small-scale spatial heterogeneity associated with variation in pH, litter accumulation, and vegetation structure makes a distinct contribution by providing a range of conditions exploited by very different life-histories, morphologies, physiologies, and regenerative characteristics. Support for this hypothesis is evident from simple comparisons of the major species recorded in the Millersdale site. *Thymus praecox* and *H. nummularium* are small, prostrate shrubs common in areas of rocky shallower soil, and provide a marked contrast with the robust tussocks of *A. pratensis* which is associated with areas of deeper soil. However, doubts have been raised by investigations (Grime, Shacklock & Band 1985; Mahdi & Law 1987; Pearce 1987) which did not find pattern in vegetation or soil factors in moister calcareous grassland. In this kind of habitat it may be that disturbance e.g. grazing, rather than spatial heterogeneity plays a major role in maintaining species diversity.

Chapter 3

A comparative study of seedling growth responses to moisture supply and temperature regimes.

3.1. INTRODUCTION:

A combination of water stress and low temperature stress is commonly experienced by the vegetation of arctic regions and it is not unusual for the vegetation of drier areas in the tropics and subtropics to experience combined effects of thermal stress and desiccation. Extremes of temperature often coincide with drought in locally xeric habitats (e.g. sand dunes, shallow soils) in temperate zones (Fitter & Hay 1981). Because of this frequent association between the two forms of stress, it is often difficult to disentangle their effects on plants growing in the field.

Previous studies have shown that limestone grasslands of the type occurring in Millersdale contain species differing considerably in seasonal timing of shoot growth (Al-Mufti *et al* 1977), and in response to water stress (Grime & Curtis 1976; Sydes & Grime 1984). Therefore the main objective of this experiment was to examine the responses of the major component species of Millersdale to temperature and moisture supply. The experiment described in this chapter utilises the 'temperature-gradient-tunnel' introduced by Mason, Grime & Lumb (1976) and improved by Grime, Hall, Hunt, Neal, Ross-Fraser & Sutton (1989). This provides a range of controlled temperatures simultaneously within one chamber, while maintaining other environmental variables constant to the standards which are current in modern plant growth cabinets (Grime *et* al 1989). In the experiment described in this chapter plants were subjectedtoa cycle of water-stress using an intermittent watering regime. This allowed the species to be ranked on the basis of their ability to survive the applied water-stress. In addition to survivorship, measurement was also made of plant production (growth) relative to that of undroughted control plants.

3.2 MATERIALS AND METHODS:

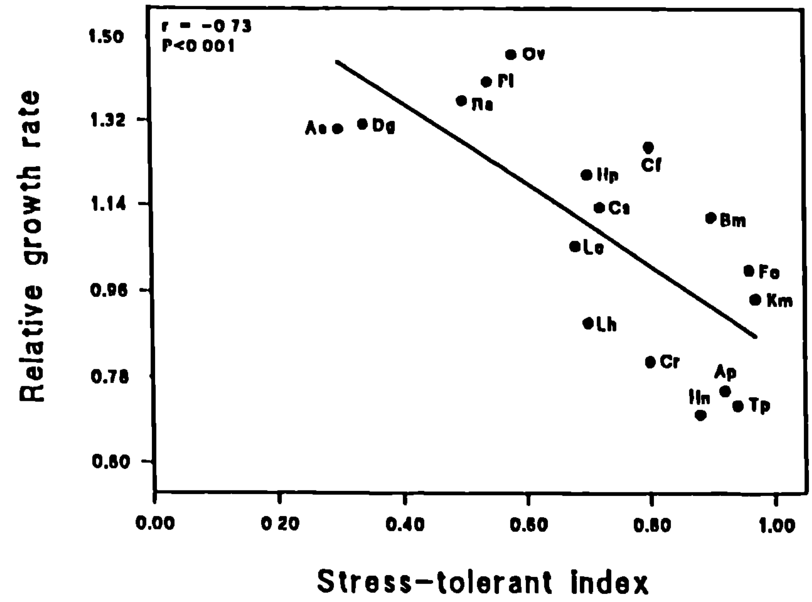
Seventeen species of herbaceous plants or small shrubs were used in the experiment (Table 3.0 and Figure 3.0). Fourteen of these were present in the studied plot on the dry south-facing slope of Millersdale (see Chapter 2). The remaining three species were selected as representatives of the very different flora situated on the adjacent north-facing slope. Seeds were germinated in de-ionized water in closed transparent boxes at 20/15 °C day/night and 29 Wm^{-2} irradiance. Two or four seedlings (according to expected biomass) of a species were planted into each 220 ml square plastic pot, which was filled with Leighton Buzzard silica sand and saturated with Rorison nutrient solution (Hewitt 1966). Pots were placed in shallow trays filled to 5 mm with de-ionized water and then transferred to the temperature-gradient-tunnel. The five tunnel compartments were adjusted to night temperatures of 5 / 10 / 15 / 20 / 25 °C respectively. Day temperature was 25 °C for all compartments, with a 14 h. photoperiod (29 $W\ m^{-2}$). At seven days after planting, two watering regimes (control and drought) were implemented. The control treatment was

Table 3.0: The 'main strategy', 'stress-tolerance index' and mean 'relative growth rate of seventeen selected species.

SPECIES	RGR ** (week^{-1})	Main Strategy *	Stress-tolerance Index *
Arrhenatherum elatius	1.30	C	0.30
Dactylis glomerata	1.31	C-S-R & C	0.34
Festuca ovina	1.00	S	0.96
Thymus praecox	0.72	S	0.94
Briza media	1.11	S	0.90
Avenula pratensis	0.75	S & S-C	0.92
Hieracium pilosella	1.20	S & C-S-R	0.70
Carex flacca	1.26	S	0.80
Helianthemum nummularium	0.70	S	0.88
Koeleria macrantha	0.94	S	0.97
Campanula rotundifolia	0.81	S	0.80
Centaurea Scabiosa	1.13	S & C-S-R	0.72
Leontodon hispidus	0.89	S	0.70
Lotus corniculatus	1.05	S & C-S-R	0.68
Plantago lanceolata	1.40	C-S-R	0.54
Origanum vulgare	1.46	C-S-R & S-C	0.58
Rumex acetosa	1.36	C-S-R	0.50

* From Grime *et al* (1988) which based on Grime's model (1979)
S; stress-tolerant, C-S-R; intermediate strategy, C; competitor
S R; stress-tolerant ruderal, S-C; stress-tolerant competitor
** Mean relative growth rate data from Grime & Hunt (1975).

Figure 3.0: The relation between variation in growth rate and variation in the stress-tolerance index



watered with 50 ml Rorison solution per pot every 5 days, and additionally with a daily replenishment of de-ionized water to 5 mm in each tray. In the drought treatment, plants were watered with 50 ml Rorison solution per pot every 5 days. The complete design was: 17 species x 5 night temperatures x 2 water regimes. The experiment was run for 28 days. Each plant was individually harvested, and root and shoot were separated and dried to 80 °C for 48 h., then weighed.

3.3. QUANTITATIVE ANALYSIS:

Fitted quadratic curves (Hunt & Parsons 1974, 1981) were used to describe the response to temperature of total dry weight per plant and root/shoot ratio at the final harvest. In addition, two arbitrary indices of response to the experimental variables were introduced:

Drought Sensitivity Index

This index described the area (mm^2) which lies between the two fitted curves obtained by plotting ln (total dry weight per plant) against night temperature for the control and droughted plants. The scale of the common y-axes is ** mm per log unit, the scale of the common x-axes is ** mm per degree Celsius, and the area is assessed between the night temperatures 5 °C and 25 °C.

Night Depression Sensitivity Index

A second index, was calculated as the vertical distance which lies between the maximum and minimum yields on the fitted curve relating ln (total dry weight per plant) of the undroughted plants to night temperature. The minimum normally lies at 5 °C and the maximum at 25 °C.

3.4. RESULTS:

In the drought treatment no plants of *Origanum vulgare, Campanula rotundifolia, Rumex acetosa, Leontodon hispidus,* and *Lotus corniculatus* survived at 25 °C.

The responses to temperature and drought of 16 of the 17 species are presented in Fig 3.1. After transplant the seedlings of *Hieracium pilosella* failed to establish. At the lowest temperature (5°C) there were no major differences in dry weight production between control and drought treatments. As we might expect, however, the effect of higher temperatures was to increase the effect of water-stress on biomass production (Fig 3.2). Seven species exhibited a distinct optimum night temperature in the control treatment, while the remainder either did not respond (e.g. *Avenula pratensis, Campanula rotundifolia),* or their dry matter production was increased by rising temperature, indicating an optimal temperature at or above 25 °C (Table 3.2). Species ranking for drought and night depression sensitivity are given in Tables 3.1, and 3.2, respectively. These two indices show positive association (except for *Thymus praecox*) (Fig 3.3c). The drought and night depression sensitivity indices are also negatively associated with stress-tolerance index (*sensu* Grime 1979,

Figure 3.1:
Fitted quadratic curves of ln (total dry weight per plant) of the species in response to temperature for control and droughted plants.

Figure 3.1:

Grasses

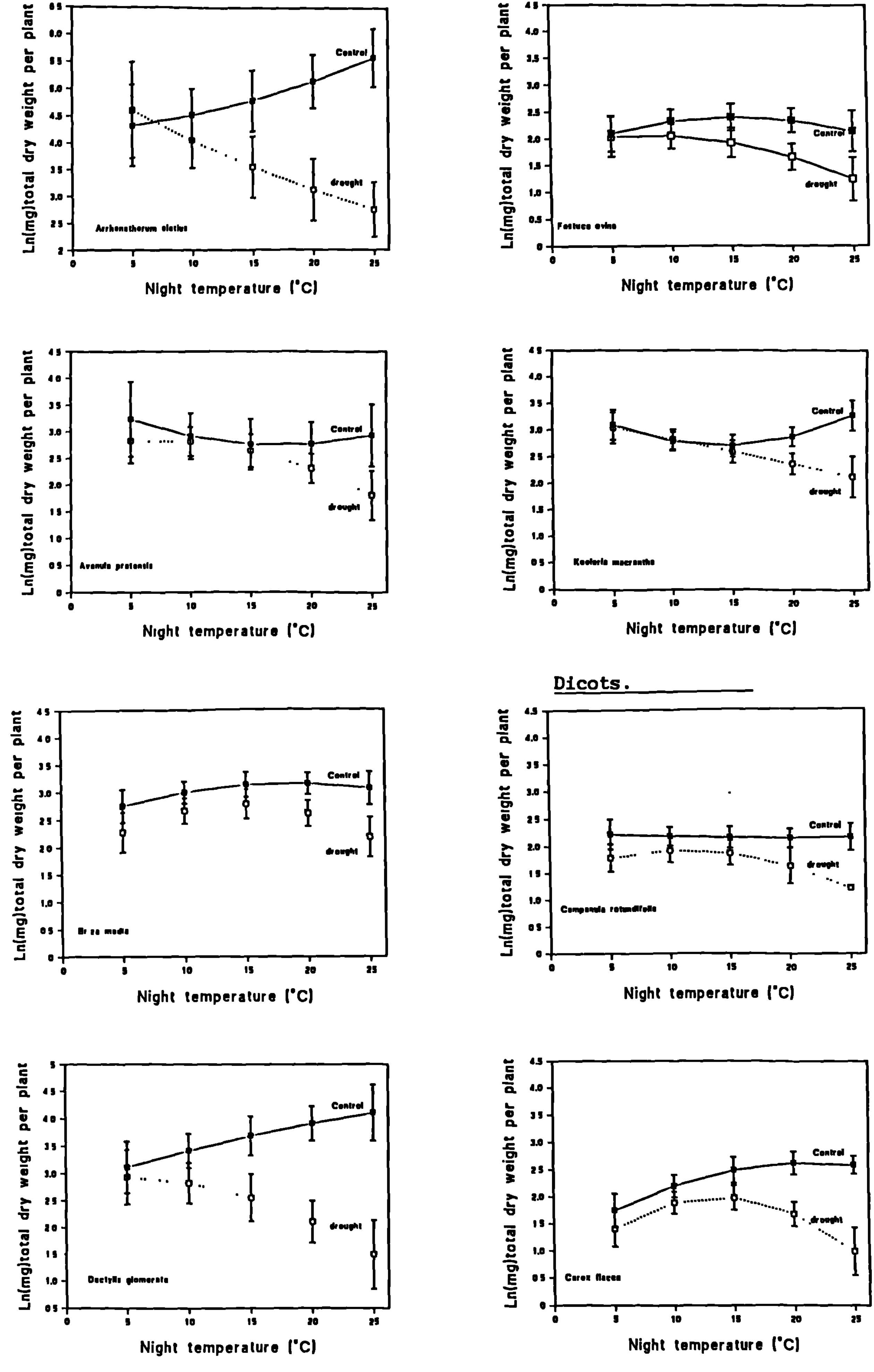
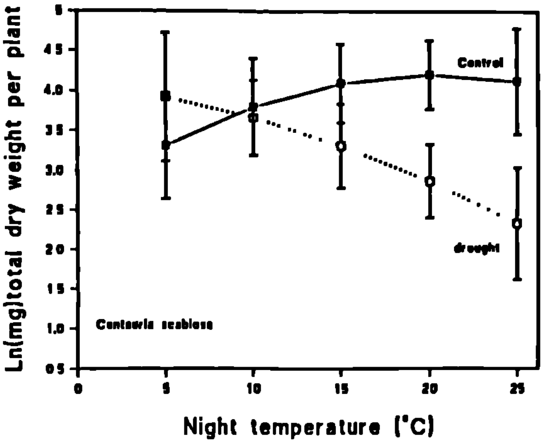
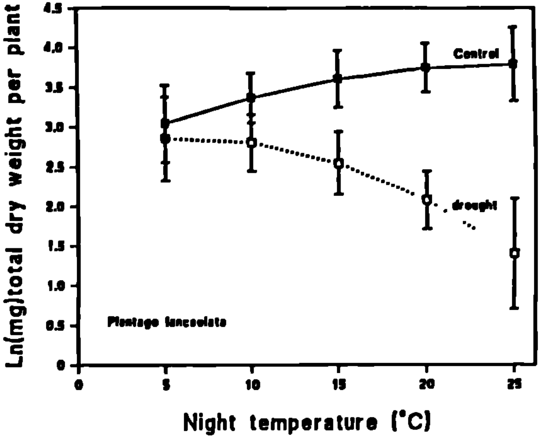
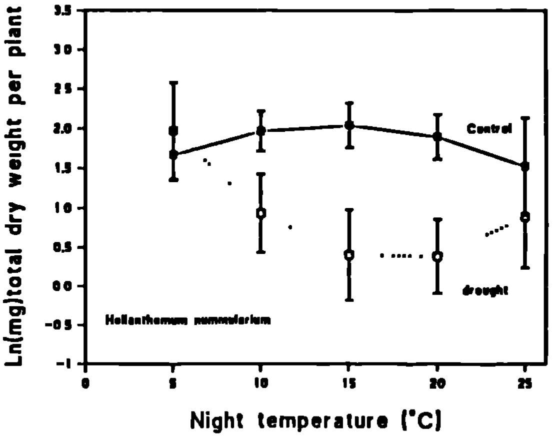
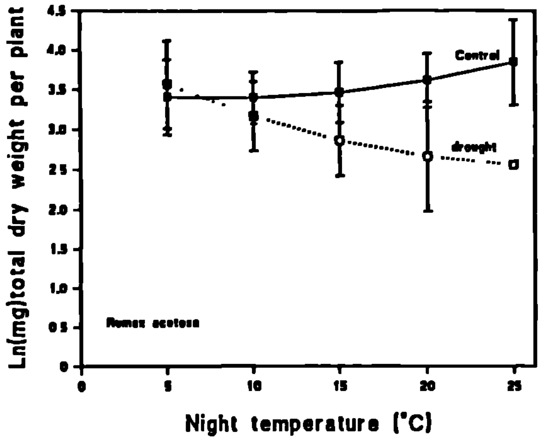


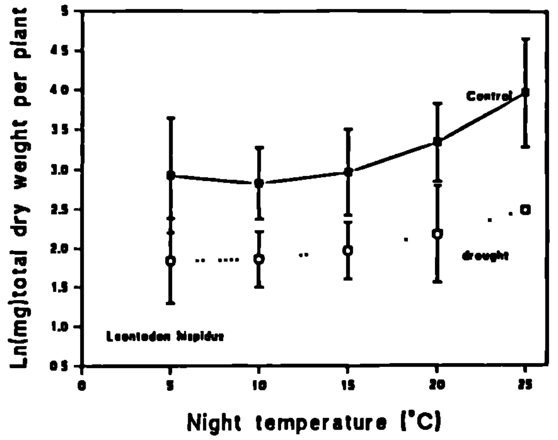
Figure 3.1 (contd.)

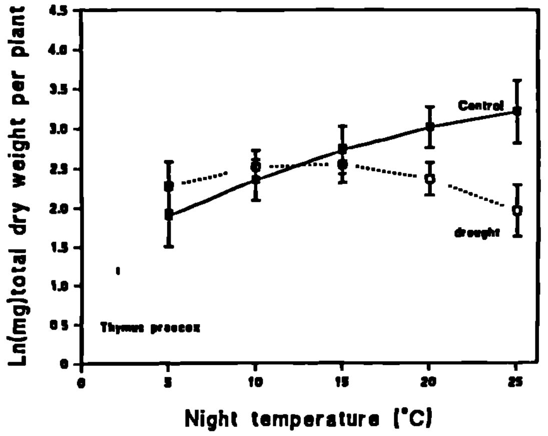


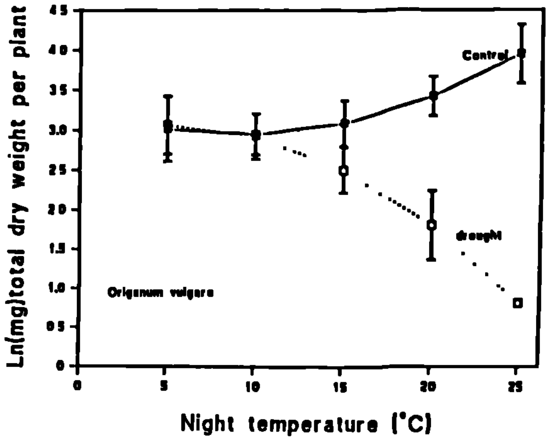




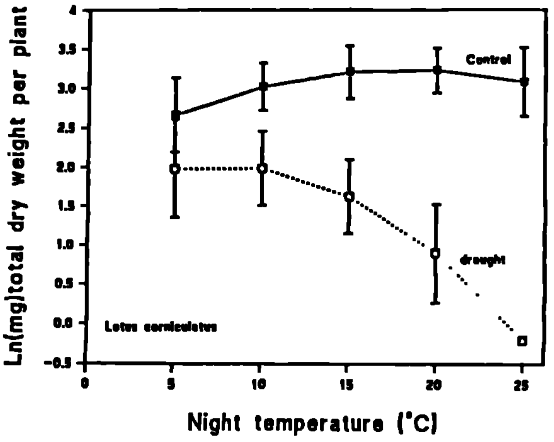


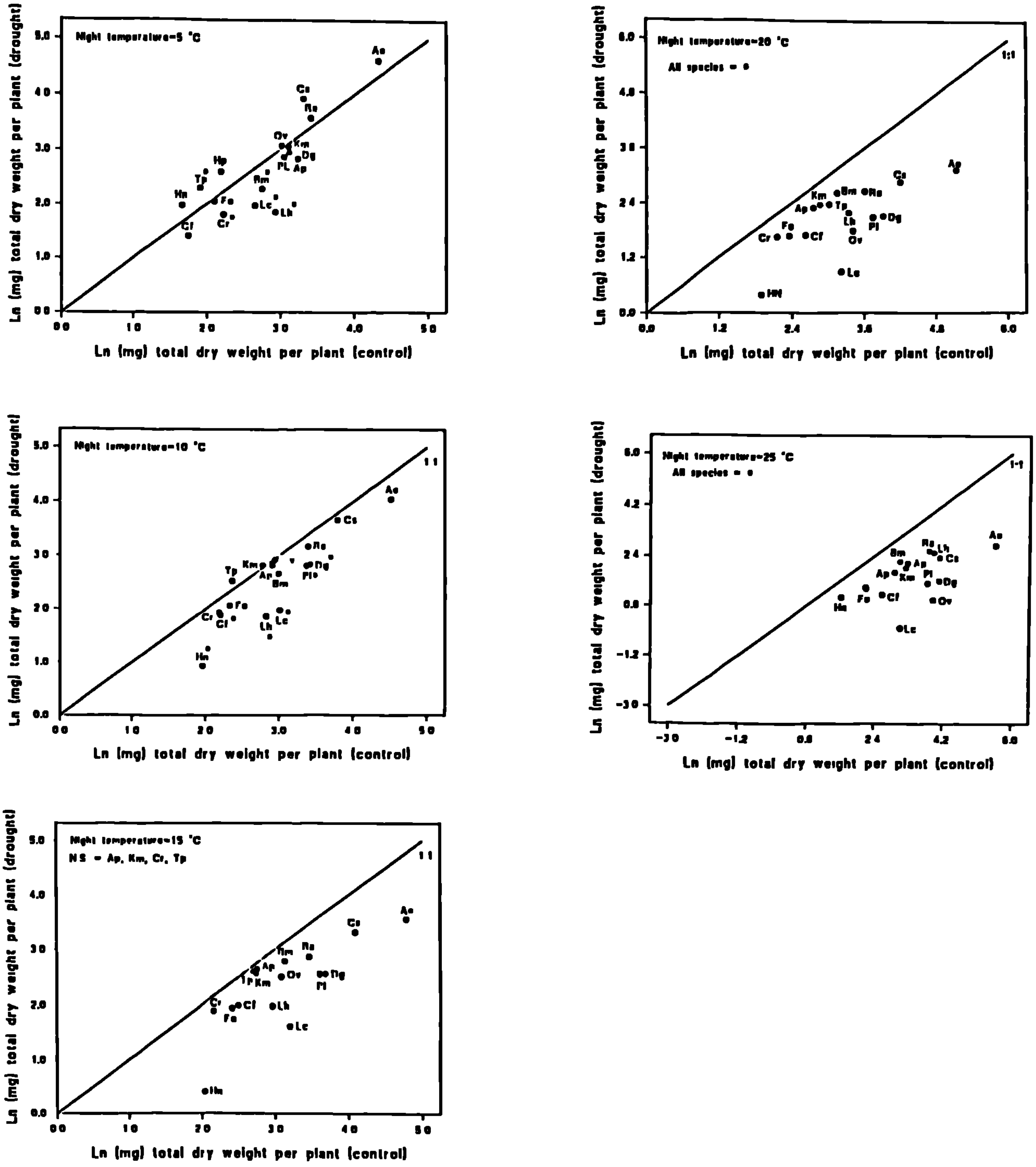






Legume





<u>Figure 3.2:</u> The effect of drought on the yield of various Millersdale species. Log (total dry weight per plant) in drought is plotted against control treatment for each night temperature regime. * indicates the statistical significant differences (P<0.05). Key to species; *Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Plantago lanceolata (Pl), Thymus praecox(Tp), Lotus corniculatus (Lc).*

Table 3.1: Species drought sensitivity rank; based on the area (mm^2) which lies between the two fitted curves (see Fig. 3.1) obtained by plotting ln (total dry weight per plant) against night temperature for the control and droughted plants.

Species	Drought Sensitivity Index	
	Area mm^2	Rank
Lotus corniculatus	6383	1
Arrhenatherum elatius	4483	2
Dactylis glomerata	4477	3
Plantago lanceolata	4151	4
Helianthemum nummularium	4029	5
Leontodon hispidus	3879	6
Origanum vulgare	3393	7
Centaurea scabiosa	2622	8
Carex flacca	2316	9
Rumex acetosa	2171	10
Festuca ovina	1739	11
Briza media	1665	12
Campanula rotundifolia	1389	13
Avenula pratensis	1101	14
Koeleria macrantha	970	15
Thymus praecox	926	16

Table 3.2: Sensitivity to night depression was calculated as the vertical distance in ln (total dry weight per plant) between the maximum and minimum yields of the fitted curve (see Fig. 3.1) relating ln (total dry weight per plant) of the undroughted plants to night temperature. The minimum normally lies at 5°C and the maximum at 25°C. (*) No detectable effect of temperature.

SPECIES	Night Depression Sensitivity		Optimum or maximum temperature (observed)	
	Index	Rank		
Thymus praecox	1.3139	1	-	25
Arrhenatherum elatius	1.2572	2	-	25
Leontodon hispidus	1.0439	3	-	25
Dactylis glomerata	0.9848	4	-	25
Origanum vulgare	0.9314	5	-	25
Centaurea scabiosa	0.8907	6	20.38	-
Carex flacca	0.8826	7	21.46	-
Plantago lanceolata	0.7482	8	24.94	-
Lotus corniculatus	0.5680	9	18.12	-
Rumex acetosa	0.4352	10	-	25
Briza media	0.4048	11	18.58	-
Helianthemum nummularium	0.3832	12	14.38	-
Festuca ovina	0.3132	13	15.47	-
Koeleria macrantha	0.1672	14	-	25
Campanula rotundifolia	-0.0580	15	*	*
Avenula pratensis	-0.3070	16	*	*

Figure 3.3:

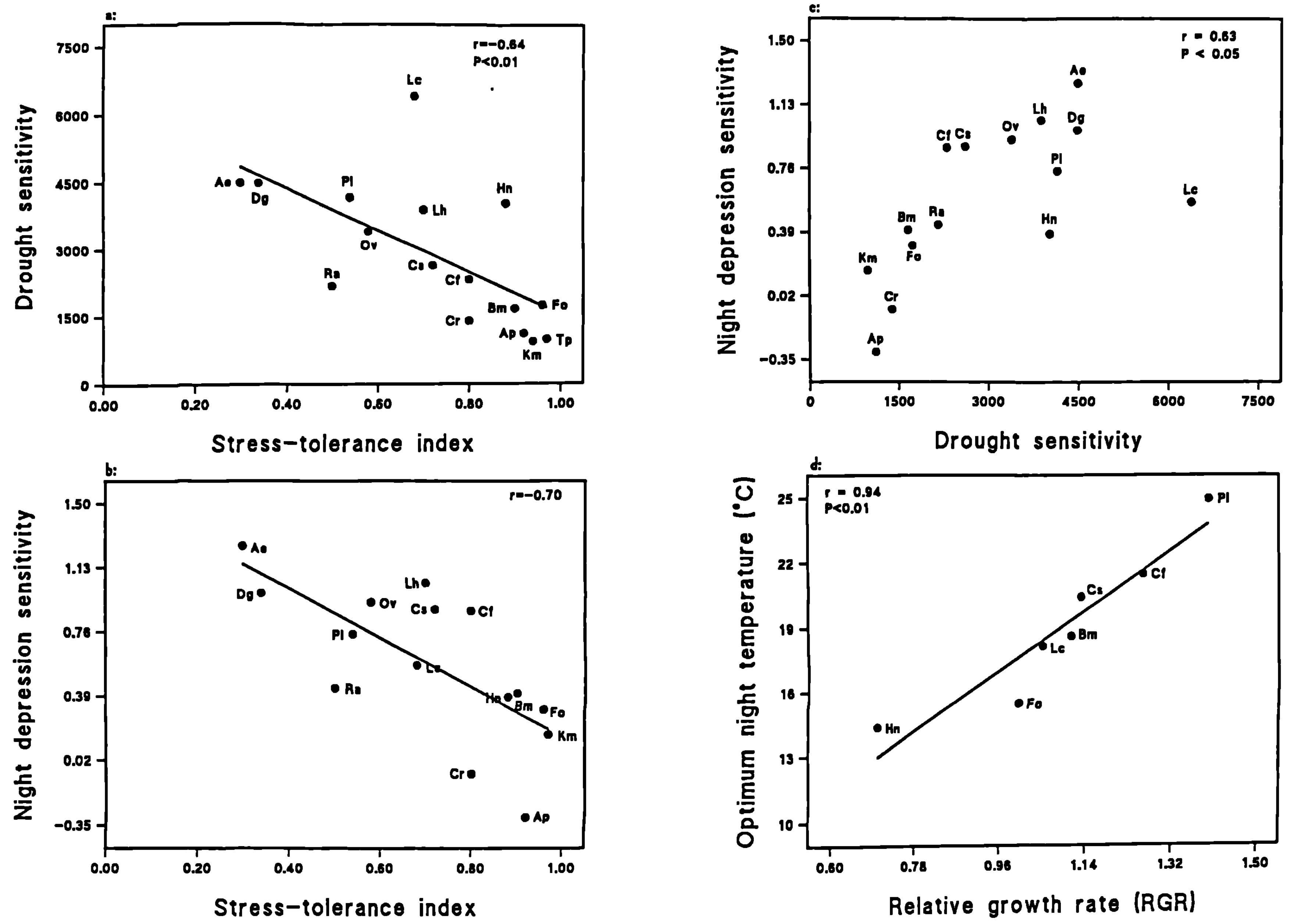
a; The relation between variation in **drought sensitivity** and variation in the **stress-tolerance index.**

b; The relation between variation in **night depression sensitivity** and variation in the **stress-tolerance index.**

c; The relation between variation in **night depression sensitivity** and variation in the **drought sensitivity.**

d; The relation between variation in **optimum night temperature** and variation in the **relative growth rate.**
Key for species;

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Plantago lanceolata (Pl), Thymus praecox(Tp), Lotus corniculatus (Lc).


a:
r=-0.64
P<0.01
Drought sensitivity
0
1500
3000
4500
6000
7500
Stress-tolerance index
0.00
0.20
0.40
0.60
0.80
1.00
Ae
Dg
Pl
Lc
Lh
Hn
Ov
Rs
Cs
Cf
Cr
Bm
Fo
Ap
Km
Tp
b:
r=-0.70
Night depression sensitivity
-0.35
0.02
0.39
0.76
1.13
1.50
Stress-tolerance index
0.00
0.20
0.40
0.60
0.80
1.00
Ae
Dg
Lh
Ov
Cs
Cf
Pl
Lc
Rs
Hn
Bm
Fo
Km
Cr
Ap
c:
r = 0.63
P < 0.05
Night depression sensitivity
-0.35
0.02
0.39
0.76
1.13
1.50
Drought sensitivity
0
1500
3000
4500
6000
7500
Ae
Lh
Dg
Cf
Cs
Ov
Pl
Lc
Bm
Rs
Hn
Fo
Km
Cr
Ap
d:
r = 0.94
P<0.01
Optimum night temperature (°C)
10
13
16
19
22
25
Relative growth rate (RGR)
0.60
0.78
0.96
1.14
1.32
1.50
Pl
Cf
Cs
Bm
Lc
Fo
Hn

data from Grime *et al* 1988) of the species (Fig 3.3a,b), and there is a positive correlation between relative growth rate (RGR) (Grime & Hunt 1975) and optimum night temperature (3.3d). Root / shoot ratio is plotted against temperature for the control and drought treatments in Fig (3.4). The response of root/shoot ratio to drought was dramatic in the majority of inherently slow-growing species, with values elevated above the controls across the range of temperature regimes. The majority of potentially fast-growing plants either did not respond, or their root/shoot ratio was decreased (Fig 3.5). In species which were less sensitive to drought, shoot biomass was usually reduced more than root biomass.

3.5 DISCUSSION:

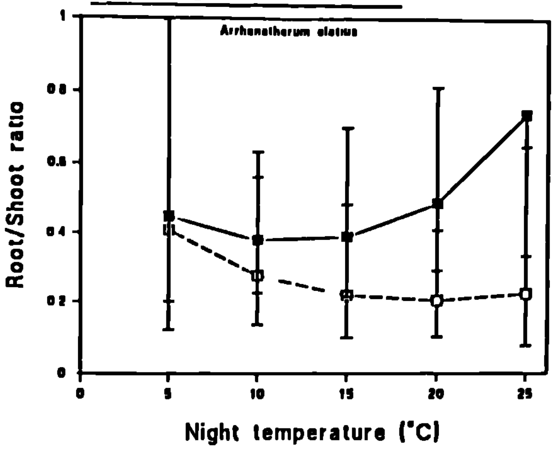
Figure 3.1 and Table 3.2 show that the species exhibit a wide range in optimal night temperature, and it is also apparent that variation in this respect is correlated with variation in potential relative growth rate (RGR) under non-limiting conditions (Fig 3.3d). In particular species such as *Plantago lanceolata, Centaurea scabiosa,* and *Carex flacca* with relatively higher RGR, occupied the top of the range in optimal night temperatures. With the exception of *Thymus praecox,* stress-tolerant species had lower night depression sensitivity indices. These results indicate that in potentially fast-growing plants dry matter production is depressed more severely than in slow-growing plants, by

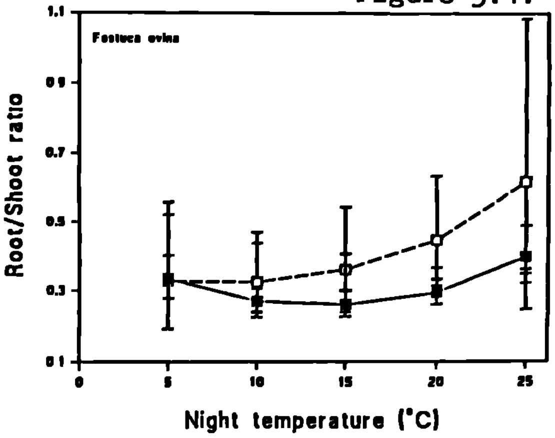
Figure 3.4:

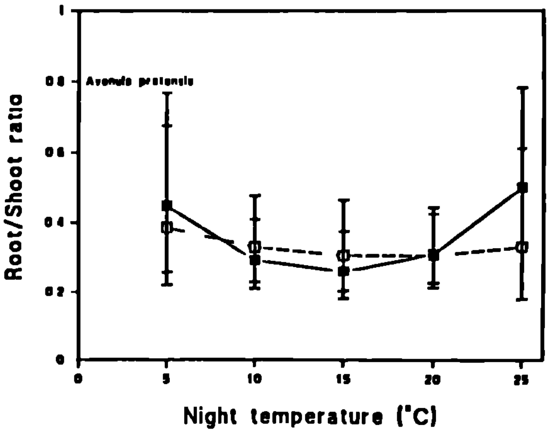
Fitted quadratic curves of root / shoot ratio of the species in response to temperature for control and droughted plants; Drought ---☐---
Control ——■——

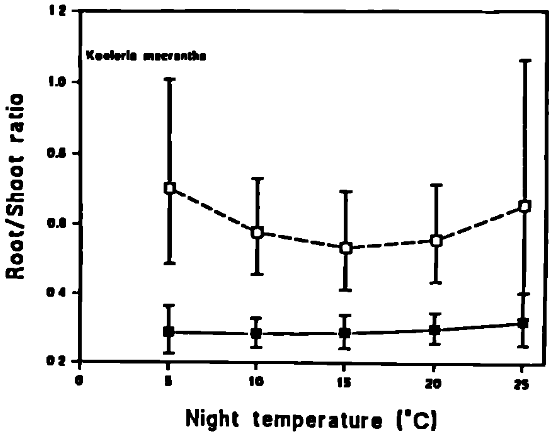
Figure 3.4:

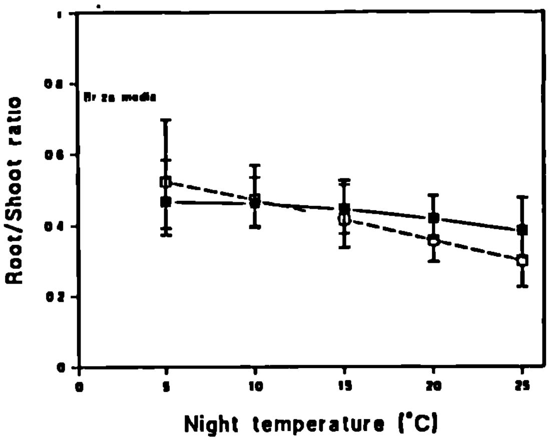
Grasses

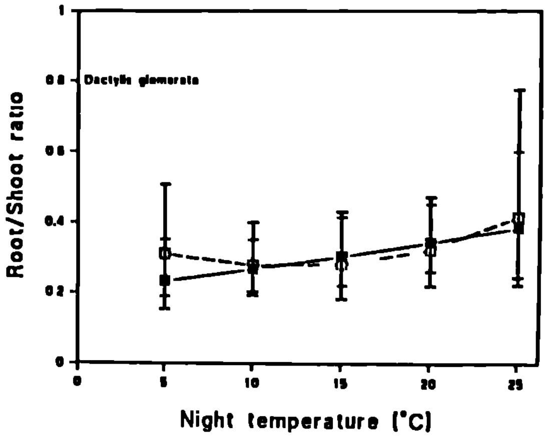




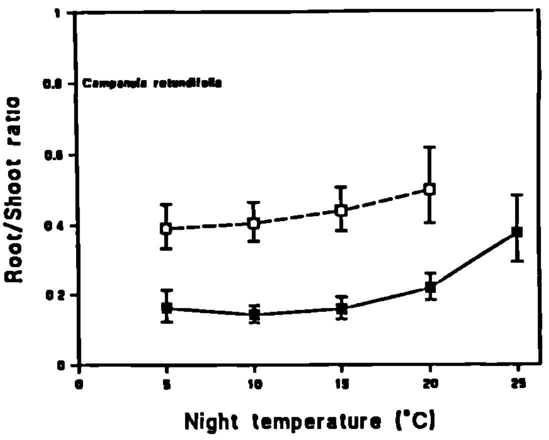








Dicots.



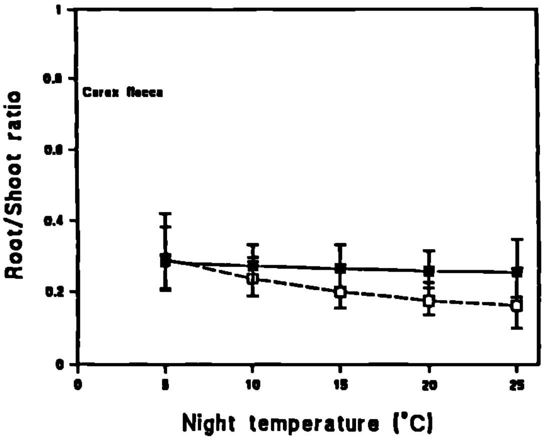
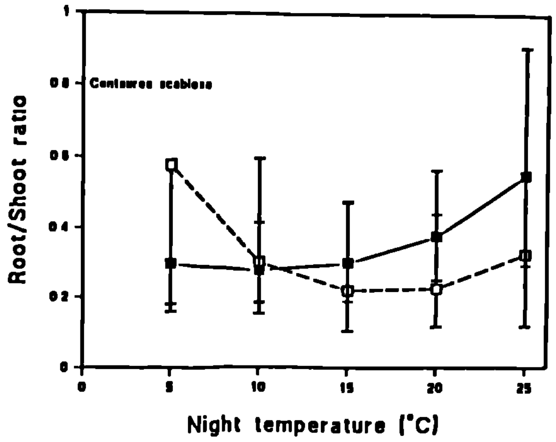
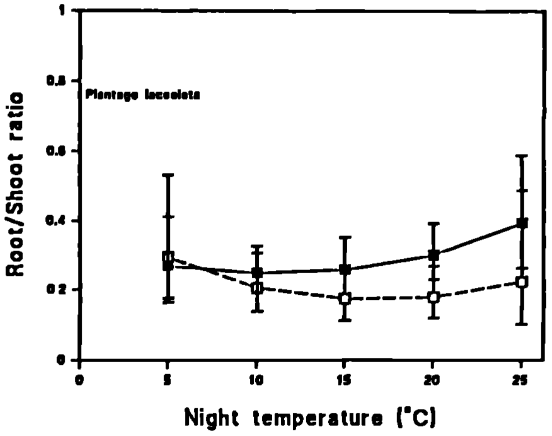
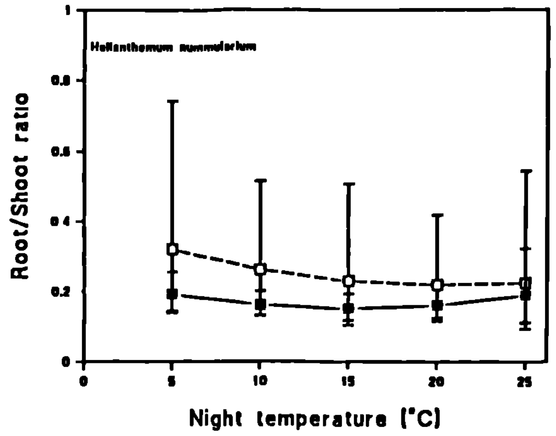
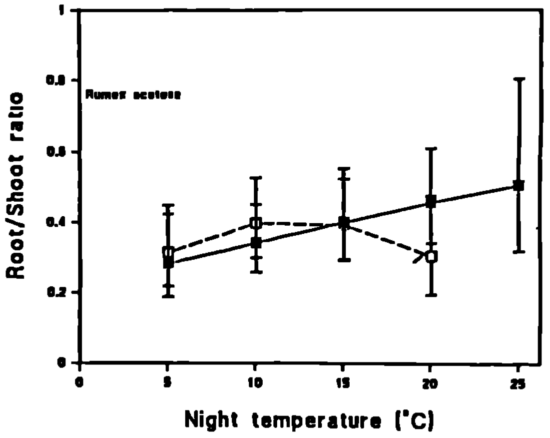


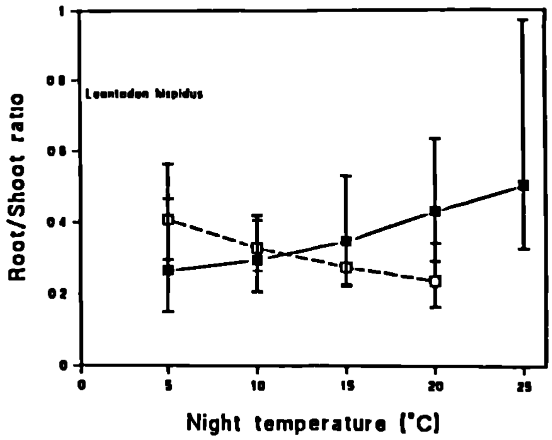
Figure 3.4 (contd.)

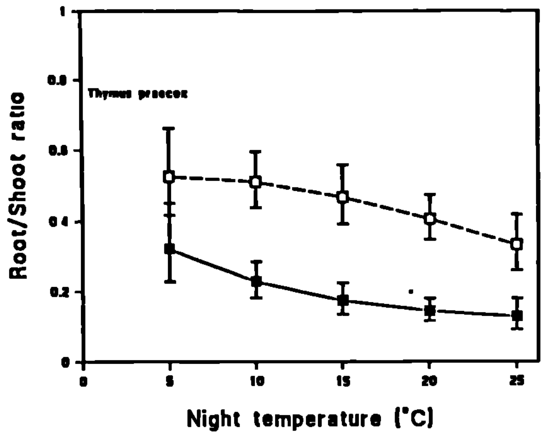


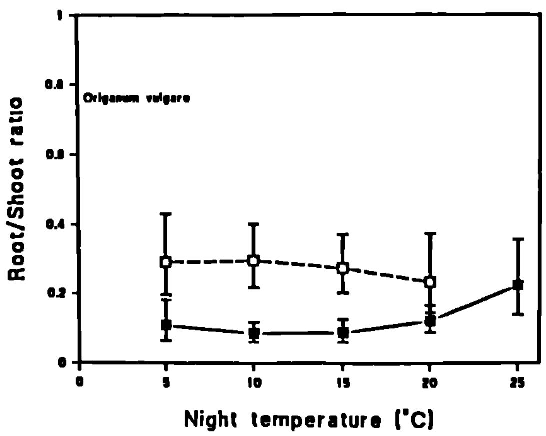




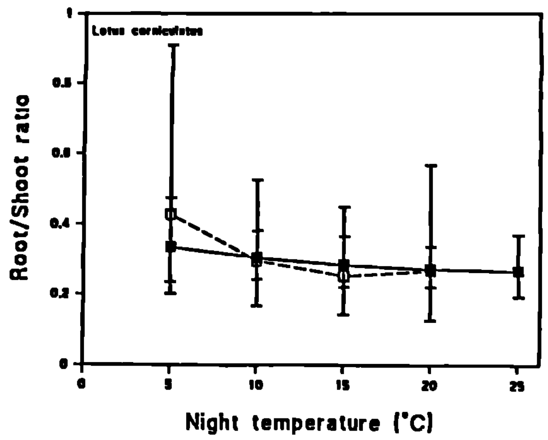








Legume



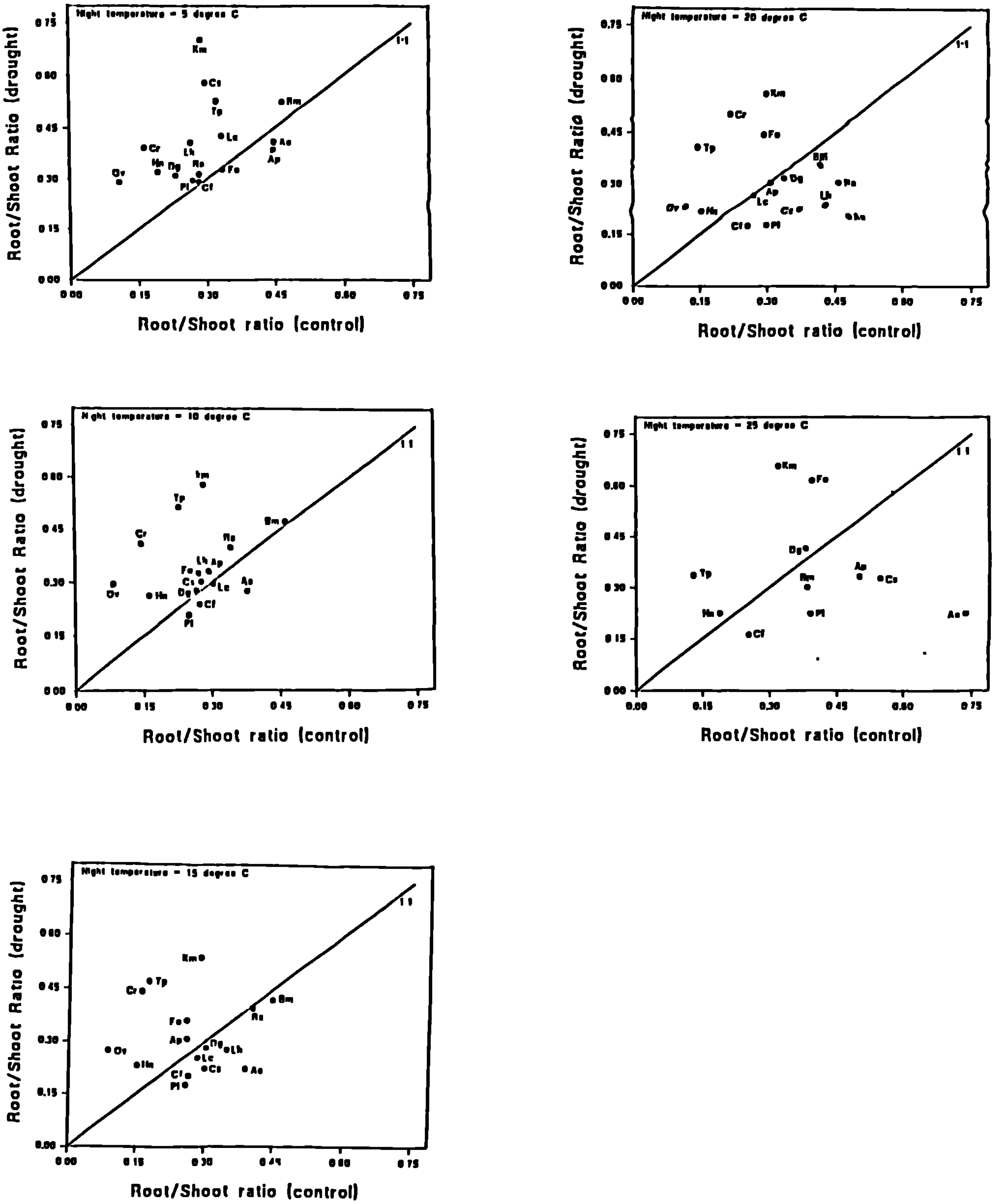


Figure 3.5: The effect of drought on the root : shoot ratio of various Millersdale species grown under five temperature regimes. Root : shoot ratio in drought treatment is plotted against control treatment for each night temperature regime. Key to species; *Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Plantago lanceolata (Pl), Thymus praecox(Tp), Lotus corniculatus (Lc).*

exposure to low night temperature. Greater reductions in RGR in response to a drop in temperature have also been reported in fast-growing species by Peterkin (1981); Rorison, Peterkin & Clarkson (1983); Kachi & Rorison (1990). Table 3.1 and Figure 3.1 indicate that the most marked responses of species to water-stress in terms of dry-matter reduction were in the potentially fast-growing plants *Arrhenatherum elatius, Dactylis glomerata, Plantago lanceolata,* and in *Lotus corniculatus,* a species which in the field may be dependent upon access to subsoil moisture through the deep tap-root. *Thymus praecox, Avenula pratensis, Campanula rotundifolia,* and *Festuca ovina* were among the most drought-tolerant of the species investigated.

As we might expect rising night temperature intensified the effect of drought (Fig 3.2). At 5°C night temperature the effect of drought on yield was negligible in all species. The main reason why effects of drought were not apparent at 5°C is that there is reduction in evaporation from the soil (and trays) and in transpiration by the plants. Clearly the plants in this treatment were not exposed to severe water stress.

Comparison of the rankings of the species with respect to sensitivity to drought and to low night temperature (Tables 3.1, and 3.2) reveals a positive correlation (Figure 3.3c) between responses to these two factors. In terms of dry matter production the slow-growing species were less affected by drought and lower temperature than the potentially fast-growing species; these results confirm earlier experimental data (e.g. Clarkson 1965; Higgs & James 1969) showing that there is a general trade-off between the capacity for a high potential relative growth rate when growing in optimal growth conditions and the degree of reduction of relative growth rate in suboptimal environments (Kruckeburg 1954; Beadle 1954; Bradshaw *et al* 1964; Grime 1965; Hackett 1967; Clarkson 1967; Parsons 1968; Higgs & James 1969; Loach 1970). The results reported in this chapter indicate that some plants sustained growth under both of the applied stresses.

An increase in root : shoot ratio in response to drought was mainly restricted to slow growing species which were less affected by drought. In comparison, potentially fast-growing species either did not respond to drought, or their root/shoot ratio decreased. This observation does not confirm the hypothesis that morphological plasticity in terms of root/shoot ratio is higher in fast-growing species than slow-growing species. It is not clear whether this was due to inherently low plasticity in root : shoot partitioning by the fast-growing species or was due to their more rapid exhaustion of water and consequently reduced opportunity for growth responses to moisture stress.

Chapter 4

A comparative study of seedling growth responses of *Arrhenatherum elatius* and *Festuca ovina* to mineral nutrients, water supply and temperature regimes.

4.1: INTRODUCTION

As explained in the first chapter the south-facing slope of Millers-dale, which is the focus of the investigation, is nutritionally poor, subjected to drought during the summer, and has dominant species which are classified (Grime, Hodgson & Hunt 1988) as relatively stress-tolerant. Fast-growing plants are either absent, or scarce at the site. The spatial analysis of the community described in Chapter 2 revealed variation in soil depth and habitat productivity, and phenological studies (Al-Mufti *et al* 1977) have shown that limestone grasslands of the type occurring in Millersdale contain species differing considerably in seasonal timing of shoot growth. It was therefore considered essential in attempting to analysis the functional characteristics of the community to examine the responses of all the major component species to factors such as temperature and moisture supply; these experiments are described in Chapters 3 and 5. This chapter addresses a rather different problem and is concerned with the role of mineral stress and drought in the failure of *Arrhenatherum elatius*, a common grassland species in Millersdale, to invade the study site. An earlier field experiment conducted by Grime and Curtis (1976) suggested that the mechanism excluding *A. elatius* involved an interaction between mineral nutrient stress and summer desiccation. The purpose of the experiment described in this chapter was to examine this phenomenon in detail by means of a multifactorial study employing the temperature gradient tunnel. Three factors; water supply, nutrient supply and night temperature were manipulated and the responses of *A. elatius* were compared with those of *Festuca ovina*, a species which is of wide occurrence within the Millersdale site.

4.2: MATERIALS AND METHODS

Seeds of *Festuca ovina* and *Arrhenatherum elatius* were germinated over de-ionized water in closed transparent boxes experiencing 20/15 °C day/night temperature and 29 Wm^{-2} irradiance. Seedlings were planted into 220 ml plastic flowerpots, each of which was filled with Leighton Buzzard silica sand and saturated with full Rorison nutrient solution (Hewitt 1966) (nutritionally-rich-treatment), or 1:25 full Rorison solution (nutritionally-poor-treatment). Pots were placed in shallow trays filled to 5 mm with de-ionized water and transferred to the temperature gradient tunnel. The five tunnel compartments were adjusted to night temperatures of 5 / 10 / 15 / 20 / 25 °C respectively. Day temperature was 25°C for all compartments, with a 14 h. photoperiod. Seven days after planting, two watering regimes (control & drought) were implemented. All plants were watered with 50 ml full Rorison solution, or 1/25 full Rorison solution for rich- and poor-nutritional treatments respectively per pot every 5 days. The controls were supplied with an additional daily replenishment of de-ionized water to 5 mm in each tray. The complete design was: 2 species x 5 night temperatures x 2 water regimes x 2 nutritional regimes each containing 8 replicates.

Fitted quadratic curves (Hunt & Parsons 1974, 1981) were used to describe the response to temperature of total dry weight per plant and root:shoot ratio. In addition a drought sensitivity index (see Chapter 3) was calculated. Analyses of variance were used to examine the responses of plants to individual stresses and their interaction.

3.3: RESULTS

Yield

In all treatments the amount of biomass achieved by *A.elatius* was higher than *F.ovina* (Fig 4.2).

Two way analysis of variance showed that, in the case of *Festuca ovina*, in dry weight production, there was no significant interaction between temperature, water, and nutrient regimes. In contrast, for *Arrhenatherum elatius*, there was interaction between water and nutrients ($P<0.001$), water and temperature ($P<0.05$), and no significant interaction between nutrients and different temperature regimes (Appendix 3.1).

The responses of the two species to the different treatments are illustrated in Fig 4.1, and 4.2. Under conditions of high nutrition and continuous water supply *Festuca ovina* was relatively unresponsive to night temperature and showed an ill-defined optimum at about 15 °C. *Arrhenatherum elatius* exhibited a positive response, Fig 4.1:

Fitted quadratic curves of ln (total dry weight per plant) of two contrasted species (*Arrhenatherum elatius* and *Festuca ovina)* in response to temperature and nutrient treatments for control and droughted plants.

Figure 4.1:

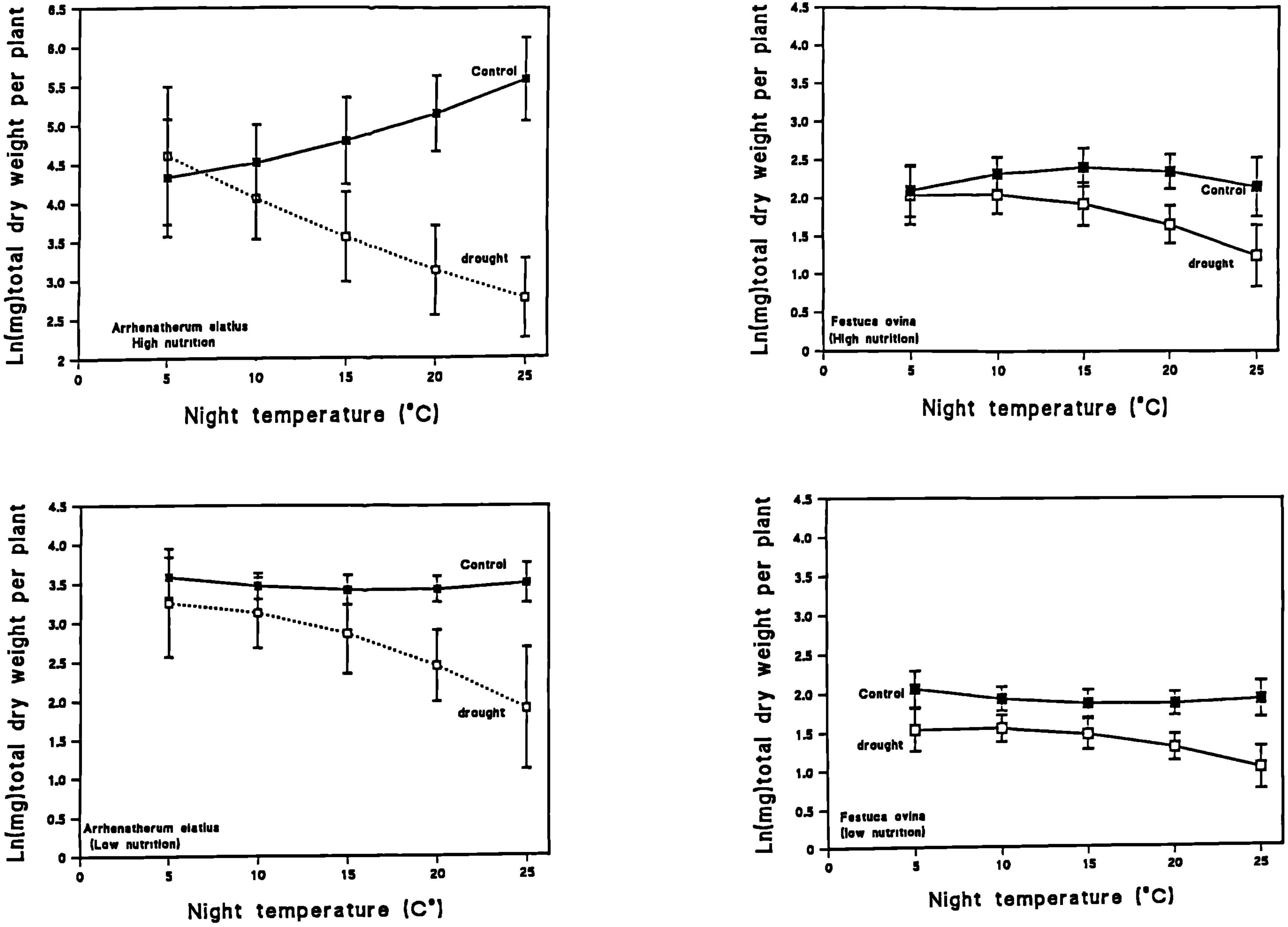
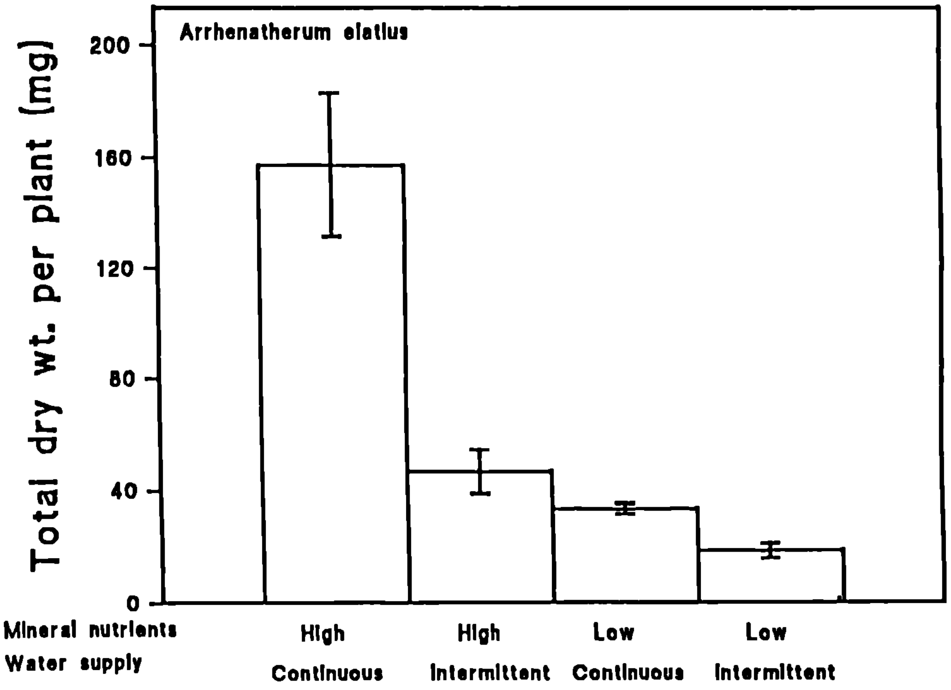

Ln(mg)total dry weight per plant
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2
0
5
10
15
20
25
Control
drought
Arrhenatherum elatius
High nutrition
Night temperature (°C)
Ln(mg)total dry weight per plant
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
Control
drought
Festuca ovina
(High nutrition)
Night temperature (°C)
Ln(mg)total dry weight per plant
Control
drought
Arrhenatherum elatius
(Low nutrition)
Night temperature (C°)
Ln(mg)total dry weight per plant
Control
drought
Festuca ovina
(low nutrition)
Night temperature (°C)

Figure 4.2:



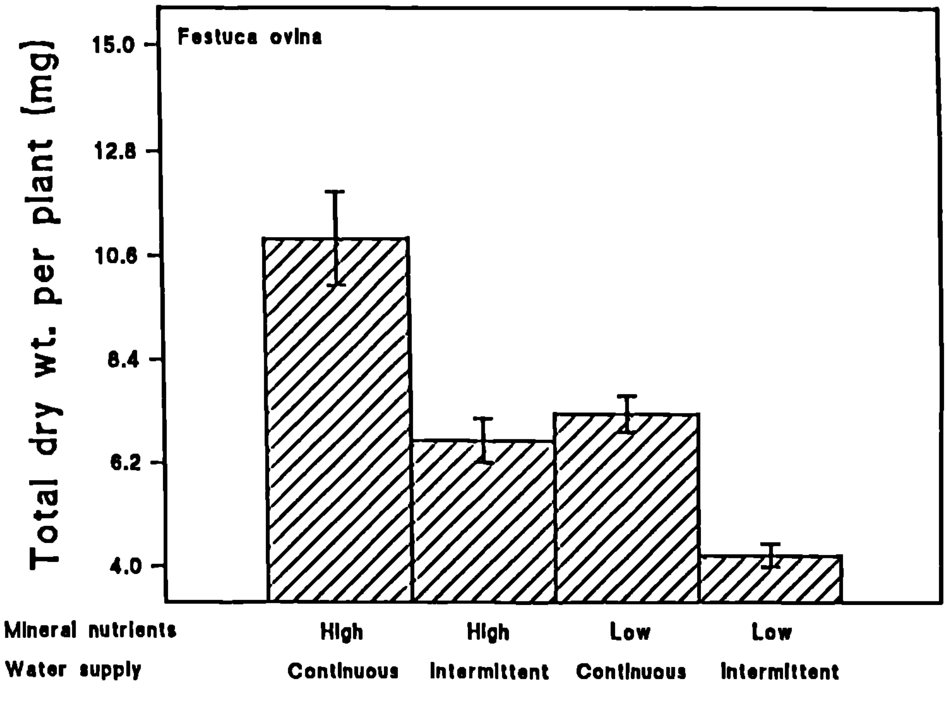


Figure 4.2:
The comparison of the biomass production of two contrasted species (*Arrhenatherum elatius* and *Festuca ovina*) in different mineral nutrient and watering regimes.

over the complete range investigated indicating an optimum night temperature >25 °C. Neither of the species showed a significant response to high temperature in the low nutrients and continuously moist treatment. Under high nutrient treatment, at the lowest temperature (5 °C) there was no significant difference in dry weight production between control and drought treatments. In contrast, at low nutrient treatment, both species as a result of drought reduced their biomass. This effect only for *Festuca ovina* was significant. As we might expect, the effect of higher temperatures is to increase the effect of water-stress on biomass production. The effect of water-stress on *A. elatius* was 2.5 fold stronger than *F. ovina* in nutritionally-rich treatment (Fig 4.2), but this effect on *A. elatius* was remarkably reduced in the nutritionally-poor treatment (Fig 4.2). In case of *F. ovina* the effects of drought in either nutritional regimes were similar (Fig 4.2).

Root : shoot ratio

The responses of the two plants to different treatments in terms of root:shoot ratio are illustrated in Fig 4.3a, 4.3b, and 4.4. Plant response to temperature in terms of root:shoot ratio did not exhibit a clear-cut pattern (Fig 4.3a,b). *Arrhenatherum elatius* failed to respond to water-stress in the nutritionally-poor treatment, and reduced its root:shoot ratio in the nutritionally-rich treatment (Fig 4.3a). In contrast, *Festuca ovina* allocated more dry weight to the root system in response to drought

Figure 4.3a:

Fitted quadratic curves of **root /shoot ratio** of ***Arrhenatherum elatius*** in response to temperature and different mineral nutrients treatment for control and droughted plants.

Figure 4.3a:

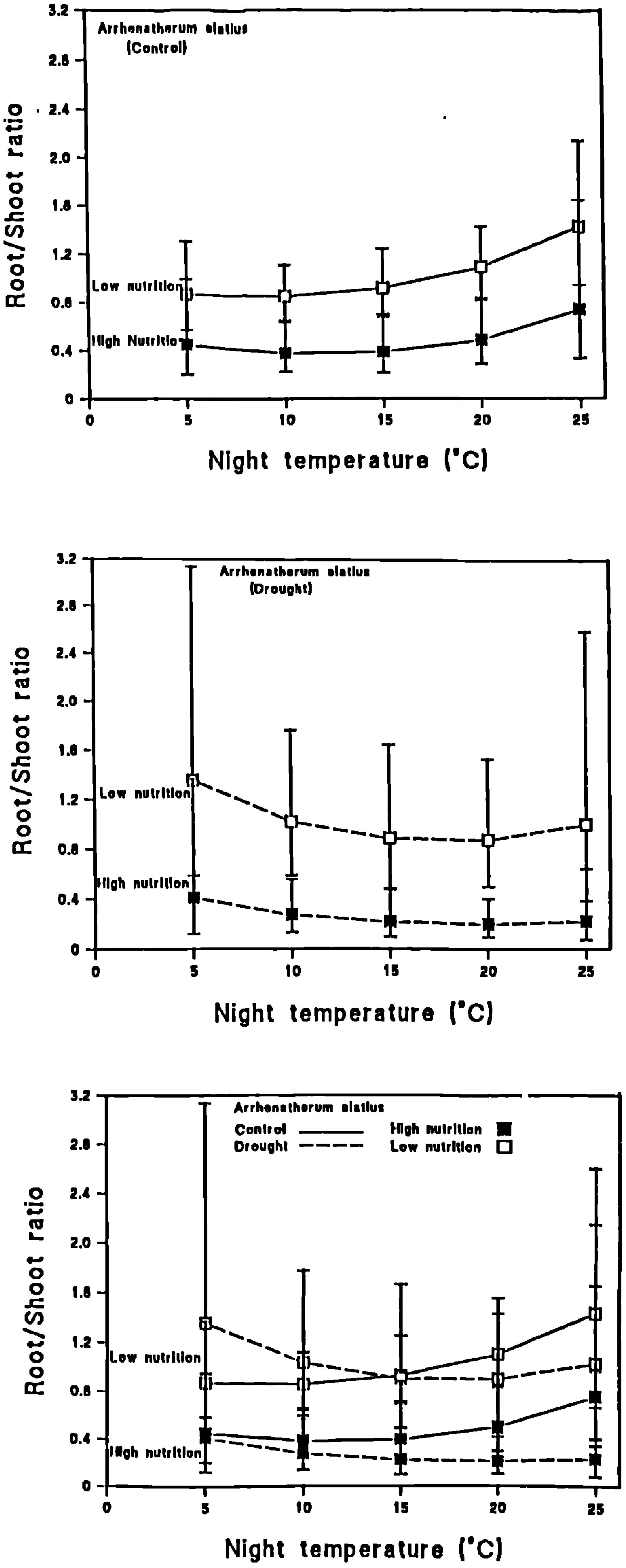
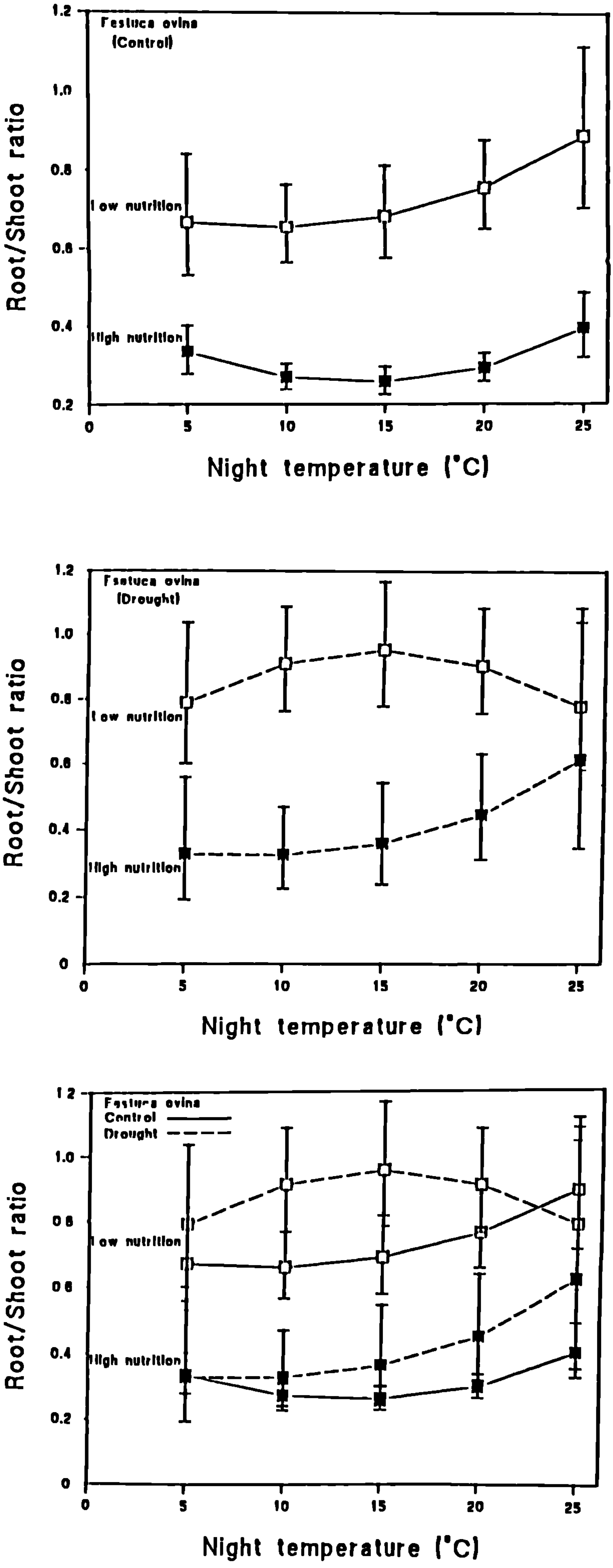

Arrhenatherum elatius
(Control)
Root/Shoot ratio
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0
Low nutrition
High Nutrition
0
5
10
15
20
25
Night temperature (°C)
Arrhenatherum elatius
(Drought)
Root/Shoot ratio
Low nutrition
High nutrition
Night temperature (°C)
Arrhenatherum elatius
Control
Drought
High nutrition ■
Low nutrition □
Root/Shoot ratio
Low nutrition
High nutrition
Night temperature (°C)

Figure 4.3b:

Fitted quadratic curves of **root /shoot ratio** of *Festuca ovina* in response to temperature and different mineral nutrients treatment for control and droughted plants.

Figure 4.3b:


Festuca ovina
(Control)
Low nutrition
High nutrition
Root/Shoot ratio
Night temperature (°C)
0.2
0.4
0.6
0.8
1.0
1.2
0
5
10
15
20
25
Festuca ovina
(Drought)
Low nutrition
High nutrition
Root/Shoot ratio
Night temperature (°C)
0
0.2
0.4
0.6
0.8
1.0
1.2
0
5
10
15
20
25
Festuca ovina
Control
Drought
Low nutrition
High nutrition
Root/Shoot ratio
Night temperature (°C)
0
0.2
0.4
0.6
0.8
1.0
1.2
0
5
10
15
20
25

in both nutritional treatments (Fig 4.3b). Both species increased their root:shoot ratio under the nutritionally stressed condition (Fig 4.3a,b); this response was highly significant in the case of *F. ovina* ($P<0.001$) and less so in *A. elatius* ($P<0.01$). Generally the response in root:shoot ratio to nutritional stress was more marked than that to water-stress (Fig 4.3a,b). *Arrhenatherum elatius* had a generally higher root:shoot ratio than *F. ovina*, but *F. ovina* showed higher plasticity in response to the different treatments (Fig 4.4).

On the basis of two way analysis of variance (Appendix 4.1) the root:shoot ratio of *A. elatius* was mainly affected by nutritional regimes, whilst other two factors (water & night temperature) had no significant effects. In *Festuca ovina* the root : shoot ratio was sharply influenced by nutrient supply ($P<0.001$), but also responded to water supply ($P<0.01$) and showed evidence of an interaction between nutrient and temperature ($P<0.05$) (Appendix 4.1).

4.4: DISCUSSION

Yield

In the nutritionally-rich and continuously moist treatment at warmer temperatures, *Arrhenatherum elatius* showed the greatest growth, and this species was more sensitive than *Festuca ovina* to low night temperature. Such differences between fast- and slow-growing plants have been reported by Rorison (1980), and Peterkin (1981). Phenological studies

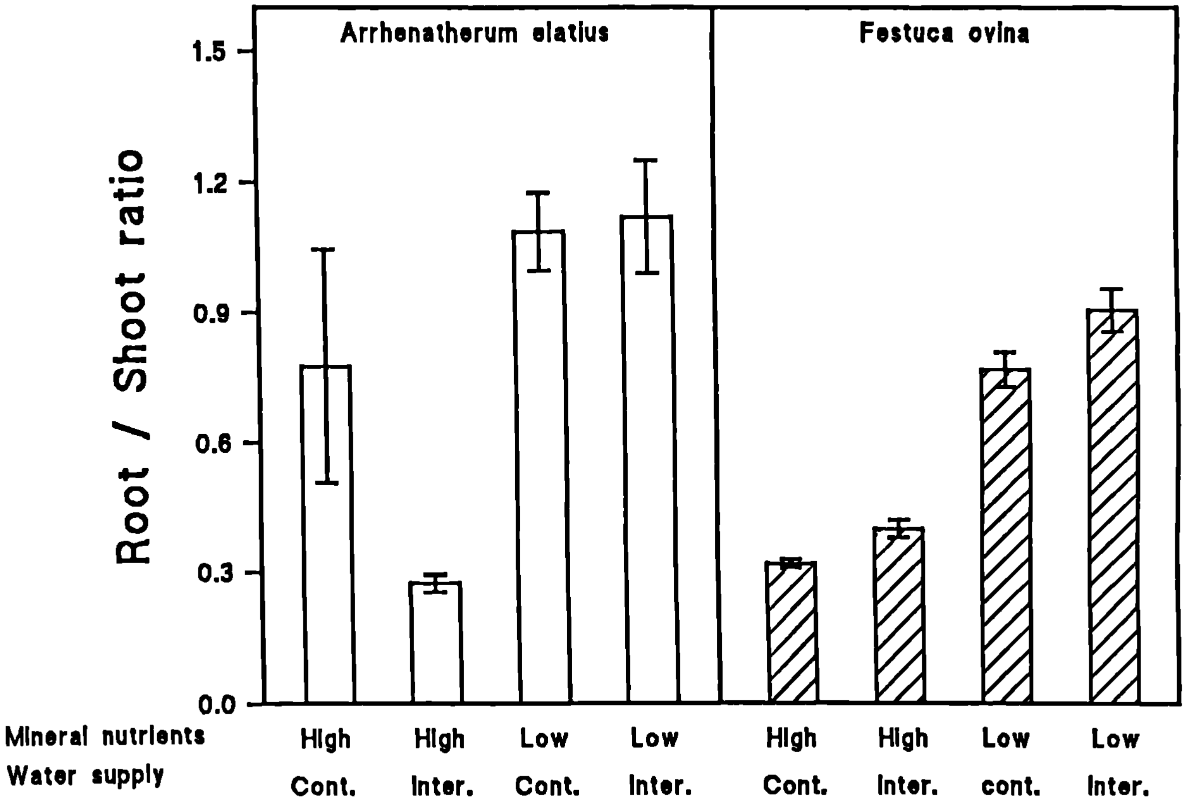


Figure 4.4:
The comparison of the root / shoot ratio variation of two contrasted species (*Arrhenatherum elatius* and *Festuca ovina*) in response to different nutrient and watering treatments.

(Al-Mufti *et al* 1977) have shown that in Millersdale these two species differ considerably in seasonal timing of shoot growth; *A. elatius* reaches a maximum standing crop in July. In contrast, *F. ovina* continues to make a major contribution to standing crop throughout the year. In low mineral nutrient supply and continuously moist conditions , there was no significant effect of temperature on growth in either species.

Both species were affected by water-stress, although *A. elatius* was more sensitive than *F. ovina,* a result similar to that reported in a field experiment by Grime and Curtis (1976). In the case of *A. elatius* there was a significant ($P<0.001$) interaction between drought and nutrient regime; In the nutrient rich condition, the effect of drought in reducing the biomass of *A. elatius* was more severe than in the nutrient poor treatment; this is not surprising since the reduced shoot growth under nutrient stress would inevitably delay the onset of desiccation.

The low sensitivity of dry matter production in *Festuca ovina* to nutrient-deficiency and low temperature and the high sensitivity of *A. elatius* to drought, nutrient-deficiency, and low temperature in the experiment are consistent with the data and conclusions of Al-Mufti *et al* (1977), Grime and Curtis (1976), and Peterkin (1981). It seems reasonable to conclude that on the south-facing slope *Arrhenatherum elatius* is severely restricted in abundance by droughting, and by mineral-nutritional stress. In contrast *Festuca ovina* through its tolerance of drought is able to persist in areas of shallower soil , but it is only able to grow slowly and in the wetter and cooler parts of the year. Although in all the experimental treatments, the total dry weights per plant achieved by *A. elatius* were higher than those of *F. ovina*, the proportional suppression as a result of the various treatments was higher in *A. elatius*..

Root : shoot ratio

Arrhenatherum elatius produced a higher root:shoot ratio than *Festuca ovina*, but despite this, *F. ovina* demonstrated higher morphological plasticity, here defined as the degree to which the root : shoot ratio changed in response to different stresses (Pearce 1987). This result is supported by the conclusion of the previous chapter, where drought tolerant plants, which were mainly slow-growing species, increased their root:shoot ratio in response to drought.

We can conclude that the response of species allocation patterns to stress depends on both genotype and environment; either *Arrhenatherum elatius* is common where drought is not a major environmental factor, or it can avoid it by means of a long root system, and this may account for its poor response to drought.

Chapter 5

A comparative study of root penetration

5.1. INTRODUCTION:

It is hypothesized in Chapter I that an important mechanism which enables some plants to avoid drought involves root systems which penetrate deeply into the soil profile. It is also possible that differences in vertical root distribution contribute to the mechanism which allows species co-existence by complementary exploitation of water, nutrients, space and season (Sydes & Grime 1984). Although there are several different factors which determine the rate at which the root system of a plant will grow and penetrate the soil, the experiment described in this chapter was designed to provide an extremely simple screening procedure to compare under standardised conditions the root penetration of seventeen species of common occurrence in Millersdale (see Chapter 3; Table 3.0). The experiment also allowed an analysis of the effects of water-stress on the development of the root system in each species.

In marked contrast to the technique applied in the experiment with the temperature gradient tunnel (Chapters 3 and 4), the experiment was conducted using a large and vertically-extensive soil volume so that (a) the profile of root growth with depth could be recorded and (b) progressive drying of the surface layer of the soil could be achieved. Previous large-scale ecological root studies have been accomplished using long boxes and tubes of various designs (see review by Bohm 1979). Cylindrical tubes of a range of materials and dimensions have been used more often than boxes. In recent years, plastic cylinders have been used with good success. In the experiment described in this chapter polythene tubing was used; this material has the advantage of being easy to cut longitudinally thus facilitating recovery of the roots at the time of the final harvest. This approach is also more economical in comparison with many others, particularly when large numbers of species are screened.

5.2. MATERIALS AND METHODS:

The pots used in the experiment were designed to simulate a soil profile with a crevice of sandy soil (Plate 5a). Each seedling was grown individually in a 1 metre long polythene tube, 7.7 cm in diameter and pre-labelled at 10 cm intervals (= 10 sections in total) (Plate 5.1). At the bottom of the tube there were drainage holes. Each tube contained 3 kg of sand, which at field capacity had an average water content of 25.44%. The experiment was conducted in a controlled growth-room; with 29 Wm^{-2} irradiance, 14 h. photoperiod, 22°C day / 17°C night temperatures, and 60 / 90% relative humidity at day and night, respectively. The tubes were housed in a specially constructed frame.

At the beginning of the experiment, the sand in each tube was saturated with Rorison solution. Seeds from the seventeen species (Table 5.1) were germinated on moist filter paper. One seedling was planted in the centre of each pot. Each species was subjected to two treatments (control

Plate 5.1: Side view of experiment with front reflecting panel removed to show the vertical tubes of sand.

and droughted). Each treatment was provided with six replicates. After planting, all tubes regardless of treatment had an identical mineral nutrient supply and watering regime for the first three weeks. Rorison solution (10 ml) was added to each pot every day, and in order to avoid drying of the sand surface, water supply was replenished by surface application of deionized water using a plastic spray-can. For the first three weeks this same treatment was maintained. After three weeks a drought regime was imposed upon half the plants (6 pots) by withholding further water supply until the end of the experiment. In the remaining half of the experiment daily watering was continued. Nutrient additions were terminated for all plants after three weeks.

After six weeks (three weeks establishment + three weeks treatment), each plant was harvested. The shoots were severed at the soil surface. The tube with its content of sand and roots was cut into ten 10 cm portions using a safety razor blade. By sieving and washing, the roots were recovered from each portion separately. Maximum root depth (in terms of root penetration) was measured. All plant materials were dried at 80°C for 48h. prior to weighing. The moisture content of the sand at various depths in each tube was measured at harvest.

The results were subjected to one-way analysis of variance, root:shoot ratio was calculated, and, finally, the pattern of root development within the tube by each species and in each moisture treatment was assessed. By comparing the quantity of root dry matter in the C_2 (11-100 cm) section as a percentage of that in the C_1 (0-10 cm) section it has been possible to obtain a measure of the degree of crevice exploitation (E) occurring in each species, where $E = C_2/C_1 \times 100$ (Sydes & Grime 1984). The morphological plasticity exhibited by the root (MPR) in response to the drought treatment can be obtained by using the ratio E_d/E_c, where E_d and E_c are the degree of crevice exploitation in drought and control conditions respectively.

5.2. RESULTS:

All plants of *C. flacca* died in the water-stress treatment. The distribution of moisture in the experimental tubes at the end of the growth period is illustrated in Fig 5.1. Moisture content was extremely low in the uppermost 10 cm (first section) of tubes in the stress treatment. In the remaining sections of the droughted tubes moisture levels were lower than the control values but the differences were far less than those occurring in the upper layer.

The depths attained by the roots of all seventeen species are given in Table 5.1. The longest and the shallowest root system belonged to *Rumex acetosa* and *Carex flacca*, respectively. In most of the species, the water-stress treatment induced greater root penetration (Figure 5.2), but statistically significant effects were detected only in *Helianthemum nummularium* and *Leontodon hispidus*. Total yield per plant and total shoot and root dry weights are given in

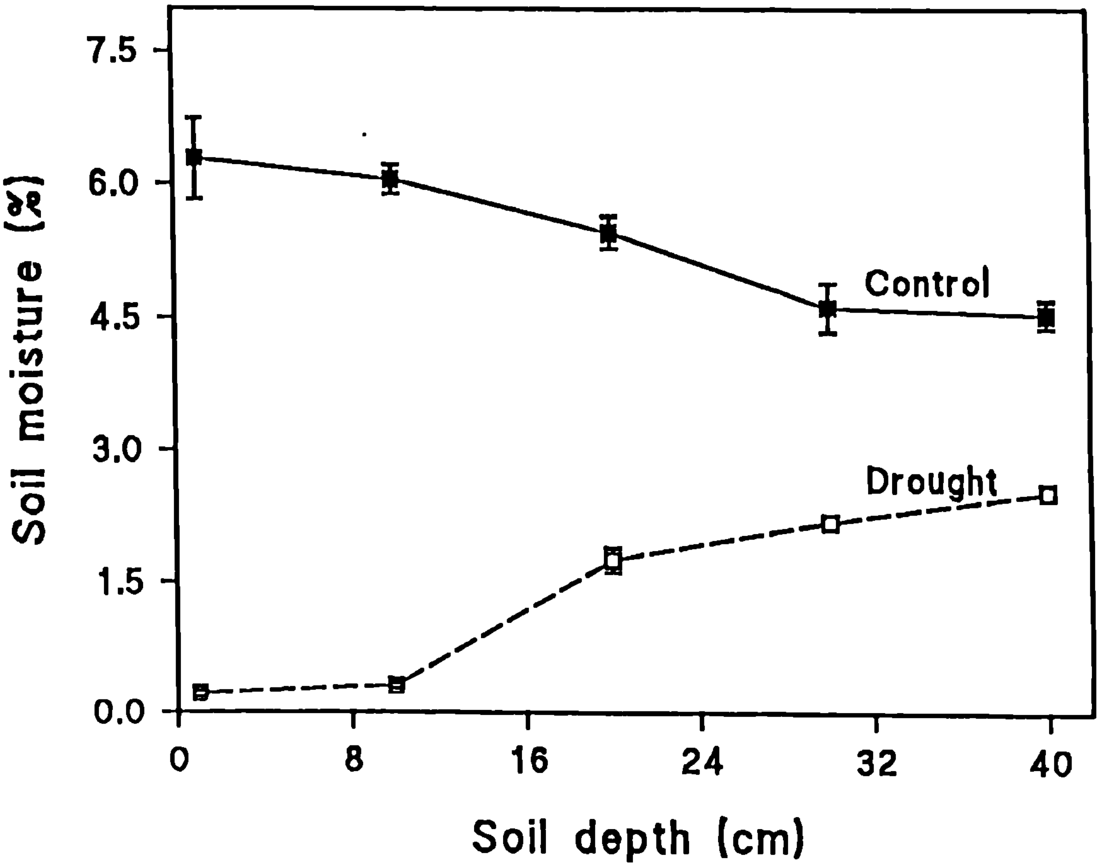


Figure 5.1: The distribution of moisture in the experimental tubes at the end of the growth period in control and drought treatments.

Bars = SE.

SPECIES	MEAN ROOT PENETRATION (mm)		
	Control	Drought	F-Test
Rumex acetosa	515.4	521.0	N.S.
Hieracium pilosella	428.3	472.2	N.S.
Arrhenatherum elatius	394.4	405.2	N.S.
Dactylis glomerata	351.0	388.6	N.S.
Plantago lanceolata	296.0	428.0	N.S.
Centaurea scabiosa	278.3	287.5	N.S.
Thymus praecox	248.6	234.0	N.S.
Avenula pratensis	224.0	316.0	N.S.
Festuca ovina	215.8	230.0	N.S.
Leontodon hispidus	199.8	299.0	***
Koeleria macrantha	186.5	224.5	N.S.
Campanula rotundifolia	184.2	223.4	N.S.
Lotus corniculatus	165.0	204.0	N.S
Origanum vulgare	155.0	164.0	N.S.
Briza media	146.0	155.0	N.S.
Helianthemum nummularium	113.8	160.0	**
Carex flacca	85.0	47.0	***

Table 5.1: The depth attained by the roots of seventeen species in control and drought treatments.
; $P<0.01$, *; $P<0.001$.

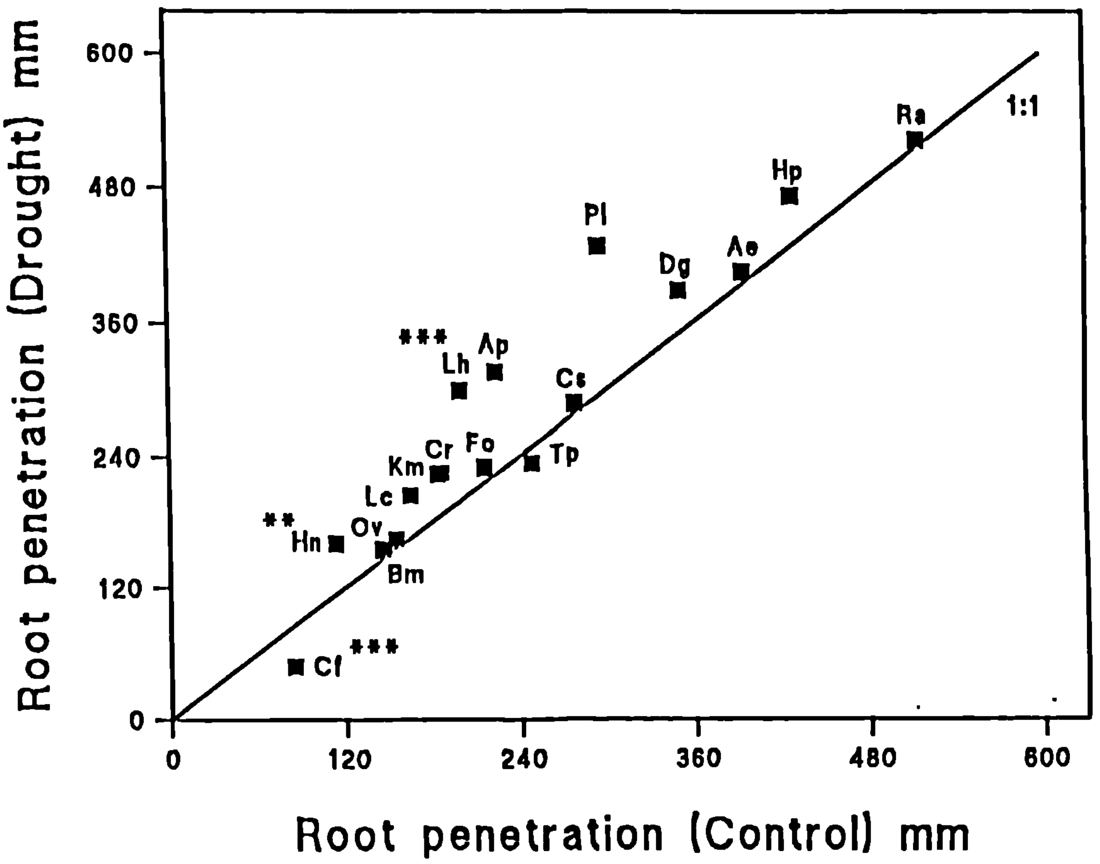


Figure 5.2: Comparison of mean root penetrationin control and drought treatments. Key to species;

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Hieracium pilosella (Hp), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Plantago lanceolata (Pl), Thymus praecox(Tp), Lotus corniculatus (Lc).

Table 5.2. Four of the seventeen species showed significant reduction in total dry weight in response to stress. Most of the reduction in *Arrhenatherum elatius* took place in the root system but in the other three, *C. flacca, Hieracium pilosella* and *Lotus corniculatus*, both shoot and root were affected (Table 5.2). Over the range of species there was a positive relationship between root depth and yield ($P<0.05$ in control and $P<0.001$ in the drought treatment), and also between root depth and (max.)relative growth rate (Grime & Hunt 1975) ($P<0.01$ in control and $P<0.02$ in drought). Root dry matter (% of total) in each of the tube sections at the end of the experiment, for each of the seventeen species investigated is presented in Figure 5.3. The pattern of distribution and redistribution of root dry weight down the profile in response to watering regime is expressed as the two indices (E) and (MPR), and is given in Table 5.4. The upper 10 cm was the dominant contributor to the total root dry weight although, as we might expect, values were lower in the control than in the stressed plants, and the contribution of the sections below 10 cm was lower in the control than in the stressed plants (Fig.5.4).

With respect to root:shoot ratio eight species responded significantly to drought, but the form of response was extremely variable, with *Plantago lanceolata, Origanum vulgare,* and *Leontodon hispidus* increasing their root : shoot ratio, and *A. elatius* , *Briza media, Festuca ovina,* and *Koeleria macrantha* showing reductions (Table 5.3). This difference between grasses and forbs was statistically

	DRY WEIGHT PER PLANT (mg)								
	TOTAL			SHOOT			ROOT		
	control	drought		control	drought		control	drought	
A.elatius	209.34	143.36	***	80.03	71.87	N.S.	129.31	73.49	***
A.pratensis	64.12	64.68	N.S.	30.29	34.19	N.S.	33.83	30.49	N.S.
B.media	29.99	20.18	N.S.	10.10	11.56	N.S.	19.90	8.62	***
D.glomerata	120.08	108.51	N.S.	59.31	54.89	N.S.	60.76	53.63	N.S.
F.ovina	26.40	23.58	N.S.	13.13	14.14	N.S.	13.27	9.44	N.S.
K.macrantha	24.57	25.07	N.S.	10.38	14.72	N.S.	14.20	10.35	N.S.
C.rotundifolia	11.94	17.99	N.S.	3.70	7.54	N.S.	8.24	10.46	N.S.
C.flacca	16.49	6.05	***	8.01	3.99	***	8.49	2.49	***
C.scabiosa	77.88	52.49	N.S.	24.98	15.27	**	52.90	37.22	N.S.
H.nummularium	8.45	9.65	N.S.	4.64	4.13	N.S.	3.81	5.52	N.S.
H.pilosella	111.96	66.96	***	50.30	26.84	***	61.66	40.12	***
L.hispidus	37.88	43.70	N.S.	12.75	18.25	N.S.	25.13	25.45	N.S.
O.vulgare	24.73	16.91	N.S.	16.20	7.17	N.S.	8.53	9.74	N.S.
P.lanceolata	89.90	75.04	N.S.	42.38	28.59	N.S.	47.52	46.45	N.S.
R.acetosa	77.55	66.10	N.S.	22.52	21.52	N.S.	55.03	44.39	N.S.
T.praecox	30.55	28.03	N.S.	16.02	14.08	N.S.	14.53	13.94	N.S.
L.corniculatus	53.87	15.40	***	29.49	8.37	***	24.38	7.04	***

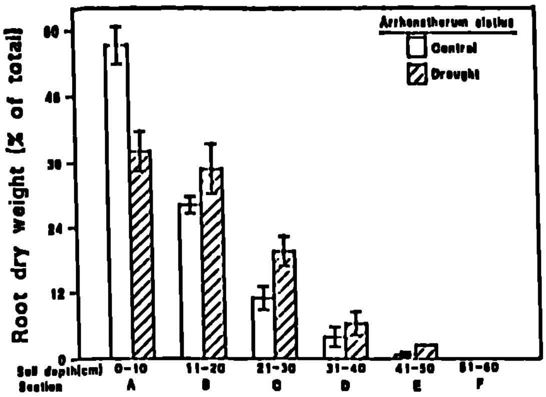
Table 5.2: The comparison of yield per plant (mg) of species in control and drought treatments after six weeks (three weeks establishment + three weeks treatment). Species in drought treatment experienced continued drought by withholding further water supply for three weeks in 1 metre long experimental tubes. The analysis of variance based on F-test;
*; P<0.05, **; P<0.01, ***; P<0.001.

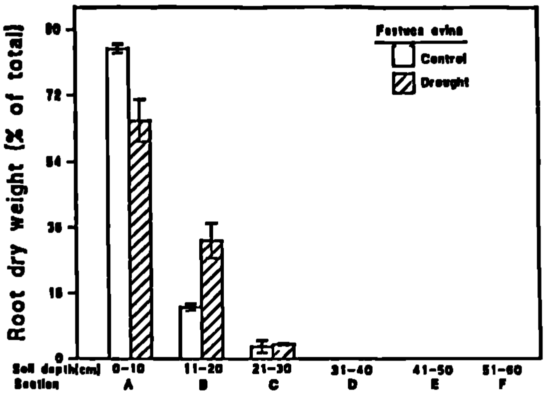
Figure 5.3:

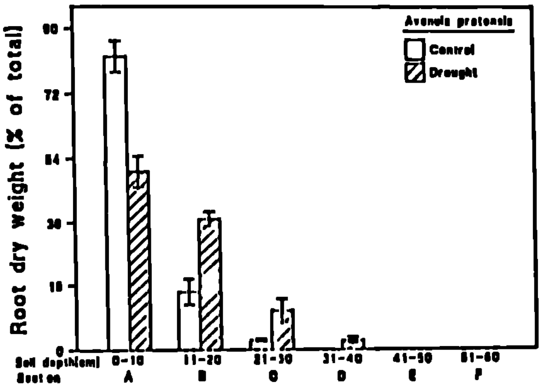
Distribution of root dry matter (% of total) of species in different sections of the experimental tubes in control and drought treatments.

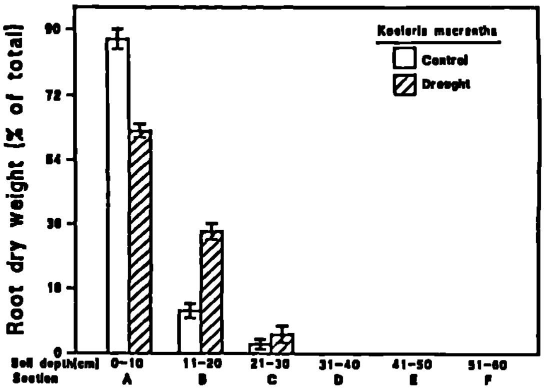
Figure 5.3:

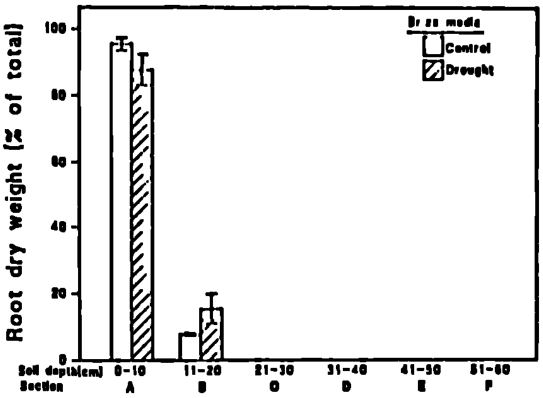
Grasses



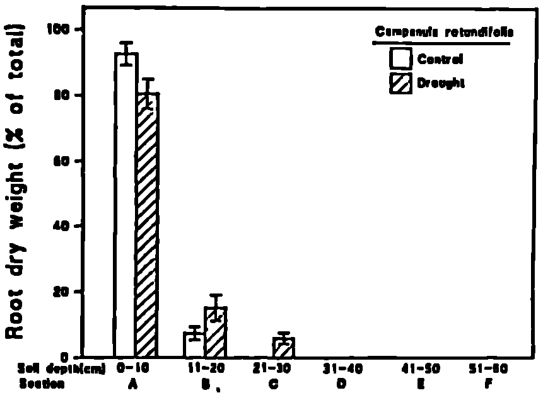


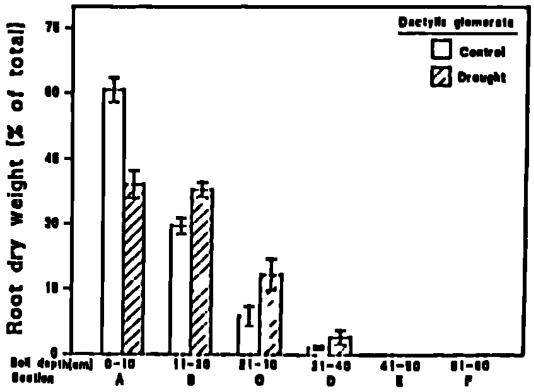






Dicots.





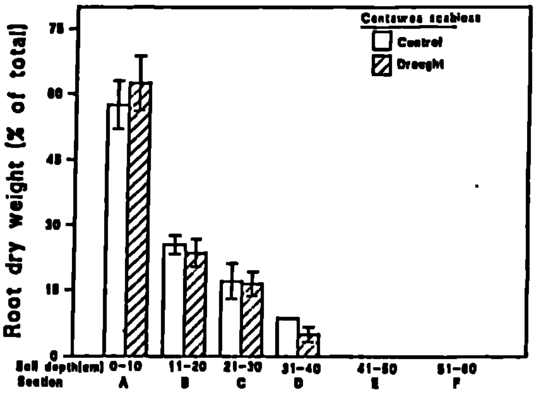
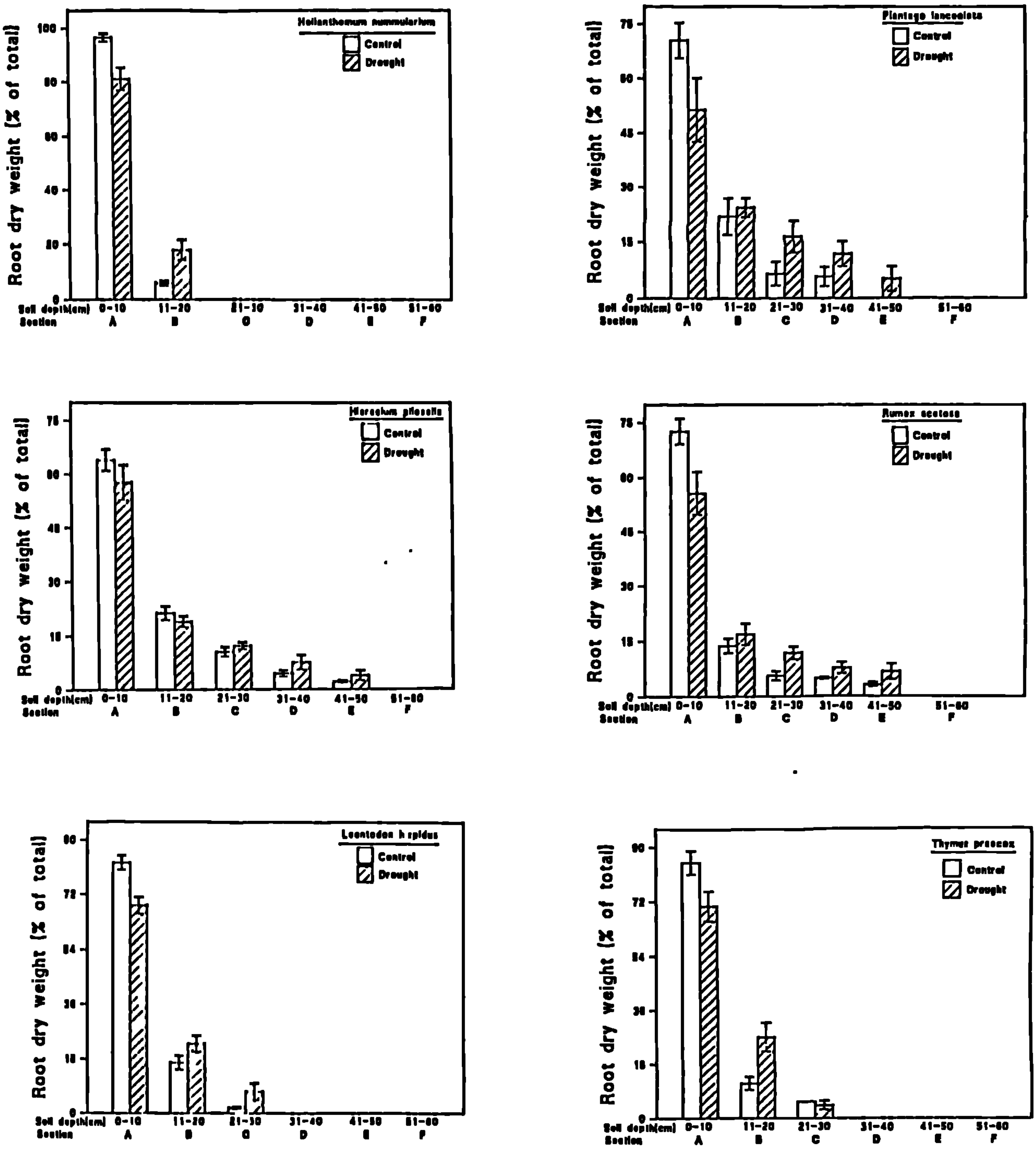
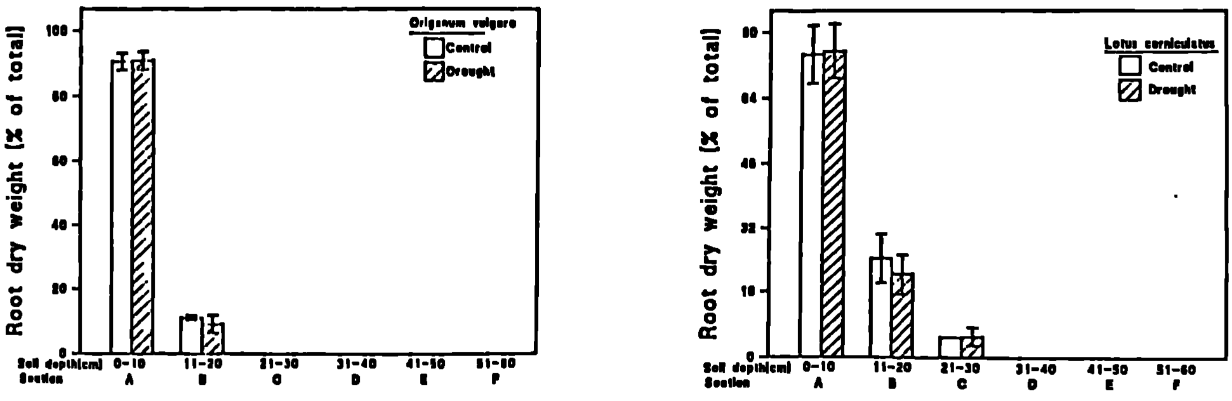


Figure 5.3 (contd.)



Legume



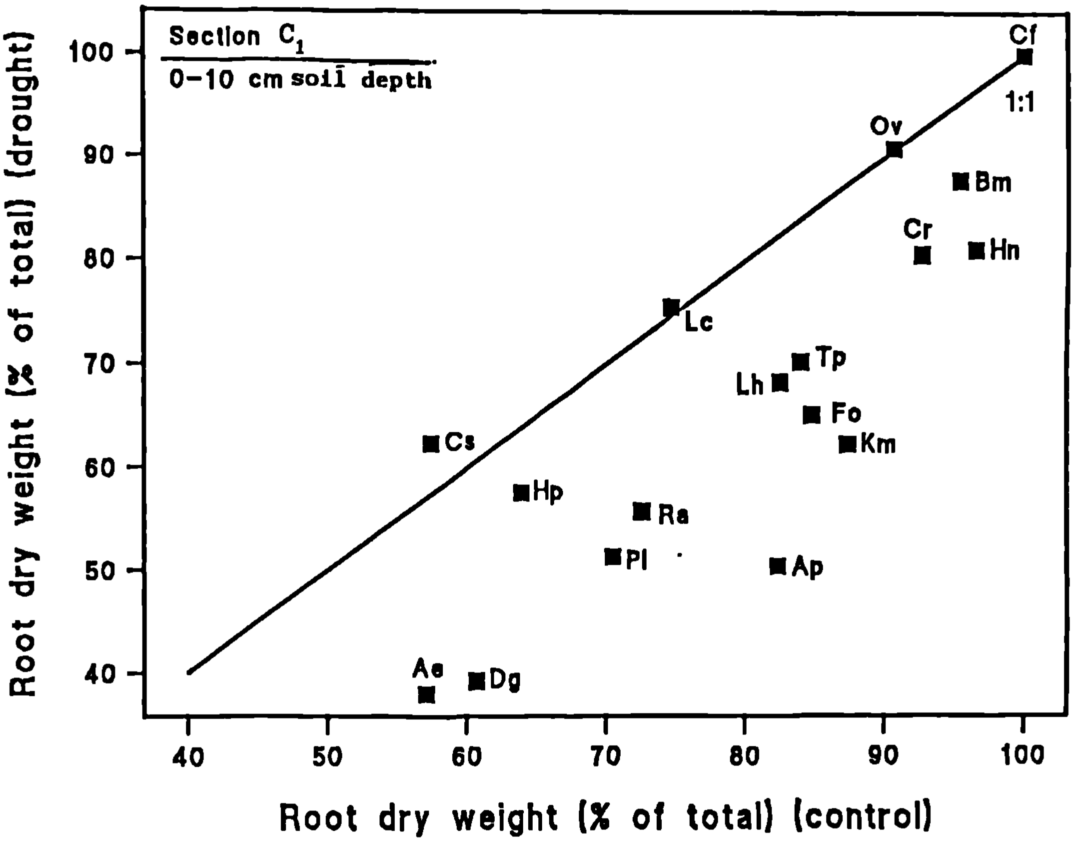


Figure 5.4: Comparison of the root dry matter allocation patterns in control and drought treatments. Key to species;

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Hieracium pilosella (Hp), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Plantago lanceolata (Pl), Thymus praecox(Tp), Lotus corniculatus (Lc).

	ROOT : SHOOT RATIO		
	control	drought	
A.elatius	1.65	1.04	***
A.pratensis	1.16	0.89	N.S.
B.media	1.99	0.75	**
D.glomerata	1.04	1.00	N.S.
F.ovina	1.01	0.67	**
K.macrantha	1.35	0.75	***
C.rotundifolia	2.40	1.54	N.S.
C.flacca	1.11	0.62(dead)	**
C.scabiosa	2.16	2.36	N.S.
H.nummularium	0.84	1.38	**
H.pilosella	1.27	1.48	N.S.
L.hispidus	2.15	1.46	N.S.
O.vulgare	0.59	1.27	**
P.lanceolata	1.19	1.71	**
R.acetosa	2.60	2.15	N.S.
T.praecox	1.09	1.03	N.S.
L.corniculatus	0.84	0.87	N.S.

Table 5.3: The comparison of root / shoot ratio of species in control and drought treatments. The analysis of variance based on F-test; *; $P<0.05$, **; $P<0.01$, ***; $P<0.001$.

	CREVICE EXPLOITATION				MORPHOLOGICAL PLASTICITY OF ROOT	
	control	rank	drought	rank		rank
A .elatius	74.99	1	163.15	1	2.17	10
A.pratensis	21.49	8	98.15	3	4.56	2
B.media	4.83	15	14.06	15	2.91	6
D.glomerata	64.70	3	155.14	2	2.39	7
F.ovina	17.92	10	53.40	8	2.97	5
K.macrantha	14.44	12	60.42	6	4.18	3
C.rotundifolia	7.96	14	24.18	13	3.03	4
C.flacca	0.00	17	0.00	17	0.00	17
C.scabiosa	74.03	2	60.30	7	0.81	16
H.nummularium	3.62	16	23.42	14	6.45	1
H.pilosella	33.47	7	33.07	11	0.98	13
L.hispidus	21.18	9	45.85	9	2.16	11
O.vulgare	10.29	13	10.07	16	0.97	14
P.lanceolata	41.86	4	94.81	4	2.26	9
R.acetosa	37.74	5	79.34	5	2.10	12
T.praecox	17.78	11	42.15	10	2.36	8
L.corniculatus	33.97	6	32.45	12	0.95	15

Table 5.4: Species rank based on two indices of crevice exploitation and morphological plasticity of root in control and drought treatments; by comparing the quantity of root dry matter in C_2 (11-100 cm) section as a percentage of the that in C_1 (0-10 cm) section it has been possible to obtain a measure of the degree of crevice exploitation. The morphological plasticity of root obtained by using the ratio $E_d:E_c$, where E_d and E_c are the degree of crevice exploitation in drought and control conditions respectively.

significant ($P<0.02$). No consistent relationships were detected between root:shoot ratio and other growth and yield parameters.

When morphological plasticity of the root (MPR) was plotted against the ratio of yield in drought : yield in control for all species, a strong correlation ($P<0.005$) was obtained (Figure 5.5), confirming that plants which redistributed root dry matter from the upper 10 cm to the lower sections, tended to sustain their yields under the droughted condition.

5.4 DISCUSSION:

As in the previous investigation of Sydes and Grime (1984) the experiment revealed consistent inter-specific differences with respect to root penetration with the potentially fast-growing species producing deeper root systems than the slow-growing plants. The differences observed between species are consistent with published results of root systems of some of the same species excavated in natural habitats (Anderson 1927; Grime 1963; Grime & Curtis 1976). In most of the species, water-stress stimulated root penetration, and there was a general tendency toward deeper root systems under the drought treatment. Lawlor, Day, Johnston & Legg (1981), Imtiyaz, Kristensen & Mogensen (1982), and Harrouni (1989) have observed that water-stressed barley, wheat and tef exhibit a deeper penetration of roots in the soil profile than

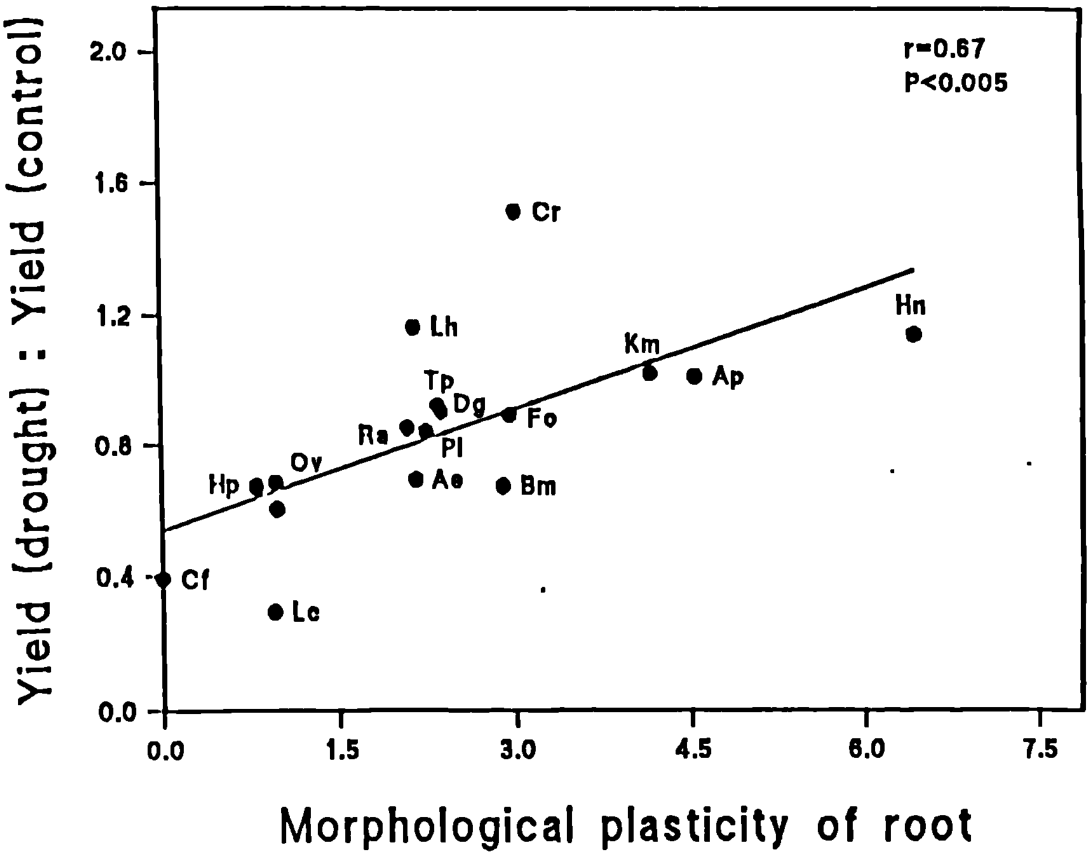


Figure 5.5: The relation between morphological plasticity of root and the ratio of yield* in drought : yield in control.
* Yield (shoot + root dry wt.). Key to species;

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Hieracium pilosella (Hp), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Plantago lanceolata (Pl), Thymus praecox(Tp), Lotus corniculatus (Lc).

irrigated plants. As soil moisture deficit builds up an increasing proportion of the upper layer of the soil becomes dry because of evaporation and exploitation by plant roots, and the availability of water is therefore restricted to deeper layers of the profile. In this circumstance survival certainly must have been dependent upon roots reaching the deeper resource of moisture supply (Harris 1967). In the extremely dry habitats occupied by phreatophytic genera such as *Acacia* or *Tamarix* the same phenomenon reaches its maximum expression where roots penetrate down to a permanent water-table (Grenot 1974).

The experiment also revealed different patterns of distribution and re-distribution of root dry weight in response to water regime. Many of the species investigated produced deeper root systems in response to drought, and located a greater proportion of the total root biomass in the lower parts of the profile. Similar results were obtained by Bennett & Doss (1960), Watts, Rodriguez, Evans & Davies (1981), Sharp & Davies (1985), Westgate & Boger (1985) and Harrouni (1989). Since many soils are very heterogeneous, restricted root growth in pockets of soil which are unfavourable for root growth and penetration (as a result of shallowness of the soil, the presences of rock fragments or nutritional limitation) may be compensated for by improved root growth in favourable pockets of soil accessible to the root system (Russell 1973). This depends upon the magnitude and rate of plastic response by the root system following drought stress. Here the strong correlation between morphological plasticity of the root and the ability of the plant to sustain biomass production indicates that in habitats where upper parts of the soil are subject to desiccation, roots within this layer may cease growth and water uptake, and the effective root system is that located in deeper parts of the soil where water remains available. In these circumstances allocation of dry weight will be from one part of the soil profile to another part rather than from above ground to below ground.

Chapter 6

Floristic diversity in a model system using experimental 'Microcosms' providing factorial combinations of soil heterogeneity, different watering and nutritional regimes.

6.1. INTRODUCTION:

As explained in Chapter I both drought and nutrient deficiency have been implicated as key factors in the majority of the experimental studies which have explored the mechanisms controlling plant diversity of calcareous grassland. Ancient species-rich calcareous grassland soils are chronically deficient in major nutrients; this is evident from soil analyses (Willis & Yemm 1961), seedling bioassays (Grime 1963a,b), and fertilizer experiments on field plots (Willis 1963; Lloyd & Piggot 1967; Grime & Curtis 1976). As a result of low precipitation : evaporation ratios, shallowness of the soil and the absorptive nature of the parent material (Donovan & Jeffrey 1990), drought would be expected to be a major feature in chalk and limestone grasslands at certain times of the year, and both meterological data and measurements of soil moisture tension (e.g. Rorison *et al* 1986) confirm this prediction. It is perhaps not surprising therefore to find that the plant communities in shallow calcareous soils tend to be dominated by hemi-cryptophytes, including both grasses and forbs, e.g. *Festuca ovina, Koeleria macrantha, Helianthemum nummularium, Thymus praecox,* and some deep-rooting forbs, e.g. *Centaurea scabiosa,* and *Lotus corniculatus* (Hillier 1990). Although the coincidence of mineral nutrient stress and drought can be related to the general morphology of these perennial plants, we are not yet in a position to explain why there are so many different species represented in each community. Therefore the purpose of this chapter is to examine the precise individual and interactional effects of drought, nutrient, and soil heterogeneity in a functional way on plant growth, abundance, and community structure by experimental studies using a range of selected species from the calcareous grassland in Millers Dale (Derbyshire, England).

Most investigations of floristic diversity have involved studies of natural vegetation. In practice, however field observations and measurements can do no more than indicate the mechanisms controlling community structure and species composition (Ford 1990); this is because some potentially important factors are not amenable to precise measurement or manipulation in the field. Here an alternative research strategy introduced by Grime *et al* (1987), was used, in which communities were allowed to develop in turf microcosms providing factorial combinations of soil heterogeneity, water supply and nutrient-treatments. In this approach the objective was to analyse the contribution of each of the three experimental variables to the control of the species composition and diversity of the synthesised vegetation.

6.2 METHODS AND MATERIALS:

-Experimental design:

Treatments involving water regimes, nutrient supply, and variation in soil depth were provided in factorial combinations. Two watering treatments (control and drought), two mineral nutritional regimes (high and low), and four soil heterogeneity treatments (I, II, III, IV), provided a total of sixteen combinations, each of which was replicated four times.

Each of the 64 containers (microcosms) in this experiment had external dimensions of 230 x 230 x 100 mm, and was filled to a depth of 85mm of which the lower 75 was sand, and upper 10mm was soil collected from the surface layer of the (Millers Dale) site. All containers were free draining; this was achieved by drilling 25 holes each 30mm in diameter (see Figure 6.1) in the base. Soil was retained by covering the base with a single layer of terylene cloth.

All microcosms were independent of each other and were maintained in a randomized block supported by a metal frame-work in a un-heated glass house with normal day light, at the Botanical garden of Sheffield University (Plate 6.2).

The seeds of sixteen species (Table 6.1) collected from Millers Dale were sown in each container. In order to allow the same chance of establishment by each species, in each part of the container one seed of each species was dropped into each of twenty five 45mm x 45mm, subsections of the soil surface. Thus a total of 400 seeds was sown in each container.

-Treatments:

There were two nutritional regimes. Half of the containers were supplied twice a week with 200 ml full Rorison solution (high nutritional treatment), and the remainder were supplied once every three weeks with 100 ml full Rorison solution (low nutrient treatment).

For each nutrient treatment, there were two watering regimes; control and drought. From the beginning of the experiment, all containers regardless of their different nutrient and soil heterogeneity treatments, had similar watering regimes; all were maintained in a uniformly moist condition with regular watering every day by deionized water. At the beginning of August, 15 weeks after sowings the drought treatment was implemented in half of the containers of each nutritional treatment by withholding water for three weeks. After three weeks, containers were re-watered and mineral nutrient supplies were recommenced until the end of the experiment which was terminated 13 weeks after the end of the drought period.

Soil heterogeneity involved 'crevices' and 'horizontal partitions' of standardized dimensions and number. The main purpose of this treatment was to simulate heterogeneity in rooting depth and soil moisture supply and to allow quantitative measurements of a kind which are not possible in natural habitats in the field. With and without crevices and horizontal partition created four possible combinations of soil heterogeneities (Plate 6.1, Diagram 6.1). Plastic water pipes of 380 mm length and 20 mm diameter were used to simulate the real crevices of the natural habitat. Each creviced container had five pipes, which were randomly positioned. For horizontal partitioning, a plastic plate 230 x 230 cm in area was used, it was positioned and sealed in the middle of the container, in order to divide the soil into shallow and relatively deep parts. Each plate had five randomly arranged perforations of 3 cm diameter. The four combinations of soil heterogeneities are, as follow;

I: No crevices and no horizontal partitions.
II: Just crevices.
III: Just horizontal partitions.
IV: With crevices and horizontal partitions.

During three weeks of the drought period the sand within the plastic pipes projecting from the unwatered containers was maintained in a moist condition in order to simulate the deep and moist crevices of a real habitat. The method of watering used for this purpose was designed to prevent significant upward movement of water to the main container.

-Procedure and time table:

20-April-1989:

Immediately after seeds were sown all containers were covered by a plastic sheet creating relatively humid and warm conditions for seed germination. This cover was removed after two weeks.

25-31 May 1989:

Each individual seedling was identified and mapped (Appendix 6.1).

1-June-1989:

Nutrient-treatments were applied, and subsequently maintained until three weeks before starting the drought treatments.

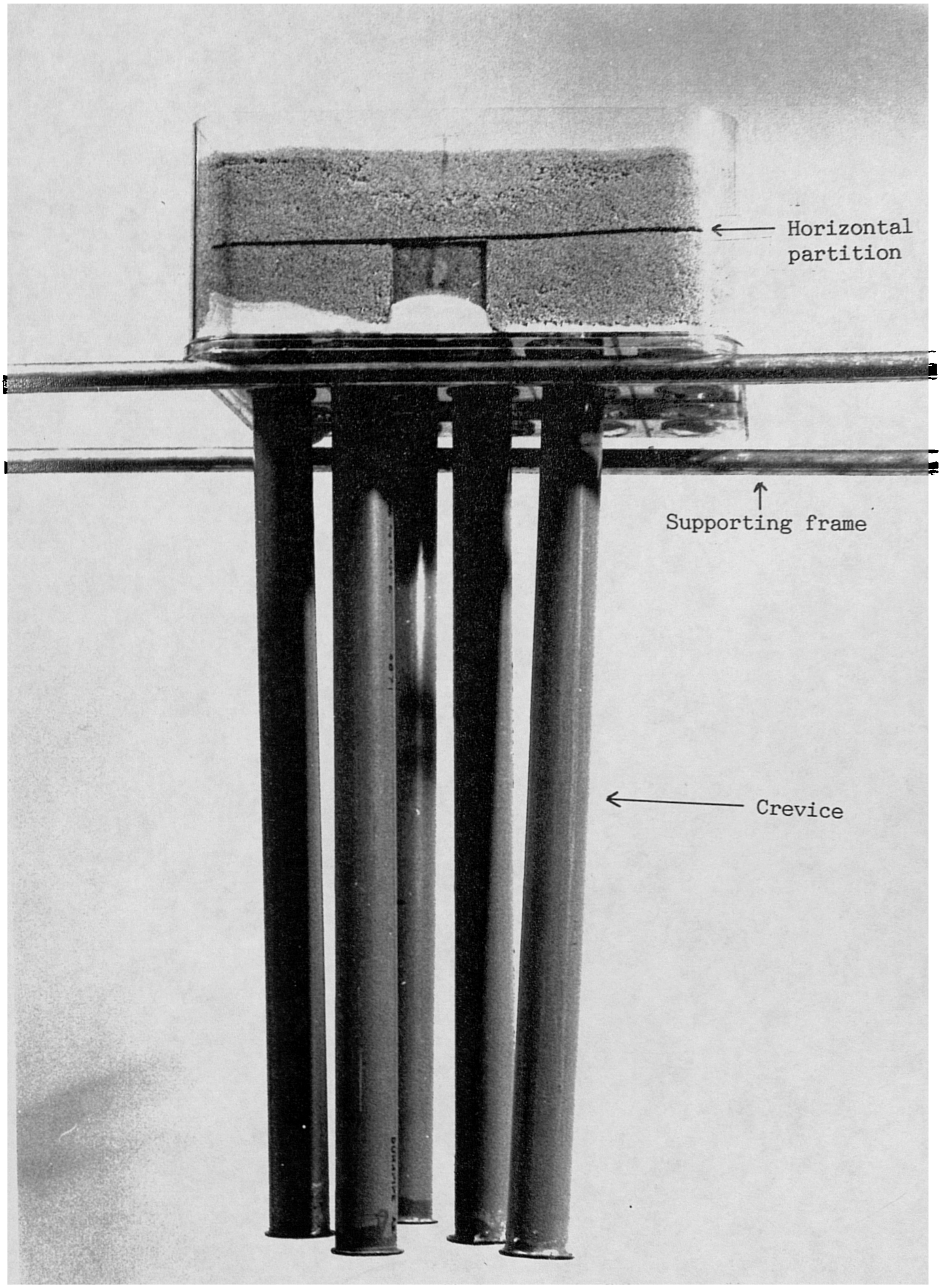


Plate 6.1: A microcosm

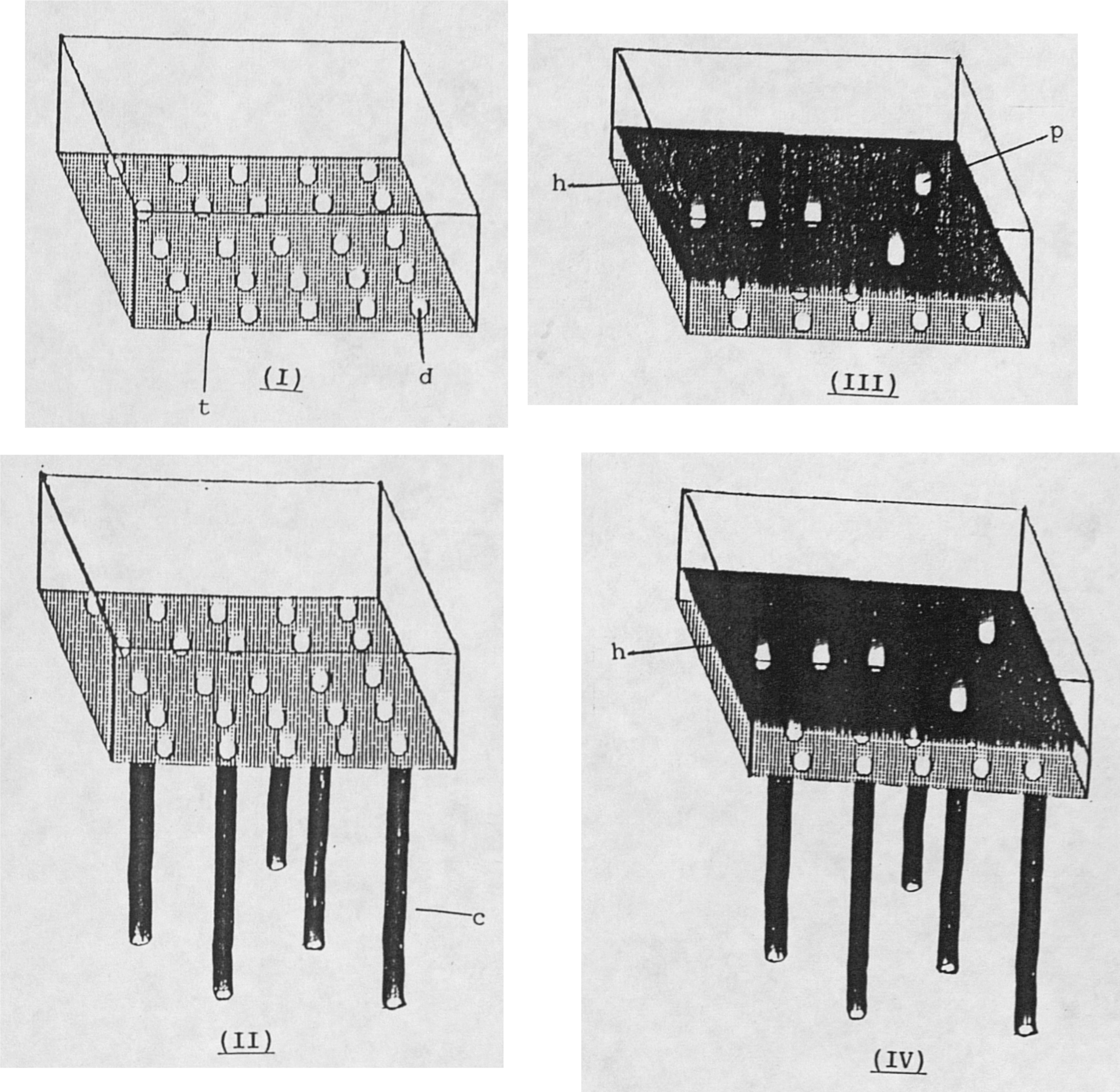


Diagram 6.1:

The four combinations of soil heterogeneity are as follows;

I: No crevices and no horizontal partitions
II: Just crevices
III: Just horizontal partitions
IV: Crevices + horizontal partitions

c: crevice.
d: drainage hole.
h: horizontal partition.
p: perforations.
t: terylene cloth.

Plate 6.2: General view of the microcosms experiment. Soil crevices can be seen in the foreground. Plastic sheets supported an a wooden frame were used to exclude any raindrops entering the greenhouse through open ventilators.

1-August-1989;

The drought treatment was implemented for three weeks.

21-August-1989:

Droughting was terminated and mineral nutrient additions were recommenced.

End of November 1989:

The second recording and mapping (Appendix 6.2) was commenced, and the shoot of each surviving plant was individually harvested and dried to 80°C for 48 h., then weighed.

-Data analysis;

Using ANOVA and GLM of the Minitab program, one- and three-way analyses of variance were carried out. Survivorship, mean shoot dry weight, and abundance values for each species were calculated, as follows:

$$\text{Survivorship of species i in control} = \frac{\text{Number of plants in second recording}}{\text{Number of plants in first recording}} \times 100$$

$$\text{Survivorship of species i in drought treatment} = \frac{\text{Number of plants after drought}}{\text{Number of plant before drought}} \times 100$$

$$\text{Abundance value of species i} = \frac{\text{Total biomass of species i}}{\text{Total biomass of all species}} \times 100$$

For each treatment Shannon diversity (H), and evenness (J) indices were calculated, as follows:

$$\text{diversity } H = -\sum_{i=1}^{S} P_i \ln P_i$$

$$\text{Evenness} \quad J = \frac{H}{H_{\max}} = \frac{-\sum_{i=1}^{S} P_i \ln P_i}{\ln S}.$$

Where S is the total number of species in the community (i.e. the richness), the proportion is P_i for the ith species.

6.3 RESULTS:

- Germination:

The number of seedlings of each species observed at the first recording is given in Table 6.1. On average the number of seedlings per container was equivalent to slightly less than 50% of the 400 seeds sown. There were great differences between species. The maximum and minimum germination rate belonged respectively to *Rumex acetosa* with 21.0, and *Carex flacca* with 6.3 seedlings per container, (Table 6.1). Three of the sixteen species (*Briza media, Hieracium pilosella* and *Thymus praecox*) failed to germinate.

Containers allocated to different water and nutrient-treatments had comparable seedling numbers and no statistically significant differences were detected (Table 6.2a,b). Although the first recording took place before implementing the watering and nutrient treatments it was observed that seedling numbers were influenced by the soil heterogeneity treatments. Those containers with crevices (II, IV), regardless of having horizontal partitions or not, had more germination than containers without crevices(I,

Table 6.1: Mean number of germinated seeds from 25 sown seeds of each species per container in different treatments. The significance level of LSD is based on P<0.05. I-IV are soil heterogeneity treatments described in text.

	CONTROL (No drought)								DROUGHT										
	High nutrition				Low nutrition				High nutrition				Low nutrition						
	I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV	LSD	Mean	%
A. *elatius*	7.2	13.0	8.2	9.2	8.0	10.7	9.2	13.5	7.0	12.7	7.5	10.2	10.7	12.0	8.5	11.7	0.7	9.9	40
A. pratensis	9.2	16.5	10.5	17.2	10.0	13.7	10.7	14.5	11.7	13.0	9.5	16.0	11.7	11.7	10.5	11.5	0.6	12.3	49
B. media	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. glomerata	15.5	17.7	11.7	16.0	15.5	20.5	13.7	17.5	16.0	19.7	10.5	13.2	13.7	15.2	14.2	9.2	0.8	15.0	60
F. ovina	20.5	19.0	16.2	18.5	20.0	16.0	19.0	18.5	18.2	17.5	10.7	8.0	15.2	9.5	13.0	8.0	0.9	15.5	62
K. macrantha	12.5	18.0	14.0	19.0	12.5	15.5	11.2	14.2	15.5	16.7	16.5	12.2	10.7	11.0	14.2	12.0	0.9	14.1	56
C. *rotundifolia*	8.2	15.0	7.5	13.0	9.5	11.7	12.7	10.5	12.7	13.2	12.0	13.2	12.7	12.0	8.7	16.2	0.8	11.8	47
C. *flacca*	7.5	3.2	6.5	3.0	12.5	3.7	6.2	4.5	7.2	4.5	9.0	3.0	9.2	5.0	11.5	5.0	0.6	6.3	25
C. *scabiosa*	14.0	16.5	15.2	18.5	15.2	18.2	18.0	14.5	15.2	16.5	14.7	14.0	15.7	17.0	14.2	13.2	0.9	15.6	62
H. nummularium	13.5	16.5	10.7	14.7	13.5	17.7	14.0	16.7	13.0	17.2	12.5	16.5	13.7	17.0	13.0	17.0	0.6	14.8	59
H. pilosella	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. hispidus	18.7	21.7	14.0	20.5	19.2	19.5	18.0	19.7	19.0	20.5	18.5	22.0	20.0	20.2	19.7	22.2	0.7	19.6	78
O. *vulgare*	11.2	12.7	9.0	18.0	12.0	11.7	13.7	15.7	13.5	13.2	12.7	14.2	13.2	15.0	13.5	14.2	1.0	13.3	53
P. lanceolata	15.5	19.0	16.7	20.0	16.0	19.5	14.2	18.2	17.7	16.7	17.2	21.7	17.7	20.2	14.0	19.0	0.7	17.7	71
R. acetosa	19.5	22.0	16.5	21.5	22.7	21.0	20.5	22.5	20.2	22.5	20.0	21.5	19.5	23.2	20.0	23.7	0.6	21.0	84
T. praecox	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total/container	173	211	157	209	186	199	181	200	187	204	171	186	184	189	175	183	3	187	47

Table 6.2: Mean number of germinated seeds from 25 sown seeds of each species in different treatments@; a, in different soil heterogeneity b, nutritional and c, water regimes $P<0.05$ *, $P<0.01$ **, $P<0.001$ ***

@ Mean number of germinated seeds based on first recording which took place before implementing the watering and nutrient treatments.

a:

	SOIL HETEROGENEITY				
	I	II	III	IV	$LSD_{P<0.05}$
A. elatius	8.2	12.1	8.3	11.1	0.7
A. pratensis	10.6	13.7	10.3	14.8	0.7
B. media	-	-	-	-	-
D. glomerata	15.1	18.3	12.5	14.0	0.9
F. ovina	18.5	15.5	14.7	13.2	1.3
K. macrantha	12.8	15.3	14.0	14.3	1.0
C. rotundifolia	10.8	13.0	10.2	13.2	0.9
C. flacca	9.0	4.1	8.3	3.8	0.6
C. scabiosa	15.0	17.0	15.5	15.0	0.8
H. nummularium	13.4	17.1	12.5	16.2	0.6
H. pilosella	-	-	-	-	-
L. hispidus	19.2	20.5	17.5	21.1	0.7
O. vulgare	12.5	13.1	12.2	15.5	1.0
P. lanceolata	16.7	18.8	15.5	19.7	0.8
R. acetosa	20.5	22.1	19.2	22.3	0.6
T. praecox	-	-	-	-	-
TOTAL/container	182	201	171	194	3.6

b:

	NUTRITION		
	High	Low	F-test
A. elatius	9.4	10.5	N.S.
A. pratensis	12.9	11.8	N.S.
B. media	-	-	-
D. glomerata	15.0	14.9	N.S.
F. ovina	16.0	14.9	N.S.
K. macrantha	15.5	12.6	**
C. rotundifolia	11.8	11.7	N.S.
C. flacca	5.4	7.1	*
C. scabiosa	15.5	15.7	N.S.
H. nummularium	14.3	15.3	N.S.
H. pilosella	-	-	-
L. hispidus	19.3	19.8	N.S.
O. vulgare	13.0	13.6	N.S.
P. lanceolata	18.0	17.3	N.S.
R. acetosa	20.4	21.6	N.S.
T. praecox	-	-	-
TOTAL/container	187	187	N.S.

c:

	WATER REGIME		
	Control	Drought	F-test
A. elatius	9.9	10.0	N.S.
A. pratensis	12.8	11.9	N.S.
B. media	-	-	-
D. glomerata	16.0	14.0	*
F. ovina	18.4	12.5	***
K. macrantha	14.6	13.6	N.S.
C. rotundifolia	11.0	12.6	N.S.
C. flacca	5.8	6.8	N.S.
C. scabiosa	16.2	15.0	N.S.
H. nummularium	14.6	15.0	N.S.
H. pilosella	-	-	-
L. hispidus	18.9	20.2	N.S.
O. vulgare	13.0	13.7	N.S.
P. lanceolata	17.4	18.0	N.S.
R. acetosa	20.7	21.3	N.S.
T. praecox	-	-	-
TOTAL/container	189	185	N.S.

III) (Table 6.2a). This difference was statistically significant. No effect was observed in *Festuca ovina*, but the remainder except for *C. flacca*, produced more seedlings in containers with crevices. In *Carex flacca* the number of seedlings was greater in the treatments without crevices. No clear explanation for these effects of treatment upon seedling number can be offered although it seems likely that differences in moisture and algal colonization at the soil surface could have arisen from the influence of the crevices upon drainage

- Survivorship in the control treatment.

The results of total survivorship per container in the control treatment for both high and low nutrient treatments are given in Figure 6.1a. In low nutrient conditions crevices increased survivorship. *Origanum vulgare*, *Helianthemum nummularium*, *Campanula rotundifolia*, and *Leontodon hispidus* experienced the lowest survivorship in the undroughted containers (Fig 6.1). In both nutritional regimes, correlation between percentage survivorship and mean dry weight (of surviving plants) of species was positive and highly significant (Fig 6.1c,d). Smaller species had higher mortality than larger species.

Two-way analysis of variance showed that the percentage survivorship was strongly affected by soil heterogeneity ($P<0.05$), and an interaction between soil heterogeneity and nutrient treatment was detected ($P<0.05$). In *Koeleria macrantha*, *Helianthemum nummularium* and *Leontodon hispidus*,

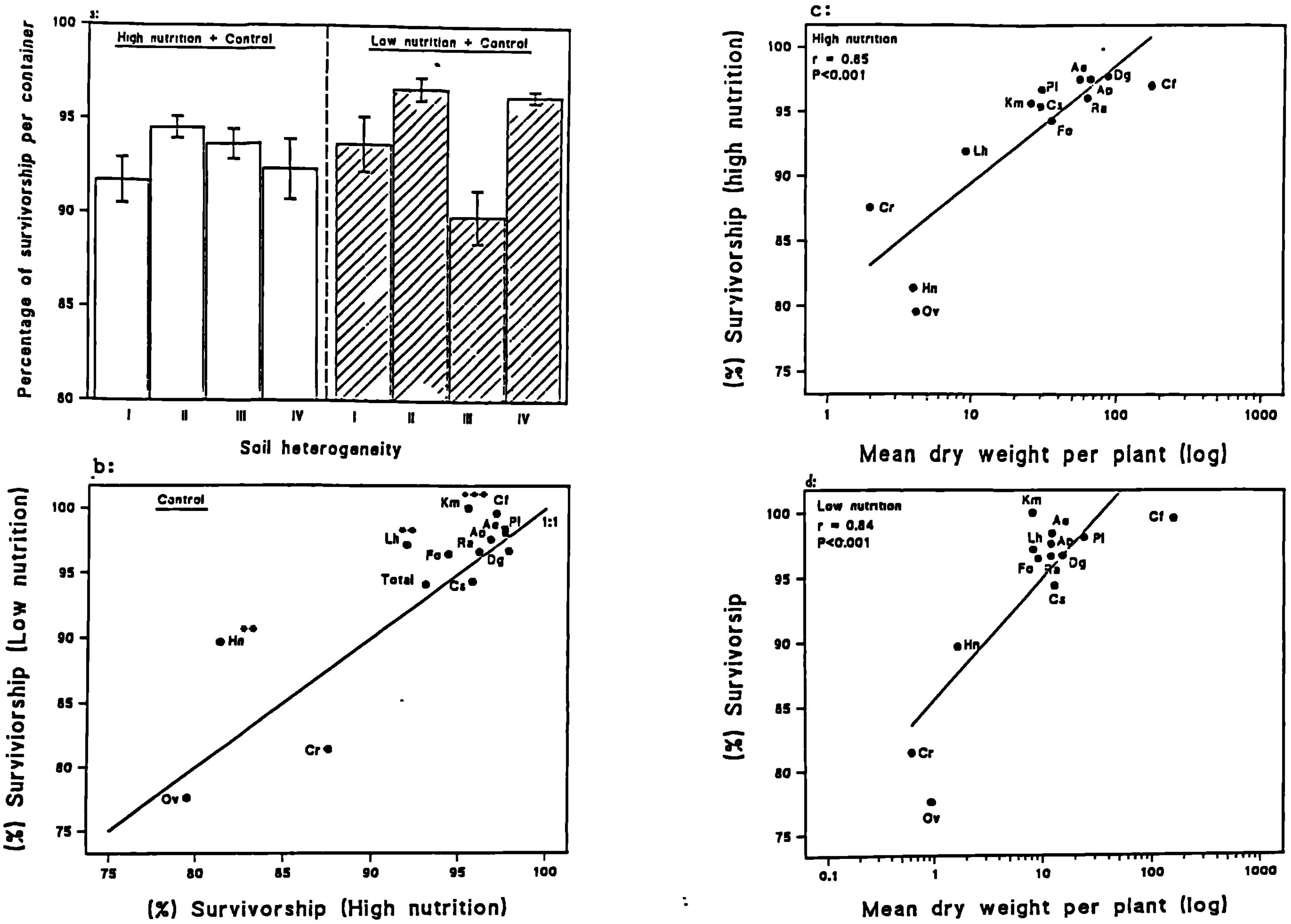
Figure 6.1: Percentage survivorship of each species in wet containers (undroughted) was calculated by using the first and final recording (see text), as follows;

a; Percentage survivorship of species in response to different soil heterogeneity at two nutrient regimes (low & high). Bars based on the SE (Standard error)

b; The differences in total survivorship of species in response to different nutrient conditions.
The significant level of F-test based on;
$P<0.05$ *, $P<0.01$ **, $P<0.001$ ***.

c & d; Correlation coefficient of species percentage survivorship with their mean dry weight at high (c), and low (d) nutrient conditions.

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Thymus praecox(Tp).


a:
Percentage of survivorship per container
100
95
90
85
80
High nutrition + Control
Low nutrition + Control
I
II
III
IV
I
II
III
IV
Soil heterogeneity
b:
Control
(%) Surviviorship (Low nutrition)
(%) Survivorship (High nutrition)
Km
Cf
Pl
1:1
Ae
Ap
Ra
Lh
Fa
Dg
Total
Cs
Hn
Cr
Ov
75
80
85
90
95
100
c:
High nutrition
r = 0.85
P<0.001
(%) Survivorship (high nutrition)
Mean dry weight per plant (log)
Ae
Dg
Pl
Ap
Cf
Km
Cs
Ra
Fa
Lh
Cr
Hn
Ov
1
10
100
1000
d:
Low nutrition
r = 0.84
P<0.001
(%) Survivorsip
Mean dry weight per plant (log)
Km
Ae
Cf
Lh
Ap
Pl
Fa
Ra
Dg
Cs
Hn
Cr
Ov
0.1
1
10
100
1000

survivorship was affected by nutritional treatment, and in *Origanum vulgare* by soil heterogeneity. An interaction between soil heterogeneity and nutrition occurred in *Campanula rotundifolia* (Table 6.3). Survivorship was lower in the nutritionally rich treatment, (e.g. *A. elatius, F. ovina* and *C. flacca*) but differences were not significant (Fig 6.1b). *Origanum vulgare* regardless of nutritional regime, and *Campanula rotundifolia* in the low-nutrient treatment had higher survivorship in the container with crevices than in those without crevices.

-Survivorship in drought treatment.

The percentage survivorship of species is given in Table 6.5. The two-way analysis of variance (Table 6.4) demonstrates that total survivorship was affected by both soil heterogeneity (P<0.001), and nutrient treatment (P<0.05). There was no statistically significant interaction between these two factors. On the basis of one-way analysis of variance (Fig 6.2b) total survivorship was higher in the high- than the low-nutrient treatment. In the containers without crevices (I, III), all plants were killed as a result of the drought. Among the containers with crevices (II, IV), those with horizontal partitions had lower survivorship. This difference was greater in the infertile condition (Fig 6.2c,d). The maximum and minimum survivorship (%) belonged to containers with crevices only (II) at high-nutrient supply, and to containers with crevices + horizontal partitions (IV) and low nutrients,

Table 6.3: The significance level of two-way analysis of variance (ANOVA) of percentage survivorship of species in control (undroughted) in response to different soil heterogeneity and nutrient treatments; $P<0.05$ *, $P<0.01$ **, $P<0.001$ ***.

	(%) SURVIVORSHIP (in control)		
	Soil hete.	Nutr.	Interaction
A. elatius	N.S.	N.S.	N.S.
A. pratensis	N.S.	N.S.	N.S.
D. glomerata	N.S.	N.S.	N.S.
F. ovina	N.S.	N.S.	N.S.
K. macrantha	N.S.	***	N.S.
C. rotundifolia	N.S.	N.S.	*
C. flacca	N.S.	N.S.	N.S.
C. scabiosa	N.S.	N.S.	N.S.
H. nummularium	N.S.	*	N.S.
L. hispidus	N.S.	**	N.S.
O. vulgare	**	N.S.	N.S.
P. lanceolata	N.S.	N.S.	N.S.
R. acetosa	N.S.	N.S.	N.S.
TOTAL/container	*	N.S.	*

TABLE 6.4: The significant level of two-way analysis of variance (ANOVA) of percentage drought survivorship of species in response to soil heterogeneity, and nutrient treatments; $P<0.05$ *, $P<0.01$ **, $P<0.001$ ***.

	(%) DROUGHT SURVIVORSHIP		
	Soil hete.	Nutr.	Interaction
A. elatius	***	N.S.	N.S.
A. pratensis	***	N.S.	N.S.
D. glomerata	***	*	***
F. ovina	***	**	**
K. macrantha	***	**	*
C. rotundifolia	N.S.	N.S.	N.S.
C. flacca	N.S.	N.S.	N.S.
C. scabiosa	***	N.S.	N.S.
H. nummularium	***	N.S.	N.S.
L. hispidus	***	N.S.	N.S.
O. vulgare	N.S.	N.S.	N.S.
P. lanceolata	***	N.S.	N.S.
R. acetosa	***	**	N.S.
Total/container	***	*	N.S.

Table 6.5: The percentage of drought survivorship of species in different nutrient and soil heterogeneity treatments. II (containers with just crevices), and IV (crevices + horizontal partitions).

	Percentage of Survivorship				
	HIGH NUTRITION		LOW NUTRITION		
	II	IV	II	IV	$LSD_{P<0.05}$
A . elatius	16.1	5.93	28.9	11.6	7.6
A. pratensis	11.4	6.2	14.2	8.9	5.5
D. glomerata	21.3	18.1	22.3	3.1	3.4
F. ovina	13.8	31.8	6.3	2.5	7.0
K. macrantha	22.7	16.5	15.4	5.3	3.2
C. rotundifolia	6.8	5.9	3.1	0.0	3.5
C. flacca	5.0	0.0	5.0	0.0	3.7
C. scabiosa	18.2	8.9	16.3	10.5	5.0
H. nummularium	8.4	10.4	12.7	4.6	3.7
L. hispidus	10.9	3.6	9.0	1.1	2.4
O. vulgare	2.9	2.0	1.1	0.0	2.0
P. lanceolata	16.2	10.2	18.4	4.0	3.2
R. acetosa	30.2	22.0	17.5	11.4	4.4
Total/container	15.7	10.8	13.9	5.2	1.7

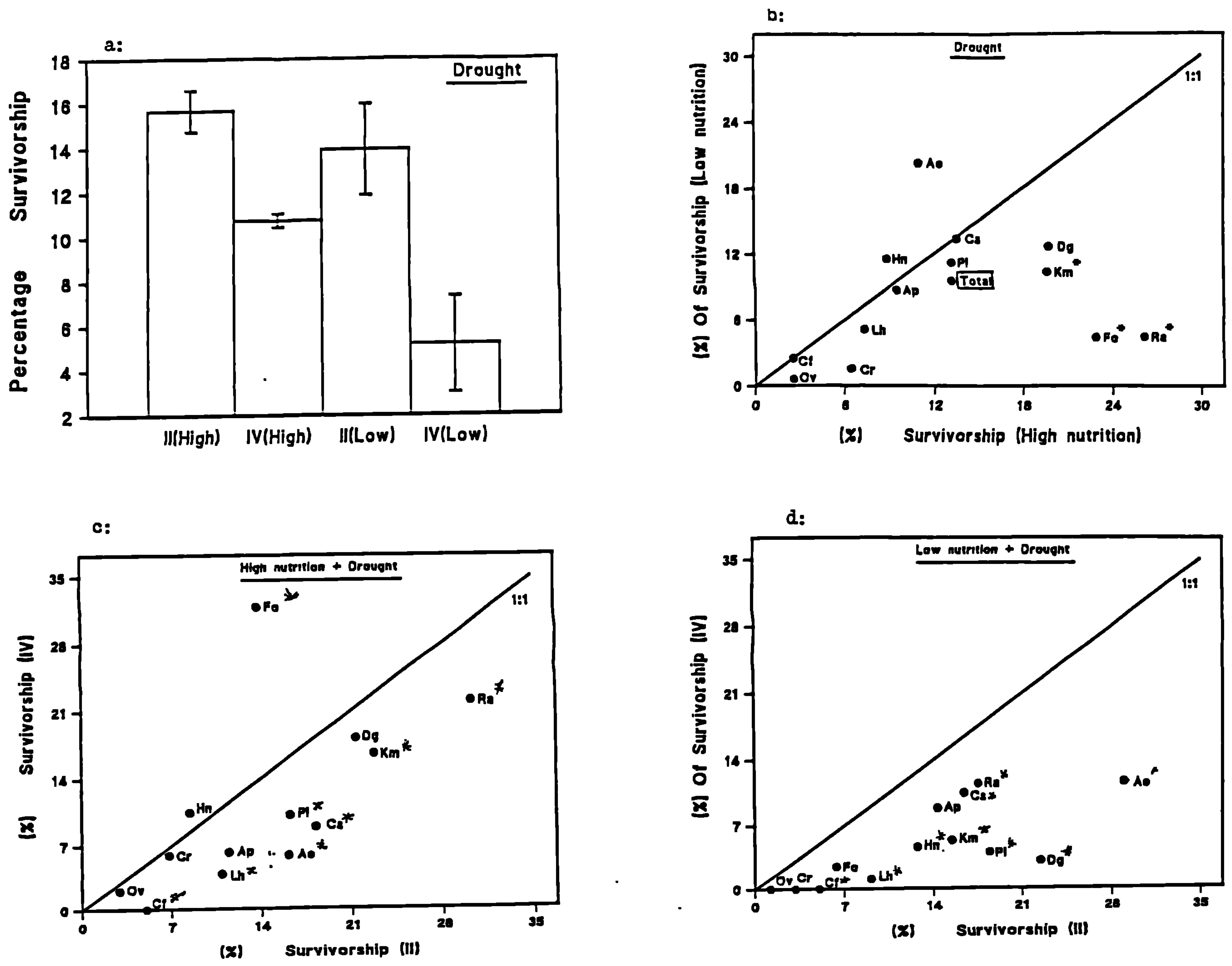
Figure 6.2 (a,b,c,d):

Percentage drought survivorship of each individual species was calculated by using the first (before drought) and final recording (after drought) (see text), for different treatments, as follow;

a; Percentage total survivorship per container in response to different soil heterogeneity at two nutrient regimes (low & high). Bars based on the SE (Standard error)

b,c,d;The differences in percentage drought survivorship of each individual species in response to different nutrient (b), and to different soil heterogeneity at high (c), and low (d) nutrient conditions. The significant differences based on LSD at P<0.05 level *.

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Thymus praecox(Tp).


a:
Percentage Survivorship
2
4
6
8
10
12
14
16
18
Drought
II(High)
IV(High)
II(Low)
IV(Low)
b:
(%) Of Survivorship (Low nutrition)
(%) Survivorship (High nutrition)
0
6
12
18
24
30
Drought
1:1
Ae
Cs
Dg
Hn
Pl
Km
Total
Ap
Lh
Fo
Ra
Cf
Ov
Cr
c:
(%) Survivorship (IV)
(%) Survivorship (II)
0
7
14
21
28
35
High nutrition + Drought
1:1
Fo
Ra
Dg
Km
Hn
Pl
Cs
Ap
Ae
Cr
Lh
Ov
Cf
d:
(%) Of Survivorship (IV)
(%) Survivorship (II)
0
7
14
21
28
35
Low nutrition + Drought
1:1
Ra
Ae
Cs
Ap
Hn
Km
Pl
Dg
Fo
Ov
Cr
Cf
Lh

respectively (Fig 6.2a). All species except *Arrhenatherum elatius* and *Leontodon hispidus*, had lower mortality in the fertile treatment, and in *Festuca ovina*, *Rumex acetosa* and *Koeleria macrantha* this effect was statistically significant (Fig 6.2b). As Figs 6.2c,d demonstrate the majority of species exhibited higher survivorship in the containers with crevices only (II) than in the containers with crevices + horizontal partitions (IV). *Festuca ovina* had the opposite result. Only one plant of *C. flacca* survived in the drought treatment.

-Biomass production:

A three-way analysis of variance was conducted in which watering regimes, nutrient supply, and soil heterogeneity, and their interactions were the independent variables (Table 6.6). If the number of statistically significant effects on yield is considered as a measure of importance the experimental variables can be ranked as; nutrient> soil heterogeneity> watering treatment. A highly significant interaction of watering regime with soil heterogeneity occurred with respect to dry matter production. The ranking of interactions was as follows; water x soil heterogeneity> nutrient x soil heterogeneity> water x nutrient supply (Table 6.6).

The response of plant size (mean dry weight of shoot) to different treatments was tested by using a one-way analysis of variance. The results are presented in Table 6.7, 6.8, and Fig 6.3, and can be summarised follows:

TABLE 6.6: The significance level of analysis of variance (ANOVA) of the mean dry weight of individual species in each treatment: *** $P<0.001$; ** $P<0.01$; * $P<0.05$.

	Water	Nutrition	Soil-hete.	Wate*Nutri	Wate*Soil	Nutr*Soil
A. elatius	***	***	**	**	***	N.S.
A. pratensis	N.S.	***	*	N.S.	**	N.S.
D. glomerata	N.S.	***	***	N.S.	***	**
F. ovina	***	***	N.S.	**	*	N.S.
K. macrantha	N.S.	***	***	N.S.	***	***
C. rotundifolia	N.S.	*	N.S.	N.S.	N.S.	N.S.
C. flacca	***	N.S.	***	N.S.	***	N.S.
C. scabiosa	N.S.	***	***	N.S.	***	*
H. nummularium	***	***	**	N.S.	**	*
L. hispidus	N.S.	N.S.	**	N.S.	**	N.S.
O. vulgare	**	**	*	*	N.S.	N.S.
P. lanceolata	**	***	***	*	***	***
R. acetosa	***	***	***	*	***	**

Table 6.7: Mean dry weight (mg) of species in different treatments. The significance level of LSD based on $P<0.05$, and F-test $P<0.05$ *, $P<0.01$ **, $P<0.001$ ***. Containers with crevices only, and crevices + horizontal partitions are II, and IV, respectively.

	CONTROL (No drought)										DROUGHT					
	High nutrition					Low nutrition					High nutrition			Low nutrition		
	I	II	III	IV	LSD	I	II	III	IV	LSD	II	IV	F-test	II	IV	F-test
A. elatius	65.1	48.6	62.2	48.1	7.1	10.8	12.7	15.6	10.1	1.4	58.8	50.8	N.S.	23.6	8.7	*
A. pratensis	38.2	32.5	25.9	24.9	3.0	12.4	12.9	12.4	9.9	0.6	82.7	45.6	N.S.	12.0	12.2	N.S.
D. glomerata	89.3	86.8	102.3	69.3	9.5	14.6	16.9	16.7	12.0	1.3	151.6	206.6	N.S.	31.6	33.9	N.S.
F. ovina	36.7	36.7	38.5	28.8	2.7	8.6	10.0	10.2	7.4	0.6	26.9	71.0	**	13.1	-	-
K. macrantha	30.9	28.4	30.9	27.8	2.5	7.3	9.0	8.2	7.4	0.7	62.7	89.7	N.S.	15.9	18.2	N.S.
C. rotundifolia	1.9	2.0	1.7	2.1	0.3	0.7	0.6	0.6	0.4	0.1	18.6	9.3	N.S.	-	-	-
C. flacca	147.9	150.4	239.8	111.2	22.8	150.1	143.9	195.8	124.2	17.8	-	-	-	-	-	-
C. scabiosa	23.1	23.5	30.2	24.2	2.6	14.7	13.0	11.5	11.7	1.1	77.7	98.3	N.S.	12.4	49.1	***
H. nummularium	4.7	3.3	3.0	4.6	0.6	1.8	1.7	1.7	1.4	0.1	3.5	4.9	N.S.	2.5	4.5	*
L. hispidus	8.7	11.5	9.3	6.4	1.0	9.9	9.0	8.5	5.1	0.6	30.5	32.1	N.S.	18.8	-	-
O. vulgare	3.0	4.6	2.5	5.0	1.0	0.7	1.0	0.7	1.1	0.1	-	-	-	-	-	-
P. lanceolata	64.9	57.8	92.1	49.5	5.2	30.4	19.1	24.6	21.8	1.7	195.5	442.7	**	57.5	121.2	**
R. acetosa	68.2	48.8	96.3	43.3	6.6	11.7	11.1	13.6	10.9	0.9	223.6	320.5	*	43.2	101.9	**
Total/container	7048	7117	8003	5796	366	3556	2511	2965	2234	145	3570	3532	N.S.	706	511	N.S.

Table 6.8: mean dry weight (mg) of species in different; nutritional (a), and water regimes (b). The significance level of F-test based on P<0.05 *, P<0.01 **, P<0.001 ***.

a:

	CONTROL			DROUGHT		
	High nut	Low nut	F-test	High nut	Low nut	F-test
A. elatius	54.65	12.09	***	56.58	19.23	**
A. pratensis	29.78	11.80	***	67.86	12.07	**
D. glomerata	85.85	15.07	***	171.97	33.05	***
F. ovina	35.05	9.00	***	39.51	15.95	N.S.
K. macrantha	29.28	8.00	***	72.09	15.58	**
C. rotundifolia	1.94	0.61	***	22.53	1.47	***
C. flacca	171.70	156.00	N.S.	-	-	-
C. scabiosa	25.24	12.63	***	83.75	25.35	***
H. nummularium	3.93	1.63	***	4.23	3.05	N.S.
L. hispidus	8.97	8.08	N.S.	30.85	19.68	N.S.
O. vulgare	4.11	0.92	***	8.93	-	-
P. lanceolata	64.82	23.61	***	312.10	68.09	***
R. acetosa	61.94	11.79	***	266.42	66.99	***

b:

	HIGH NUTRITION			LOW NUTRITION		
	Control	Drought	F-test	Control	Drought	F-test
A. elatius	54.85	56.58	N.S.	12.09	19.23	**
A. pratensis	29.78	67.86	***	11.81	12.04	N.S.
D. glomerata	85.85	171.97	***	15.10	33.05	***
F. ovina	35.05	39.51	N.S.	8.99	15.95	**
K. macrantha	29.28	72.09	***	7.99	16.58	***
C. rotundifolia	1.94	22.53	***	0.61	2.82	***
C. flacca	171.70	-	-	156.00	-	-
C. scabiosa	25.24	83.75	***	12.68	25.35	***
H. nummularium	3.93	4.23	N.S.	1.63	3.05	***
L. hispidus	8.97	30.85	***	8.07	19.68	***
O. vulgare	4.11	8.93	N.S.	0.92	-	-
P. lanceolata	64.61	312.10	***	23.61	68.09	***
R. acetosa	61.94	266.42	***	11.82	67.10	***

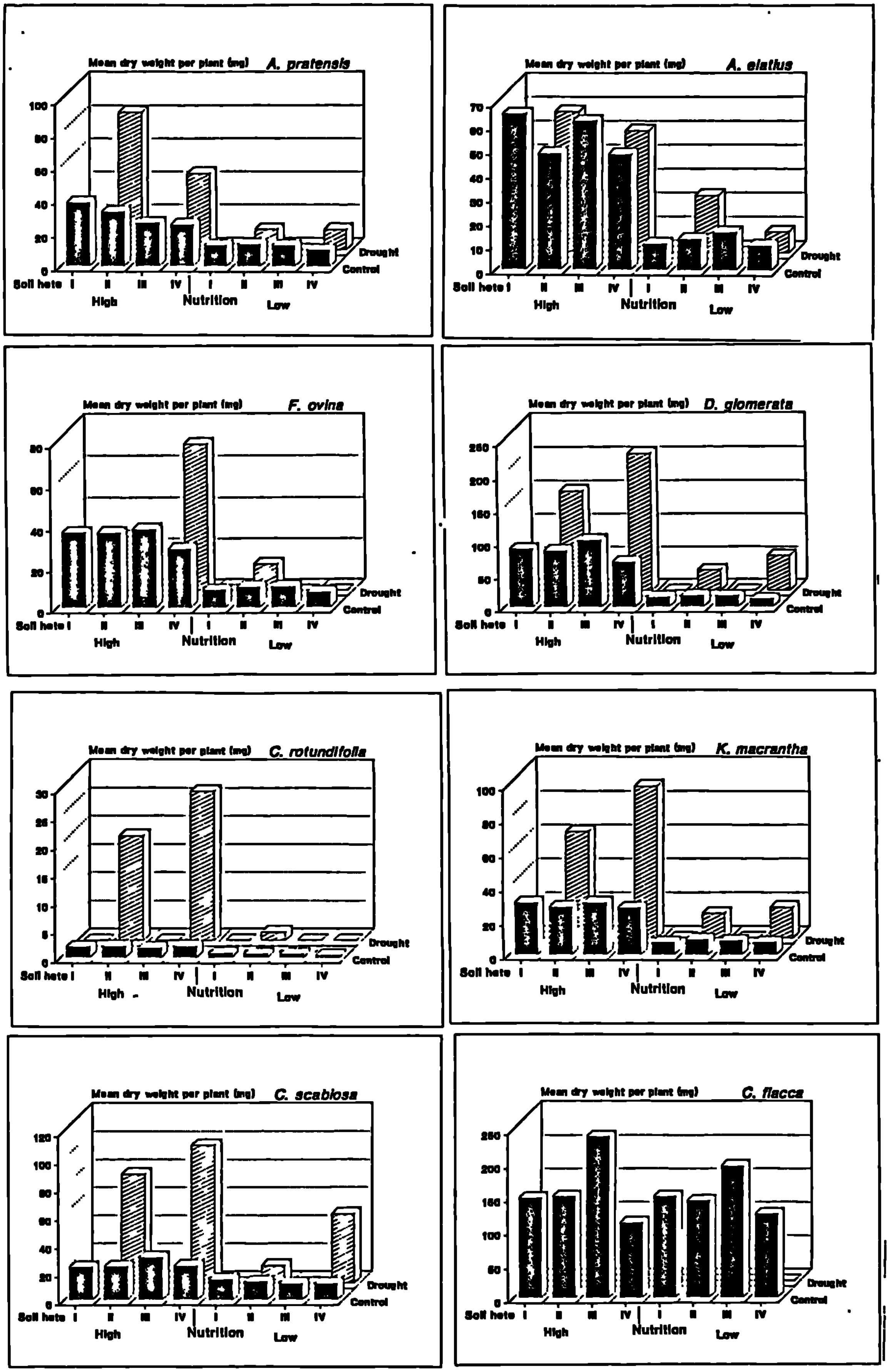
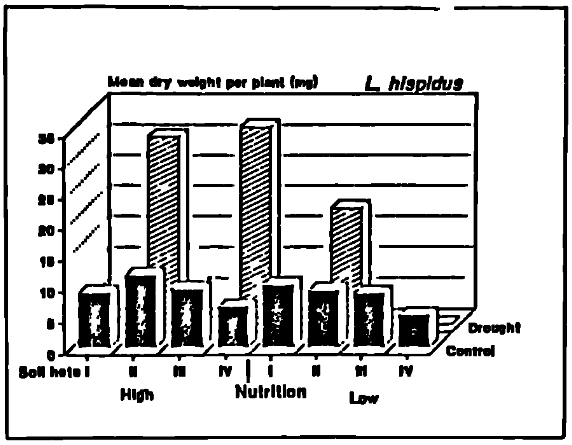
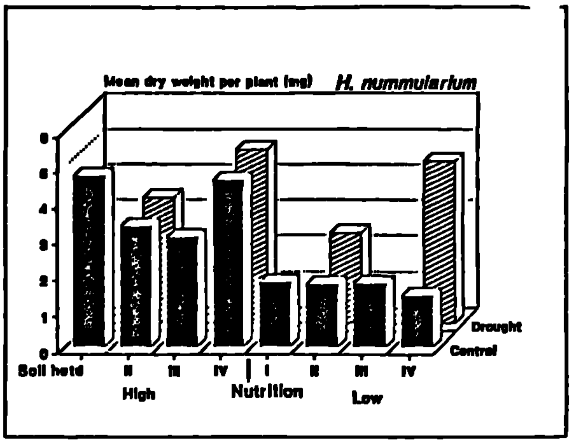
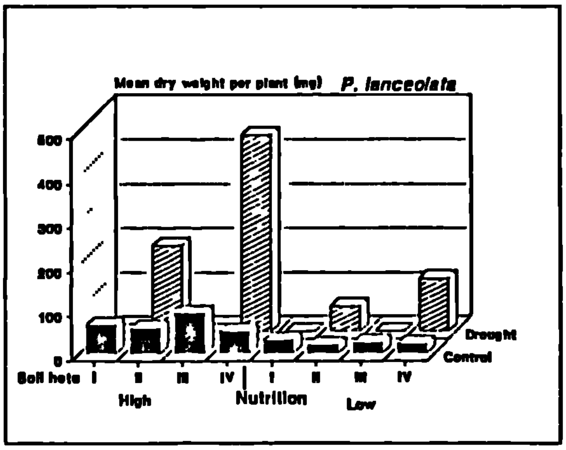


Figure 6.3: A graphical representation of mean dry weight (mg) of species in response to different treatments.


Mean dry weight per plant (mg)
L. hispidus
35
30
25
20
15
10
5
0
Soil hete I
II
III
IV
I
II
III
IV
High
Nutrition
Low
Drought
Control


Mean dry weight per plant (mg)
H. nummularium
6
5
4
3
2
1
0
Soil hetd
II
III
IV
I
II
III
IV
High
Nutrition
Low
Drought
Control


Mean dry weight per plant (mg)
P. lanceolata
500
400
300
200
100
0
Soil hete
I
II
III
IV
I
II
III
IV
High
Nutrition
Low
Drought
Control

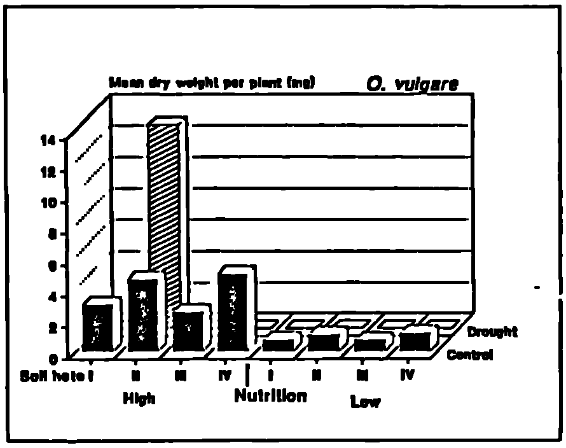
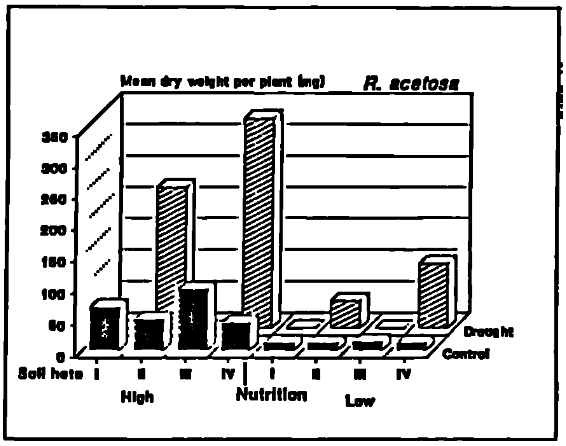

Mean dry weight per plant (mg)
O. vulgare
14
12
10
8
6
4
2
0
Soil hete I
II
III
IV
I
II
III
IV
High
Nutrition
Low
Drought
Control

Fig 3.6 (contd.)


Mean dry weight per plant (mg)
R. acetosa
350
300
250
200
150
100
50
0
Soil hete
I
II
III
IV
I
II
III
IV
High
Nutrition
Low
Drought
Control

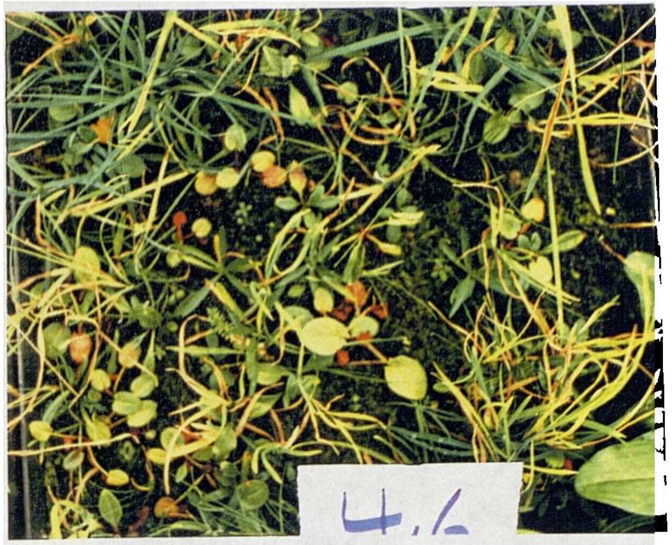
1. In the control treatment (no drought) all species, except *Carex flacca* and *Leontodon hispidus*, produced significantly larger plants in response to the high nutrient treatment (Table 6.8a and Plate 6.3a,b). 2. In the drought treatment as a result of drought mortality several species, including *Carex flacca* and *Origanum vulgare*, had too few replicates to give reliable estimate of shoot yield. *Leontodon hispidus*, *Helianthemum nummularium* and *Festuca ovina*, were considerably smaller in the low-nutrient regime, but the differences were not statistically significant. The remaining species had significantly higher mean dry weight in nutritionally rich conditions (Table 6.8a).

Heterogeneity in the rooting zone was associated with low biomass in both nutrient treatments (Table 6.7). The highest and lowest mean shoot dry weights of individual species, except *Origanum vulgare*, *Campanula rotundifolia* and *Helianthemum nummularium* were achieved in the soil heterogeneity treatments III and IV respectively (Table 6.7). In considering the response to the watering-treatments, it is necessary to recognize that many of the effects of drought reflected the response of plant dry matter production to the change in plant density, resulting from drought mortality. All surviving plant species responded to the reduction in plant density caused by drought, by increasing their mean dry weight (Plate 6.3c,d). The level of response varied between species and with nutrient regime (Table 6.8b). In the nutritionally-rich condition, *Arrhenatherum elatius*, *Festuca*

Plates 6.3 (a-d): Vertical views the vegetation developed after seven months in four of the treatments included in the microcosm experiment. (a) high nutrients, undroughted (b) Low nutrients, undroughted (c) high nutrients, droughted (d) low nutrients, droughted.

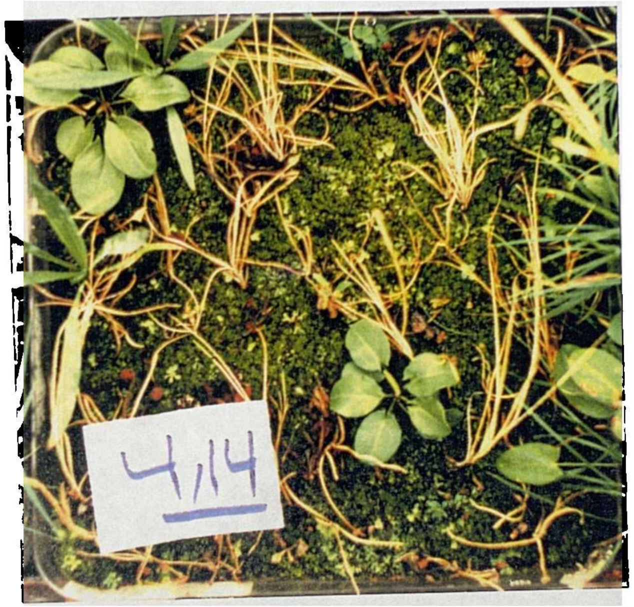
a

b



c

d



ovina, *Helianthemum nummularium* and *Origanum vulgare* exhibited statistically insignificant responses. In the nutrient-poor condition, by contrast, all species except *Avenula pratensis* responded significantly (Table 6.8b).

In undroughted control treatments in both nutrient regimes total dry weight and total number of plants per container were negatively associated ($P<0.05$). At high fertility in the droughted containers there was no such relationship whereas a positive correlation ($P<0.001$) developed between these two variables in the low fertility treatment.

Under high nutrient supply the relationship between total number of plants of all species per container and mean shoot dry weight per plant was negative in *Arrhenatherum elatius* ($P<0.05$), *Plantago lanceolata* ($P<0.01$), *Carex flacca* ($P<0.01$), and *Rumex acetosa* ($P<0.001$), and positive in *Origanum vulgare* ($P<0.05$). At low nutrient status, however, there was no statistically significant association between mean dry weight per plant of any species and total number of plants per container.

-Abundance and Diversity.

The mean relative abundance of each species, based on its percentage contribution to the total shoot biomass per container, was calculated in each treatment and is given in Table 6.10 . A Three-way analysis of variance was conducted (Table 6.9) in which effects of water supply, mineral nutrients, soil heterogeneity, and their interactions were examined. Soil heterogeneity and water supply emerged as

TABLE 6.9: Analysis of variance of proportional contribution (% of total dry weight) of individual species in each treatment: *** P<0.001; ** P<0.01; * P<0.05.

	Water	Nutrition	Soil-hete.	Wate*Nutri	Wate*Soil	Nutr*Soil
A. elatius	***	N.S.	***	**	*	N.S.
A. pratensis	***	N.S.	***	N.S.	N.S.	N.S.
D. glomerata	***	***	***	*	***	N.S.
F. ovina	***	**	*	*	N.S.	N.S.
K. macrantha	***	***	***	N.S.	*	N.S.
C. rotundifolia	*	N.S.	**	N.S.	N.S.	N.S.
C. flacca	***	***	***	***	**	N.S.
C. scabiosa	**	N.S.	**	N.S.	N.S.	N.S.
H. nummularium	***	**	**	N.S.	N.S.	N.S.
L. hispidus	***	***	**	*	N.S.	N.S.
O. vulgare	***	N.S.	***	*	***	N.S.
P. lanceolata	N.S.	N.S.	***	N.S.	***	N.S.
R. acetosa	***	*	***	N.S.	***	*

Table 6.10: (%) proportional contribution (abundance value) of each species to total shoot biomass in four treatments; I (no crevices or horizontal partitions), II (crevices), III (horizontal partitions), and IV (crevices + horizontal partitions).

	CONTROL (No drought)								DROUGHT				
	High nutrition				Low nutrition				Low nutrition		High nutrition		$LSD_{P<0.05}$ for all treatments
	I	II	III	IV	I	II	III	IV	II	IV	II	IV	
A. elatius	6.44	8.35	6.22	7.50	2.34	5.20	4.59	6.39	3.29	1.98	0.00	2.12	0.89
A. pratensis	4.85	7.19	3.32	6.88	3.57	6.82	4.18	6.59	3.47	1.27	2.83	2.38	0.61
D. glomerata	19.90	21.64	14.09	18.29	6.08	13.46	7.62	9.54	18.04	14.44	17.38	2.63	1.50
F. ovina	8.57	9.01	7.58	8.72	4.38	6.39	6.00	6.36	1.88	1.98	1.54	1.20	0.68
K. macrantha	5.34	6.87	5.41	8.67	2.56	5.54	3.12	4.92	6.58	5.01	4.59	2.66	0.58
C. rotundifolia	0.15	0.40	0.14	0.39	0.15	0.32	0.16	0.17	0.51	0.74	0.11	0.00	0.08
C. flacca	15.17	6.86	18.02	5.29	48.54	21.49	41.27	21.83	0.07	0.35	0.00	0.00	2.27
C. scabiosa	4.24	5.20	5.57	7.22	5.97	8.91	6.60	7.66	6.52	3.43	5.36	14.42	1.49
H. nummularium	0.71	0.65	0.31	0.89	0.60	1.12	0.68	1.01	0.14	0.23	0.78	0.66	0.12
L. hispidus	2.16	3.10	1.33	2.08	4.94	6.92	4.88	4.63	1.91	0.67	5.90	1.33	0.78
O. vulgare	0.31	0.69	0.19	1.31	0.16	0.39	0.19	0.69	0.18	0.01	0.37	0.00	0.09
P. lanceolata	13.76	15.23	18.45	17.14	13.44	14.43	11.61	18.90	13.62	27.84	33.92	17.80	2.93
R. acetosa	18.33	14.73	19.29	15.55	7.23	8.95	9.04	11.26	43.72	42.01	27.17	54.75	2.68

the most influential factors on the proportional contribution of species to total biomass. There is no statistically significant interaction between nutrient and soil heterogeneity, but some interactions between these three variables have significant effects on the abundance values of some species (e.g. *C. flacca, D. glomerata, R. acetosa)*.

The response of the abundance value of each species to different treatments was tested by using one-way analysis of variance, and the results are given in Tables 6.10 and 6.11. In the control, abundance values of *Arrhenatherum elatius, Dactylis glomerata, Festuca ovina, Koeleria macrantha, Origanum vulgare* and *Rumex acetosa* increased significantly in the high nutrient-treatment. In contrast *Carex flacca* and *Leontodon hispidus* increased their contribution in low nutrient treatments (Table 6.11a). *Carex flacca* dominated the nutrient-poor containers particularly in treatments I and III in continuously moist conditions. In the droughted containers, there was no significant response to nutritional treatment (Table 6.11a), *Carex flacca* was eliminated, and *Rumex acetosa* dominated the microcosms by contributing above 40 percent to total biomass. Figure 6.4 presents ranking of the species on the basis of their abundance values in each treatment.

Shannon diversity (H) and Evenness (J) indices were also calculated and these are given in Table 6.13. Three-way analysis of variance, including soil heterogeneity, water, mineral nutrients and their interactions are presented in

Table 6.11: (%) Proportional contribution of each species to total shoot biomass in different treatments; a; nutritional, and b; water regimes. The significant level of F-test based on P<0.05 *, P<0.01 **, P<0.001 ***.

a:

	CONTROL			DROUGHT		
	High nut	Low nut	F-test	High nut	Low nut	F-test
A. elatius	7.19	4.56	**	2.47	6.06	N.S.
A. pratensis	5.61	5.29	N.S.	2.75	2.45	N.S.
D. glomerata	18.36	9.04	***	17.67	9.00	N.S.
F. ovina	8.51	5.73	***	2.45	1.28	N.S.
K. macrantha	6.58	3.95	***	4.72	3.26	N.S.
C. rotundifolia	0.28	0.21	N.S.	0.32	0.16	N.S.
C. flacca	11.18	33.79	***	0.0	0.0	N.S.
C. scabiosa	5.61	7.61	N.S.	5.39	8.97	N.S.
H. nummularium	0.64	0.86	N.S.	0.22	0.57	N.S.
L. hispidus	2.22	5.37	***	1.33	3.01	N.S.
O. vulgare	0.63	0.35	N.S.	0.08	0.16	N.S.
P. lanceolata	16.18	14.41	N.S.	20.34	23.15	N.S.
R. acetosa	16.84	9.11	***	41.64	40.53	N.S.

b:

	HIGH NUTRITION			LOW NUTRITION		
	Control	Drought	F-test	Control	Drought	F-test
A. elatius	7.19	2.47	***	4.56	6.06	N.S.
A. pratensis	5.61	2.75	*	5.29	2.45	**
D. glomerata	18.36	17.67	N.S.	9.04	9.00	N.S.
F. ovina	8.51	2.45	***	5.73	1.28	***
K. macrantha	6.58	4.72	N.S.	3.95	3.26	N.S.
C. rotundifolia	0.28	0.32	N.S.	0.21	0.16	N.S.
C. flacca	11.18	0.0	***	33.79	0.0	***
C. scabiosa	5.61	5.39	N.S.	7.61	8.97	N.S.
H. nummularium	0.64	0.22	**	0.86	0.57	N.S.
L. hispidus	2.22	1.33	*	5.37	3.01	N.S.
O. vulgare	0.63	0.08	**	0.35	0.16	N.S.
P. lanceolata	16.18	20.34	N.S.	14.41	23.15	*
R. acetosa	16.84	41.64	***	9.11	40.53	***

TABLE 6.12: The significant level of three-way analysis of variance (ANOVA) of Shannon diversity (H) and evenness indexes in the microcosm experiment: *** P<0.001; ** P<0.01; * P<0.05.

	Water	Nutrition	Soil-hete.	Wate*Nutri	Wate*Soil	Nutr*Soil
DIVERSITY (H)	***	*	***	N.S.	***	N.S.
EVENNESS (J)	***	N.S.	***	**	***	*

Table 6.13: Shannon diversity (H) and evenness (J) indices were calculated for different soil heterogeneities (a) water treatments (b), and different nutritional regimes (c). LSD based on $P<0.05$, and the significant level of F-test based on $P<0.05$ *, $P<.0.01$ **, $P<0.001$ ***.

		CONTROL (No drought)					DROUGHT				
a:		I	II	III	IV	LSD.	I	II	III	IV	F-test
DIVERSITY (H)	HIGH NUTRITION	2.14	2.20	2.10	2.22	0.03	-	1.69	-	1.37	N.S.
	LOW NUTRITION	1.78	2.22	1.94	2.15	0.06	-	1.73	-	0.98	*
EVENNESS (J)	HIGH NUTRITION	0.84	0.86	0.82	0.87	0.01	-	0.73	-	0.64	N.S.
	LOW NUTRITION	0.69	0.86	0.76	0.84	0.02	-	0.76	-	0.67	N.S.

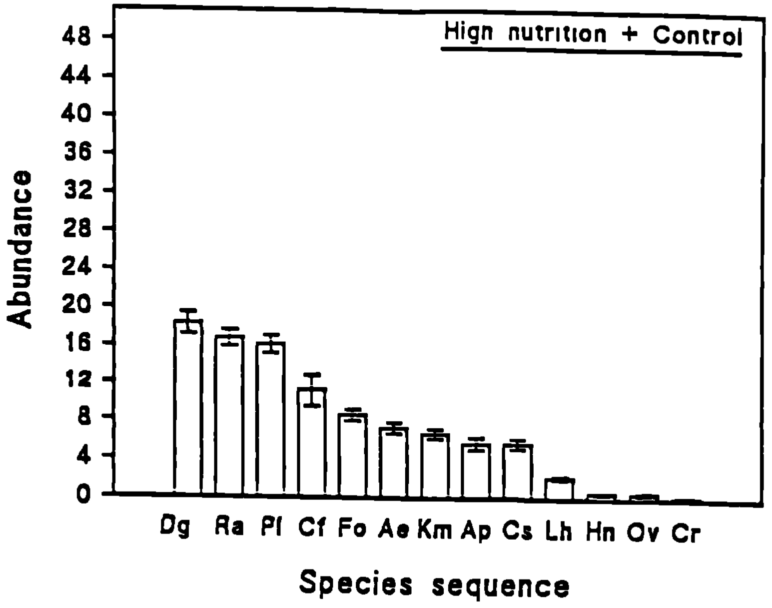
	HIGH NUTRITION			LOW NUTRITION		
b:	CONTROL	DROUGHT	F-TEST	CONTROL	DROUGHT	F-test
DIVERSITY (H)	2.16	1.53	***	2.02	1.35	***
EVENNESS (J)	0.84	0.68	***	0.76	0.71	*

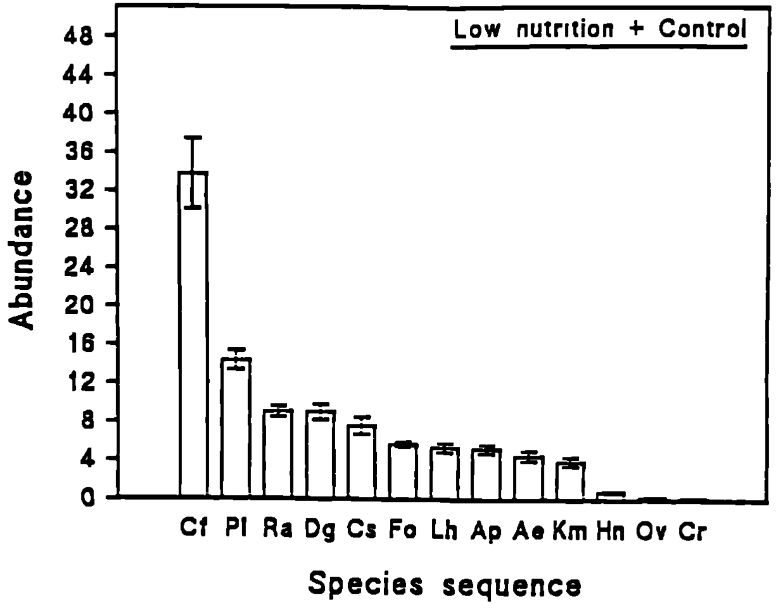
	CONTROL			DROUGHT		
c:	HIGH NUT	LOW NUT	F-test	HIGH NUT	LOW NUT	F-test
DIVERSITY (H)	2.16	2.02	**	1.53	1.35	N.S.
EVENNESS (J)	0.84	0.76	*	0.68	0.71	N.S.

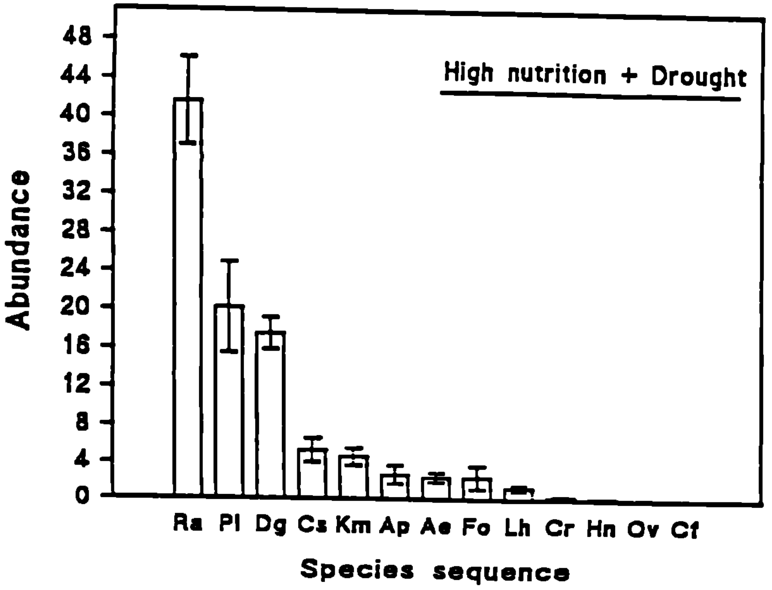
Figure 6.4:

Species ranks based on individual species proportional contribution (%) to the total biomass per container at different treatments.

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Thymus praecox(Tp).


Hign nutrition + Control
Abundance
0
4
8
12
16
20
24
28
32
36
40
44
48
Dg Ra Pl Cf Fo Ae Km Ap Cs Lh Hn Ov Cr
Species sequence


Low nutrition + Control
Abundance
0
4
8
12
16
20
24
28
32
36
40
44
48
Cf Pl Ra Dg Cs Fo Lh Ap Ae Km Hn Ov Cr
Species sequence


High nutrition + Drought
Abundance
0
4
8
12
16
20
24
28
32
36
40
44
48
Ra Pl Dg Cs Km Ap Ae Fo Lh Cr Hn Ov Cf
Species sequence

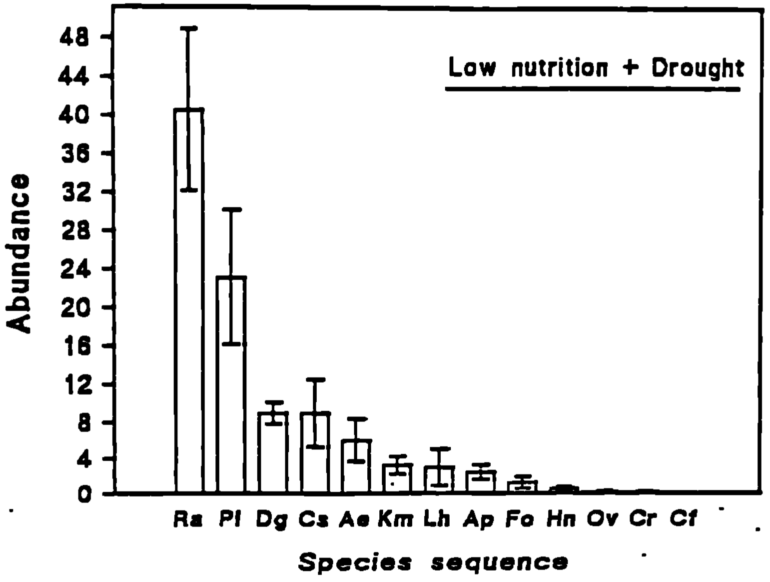

Low nutrition + Drought
Abundance
0
4
8
12
16
20
24
28
32
36
40
44
48
Ra Pl Dg Cs Ae Km Lh Ap Fo Hn Ov Cr Cf
Species sequence

Table 6.12. On the basis of these analyses, it is apparent that diversity was affected by water supply, soil heterogeneity, and nutrient supply in descending order. Only the interaction of water and soil heterogeneity had a significant effect on diversity.

In order to clarify the result of the three-way analysis of variance, a one-way analysis of variance was carried out on the response of the two indices to the individual experimental variables. The results presented in Table 6.13 indicate that in the control condition (no drought) containers with crevices (II, IV) become more diverse than the other two (I, III). Figure 6.5 and Table 6.3b show that, as we might expect, diversity was reduced by the mortalities inflicted by the drought treatment. In the droughted microcosms with soil heterogeneity treatments I and III there was no surviving vegetation (and therefore no diversity !). Of the remaining treatments, II (crevices only) was more diverse than treatment IV (crevices + horizontal partitions), but this differences was significant (Table 6.13a) only in the low-nutrient treatment. Containers supplied with nutrients at high concentrations had higher diversity than those maintained at low nutrient levels (Table 6.13c).

Figures 6.6, and 6.7 demonstrate that in more productive treatments the abundance of species of high potential RGR shows an inverse relationship to species diversity. In contrast, at low nutrients *Carex flacca* was the only species which was negatively correlated with diversity. There were

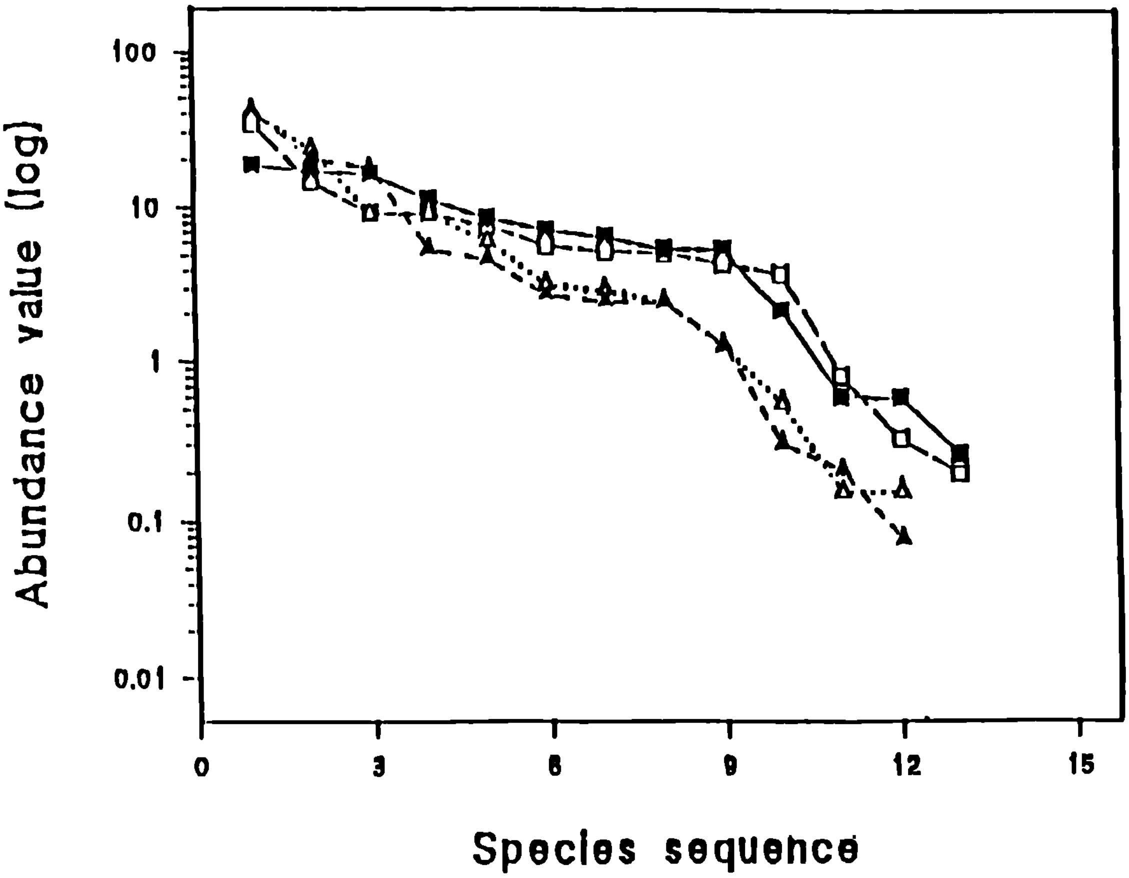


Figure 6.5:
Comparison of dominance diversity curves (Whittaker 1965) based on species abundance value at different water regimes.

High nutrition + control ————
Low nutrition + control — — — —
High nutrition + drought - - - - - -
Low nutrition + drought ....

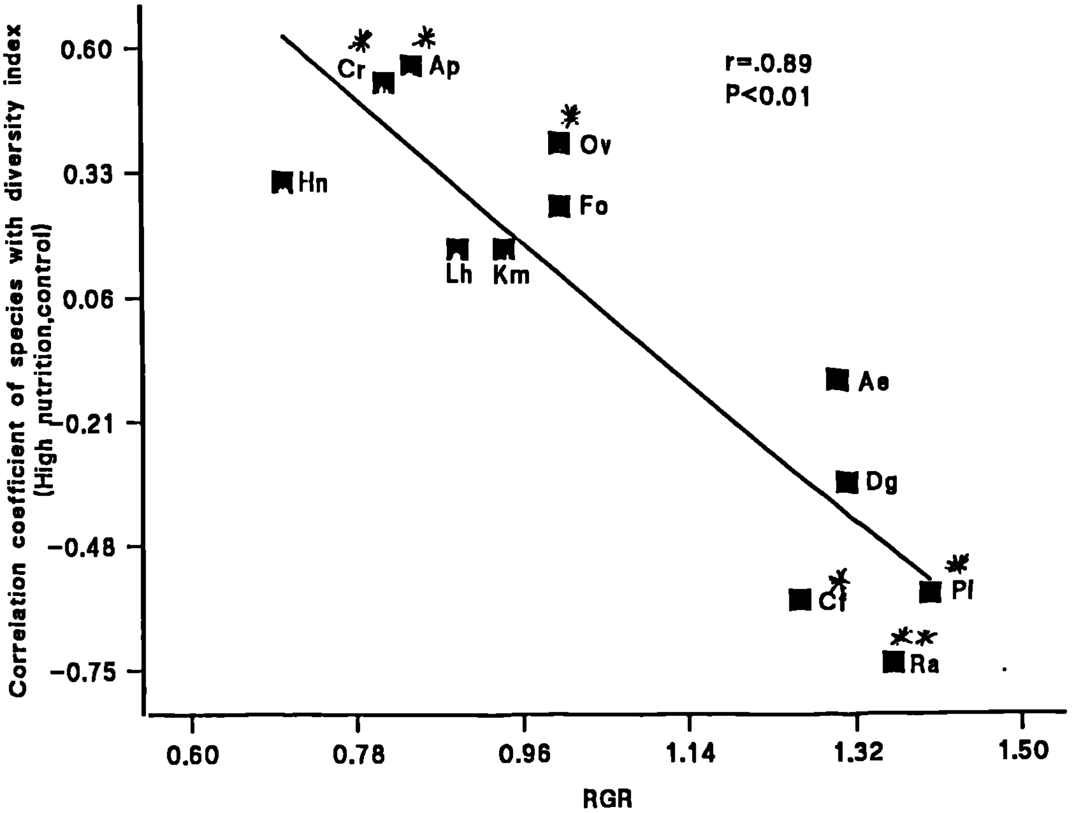


Figure 6.6:
The correlation coefficient of species with diversity index plotted against their RGR (relative growth rate). As the figure shows, the fast-growing species were associated negatively with diversity in the nutritionally rich condition.

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Thymus praecox(Tp).

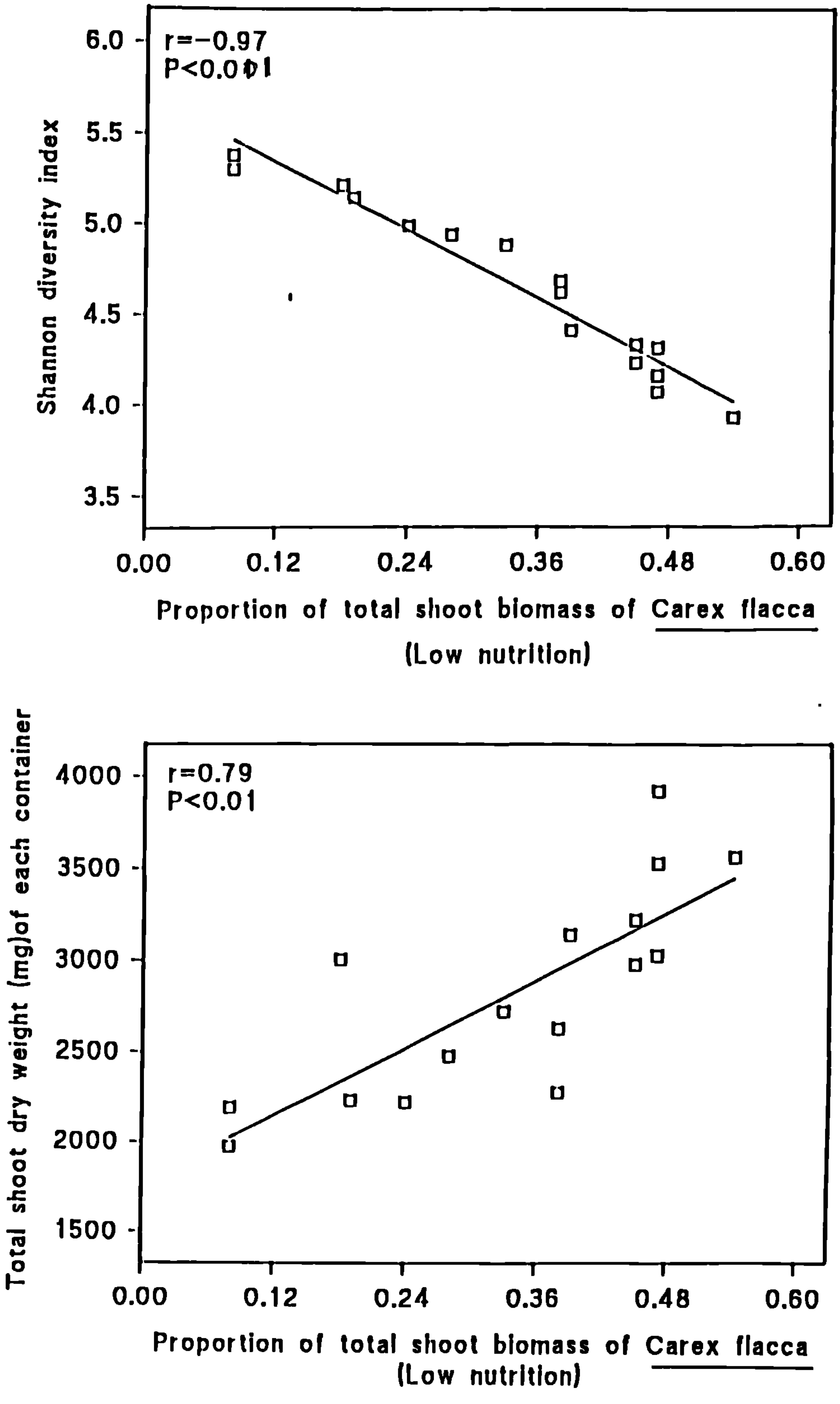


Figure 6.7: a, Relationship between diversity index and *Carex flacca* abundance value (proportional contribution) in low nutrient containers. b, Relationship between total biomass per container in low nutrient conditions and *C. flacca* abundance value (proportional contribution to total biomass)

no significant differences in diversity between the two nutritional treatments In general the highest diversity corresponded to soil heterogeneity treatment IV under continuously moist conditions and high mineral nutrient supply, and the lowest to soil heterogeneity treatment IV in the droughted, nutrient poor condition. Diversity had positive and negative associations respectively with total plant density and total biomass per container in the control treatment, but these relationships in the drought treatment were not statistically significant (Table 6.14)

6.4 DISCUSSION :

- Germination :

As explained on page 7, despite having the same water supply, an effect of soil-heterogeneity on germination was evident and must be taken into account in interpreting the results. Containers with crevices had higher germination rates than those without crevices. At the end of the experiment diversity was higher in containers with crevices. Also there was a positive correlation between diversity and total plant density per container. It is now difficult to isolate the consequences of differences in initial germination from the effects of other treatments.

- Drought survivorship :

The effect of drought on a plant community may be evidenced by the death of individuals (disturbance sensu Grime 1977)

TABLE 6.14: Correlation coefficient (r) of two Shannon diversity (H) and evenness indices with total biomass and total number of plants per container. The significant level of r value based on * P<0.05, ** P<0.01, *** P<0.001, df=14 (in control condition) and df=6 (in drought condition)

		CONTROL				DROUGHT			
		HIGH NUT	P<	LOW NUT	P<	HIGH NUT	P<	LOW NUT	P<
Total biomass per container	DIVERSITY (H)	-0.70	**	-0.84	***	-0.40	N.S.	0.62	N.S.
	EVENNESS (J)	-0.66	**	-0.84	***	-0.40	N.S.	0.56	N.S.
Total number of plant per container	DIVERSITY (H)	0.68	**	0.78	***	0.58	N.S.	0.69	N.S.
	EVENNESS (J)	0.69	**	0.78	***	0.65	N.S.	0.86	N.S.

or by reduction of growth (stress sensu Grime 1977). Here the former definition is relevant. Survivorship varied between species and between different nutrient- and soil heterogeneity-treatments. *Rumex acetosa* and *Carex flacca* respectively had the highest and lowest survivorship rates. This hierarchy of survivorship appears to be related to root length (depth of penetration); this hypothesis is tested later (Chapter 8) using data from the root penetration study (Chapter 5).

Soil heterogeneity also affected survivorship. No plants survived drought in those containers without crevices, and more individuals survived in containers provided with crevices alone than in containers where access to crevices was partially obstructed by horizontal partitions. It is clear therefore that horizontal partitions intensified drought mortality. This is consistent with the observation that in arid and semi-arid ecosystems, after early growth in spring where moisture is readily available in the upper soil horizons, summer deaths of seedlings tend to be most common in individuals that do not have access to subsoil moisture (Salihi & Norton 1987; Owens & Norton 1989; Reichenberger & Pyke 1990; Pyke 1990). Unlike shallow-rooted species (Dodd *et al* 1984; Moll & Sommerville 1985: Hart & Rodosovich 1987), deep-rooted plants retain contact with water stored at depth (Crombie *et al* 1988). Since the surface root systems were unlikely to have been functional in the absence of rain over summer (Lamont 1976), it is sinkers and tap roots that must have sustained shoot growth at this time

(Lamond & Bergel 1991).

Survivorship in the experiment was also affected by nutrient supply. Particularly in soil heterogeneity treatment IV (crevices + horizontal partitions), containers in the high-nutrient treatment had higher survivorship rates than those in the low-nutrient condition. Effects of mineral nutrient supply on ability to avoid drought mortality have been suggested by previous studies (Peak *et al* 1975; Grime & Curtis 1976; Wellington 1985). It was found by Wellington (1985) that the addition of nutrients to soils reduces seedling mortality, presumably by promoting root growth, thus enhancing exploitation of deeper soil moisture.

- Competition and diversity :

In case of competition and nutrients, there are two controversial theories; Grime (1973, 1979), Huston (1979), and Keddy (1989) have suggested that the intensity of interspecific competition increase along a productivity gradient. Competition may be most important in productive habitats, which support high growth rates, and high biomass production. In contrast Newman (1973, 1983), and Tilman (1988) suggest that there may be no quantitative change in the intensity of competition along a productivity gradient but there may be an important qualitative change.

It is obvious that neither side has ruled out the existence of competition as a factor in unproductive conditions, but the differences lie in the degree of emphasis on the intensity and the quality of competition in nutrient poor habitats. The results of this experiment provide two lines of evidence to suggest that plant growth is constrained by competition; first, removal of plants by means of drought mortality improved the above-ground productivity of their surviving neighbours. Second, there was a negative correlation between total density and total biomass production in both nutritional treatments. Therefore the results of this experiment may suggest that competition occurred in both low and high nutritional treatments. Despite the evidence of existence of competition in both nutritional treatment, some features of the data indicate that competition was more intense in the productive than in the unproductive conditions. Fig 6.3 indicates that the greatest increases in plant sizes in all species following drought mortality occurred in the nutritionally rich conditions. Second, there was a strong negative association between mean dry weight of individual species and total plant density per container in the high nutrient treatment, but there was no such relationship in the low nutrient treatment. Third, in the continuously moist conditions, mortality was higher in rich than poor treatments.

In any attempt to explain the dominance of *Carex flacca* in the low nutrient conditions, it may be important to draw a distinction between the ability of plants to compete for resources and the capacity for dominance. Many of the plants which eventually dominate unproductive habitats of low biomass, achieve their status not through any exceptional ability to monopolize resource capture in competition with neighbours; rather they assume dominance through the capacity to retain and protect captured resources (Grime 1979, Grime *et al.* 1990). Therefore the reason for great reduction in abundance of some species, e.g. *Rumex acetosa* may arise from its sensitivity to nutrient deficiency (Grime 1963) rather than its failure in direct competition for resources with species such as *Carex flacca*. Also, where drought disturbance, as in this experiment takes place during summer time (growing season), resulting in higher density independent mortality , the chance for competition within and between species is considerably reduced.

Diversity was affected by drought, soil heterogeneity and nutrients. Also the interaction of drought and soil heterogeneity is likely to have played played a significant role (Evenari *et al.* 1971; Yair *et al.* 1978; Whittaker *et al.* 1983; Erschbamer *et al.* 1983). As a result of drought disturbance considerable numbers of plants were killed, therefore diversity was reduced significantly compared to wet conditions. The effect of drought was intensified by the shallowness of the soil either because of the absence of crevices and/or as result of the presence of horizontal partitions.

In the continuously moist conditions soil heterogeneity and nutrient supply influenced plant diversity. Dominance by one single species (*Carex flacca*) in nutrient poor containers, reduced diversity significantly compared to rich conditions.

In response to soil-heterogeneity all species except *Origanum vulgare*, *Campanula rotundifolia* and *Helianthemum* *nummularium*, achieved the highest and lowest mean dry weight in treatments III and IV respectively. If the higher density was the only reason for the low biomass production in soil heterogeneity treatment IV, then we should have a similar result in soil heterogeneity II, which had similar density to treatment IV, but produced relatively higher biomass. Perhaps the higher density and horizontal partitions acted together to restrict the growth of plants, particularly larger plants, and gave an opportunity for smaller plants like *Origanum vulgare*, *Campanula rotundifolia*, and *Helianthemum nummularium* to grow relatively free from competition from other dominant plants. Consequently diversity was increased in both nutritional treatments.

Chapter 7

Floristic diversity in a model system using experimental 'Microcosms' providing factorial combinations of different watering regime and species input.

7.1: INTRODUCTION:

Generally, grassland vegetation contains different grass species together with several dicotyledons. It is difficult to identify the factors determining both species composition and the abundance of these functional groups. Published studies have generally put more emphasis on studying either the relationship between one grass and one legume or between grasses and short-lived annual forbs. In the experiment which is discussed in this chapter the main objective is to study the influence of perennial grasses on survivorship and abundance of perennial forbs and *vice versa*. The selected species coexist at the studied site.

In the experiment discussed in the previous chapter, species responses in a "plant community" synthesised in microcosms were examined in a multifactorial experiment, using water, nutrient, and soil depth treatments. In the experiment which is discussed here, the nutritional and soil depth conditions of all turf microcosms were kept constant, but species input was varied. All microcosms contained crevices and horizontal partitions, and were supplied with 100 ml Rorison solution once every three weeks, in order to simulate a heterogeneous nutrient-deficient soil of the kind encountered in Millersdale (Chapter 2). In each species drought survivorship, growth, and abundance in response to different plant community (and density) treatments were tested under the influence of two moisture supply treatments (control, drought).

7.2:METHODS AND MATERIALS:

Experimental design

Two watering treatments (control and drought), and the four plant composition treatments shown in Table 7.0 provided a total of eight combinations, each of which was replicated five times.

Each of the 40 microcosms in the experiment had external dimensions of 230 x 230 x 100 mm with crevices and horizontal partitions (for further details see Chapter 6), and was filled to a depth of 85 mm, of which the lower 75 mm was sand, and upper 10 mm was soil collected from the surface layer of the Millers Dale site.

All containers were free draining; this was achieved by drilling 25 holes each 30 mm diameter (see Fig. 6.1) in the base. Soil was retained by covering the base with a single layer of terylene cloth.

All microcosms were independent of each other and were maintained in a randomized block supported by a metal frame-work in an unheated glass house with natural day light at the Sheffield University Botanical Garden.

Treatments

Studies of plant composition have used a limited number of experimental designs. The two principal types are additive and substitutive. In the additive, the densities of species in mixture is greater than in monoculture. In the substitutive experimental design (de Wit 1960), the relative proportions of the components of a mixture are varied, but the total density is kept constant. the substitutive (replacement series) approach has been criticized recently because of the sensitivity of the results to the total mixture density (Suehiro & Ogawa 1980; Inouye & Schaffer 1981; Spitters 1983; Joliffe, Minjas & Runeckles 1984; Firbank & Watkinson 1985; Connolly 1987; Law & Wakinson 1987) and its restriction when numerous species are included in the mixture (Austin & Austin 1980). In this experiment, an additive design with equal proportions was used (Austin & Austin 1980; Newman 1983); density in different mixtures is the same for all species. There were four plant community (composition) treatments;

- Grasses + Forbs + Legume (GFL).
- Grasses + Forbs (GF).
- Grasses (G).
- Forbs (F).

The grasses and forbs contained six and ten species, respectively, and only one legume was involved (Table 7.0). Four different plant communities with different total plant densities were sown as shown below. Each species was sown at a constant rate of 25 seeds per container.

Treatments	number of species	density (sown seeds/container)
GFL	17	425
GF	16	400
G	6	150
F	10	250

In order to allow the same chance of establishment by each species, in each part of the container one seed of each species was dropped into each of twenty five 46 mm x 46 mm,

Table 7.0: Different plant community treatments. The symbol (+) opposite any species indicates that species was present in that particular community.

Grasses + Forbs + Legume	Grasses + Forbs	Grasses	Forbs
Grasses:			
Arrhenatherum elatius	+	+	
Avenula pratensis	+	+	
Briza media	+	+	
Dactylis glomerata	+	+	
Festuca ovina	+	+	
Koeleria macrantha	+	+	
Forbs :			
Campanula rotundifolia	+		+
Carex flacca	+		+
Centaurea scabiosa	+		+
Helianthemum nummularium	+		+
Hieracium pilosella	+		+
Leontodon hispidus	+		+
Origanum vulgare	+		+
Plantago lanceolata	+		+
Rumex acetosa	+		+
Thymus praecox	+		+
Legume:			
Lotus corniculatus			

subsections of the soil surface.

For each plant community treatment, there were two water regimes; control and drought. In the initial phase of the experiment all containers had the same watering regime in which they all were maintained in a uniformly moist condition with regular watering every day with deionized water. At the beginning of August, 15 weeks after sowing, the drought treatment was implemented in half of the containers by withholding water for three weeks. During the three weeks of the drought period the sand within the crevices of the unwatered containers was maintained in a moist condition, in order to simulate the deep and moist crevices of a natural habitat. The method of watering used for this purpose was designed to prevent significant upward movement of water to the main containers. After three weeks, the droughted containers were re-watered and mineral nutrient supplies were recommenced.

All containers, regardless of watering treatment and plant species input, had similar low nutrient supply regime; they were supplied once every three weeks with 100 ml full Rorison solution.

Time table

20-April 1989:

Immediately after seeds were sown, all containers were covered by a plastic sheet, creating relatively humid and warm conditions for seed germination. This cover was removed after two weeks.

1-June 1989:

Mineral nutrients were supplied, and subsequently maintained until three weeks before starting the drought treatments.

1-August 1989:

The drought treatment was implemented for three weeks.

21-August 1989:

Droughting was terminated and mineral nutrient supplies were recommenced.

20-30 Number 1989:

Each surviving plant was individually harvested and dried to 80°C for 48 h., then weighed.

Data analysis

Using the Minitab program, analyses of variance were carried out. Drought survivorship, mean shoot dry weight and abundance values for each species, and Shannon diversity (H), and evenness (J) indices for each treatment were calculated (see Chapter 6 for further details).

6.3: Results:

I. General features:

Seedling densitiy

Total density per container for each treatment is given in Table 7.1. Three of seventeen species; *Briza media, Hieracium pilosella,* and *Thymus praecox* failed to germinate. Two-way analysis of variance (Table 7.2) indicates that total density per container was affected by individual and interactional effect of the two experimental factors; water and species input. Table 7.1 confirms that the very

Table 7.1: The calculated Shannon diversity (H), and evenness (J) indices, with total biomass per container (mg), and total number of plants per container (density) of different treatments. GFL (grasses + forbs + legume), GF (grasses + forbs), G (just grasses), and F (just forbs).

	CONTROL (no drought)					DROUGHT					$LSD_{P<0.05}$ of all treatments
	GFL	GF	G	F	$LSD_{P<0.05}$	GFL	GF	G	F	$LSD_{P<0.05}$	
Diversity (H)	2.12	2.13	1.56	1.48	0.19	1.38	1.19	1.17	0.42	0.48	0.34
Evenness (J)	0.80	0.83	0.97	0.71	0.08	0.69	0.74	0.89	0.39	0.21	0.13
Total biomass per container (mg)	2729.7	2315.5	1374.4	2081.7	551.1	285.9	551.4	413.3	265.4	291.9	426.0
Total number of plants per container	217.6	194.8	73.3	126.4	14.9	13.0	12.2	13.4	7.8	11.6	13.0

	Water	PLant composition	Interaction
Diversity (H)	***	***	N.S.
evenness (J)	**	***	N.S.
Total biomass	***	***	***
total density	***	***	***

Table 7.2: Result of two-way analysis of variance (ANOVA) of individual and interactional effect of different water regimes, and plant composition on diversity indices, biomass production and plant density per container.
$P<0.01$ **, $P<0.001$ ***.

different inputs of seeds resulted in different seedling densities according to treatment. In the non-droughted treatment, the highest density with average 217 seedlings, and the lowest with 73 seedlings per container belonged respectively to the 'GFL' and 'G'. Drought reduced the total density so dramatically (Table 7.1) that a after implementing the drought treatment the differences in density between different plant composition treatments were no longer significant.

Survivorship in drought treatment

Drought survivorship varied between major functional components and among individual species (Table 7.3). GFL and GF treatments had similar mean drought survivorship. Table 7.3 and Figure 7.1b show that drought survivorship was higher in 'G' and 'F' than 'GFL' and 'GF' treatments, although the response was significant only for the grasses (G) group. The highest and the lowest mean survivorship belonged respectively to *Rumex acetosa* and *Carex flacca* at 14.00 and 0.00 percent. Only *Campanula rotundifolia* increased its drought survivorship significantly in the containers in which legume was present (Figure 7.1a)

Biomass production and diversity

Total biomass per container is presented in Table 7.1. Two-way analysis of variance indicates that biomass production was affected by the different species input, watering treatment and the interaction between these two experimental factors. In the control treatment a positive association ($P<0.05$) between total biomass and total

Table 7.3: The drought survivorship (%) of species in various synthesised "communities" containing different functional elements: GFL (grasses + Forbs + legume), GF (grasses + Forbs), G (just grasses), and F (just Forbs). * $LSD_{P<0.05}$, ** $LSD_{P<0.01}$, *** $LSD_{P<0.001}$.

	DROUGHT SURVIVORSHIP (%)				The level of statistical significant differences					
	GFL	GF	G	F	$LSD_{P<0.05}$	G vs GFL	G vs GF	F vs GFL	F vs Gf	GF vs GFL
A. elatius	9.3	6.7	8.9	-	10.1	N.S.	N.S.	-	-	N.S.
A. pratensis	6.7	5.6	15.9	-	12.5	N.S.	N.S.	-	-	N.S.
D. glomerata	4.2	2.8	19.8	-	14.1	*	*	-	-	N.S.
F. ovina	3.1	6.2	7.8	-	11.6	N.S.	N.S.	-	-	N.S.
K. macrantha	6.6	4.3	18.2	-	10.2	*	*	-	-	N.S.
C. rotundifolia	8.9	0.0	-	1.8	3.1	-	-	***	N.S.	***
C. flacca	0.0	0.0	-	0.0	0.0	-	-	N.S.	N.S.	N.S.
C. scabiosa	11.0	8.2	-	12.3	12.8	-	-	N.S.	N.S.	N.S.
H. nummularium	4.2	5.6	-	2.8	8.2	-	-	N.S.	N.S.	N.S.
L. hispidus	0.0	2.2	-	2.2	3.2	-	-	N.S.	N.S.	N.S.
O. vulgare	1.5	1.5	-	0.0	3.7	-	-	N.S.	N.S.	N.S.
P. lanceolata	9.7	5.6	-	11.6	10.9	-	-	N.S.	N.S.	N.S.
R. acetosa	8.6	14.6	-	18.9	12.1	-	-	N.S.	N.S.	N.S.
L. corniculatus	6.9	-	-	-	-	-	-	N.S.	N.S.	N.S.
Mean/container	5.9	5.7	15.4	7.6	7.7	**	**	N.S.	N.S.	N.S.

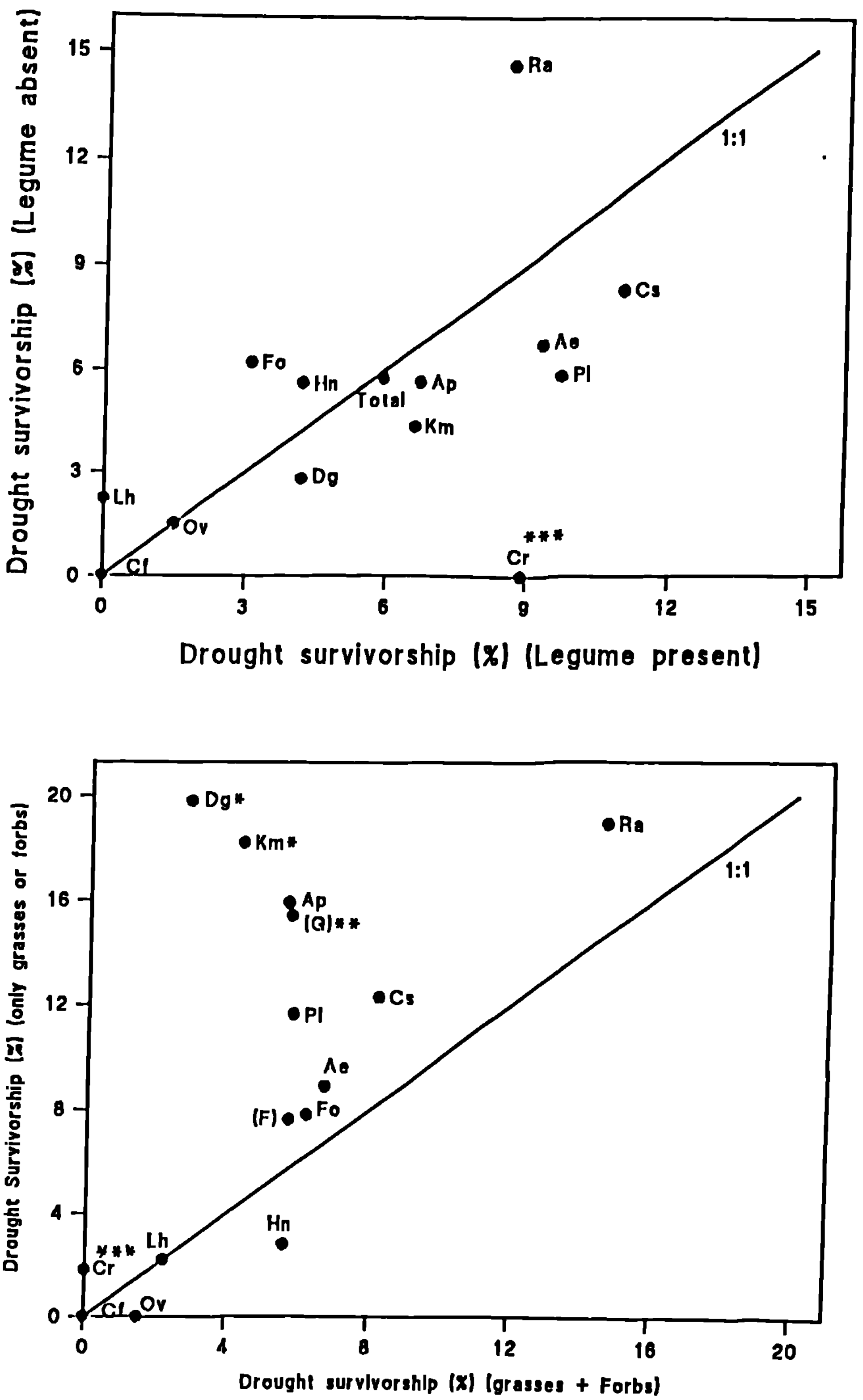


Figure 7.1: The differences in percentage drought survivorship of each individual species in response to presence or absence of legume (a), and to different plant compositions (b).
$P<0.05$ *, $P<0.01$ **, and $P<0.001$ ***.

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Plantago lanceolata (Pl), Rumex acetosa (Ra), Grasses (G), and Forbs (F).

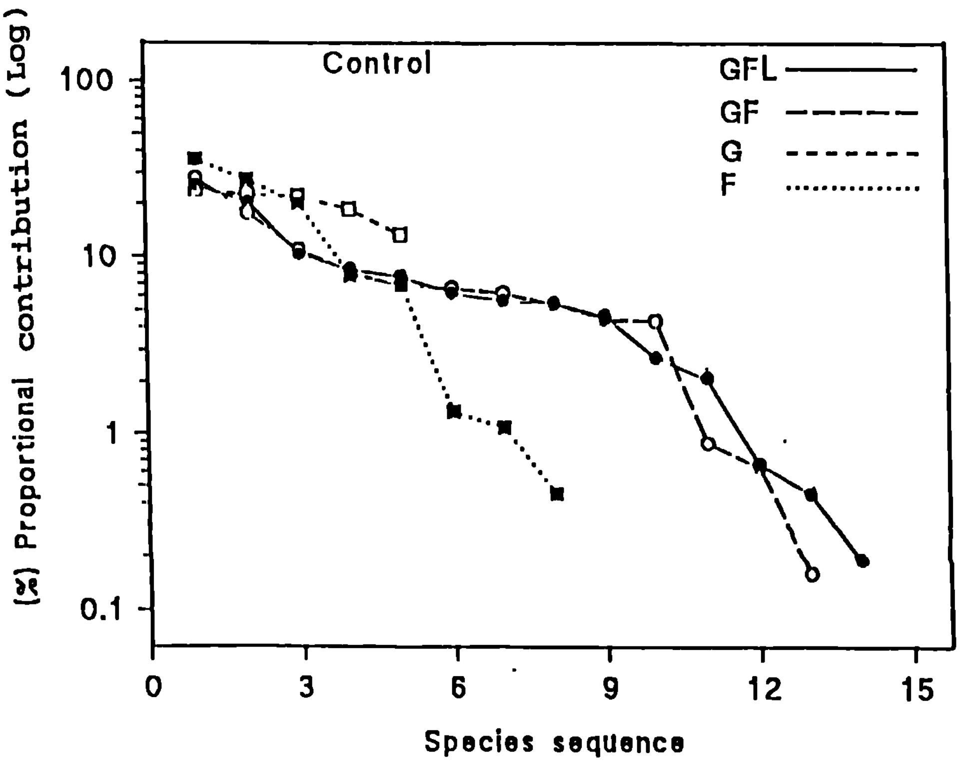
seedling density per container showed that treatments with higher seedling numbers such as GFL and GF produced higher biomass. Drought considerably reduced total biomass, and the differences from the control treatment were highly significant (Table 7.1). In droughted containers differences in total biomass production between different species input treatments was not statistically significant. Two-way analysis of variance of diversity and evenness indices is given in Table 7.2, and shows that both were affected by water and different species input treatments. There was a statistically insignificant interaction between these two experimental factors.

Shannon diversity (H) and evenness (J) indices were calculated for each community, and are given in Table 7.1. The 'GFL' and 'GF' treatments, as expected, had higher diversity (H) index than 'G' and 'F' treatments in control condition. In the drought treatment, as a result of higher seedling mortality, the differences in density and diversity (H) between different species input treatments disappeared (Table 7.1). The 'G' treatment had the highest, and 'F' treatment had the lowest evenness (J) index in both control and drought treatments (Figure 7.2 and Table 7.1). Both indices were reduced by drought. This reduction was higher in 'F' treatment (7.1).

II. Species responses:

Species yield

Two-way analysis of variance indicates that grasses and



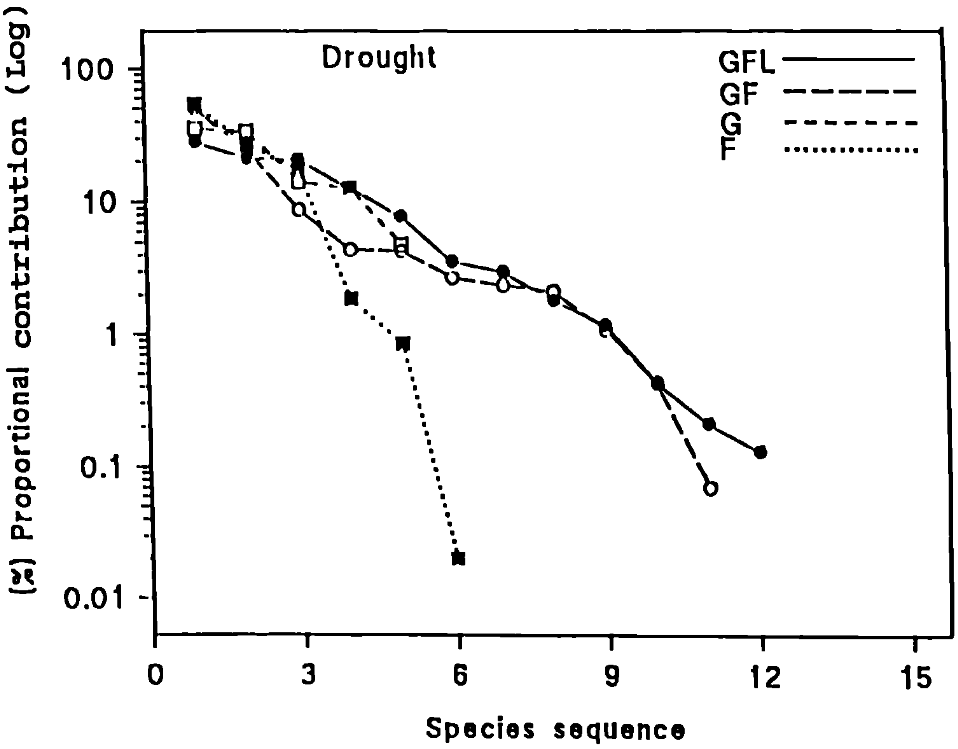


Figure 7.2: Comparison of dominance diversity curves (Whittaker 1965) based on species abundance values in different plant community treatments.

forbs biomass production were mainly influenced by species input and watering treatment respectively (Table 7.4). Mean shoot dry weight of some species, such as *Koeleria macrantha, Campanula rotundifolia, Plantago lanceolata* and *Rumex acetosa* were affected by individual and interactional effect of these two experimental factors; water and species input treatments (Table 7.4). In the control treatment (Table 7.5) the mean shoot dry weights (mg) of the majority of species were reduced in containers in which legume (*Lotus corniculatus)* was present. Only for *Plantago lanceolata* was this reduction statistically significant.

Grasses produced the highest yield in the 'G' treatment in which forbs and legume were absent. Among forbs *Carex flacca, Centaurea scabiosa* and to some extent *Helianthemum nummularium* and *Origanum vulgare* did not respond to different species input treatment (or different densities) significantly. *Campanula rotundifolia, Leontodon hispidus, Plantago lanceolata* and *Rumex acetosa* had the highest mean shoot biomass in treatment 'F'. These responses were highly significant (Table 7.5). The maximum mean shoot dry weight were achieved by *Carex flacca* and *Lotus corniculatus* at about 131.00 and 43.00 mg per plant respectively.

The yields of the majority of species in the drought treatment (Table 7.6) in contrast to control (Table 7.5) were not significantly different in different species input treatments. *Carex flacca* was killed by drought, and *Campanula rotundifolia, Origanum vulgare* and *Leontodon hispidus* had only a few survivors. Among the species which

TABLE 7.4: The significant level of analysis of variance (ANOVA) of individual and interactional effects of species input and watering regime on biomass production (mean dry weight) of each species: *** $P<0.001$; ** $P<0.01$; * $P<0.05$.

	Species input	Water	Interaction
A. elatius	***	N.S.	N.S.
A. pratensis	*	N.S.	N.S.
D. glomerata	*	N.S.	N.S.
F. ovina	N.S.	N.S.	N.S.
K. macrantha	***	*	*
C. rotundifolia	*	*	**
C. flacc	N.S.	***	N.S.
C. scabiosa	N.S.	*	N.S.
H. nummularium	N.S.	*	N.S.
L. hispidus	N.S.	N.S.	N.S.
O. vulgare	N.S.	***	N.S.
P. lanceolata	*	**	*
R. acetosa	**	***	***
L. corniculatus	-	N.S.	-
Total/container	***	***	***

Table 7.5: The mean dry weight (mg) of species in control condition in response to various synthesised "communities"; GFL (grasses + Forbs + legume), GF (grasses + Forbs), G (just grasses), and F (just Forbs). * $LSD_{P<0.05}$, ** $LSD_{P<0.01}$, *** $LSD_{P<0.001}$.

	Mean dry weight (mg)				The level of statistical significant differences					
	GFL	GF	G	F	$LSD_{P<0.05}$	G vs GFL	G vs GF	F vs GFL	F vs Gf	GF vs GFL
A. elatius	9.42	10.38	22.98	-	2.97	***	***	-	-	N.S.
A. pratensis	10.08	10.03	15.40	-	1.58	***	***	-	-	N.S.
D. glomerata	12.16	11.49	25.33	-	4.12	***	***	-	-	N.S.
F. ovina	6.53	7.47	14.25	-	2.15	***	***	-	-	N.S.
K. macrantha	6.89	7.05	17.30	-	2.18	***	***	-	-	N.S.
C. rotundifolia	0.47	0.41	-	0.74	0.14	-	-	***	***	N.S.
C. flacca	129.31	139.17	-	128.39	52.62	-	-	N.S.	N.S.	N.S.
C. scabiosa	8.92	10.39	-	10.86	2.17	-	-	N.S.	N.S.	N.S.
H. nummularium	1.37	1.31	-	1.63	0.27	-	-	N.S.	*	N.S.
L. hispidus	4.79	5.20	-	7.25	1.07	-	-	***	***	N.S.
O. vulgare	1.19	1.09	-	1.61	0.45	-	-	N.S.	*	N.S.
P. lanceolata	14.10	20.21	-	25.44	3.64	-	-	***	**	***
R. acetosa	10.11	11.09	-	16.33	1.98	-	-	***	***	N.S.
L. corniculatus	42.83	-	-	-	-	-	-	-	-	-

had more survivors in the drought treatment and whose biomass production responded significantly to different plant community treatment ; *Dactylis glomerata, Plantago lanceolata* and *Rumex acetosa* produced the highest mean shoot dry weight in 'GF' treatment, and *Arrhenatherum elatius* and *Koeleria macrantha* in 'G' treatment (Table 7.6). An analysis of variance of the dry weights of species in all of the treatments, listed in Table 7.7, indicated that most species were larger in the droughted than in the control treatment (table 7.7). This result was not, however statistically significant for *Arrhenatherum elatius, Campanula rotundifolia, Origanum vulgare,* and *Lotus corniculatus*. The most extreme responses were associated with 'Grasses + Forbs' (GF) treatment. This may indicate that competition was more intense in 'GF" than in the other treatments (Table 7.7).

Species abundance

Two-way analysis of variance (ANOVA) of abundance value of each species listed in Table 7.8, indicates that grasses are mainly influenced by species input. In contrast, the forbs, particularly *Carex flacca, Leontodon hispidus, Origanum vulgare* and *Rumex acetosa* were affected by watering treatment (table 7.8). There was a statistically insignificant interaction between water and plant community treatments, except for *Campanula rotundifolia* (Table 7.8). In the control treatment, *Carex flacca* and *Lotus corniculatus* dominated the 'GFL' treatment (Table 7.9). In the 'GF' treatment, as a result of the absence of legume

Table 7.6: The mean dry weight (mg) of species in droughted containers in response to various synthesised "communities"; GFL (grasses + Fotbs + legume), GF (grasses + Forbs), G (just grasses), and F (just Forbs). * $LSD_{P<0.05}$, ** $LSD_{P<0.01}$, *** $LSD_{P<0.001}$.
The symbol (-) indicates that either the species was absent in the treatment, or there were not enough replicates (as result of drought mortality) for statistical comparison

	Mean dry weight (mg)				The level of statistical significant differences					
	GFL	GF	G	F	$LSD_{P<0.05}$	G vs GFL	G vs GF	F vs GFL	F vs Gf	GF vs GFL
A. elatius	13.17	8.64	24.56	-	13.23	N.S.	*	-	-	N.S.
A. pratensis	8.57	13.15	20.34	-	6.77	**	*	-	-	N.S.
D. glomerata	10.55	62.98	44.53	-	31.59	*	N.S.	-	-	**
F. ovina	10.25	29.15	20.28	-	30.98	N.S.	N.S.	-	-	N.S.
K. macrantha	12.74	16.76	33.29	-	13.97	**	*	-	-	N.S.
C. rotundifolia	0.74	0.00	-	0.34	1.12	-	-	N.S.	-	-
C. flacca	0.00	0.00	-	0.00	-	-	-	-	-	-
C. scabiosa	26.94	49.09	-	23.98	26.31	-	-	N.S.	N.S.	N.S.
H. nummularium	1.22	3.57	-	2.05	3.42	-	-	N.S.	N.S.	N.S.
L. hispidus	0.00	17.15	-	18.43	-	-	-	-	N.S.	-
O. vulgare	2.21	1.74	-	0.00	-	-	-	-	-	N.S.
P. lanceolata	36.12	106.95	-	38.93	36.71	-	-	N.S.	***	***
R. acetosa	18.42	68.75	-	19.33	30.66	-	-	N.S.	**	**
L. corniculatus	64.40	-	-	-	-	-	-	-	-	-

Table 7.7: The comparison of biomass production (mg) (mean dry weight) of each species in response to different water regimes (control & drought) in various synthesised "communities".
* P< 0.05, ** P< 0.01, *** P<0.001.
The symbol (-) indicates that the either species was absent in the treatment, or there were not enough replicates (as a result of drought mortality) for statistical comparison.

	All Treatments			Grasses + Forbs + Legume			Grasses + Forbs			Grasses or Forbs		
	Control	Drought	F-test	Control	Drought	F-test	Control	Drought	F-test	Control	Drought	F-test
A. elatius	13.42	16.60	N.S.	9.42	13.17	*	10.38	8.67	N.S.	22.98	24.56	N.S.
A. pratensis	11.47	16.39	***	10.08	8.57	N.S.	10.03	13.15	N.S.	15.40	20.34	*
D. glomerata	15.03	41.57	***	12.16	10.55	N.S.	11.49	62.99	***	25.33	44.53	**
F. ovina	9.17	21.57	***	6.53	10.26	N.S.	7.47	29.15	***	14.25	20.28	N.S.
K. macrantha	9.82	27.47	***	6.89	12.74	**	7.05	16.76	***	17.30	33.29	***
C. rotundifolia	0.56	0.68	N.S.	0.47	0.74	N.S.	0.41	-	-	0.74	-	-
C. flacca	131.19	-	-	129.31	-	-	139.17	-	-	128.39	-	-
C. scabiosa	10.04	31.56	***	8.92	26.94	***	10.39	49.09	***	10.86	23.98	**
H. nummularium	1.43	2.45	***	1.37	1.22	N.S.	1.31	3.57	***	1.63	2.05	N.S.
L. hispidus	5.79	17.79	***	4.79	-	-	5.20	17.16	***	7.25	18.43	***
O. vulgare	1.32	1.98	N.S.	1.19	-	-	1.09	-	-	1.61	-	-
P. lanceolata	19.99	52.50	***	14.10	36.12	***	20.21	106.95	***	25.44	38.93	**
R. acetosa	12.55	49.64	***	10.11	26.17	***	11.09	79.52	***	16.33	37.20	**
L. corniculatus	42.83	64.42	N.S.	42.83	64.42	N.S.	-	-	-	-	-	-
Total/container												

TABLE 7.8: The significant level of analysis of variance (ANOVA) of individual and interactional effects of species input and watering regime on proportional contribution (% of total dry weight) of each species:
*** $P<0.001$; ** $P<0.01$; * $P<0.05$.

	Species input	Water	Interaction
A. elatius	***	N.S.	N.S.
A. pratensis	***	**	N.S.
D. glomerata	***	N.S.	N.S.
F. ovina	**	*	N.S.
K. macrantha	***	N.S.	N.S.
C. rotundifolia	N.S.	N.S.	**
C. flacca	N.S.	***	N.S.
C. scabiosa	N.S.	N.S.	N.S.
H. nummularium	N.S.	N.S.	N.S.
L. hispidus	**	***	N.S.
O. vulgare	N.S.	***	N.S.
P. lanceolata	N.S.	N.S.	N.S.
R. acetosa	*	***	N.S.
L. corniculatus	-	N.S.	-

Table 7.9: The proportional (%) contribution of each species in total biomass per container (in control condition) in response to various synthesised "communities"; GFL (grasses + Forbs + legume), GF (grasses + Forbs), G (just grasses) and F (just Forbs). The significant level based on $LSD_{P<0.05}$ *.

	Proportion (%)				The level of statistical significant differences					
	GFL	GF	G	F	$LSD_{P<0.05}$	G vs GFL	G vs GF	F vs GFL	F vs Gf	GF vs GFL
A. elatius	5.59	6.19	23.92	-	4.85	*	*	-	-	N.S.
A. pratensis	7.65	6.65	18.55	-	3.90	*	*	-	-	N.S.
D. glomerata	6.22	8.12	22.38	-	6.75	*	*	-	-	N.S.
F. ovina	2.10	5.38	13.20	-	1.99	*	*	-	-	*
K. macrantha	5.43	4.38	21.96	-	5.39	*	*	-	-	N.S.
C. rotundifolia	0.19	0.16	-	0.45	0.15	-	-	*	*	N.S.
C. flacca	25.39	27.93	-	35.45	21.44	-	-	N.S.	N.S.	N.S.
C. scabiosa	4.64	6.74	-	7.74	4.80	-	-	N.S.	N.S.	N.S.
H. nummularium	0.67	0.89	-	1.08	0.57	-	-	N.S.	N.S.	N.S.
L. hispidus	2.73	4.44	-	6.93	2.73	-	-	*	N.S.	N.S.
O. vulgare	0.45	0.64	-	1.34	0.96	-	-	N.S.	N.S.	N.S.
P. lanceolata	10.17	17.55	-	27.07	5.70	-	-	*	*	*
R. acetosa	8.43	10.92	-	19.96	5.88	-	-	*	*	N.S.
L. corniculatus	20.33	-	-	-	-	-	-	-	-	-

species, *Festuca ovina* and *Plantago lanceolata* benefitted (Table 7.9, 7.10). In the 'G' and 'F' monocultures, the abundance values of all species were increased in contrast to other treatments (Table 7.9). The most extreme responses were associated with the 'Grasses' rather than the 'Forbs' (Table 7.9). The total biomass was more evenly distributed among grasses than among forb species.

In the drought treatment, as a result of elimination of *Carex flacca* by drought mortality, the abundance values of *P. lanceolata*, *R. acetosa* and *Centaurea scabiosa* were increased (Table 7.11). In 'GF' treatment the legume species was absent, and *C. flacca* killed by drought, and as a result *Rumex acetosa* with the highest abundance value (50 %) dominated the droughted containers (Table 7.11)

7.4: DISCUSSION:

Harper (1968) commented on the "powerful role of the grass flora in limiting the realized niche of the dicotyledonous species," and Keever (1950) and Pinder (1975) reported that the increased net productivity of forbs in the absence of grasses indicates that the presence of the perennial grasses reduced the productivity of the forb species. In contrast, the results of this experiment showed that the high variation in survivorship and biomass production of grasses in responses to different plant composition treatments in comparison to forbs, may demonstrate that grasses are more sensitive to competition than forbs in nutrient-deficient conditions. It seems likely therefore that nutrient

Table 7.10: The proportional (%) contribution of each species in total biomass per container (in drought condition) in response to various synthesised "communities"; GFL (grasses + Forbs + legume), GF (grasses + Forbs), G (just grasses) and F (just Forbs). The significant level based on $LSD_{P<0.05}$ *.

	Proportion (%)				The level of statistical significant differences					
	GFL	GF	G	F	$LSD_{P<0.05}$	G vs GFL	G vs GF	F vs GFL	F vs Gf	GF vs GFL
A. elatius	7.68	2.13	14.11	-		N.S.	*	-	-	N.S.
A. pratensis	2.98	2.70	12.51	-		*	*	-	-	*
D. glomerata	1.81	4.38	35.38	-		*	*	-	-	*
F. ovina	1.17	4.28	4.78	-		N.S.	N.S.	-	-	N.S.
K. macrantha	3.56	2.37	33.23	-		*	*	-	-	*
C. rotundifolia	0.43	0.00	-	0.02		-	-	N.S.	N.S.	*
C. flacca	0.00	0.00	-	0.00		-	-	N.S.	N.S.	N.S.
C. scabiosa	12.61	8.69	-	17.19		-	-	N.S.	N.S.	N.S.
H. nummularium	0.21	0.42	-	0.84		-	-	N.S.	N.S.	N.S.
L. hispidus	0.00	1.08	-	1.83		-	-	N.S.	N.S.	N.S.
O. vulgare	0.13	0.07	-	0.00		-	-	N.S.	N.S.	N.S.
P. lanceolata	27.88	24.12	-	27.07		-	-	N.S.	N.S.	N.S.
R. acetosa	20.98	49.77	-	53.05		-	-	N.S.	N.S.	N.S.
L. corniculatus	20.57	-	-	-	-	-	-	N.S.	N.S.	N.S.

Table 7.11: The comparison of of proportional (%) contribution of each species in total biomass per container in response to different water regimes (control & drought) in various synthesised communities.
* P< 0.05, ** P< 0.01, *** P<0.001.

	Grasses + Forbs + Legume			Grasses + Forbs			Grasses or Forbs		
	Control	Drought	F-test	Control	Drought	F-test	Control	Drought	F-test
A. elatius	5.59	7.68	N.S.	6.19	2.13	*	23.99	14.11	N.S.
A. pratensis	7.65	2.98	*	6.65	2.70	**	18.55	12.51	N.S.
D. glomerata	6.22	1.81	**	8.12	4.38	N.S.	22.37	35.38	N.S.
F. ovina	2.10	1.17	N.S.	5.38	4.28	N.S.	13.20	4.78	N.S.
K. macrantha	5.43	3.56	N.S.	4.38	2.37	N.S.	21.96	33.23	N.S.
C. rotundifolia	0.19	0.42	N.S.	0.16	0.00	***	0.45	0.02	***
C. flacca	25.39	0.00	***	27.93	0.00	***	35.45	0.00	***
C. scabiosa	4.64	12.61	*	6.74	8.69	N.S.	7.74	17.19	N.S.
H. nummularium	0.64	0.21	*	0.89	0.42	N.S.	1.08	0.84	N.S.
L. hispidus	2.73	0.00	***	4.44	1.08	**	6.93	1.83	*
O. vulgare	0.45	0.13	N.S.	0.64	0.07	***	1.34	0.00	*
P. lanceolata	10.17	27.88	N.S.	17.55	24.12	N.S.	27.07	27.07	N.S.
R. acetosa	8.43	20.98	N.S.	10.92	49.77	***	19.96	53.05	*
L. corniculatus	20.33	20.57	N.S.	-	-	-	-	-	-

Table 7.10: The proportional (%) contribution of each species in total biomass per container (in drought condition) in response to various synthesised "communities"; GFL (grasses + Forbs + legume), GF (grasses + Forbs), G (just grasses) and F (just Forbs). The significant level based on $LSD_{P<0.05}$ *.

	Proportion (%)				The level of statistical significant differences					
	GFL	GF	G	F	$LSD_{P<0.05}$	G vs GFL	G vs GF	F vs GFL	F vs Gf	GF vs GFL
A. elatius	7.68	2.13	14.11	-		N.S.	*	-	-	N.S.
A. pratensis	2.98	2.70	12.51	-		*	*	-	-	*
D. glomerata	1.81	4.38	35.38	-		*	*	-	-	*
F. ovina	1.17	4.28	4.78	-		N.S.	N.S.	-	-	N.S.
K. macrantha	3.56	2.37	33.23	-		*	*	-	-	*
C. rotundifolia	0.43	0.00	-	0.02		-	-	N.S.	N.S.	*
C. flacca	0.00	0.00	-	0.00		-	-	N.S.	N.S.	N.S.
C. scabiosa	12.61	8.69	-	17.19		-	-	N.S.	N.S.	N.S.
H. nummularium	0.21	0.42	-	0.84		-	-	N.S.	N.S.	N.S.
L. hispidus	0.00	1.08	-	1.83		-	-	N.S.	N.S.	N.S.
O. vulgare	0.13	0.07	-	0.00		-	-	N.S.	N.S.	N.S.
P. lanceolata	27.88	24.12	-	27.07		-	-	N.S.	N.S.	N.S.
R. acetosa	20.98	49.77	-	53.05		-	-	N.S.	N.S.	N.S.
L. corniculatus	20.57	-	-	-	-	-	-	N.S.	N.S.	N.S.

between *Campanula* and *Lotus* in field conditions (Chapter 2), may simply reflect their similar habitat requirements, or it may indicate that there is some unexplained interaction between these two species.

The value of the experiment described in this chapter is that it attempts to derive insights into plant community structure by manipulating the composition of synthesised communities. This is a novel, but therefore inevitably relatively high-risk, approach. It is also the most difficult experiment in the thesis to interpret satisfactorily, partly because it involves simultaneous changes in both functional composition and density of individuals. The resulting problems of interpretation need to be addressed and overcome in any future investigations of a similar nature.

Chapter 8

'General discussion'

8.1: Drought plant strategy theory and plant community structure:

In the first chapter the impacts of drought were divided between two categories; stress, in which plant growth is restricted by moisture limitation, and disturbance, where plants are partially or totally killed. On the basis of this classification, it may be hypothesised that different evolutionary paths or strategies have evolved in relation to moisture stress and that the fitness of particular individuals, populations or species will depend upon the past and present circumstances in which they have encountered drought. These circumstances will include site productivity, the duration, severity and periodicity of drought and the distribution of subsoil moisture. There are at least three primary evolutionary responses to drought; (1) ephemerals (2) drought avoiders (3) drought tolerators. Here, because annuals are not major contributors to the system, therefore this project concentrated on drought avoiders and drought tolerators and their role in the community at Tongue End. Drought avoiders includes those plants which can avoid the drought by a root system which penetrates into the deeper parts of the soil including rock crevices. Drought tolerators includes those which manage to survive and to some extent build up biomass under water-stressed treatment. in compare to control condition.

In this chapter an attempt will be made to integrate results from the experiments described in previous chapters; therefore this chapter has its own tables and figures, and to this extent is a departure from the established tradition of thesis preparation. Some of these results are presented in Table 8.1. As in the previous investigation of Sydes and Grime (1984) the root penetration measurements of Chapter 5 revealed consistent inter-specific differences. In general the fast-growing plants producing deeper root systems than the slow-growing plants. The differences observed between species were consistent with published records of root systems excavated in natural habitats (Anderson 1927; Grime & Curtis 1976). In most of the species, water-stress stimulated greater root penetration, and there was a general tendency toward deeper root systems under the drought treatment. Lawlor *et al* (1981), Imtiyaz *et al* (1982), and Harroni (1989) have observed that water-stressed barley (*Hordeum distichum*), wheat (*Triticum aestivum*), and tef (*Eragrostis tef*) exhibit a deeper penetration of roots in the soil profile than irrigated plants. As soil moisture deficit builds up an increasing proportion of the upper layer of the soil becomes dry because of evaporation and exploitation by plant roots, and the availability of water is therefore restricted to deeper layers of the profile. In this circumstance survival becomes increasingly dependent upon roots reaching subsoil sources of moisture supply (Harris 1967). In order to test the importance of root penetration in the Tongue End community, success in seedling establishment in permanent quadrats (Table 8.1) was plotted against depths of root penetration achieved by the same species in the root penetration

Table 8.1: Integration of experimental results discussed in earlier chapters (for full details see the relevant chapters). (-) no available information.

	Grime *et al* (1988)		Hillier (1984)		Chapter 2		Chapter 3		Chapter 5		Chapter 6	
	Stress-tolerant Index		(%) Establishment In the field		(%) Frequency in the field		Drought sensitivity Index		Root length (control(mm		(%) Drought survivorship	
		Rank		Rank		Rank		Rank		Rank		Rank
A. elatius	0.30	17	-	-	0	17	4483	2	394	3	16.1	6
A. pratensis	0.92	4	27	9	62	4	1101	13	224	8	11.4	8
B. media	0.90	5	10	14	67	3	-	-	146	15	-	-
D. glomerata	0.34	6	26	10	0	16	4477	3	351	4	21.3	3
F. ovina	0.96	2	21	12	90	1	1739	11	215	9	13.8	7
K. macrantha	0.97	1	43	4	22	8	970	13	186	11	22.7	2
C. rotundifolia	0.80	7	23	11	22	9	1389	12	184	12	6.8	11
C. flacca	0.80	8	-	-	38	6	2316	9	85	17	5.0	12
C. scabiosa	0.72	9	100	1	18	10	2622	8	278	6	18.2	4
H. nummularium	0.88	6	42	5	34	7	4029	5	113	16	8.4	10
H. pilosella	0.70	10	67	3	46	5	-	-	428	2	-	-
L. hispidus	0.70	11	41	6	17	11	3879	6	199	10	10.9	9
O. vulgare	0.58	13	20	13	1	14	3393	7	155	14	2.9	13
P. lanceolata	0.54	14	71	2	7	13	4151	4	296	5	16.2	5
R. acetosa	0.50	15	-	-	0	15	2171	10	515	1	30.2	1
T. praecox	0.94	3	33	7	79	2	926	14	248	7	-	-
L. corniculatus	0.68	12	31	8	17	12	6383	1	165	13	-	-

experiment of Chapter 5 (see Table 8.1). The results (Figure 8.1a) indicate greatest mortality in the small, shallow-rooted seedlings of *Briza media* and *Origanum vulgare*, with much higher survival in species with deep roots, such as *Centaurea scabiosa* and *Plantago lanceolata*. However, the relationship is only weakly defined, as we might expect from local observations based upon a single cohort of naturally-established seedlings. This analysis is further complicated by the small number seedlings observed for some species and the presence of other sources of mortality such as seed and seedling predation.

In a second phase of the investigation, the estimates of root penetration were compared with the survivorship of seedlings (Table 8.1) subjected to controlled drought in experimental plant communities replicated in a greenhouse environment. These were synthesised from seed in experimental microcosms (full details in Chapter 6) which provided local, randomly-located opportunities for root penetration into continuously moist subsoil. The results revealed an even more consistent relationship between seedling survivorship and rooting habit (Figure 8.1b), and a hierarchy of survivorship based upon depth of root penetration. These results indicate greatest mortality in the shallow-rooted plants *Carex flacca* and *Origanum vulgare*, and higher survivorship in deep-rooted species such as *Rumex acetosa*, *Dactylis glomerata*, *Plantago lanceolata* and *Centaurea scabiosa*. These data are consistent with the general observation that in arid and semi-arid ecosystems

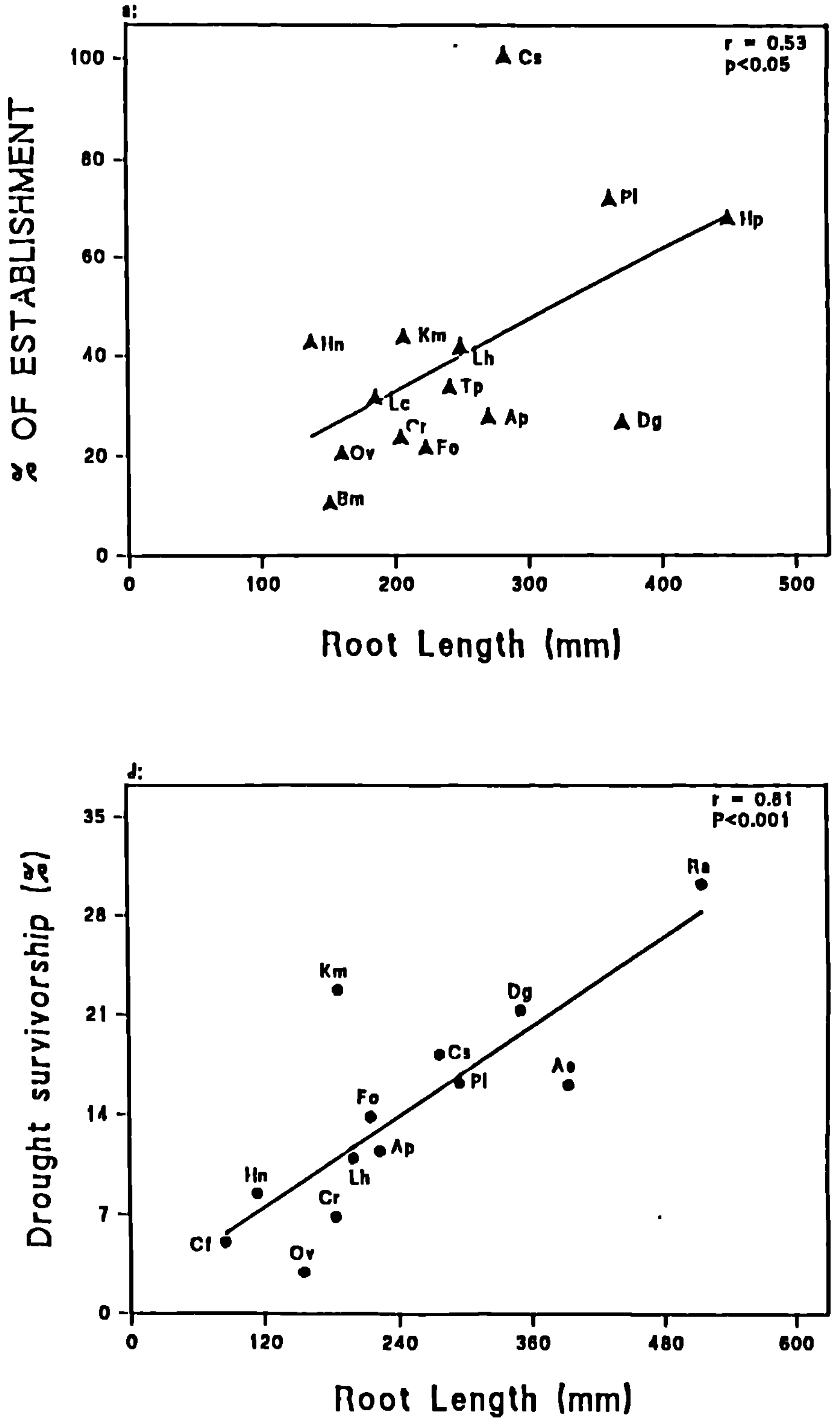


Figure 8.1:
Percent establishment at the Millers Dale site (a), and percent survivorship in droughted experimental communities in microcosms (b), as a function of root penetration measured under control conditions in the Integrated Screening Programme.
Key to species:

Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Briza media (Bm) Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Hieracium pilosella (Hp), Leontodon hispidus (Lh), Origanum vulgare (Ov), Rumex acetosa (Ra), Plantago lanceolata (Pl), Thymus praecox (Tp).

seedling growth occurs rapidly in the season in which moisture is readily available in the upper horizons but is followed by the death of those seedlings which have not gained access to subsoil moisture (Salihi & Norton 1987; Owens & Norton 1989; Reichenberger & Pyke 1990; Pyke 1990). In marked contrast to shallow-rooted annual species (Dodd *et al* 1984; Moll & Sommerville 1985; Hart & Rodosvich 1987), deep roots often establish contact with stored water at considerable depth (Crombie 1988). Some of these desert plants have surface root systems but they are unlikely to have been continuously functional in the absence of rain (Lamont 1976); it is sinkers and tap roots which sustain shoot growth at this time (Lamont & Bergel 1991).

Despite the general conclusion that deep-rooted species usually have a higher chance of establishment in a droughted habitat the results from the field experiment (Chapter 2) reveal that deep-rooted species are of restricted frequency on the south-facing slope at Tongue End. Relatively shallow-rooted species contribute a large proportion of the total shoot biomass of the community. Previous studies in this site (e.g. Grime & Curtis 1976) and the results obtained in this investigation, indicate that the contribution of deep-rooted species may be restricted by the scarcity of suitable soil conditions; this is due to a combination of edaphic factors, including areas of shallow soil and exposed bedrock. The results of the field sampling (Chapter 2) showed that eleven percent of the samples which were taken from the site consisted of exposed rocks. Soil depth ranged from 0-200 mm, with nearly 50 percent of the samples occurring in the range 0 to 60 mm. This strongly suggests that the shallowness of the soil at Tongue End restricts vertical penetration by potentially deep-rooted species. It seems reasonable to conclude that this limitation makes them susceptible to summer drought over much of the site and as a result reduces their frequency within the studied site. In the microcosm experiment (Chapter 6) the manipulation of soil depth had a precise and localised effect on drought survivorship. No individual of any species survived exposure to drought in containers without crevices and drought survivorship was reduced by nutrient-deficiency. This effect was most pronounced in containers with crevices and horizontal partitions with local perforations. This suggests that in the field the nutrient deficient soils at Tongue End may further reduce the abundance of deep-rooted species by limiting root growth and the chance of access to the crevices. Effects of low nutritional level on the ability to avoid drought by deep root growth have been suggested in previous studies (Peak *et al* 1975; Grime & Curtis 1976; Wellington 1985). Grime and Curtis (1976) found that the addition of nutrients to the soil reduced seedling mortality, presumably by promoting root growth and thus enhancing exploitation of deeper soil moisture.

A similar conclusion can be drawn from the comparative studies of drought sensitivity described in Chapter 3. From the results summarized in Figure 8.2 it is apparent that

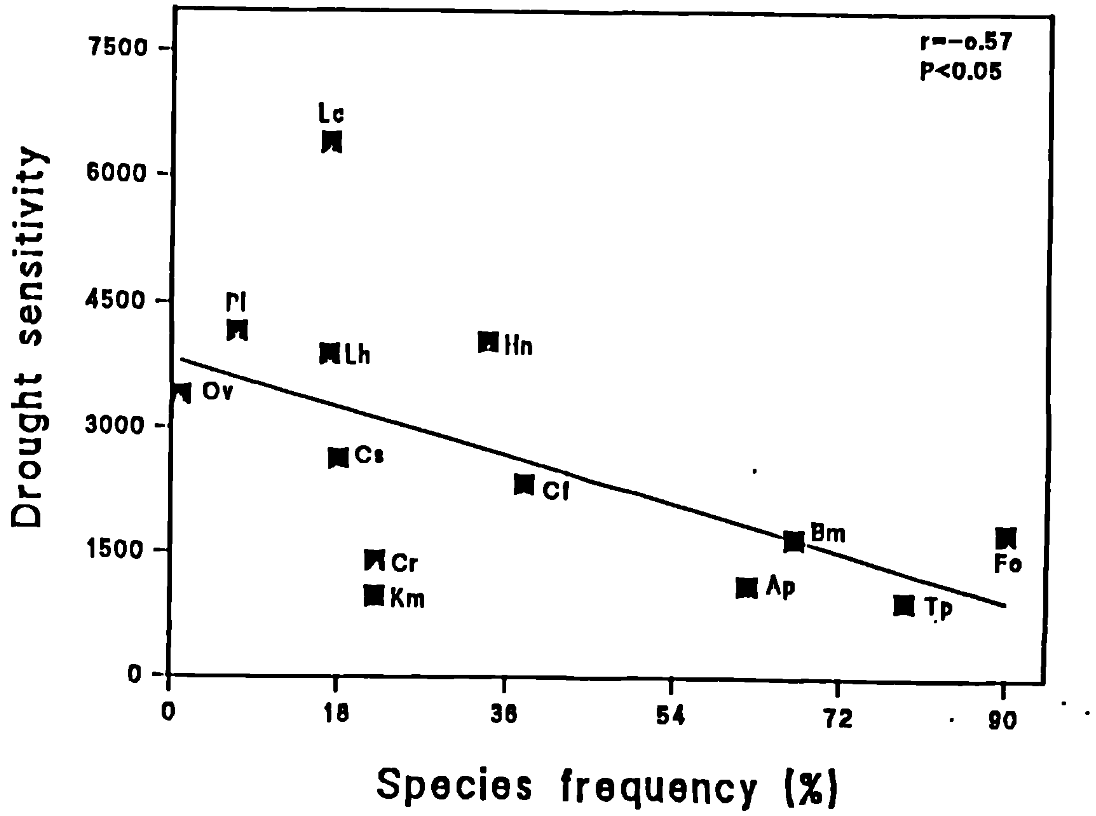


Figure 8.2:
The relationship between species frequency in the field site at Tongue End and their sensitivity to drought. Key for species:
Avenula pratensis (Ap), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Plantago lanceolata (Pl) and *Lotus corniculatus (Lc)*

the most frequent species in the turf at Tongue End are relatively resistance to drought. As Table 3.1, and Figure 3.1 of Chapter 3 indicate, the most marked response of species to water-stress in terms of dry matter reduction were in the potentially fast-growing plants. *Arrhenatherum elatius, Dactylis glomerata, Plantago lanceolata* and *Lotus corniculatus*, species which in field may be dependent upon access to subsoil moisture through the deep tap-root, were the most drought sensitive plants. *Thymus praecox, Avenula pratensis, Campanula rotundifolia* and *Festuca ovina* were among the most drought tolerant of the species of plants investigated. In a multi-factorial experiment (chap. 4) in which water- and nutrient-stress were the independent variables, the responses of *Arrhenatherum elatius* and *Festuca ovina*, the two contrasted fast- and slow-growing species respectively, were investigated. The results of this experiment concur with the conclusion of Grime and Curtis (1976), Al-Mufti *et al* (1977), and Peterkin (1981) that development of *A. elatius* on south-facing slopes can be severely restricted by droughting. In contrast *F. ovina*, even in areas of shallow soil, is relatively tolerant of drought.

When the results summarized in Figures 8.1 and 8.2 are considered in relation to the results of the principal correspondence analysis (Figure 8.3) on the local distribution of species within the sampled site, and combined with results from the microcosms experiments (Chapter 6) and the comparative autecological studies

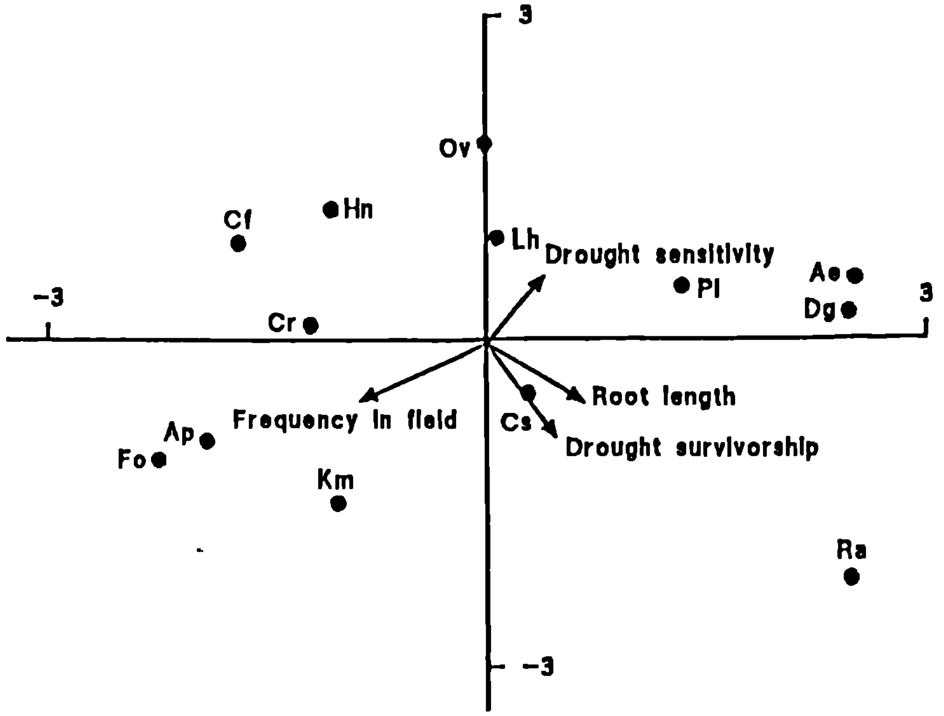


Figure 8.3:
Principal Components Analysis (PCA) ordination diagram with vascular plant species (o), and plant characteristics (arrowed). The first axis is horizontal, the second vertical. Key for species: *Arrhenatherum elatius (Ae), Avenula pratensis (Ap), Dactylis glomerata (Dg), Festuca ovina (Fo), Koeleria macrantha (km), Campanula rotundifolia (Cr), Carex flacca (Cf), Centaurea scabiosa(Cs), Helianthemum nummularium (Hn), Leontodon hispidus (Lh), Origanum vulgare (Ov), Plantago lanceolata (Pl), Rumex acetosa (Ra).*

(Chapters 3, 5) it is apparent that there is a strong association between root depth and drought survivorship on one side, and the frequency of species and drought tolerance on the other. From these data we may formulate the hypothesis that, under the drought conditions, species with the potential to develop deep-root systems would dominate the community, if the soil were deep and rich enough to allow the penetration into the deeper and continuously moist areas (Plate 8.1). Similar results obtained by Bunce *et al (1977)*, who studied young tree species native to the community (a dry ridge-top community near Ithaca) and from a wetter community which were transplanted into the study site, demonstrated that moderate drought is sufficient to exclude drought-sensitive deciduous tree species from a site with shallow soils.

8.2: Drought, vegetation structure and species diversity:

Popular theories of the maintenance of species diversity fall into two distinct groups. On one side are those (e.g. Grubb 1977; Connell 1978; Huston 1979) who argue that only non-equilibrium approaches can explain the patterns of species diversity observed in plant communities. Connell (1978) and Huston (1979) suggest that continual, small-scale disturbances, which prevent competitive displacement and provide randomly distributed opportunities for regeneration and establishment, maintain the diversity of plant communities. The humped-back model of Grime (1973a,1979) which recognizes such a role for disturbance in

Plates8.1 (a-c): Three examples of drought avoidance by deep-rooted species (a) *Taraxacum officinale* in a lawn (Weston Park, Sheffield)(b) *Hieracium pilosella* at Tongue End (c) *Plantago lanceolata, Rumex acetosa* And *Dactylis glomerata* in droughted microcosms.

a

b

c

controlling species diversity also qualifies as a non-equilibrium model. In contrast, the other group (e.g. Whittaker 1975; Tilman 1982) suggest that many species-rich communities are at equilibrium, and that the maintenance of diversity involves a high degree of niche differentiation. Evidence of niche structure in complex plant communities has been sought in many plant communities, particularly those of limestone grassland in Northern England (Al-Mufti *et al* 1977; Grime *et al* 1981; Sydes & Grime 1984; Mahdi & Law 1987; Pearce 1987) . Some of these these studies have failed to detect niche-differentiation, but others have yielded data which have been interpreted as being consistent with niche differences in attributes such as root penetration, temperature thresholds for germination, response to defoliation and shoot phenology.

On the south-facing slope at Tongue End, it seems that floristic diversity is being maintained by naturally occurring phenomena, primarily drought, and low nutrient status (Grime & Curtis 1976; Hillier 1984). These factors are responsible for high seedling mortality, gap creation, and spatial heterogeneity. As the present investigation has established, the distribution and ecology of the species present at this site appear to be strongly influenced by both drought and mineral nutrient stress. Evidence presented in earlier chapters strongly supports the hypothesis that, at Tongue End summer drought interacts with mineral nutrient stress to impose high seedling mortality and to reduce the size and vigour of the established vegetation thus reducing the intensity of competition, and preventing any individual species from becoming dominant over a high proportion of the habitat.

Data collected from the field site, presented in Chapter 2 and discussed in Campbell *et al* 1991, reveal that there is a strong positive association at Tongue End between soil depth, litter accumulation and the presence of the tussock grass *Avenula pratensis*. It is also evident that a majority of the other vascular plants present within the site are negatively associated with *Avenula pratensis* and tend to occur in locally species-rich microsites on shallower, more calcareous soil. On this basis we may suggest that, even in this nutritionally-deficient site, under the more productive conditions afford by patches of deeper soil, the robust tussocks of *Avenula pratensis* are attaining local dominance and excluding other species. Additional evidence of a role for competition in the vegetation at Tongue End was obtained in the microcosm experiments described in Chapters 6 and 7. Here it was apparent that losses of shallow-rooted species caused by imposition of drought resulted in substantial increase in the vigour of the surviving deep-rooted, crevice exploiting species. The microcosm experiments also provided evidence that in the absence of drought, dominance may begin to be expressed even in areas of shallow nutrient-deficient turf. This effect was well-developed in the shallow-rooted species *Carex flacca,* which was quite exceptional in its ability to maintain vigorous growth and to suppress neighbouring individuals in the microcosms providing shallow, nutrient-deficient, continuously moist soil. We may conclude, therefore, that at Tongue End, the occurrence of drought on the south-facing slope is a key factor maintaining floristic diversity in part by restricting the vigor of species such as *Avenula pratensis* and *Carex flacca*. As observed at other sites where root penetration is limited by factors such as nutrient-deficiency and shallowness of the soil (Mukerji 1963; Moore & Rhoades 1966; Fitter and Bradshaw 1974), occasional environmental fluctuations such as surface drought reduce the competitiveness of the dominant species and permit otherwise subordinate species to survive (Grime 1973; Fitter 1982). This phenomenon is complex since it includes not only reduced vigour of the potential dominants but also drought mortalities and creation of bare ground. Gap creation is a regular and recurring natural feature of the turf at the Tongue End site where disturbance has been observed in summer drought and after winter frost-heaving and solifluction (Hillier 1990). As well as reducing the intensity of the impact of potential dominants upon subordinates, it seems likely some species, particularly those of limited life-span (e.g. *Linum catharticum, Gentianella amarella)* are dependent for their continued existence in the turf on regeneration from seed in such local bare patches (Verkaar *et al* 1983; van Tooren 1990; Hillier 1990). This interpretation is strongly supported by observations on the markedly contrasted vegetation of the south- and north-facing slopes. Annual species are locally prominent on the south-facing slope at Tongue End whereas, except in the circumstances following occasional fires, gaps are exceedingly rare on the north-facing slope and annual species and the seedlings of perennials are relatively scarce. Such dependency on gaps for opportunities for seed regeneration corresponds with the patterns observed for smaller or short-lived forbs such as *Scabiosa columbaria* and *Linum catharticum* in earlier studies on chalk grassland (e.g. Verkaar *et al* 1983). It would be a mistake to suggest that disturbance events and the resulting gap dynamics alone provide the mechanism of species-coexistance at Tongue End. At the studied site soil nutrient deficiencies together with drought, appear to determine that species exhibiting the stress-tolerant strategy (*sensu* Grime 1974), with attributes such as small stature and low growth rate, (Grime & Hunt 1975) dominate the system (Chapter 2). The resulting compact plant morphologies (Tansley & Adamson 1925; Grime 1979) and 'slow-dynamics' (Huston 1979; Williamson 1976; Sydes 1984) are likely to allow a dense packing of individual plants and will lead to slow-healing of any vegetation gaps created by summer drought (Plate 8.2) or other disturbance events, thus creating periods long enough for some to provide micro-habitats for short-lived species and for the initial establishment of the seedlings of perennials (Hillier 1990). Plate 8.2 illustrates the two turf microcosms identical except in mineral nutrient supply and photographed after three months of recovery from a drought treatment. It is apparent that the gaps created by

Plate 8.2: Comparison of the turf structure in droughted microcosms maintained at high (above) and (below) nutrient suppl. The photographs were taken three months after the end of the drought treatment.

drought in the high-nutrient treatment had become occupied by the canopies of the surviving plants, a result of both high survivorship (Table 6.) and large plant size (Figure 6.). In contrast, the turf in the low-nutrient treatment shows slow post-drought recovery with much of the area within the container still consisting of bare ground.

Another role which can be suggested for drought in promoting vegetation coexistence on the south-facing slope at Tongue End is its interaction with the mosaic of soil depth and rock exposure within the studied site. In previous studies such environmental heterogeneity has often been shown to be correlated with the distribution of herbaceous plants within plant communities (Struick & Curtis 1962; Onyekwelu 1972) and in the first section of this chapter it was concluded that relationships between soil depth and genetic differences between species in root penetration contribute to the vegetation patterns at Tongue End. Soil moisture variations may be caused by micro-topography (Harper & Sagar 1953) e.g. ant hills, soil depth (Kershaw 1958) and presence of rock fragments (Olsvig-Whittaker *et al* 1983; and Fowler 1990). As a result the soil water conditions in the study area can be divided into two niches; the 'soil layer water source, and the 'rock crevices' water source. The species with fibrous root system, e.g. grasses are restricted to the former (Erschbamer *et al* 1983), as indicated by the close linear correlation found between soil depth and the distribution of the tussock grass *Avenula pratensis*. other species can exploit water reserves present in the deep rock crevices, because of their extensive, deep rooting system (Sydes & Grime 1984). The few and isolated deep crevices are occupied by deep-rooted, fast-growing and drought sensitive species, such as *Plantago lanceolata* and *Centaurea scabiosa*. The narrow deep fissure are usually exploited by *Lotus corniculatus* and *Hieracium pilosella* which develop thin persistent tap roots. The micro-habitat restricted to areas of extremely shallow soil and colonized by winter annuals (Grime 1979). The drought tolerant species *Festuca ovina, Koeleria macrantha* and *Thymus praecox* are located in the common patches where the soil is slightly deeper and the effects of summer desiccation are less severe. Finally species such as *Carex flacca* which performed well in wet and low nutrient condition, but was eliminated from droughted microcosms, would occupy the isolated wet patches within the system.

Evidence from this investigation suggests that the species-rich community established on the south-facing slope at Tongue End contains an assemblage of plants attuned to both regular and predictable disturbance and chronic nutrient-deficiency, interacting with the mosaic of soil depth and rock exposure within the studied site. Therefore it seems fair to conclude that in general terms the vegetation of the south-facing slope at Tongue End represents an equilibrium community. However to some extent one must take into account the more pervasive role of drought in maintaining species diversity, by restricting the growth of potentially dominant species and imposing seedling mortality, thus creating gaps within the system. On the basis of our extensive knowledge of the plant community at Tongue End, a role clearly exists for both equilibrium and non-equilibrium mechanisms of maintenance of diversity. Recognition of the precise boundaries and relative contributions of these mechanisms must await further research.

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APPENDICES

APPENDIX 2.1 (data from Grime & Curtis 1976)

Some physical and chemical characteristics of the topsoil (0–10 *cm*) *at the experimental site**

(1) % of soil volume occupied by stones of > 2 mm diameter	24·6
(2) % $CaCo_3$	21·5
(3) % loss on ignition	28·4
(4) % loss on H_2O_2 treatment	16·8
(5) % coarse sand	1·8
(6) % fine sand	10·2
(7) % silt	18·0
(8) % clay	31·2
(9) Ammonium-nitrogen ($\mu g\ g^{-1}$)	147·5
(10) Nitrate-nitrogen ($\mu g\ g^{-1}$)	48·2
(11) Labile phosphorus ($\mu g\ g^{-1}$)	3·68
(12) Soluble phosphorus ($\mu g\ g^{-1}$)	None detected

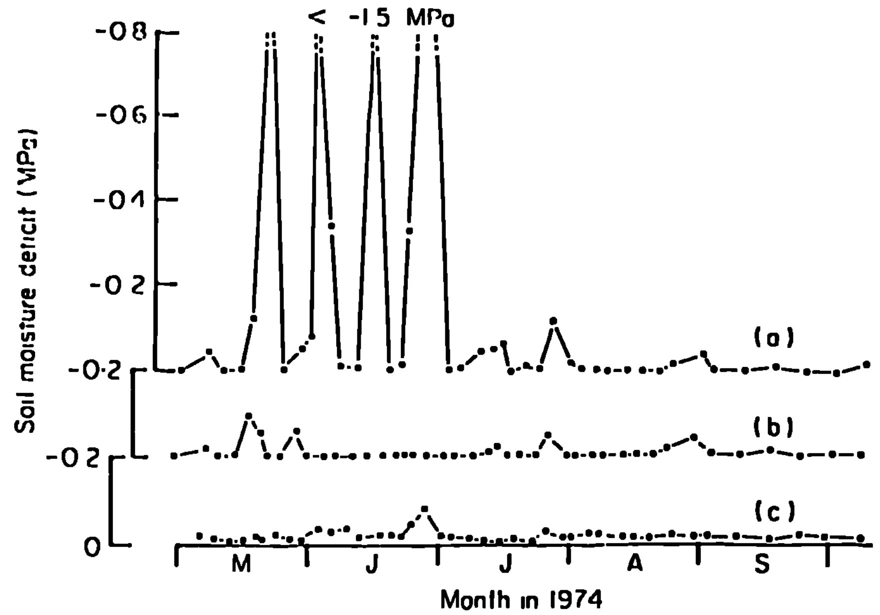
* (1) and (9)–(12) are based upon determinations on five samples of fresh soil, (2)–(8) are based upon duplicate analyses of air-dried soil.

Extractants were as follows: (9), (10), 2 M KCl; (11), 0·5 M $NaHCO_3$ (pH 8·5); (12) 0·01 M $CaCl_2$.

Monthly rainfall totals (*mm*) *at Chatsworth, North Derbyshire, over the two experimental periods*

	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
1962–63	98·0	94·2	34·5	57·4	68·8	29·5	26·2	90·9	69·3	37·6	98·8	33·8	74·2
1972–73	57·2	44·7	25·2	104·1	83·8	49·0	66·0	13·2	92·2	77·7	5·13	131·3	59·7

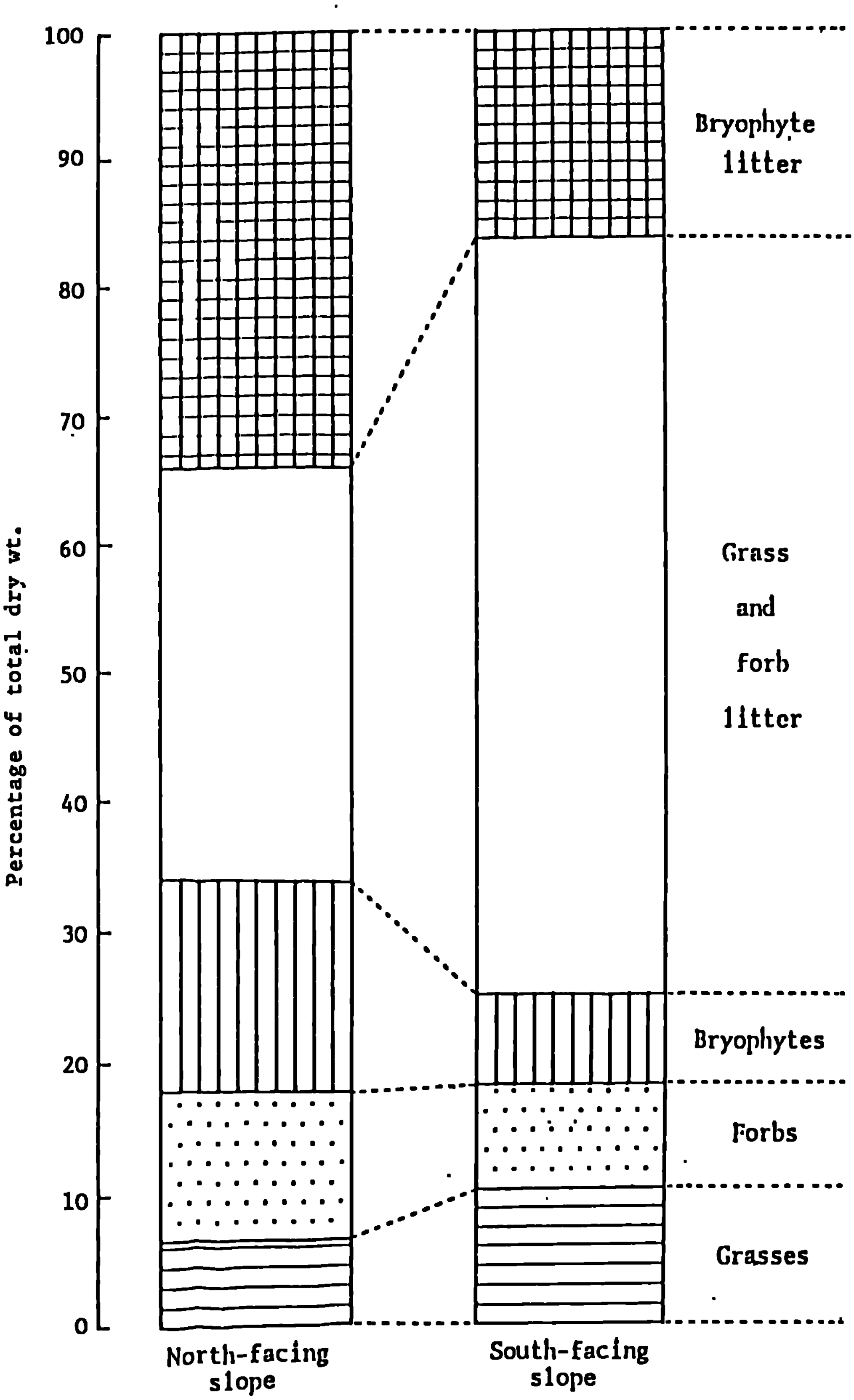
Appendix 2.1.1: (data from Rorison *et al* 1986a)



Soil moisture deficits in Lathkill Dale during 1974: points indicate occasions when representative measurements were made from (a) unwatered pots on the south slope, (b) unwatered pots on the north slope, and (c) watered pots on the south slope. Negligible deficits were recorded beyond the period shown. The method used to record deficits were not effective below −1.5 MPa.

Appendix 2.1.2: (data from Hillier 1984)

Percentage contributions of the different plant groups to the established vegetation of the experimental areas (October 1978).



Appendix 2.1.3: (data from Hillier 1984)

Total numbers of seedlings recorded in all treatments on the two slopes in autumn and spring.

NORTH-FACING SLOPE

	Autumn treatments		Spring treatments
Grasses	86	***	160
Annual and biennial forbs	0	***	12
Perennial forbs	258	***	873
TOTAL	344	***	1045

SOUTH-FACING SLOPE

	Autumn treatments		Spring treatments
Grasses	670	***	144
Annual and biennial forbs	316	***	416
Perennial forbs[a]	202	***	418
TOTAL	1188	***	834

a Including _Thymus praecox_, _Helianthemum nummularium_ and _Ulmus glabra_.

*** Significance level (Chi-square) P<0.001

Appendix 2.1.4: (data from Hillier 1984)

A comparison of some of the more common species recorded on the two slopes in autumn and spring gaps.

Species	Total number of seedlings recorded Autumn gaps		Spring gaps	Temperature range[1] (°C)
NORTH-FACING SLOPE				
Grasses				
Agrostis capillaris	29	*	50	7-31
Anthoxanthum odoratum	2	***	18	7-31
Danthonia decumbens	0	***	20	13-29
Holcus lanatus	36	NS	52	<5-35
Forbs				
Campanula rotundifolia	3	***	51	11-24
Carex flacca	1	***	83	16-28
Centaurea nigra	10	***	54	11-34
Origanum vulgare	95	***	238	13-33
Plantago lanceolata	124	***	349	10-25
SOUTH-FACING SLOPE				
Grasses				
Avenula pratensis	43	**	18	8-26
Briza media	59	***	4	-
Festuca arundinacea	26	***	3	10-32
Festuca ovina	371	***	76	7-33
Koeleria macrantha	146	***	31	6-31
Forbs				
Arabidopsis thaliana	53	***	0	7-31
Campanula rotundifolia	35	NS	29	11-24
Gentianella amarella	241	***	1	-
Hieracium pilosella	48	***	10	6-27
Linum catharticum	1	***	401	7-36^{c}
Lotus corniculatus	2	***	48	<5-34^{s}
Pimpinella saxifraga	2	***	66	-
Sonchus asper	20	*	9	9-35
Dwarf shrubs				
Helianthemum nummularium	9	*	22	<5-36^{s}
Thymus praecox	43	***	14	9-28

[1] Temperatures refer to the range of constant temperatures over which germination in light exceeds 50% of maximum in standardized laboratory tests (Grime _et al_. 1981).

c = seeds germinate only after extended chilling

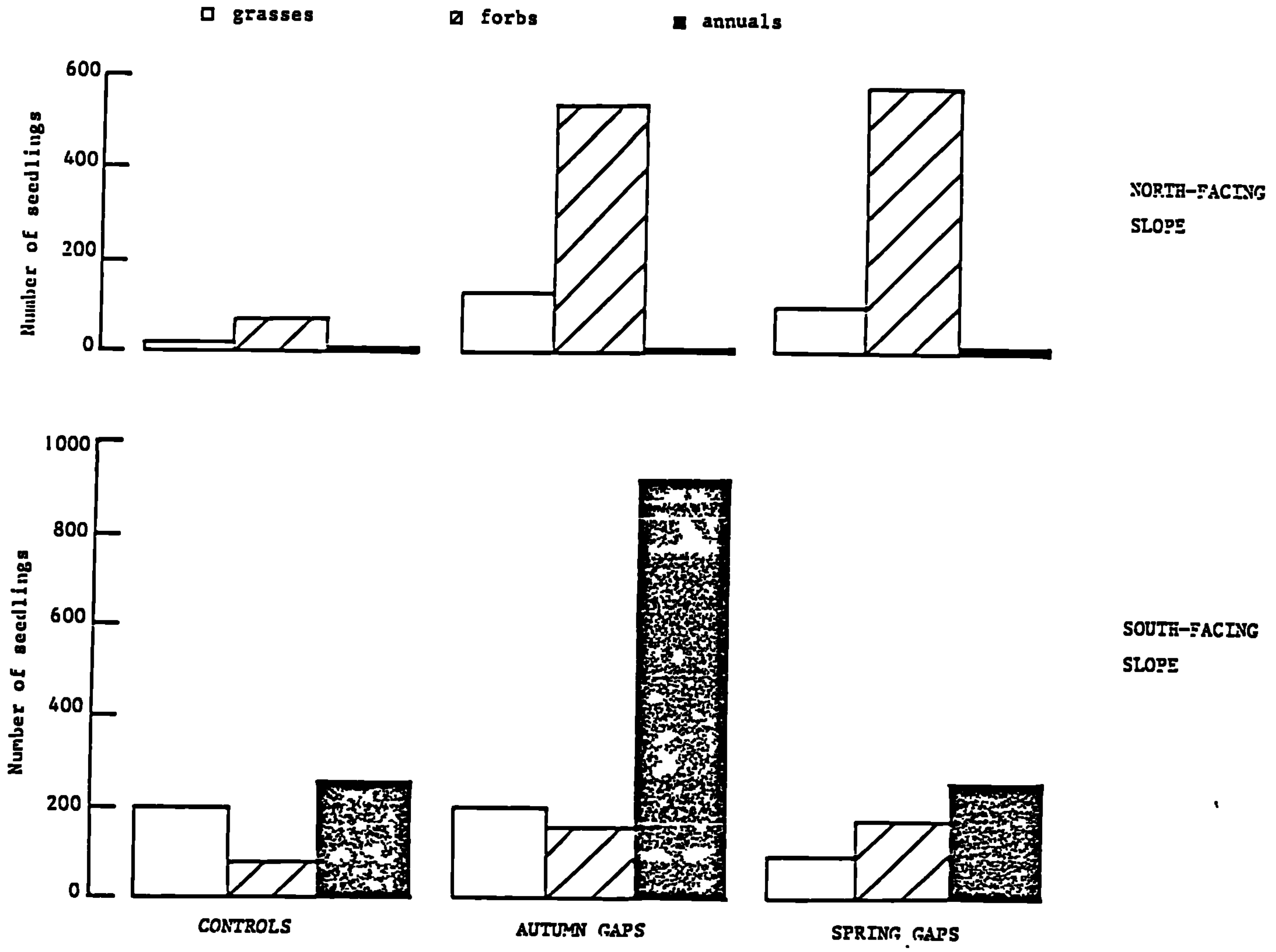
s = seeds scarified prior to test

- = no available data.

Significance levels (Chi-square): NS P>0.05; * P<0.05
** P<0.01; *** P<0.001

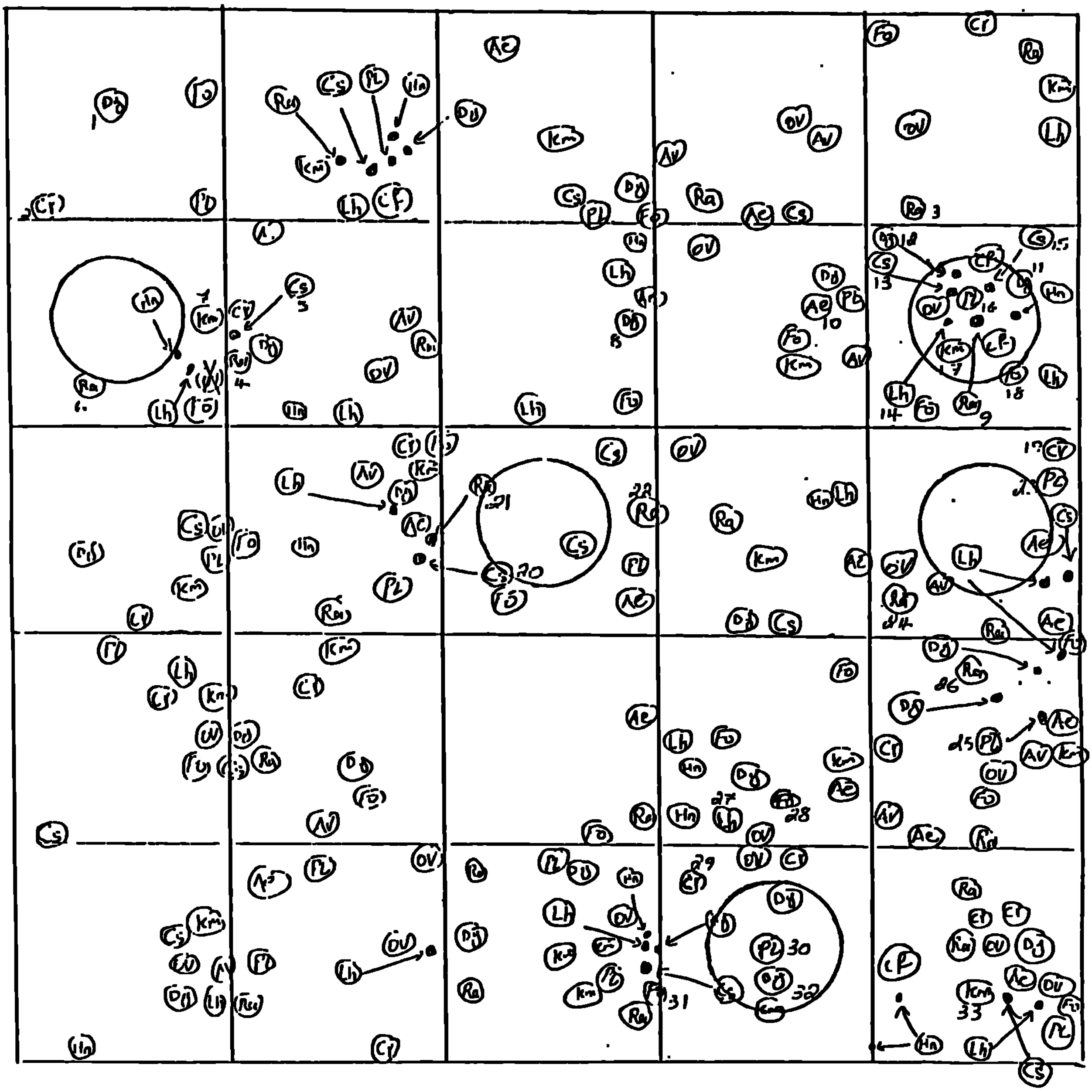
Appendix 2.1.5: (data from Hillier 1984)

Seedling numbers recorded in June 1979 in ten-month-old autumn-cut 40 cm diameter gaps, four-month-old spring-cut 40 cm diameter gaps and 40 cm diameter controls.



Appendix 4.1: the significant level of two-way analysis of variance of dry matter production and root : shoot ratio of *Arrhenatherum elatius* and *Festuca ovina* in response to water supply, mineral nutrient and temperature treatments; $P<0.05$ *, $P<0.01$ **, $P<0.001$ ***.

	Arrhenatherum elatius		*Festuca ovina*	
	Dry weight per plant	root : shoot ratio	dry weight per plant	root : shoot ratio
Water	***	n.s.	***	*
Temperature	n.s.	n.s.	*	n.s.
Interaction	*	n.s.	n.s.	n.s.
Nutrition	***	***	***	***
Temperature	n.s.	n.s.	n.s.	n.s.
Interaction	n.s.	n.s.	n.s.	*
Water	***	n.s.	***	**
Nutrition	***	***	***	***
Interaction	***	n.s.	n.s.	n.s.



Appendix 6.1: Map showing the distribution of seedlings in one of the microcosms in the experiment described in Chapter 6. Small circles indicate positions of established seedlings one month after the beginning of the experiment. Coloured circles identify seedlings which survived the drought . Large circle indicate the positions of the crevice tubes.