VEGETATION AND CLIMATE: A THIRTY-SIX YEAR STUDY IN ROAD VERGES AT BIBURY, GLOUCESTERSHIRE

By

Nigel Dunnett

N.E.R.C Unit of Comparative Plant Ecology,
Department of Animal and Plant Science,
University of Sheffield.

Thesis submitted for the Degree of Doctor of Philosophy
December 1995

CONTENTS

SUMMARY

The long-term study, initiated by Professor Arthur Willis in 1958, of the vegetation of permanent plots in road verges at Akeman Street, near Bibury, Gloucestershire, is a unique and valuable record of annual variations in shoot biomass of individual species, and of the vegetation as a whole, over a 38-year period. The study was originally devised to monitor the effects of herbicides and a growth regulator on roadside vegetation. However, more recently, in the context of the possible effects of climate change on indigenous vegetation, interest has centred on data from the untreated control plots and their potential in detecting long-term plant/weather relationships.

In Part 1 of this thesis, annual fluctuations in the de-trended or flat-trended above-ground biomass of over 40 plant species at Bibury are compared with three orders of climatic variables: individual weather variables such as temperature, rainfall and sunshine; the frequency of 'Lamb weather types' (anticyclonic, cyclonic and westerly weather), which in large part determines rainfall, sunshine and temperature; and with the changing position of the Gulf Stream in the North Atlantic, which may, in part, determine the frequency of weather types over the UK. In all comparisons, markedly non-random climate/plant relationships were detected. The responses of Bibury taxa to individual weather variables matched closely their responses to weather types. The analyses presented here agree with other studies which link a northerly Gulf Stream with increased frequencies of anticyclonic weather in spring and autumn and reduced frequencies in summer. It is suggested that plant species promoted by a more northerly Gulf Stream tend to be robust perennials with early phenologies or deep-rooted species which may exhibit a degree of drought avoidance, but which may also respond rapidly to favourable conditions in spring and summer. Overall, settled, hot, dry summers appear at Bibury to decrease the total productivity of the vegetation and promote the amount of bare ground in the ecosystem.

Part 2 of the thesis describes experiments designed to explore the mechanistic basis of the plant/weather relationships at Bibury and to extend the relevance of the data-set beyond the site itself. Five species were selected which exhibit a range of responses to individual weather variables. The plants were grown in deep containers (rigid plastic bins) in monoculture and in five-species mixture. Treatments were applied out of doors to establish whether the responses observed in the field could be repeated under semi-controlled conditions. The species were: *Achillea millefolium* (promoted by warm dry springs and summers), *Cirsium arvense* (retarded by warm dry springs and summers and promoted by mild winters), *Dactylis glomerata* (retarded by mild winters), *Festuca rubra* (retarded by mild winters) and *Poa pratensis* (retarded by warm dry springs and summers). The treatments were: heating with electric cables at the soil surface in late winter and spring; application of a severe frost in late spring; and the imposition of a severe drought in summer. The treatments affected both the vegetative and reproductive vigour of the species involved. In the great majority of cases predicted responses were fulfilled under the experimental conditions (for example, *Dactylis glomerata* was shown to be dependant on winter chilling to achieve maximum reproductive potential, reflecting its reduced performance in the field at Bibury following mild winters).

The five species were used to test current theories on genome size and plant response to unusually high temperatures in late winter and spring, and to severe late frosts. As predicted, species with low nuclear DNA content tended to gain competitive advantage in mixture following the warming treatment, while those species with high nuclear DNA content showed evidence of reduced competitive ability. Also, as predicted, small genome species tended to exhibit greater sensitivity to the late frost treatment. The experimental results provide valuable insights into the potential effects of weather on plant community dynamics and the relative competitive abilities of potential vegetation dominants and subordinates.

ACKNOWLEDGEMENTS

I wish to thank my supervisor, Professor J. P. Grime, for inspiration, criticism and much encouragement in developing the work described in this thesis. I am also particularly grateful to Professor Arthur Willis for sharing his great experience, and for his support and enthusiasm for the current study. Thanks also go to all friends and colleagues in the Unit of Comparative Plant Ecology for making my time there so enjoyable and stimulating.

I owe particular gratitude to Mr. Chris Thorpe (UCPE) for devotion beyond the call of duty in the development and operation of the frosting equipment; Mr. David Corker (UCPE) for electronic expertise; Gus Tasker (UCPE) for practical help; Dr. Rod Hunt (UCPE) for getting me started on the statistical analysis of the data-set; Dr Arnold Taylor (Plymouth Marine Laboratory) for Gulf Stream data; Dr Nicholas Aebisher (Game Conservancy Trust) and Mr Declan Conway (Climatic Research Unit, University of East Anglia) for weather type data. Special thanks are reserved to Helen Dunnett (Sanderson at the start of the project!) for much patience and support and for help in seemingly endless vegetation recording sessions.

I am very grateful to the Esmee Fairbairn Charitable Trust and to the Lindeth Charitable Trust who made this work possible through financial support for the project.

PUBLICATIONS ARISING FROM WORK DESCRIBED IN THIS THESIS

Grime, J, P., Willis, A, J., Hunt, R. & Dunnett, N, P. (1994) Climate-Vegetation Relationships in the Bibury Road Verge Experiments. In *Long Term Experiments in Agricultural and Ecological Sciences.* Ed. Leigh, R, A. & Johnston, A. E. CAB International, Wallingford.

Willis, A. J., Dunnett, N. p., Hunt, R. & Grime, J. P. (1995) Does Gulf Stream position affect vegetation dynamics in Western Europe? *Oikos* **73**, 408-410.

PART ONE: A LONG-TERM STUDY OF CLIMATE/VEGETATION RELATIONSHIPS IN THE BIBURY ROAD VERGES

CHAPTER ONE: INTRODUCTION

1.1 Introduction

1.2 Long-term Studies in Ecology

  1.2.1 Climate-related Long-term Studies in Ecology

  1.2.2 The Bibury Data-set

  1.2.3 Long-term studies and Vegetation Response to Environmental Change

1.3 Aims of the Study

1.1 INTRODUCTION

The long-term study, initiated by Professor Arthur Willis in 1958, of the vegetation of the Bibury road verges is a unique and valuable record of the performance of individual species within the verges, and of the vegetation as a whole, over a 38-year period. Results from the first 20 years or so of the study were widely quoted and applied, concerning as they did the management of roadside vegetation through the application of herbicides and a growth regulator. However, in the late 1980s, as interest increased in the possible effects of climate change on the functioning of ecosystems, the Bibury records received a new lease of life with the realisation, by Professor J. P. Grime, that the data from the control plots may yield valuable insights into the relationships between plant performance and climate. Dr Rod Hunt of the NERC Unit of Comparative Plant Ecology, University of Sheffield, performed an initial analysis in which the performance of the vegetation in the verges was compared with weather records from nearby RAF Lyneham. The results demonstrated markedly non-random plant/climate relationships in the verges (Hunt *et al.*, 1992). The investigation presented in this thesis seeks to build upon that initial analysis, and to clarify and verify the relationships discovered.

The work described in this thesis follows two of the approaches in an ideal 'three pronged' strategy for a programme of research on the impacts of climate change on British vegetation: monitoring, modelling and manipulation (Grime *et al.*, 1994). Effective long-term monitoring is the basis of the study presented here. Manipulation of synthesised vegetation communities has been used to test whether plant responses observed in the field can be repeated under controlled experimental conditions. Modelling of the Bibury system, although desirable, was not attempted.

1.2 LONG TERM STUDIES IN ECOLOGY

The importance of long-term studies in ecology has received wide recognition in recent years. This is partly the result of the short-comings of shorter-term experiments. As van der Meijden states (1989):

> "Many recent studies in plant ecology cover only a very short period and are not replicated. It is very likely that the literature is becoming enriched with information on many unique events that cannot properly be placed in perspective and will hamper formulation of unifying concepts."

The recognition is also a result of the awareness that long-term monitoring of biological systems is an essential prerequisite for understanding and eventually predicting responses of such systems to long-term climatic change. There have, however, been relatively few studies in which changes have been documented over more than two or three decades (Goldberg & Turner, 1986).

The earliest examples of long-term studies made little or no reference to the effect of climate or weather on plants. The longest long-term experiments of all, those of Lawes and Gilbert, started in the mid 1800s at various sites at the Rothamsted Experimental Station set out to investigate the effects of different fertiliser treatments on crop and hay yields (Johnston, 1994). The classic work of Tamm on perennial herbs was primarily demographic, monitoring survival and flowering of selected perennial herbs. Only passing mention is made of the effects of weather, as for example when changes in the numbers of individuals of *Primula veris* over the period 1943-1971 are attributed to the possible effects of sequences of years with 'special climatic conditions' (Tamm, 1972). The aim of some long-term studies has been to aid management of semi-natural vegetation, for example roadside verges (Parr & Way, 1988), while others have conservation value, such as those which monitor species diversification of agricultural grasslands following cessation of fertiliser applications (Olff & Bakker, 1991, van der Woude *et al.*, 1994).

1.2.1 Climate-related long-term studies in ecology

The earliest long-term studies to compare changes in plant performance with changes in weather in a comparable way to that of the Bibury study were probably those conducted by Watt (1971). For example, the percentage cover of *Festuca ovina* (recorded in early July in Breckland plots over the period 1949-1969) was compared with rainfall in May and the first half of June of the same year. Drier springs were associated with reduced cover of *Festuca*, a finding that Watt attributed to increased litter accumulation in dry springs resulting in reduced establishment of seedlings. Other studies have linked plant performance with meteorological variables, particularly rainfall (e.g. Noble, 1977; Hunt *et al.*, 1985; Goldberg & Turner, 1986; Svensson *et al.*, 1993; O'Connor & Roux, 1995). In addition to plant/weather relationships, studies have been published on, for example, climate and birds (Peach *et al.*, 1994), insects (Woiwood & Harrington, 1994, Pollard, 1988) and plankton in Lake Windemere and elsewhere (George *et al.*, 1990, Maberly *et al.*, 1994). Other studies have linked predator-prey relationships with climate (Spiller & Schoener, 1995).

In recent years a number of studies have been published that place long-term studies directly in the context of climate change (e.g. Fitter *et al.*, 1995, Sparks & Carey, 1995). These have been based upon the premise that, in order to predict future responses of species to a changed climate, it must first be understood how those species have responded to climate in the past (Sparks & Carey, 1995).

The work that is probably most comparable to that presented here is the series of latter-day analyses that have been carried out on the Park Grass plots at Rothamsted. Like the Bibury plots, and unlike most other studies, the Park Grass plots represent nonsuccessional communities that are not dominated by directional changes in species composition (Dodd *et al.*, 1994a). The original aim of this experiment was to monitor the effects of different amounts and combinations of mineral fertilisers and organic manures on the productivity of permanent grassland (Lawes & Gilbert, 1880). However, now, the unrivalled length of this study has enabled present-day analyses to be carried out in the context of community stability (Silvertown, 1980; Dodd *et al.*, 1994a; Tilman *et al.*, 1994; Dodd *et al.* 1995) and climate (Silvertown *et al.*, 1994). The last authors found that, although rainfall was positively correlated with grassland productivity, it was little better than biomass as an explanatory variable for community composition. According to their analysis, rainfall enhanced the effect of biomass, favouring better competitors in more productive plots.

1.2.2 The Bibury Data-set

Despite the number of long-term studies now being published, the Bibury data-set has a number of features which make it unique. Although some of these features may be shared by other long-term studies, no other studies combine them to the same extent as the Bibury data-set. Some of the features of the Bibury study include:

- **A single recorder over the entire period.** Professor Arthur Willis has been responsible for collecting the vegetation records (with various assistants) over the entire period of the study, from 1958-1995. Much error in botanical surveys results from recorder bias (Rich & Woodruff, 1992). The fewer recorders there are involved in a study the less risk of error. Moreover, a consistent sampling method has been used throughout (see Chapter 2), again minimising risk of error. The method of recording biomass in the Park Grass plots changed in 1960 with the introduction of a mechanical forage harvester. The recorded biomass per plot immediately increased, potentially complicating analysis of the results (Silvertown *et al.*, 1994).

- **Continuous annual records.** Records are available, collected in the same week each year (the third week of July), from the Bibury plots for every year from 1958-1995 (with the exception of 1961). Additional records are available for other times of the year but are not used in the present analysis. Parts of the Park Grass data series are not complete (see below).

- **Detailed records of community composition.** The Bibury data-set includes annual records of the performance of all species present in permanent quadrats, in addition to annual estimates of total above-ground biomass from those same plots. In the Park Grass experiment, continuous records exist only for total vegetation biomass. The record of community composition is far from complete and only very recently has the species composition of every plot and subplot been sampled in the same year (Silvertown *et al.*, 1994). No detailed continuous record of individual species is available for more than a few years at a time (Dodd *et al.*, 1995). A newly-discovered series of visual surveys of presence/absence data for individual species for the period 1920-1979 has been the subject of a recent paper on community stability (Dodd *et al.*, 1995); however, in an earlier paper the same authors stated that the visual surveys were less reliable than the hay samples from the Park Grass Plots, occasionally missing common species (Dodd *et al.*, 1994b).

Many long-term studies involve one or a small number of species, or the overall productivity of a system. The Bibury data-set contains information on the dynamics of a complete plant community.

1.2.3 Long-term studies and vegetation response to environmental change

As mentioned above, long-term studies have received much recent attention as concern has increased about the possible effects on individual species, communities and ecosystems of climate change. Scientists wishing to investigate, understand or predict responses to climate change may use laboratory-based studies or manipulate patches of vegetation in the field. However much can be learnt from existing ecosystems, given appropriate historical records and climate data (Woodward, 1992). By understanding how biological systems have responded in the past to environmental change, it may be possible to use this knowledge to predict the future effects of human activities (Adams & Woodward, 1992). In the shorter term, knowledge of relationships between the performance of biological systems and year-to-year fluctuations in weather may aid understanding of how such systems may respond to climate change in the future. For example, if a long-term study suggests that a particular species is promoted by hot, dry summers, a greater frequency of such summers in the future may result in expansion of that species.

A number of scenarios have been suggested for the future climate of the UK. In the early 1970s it was thought that the activities of man may lead to the British climate becoming cooler, wetter and more humid (Lamb, 1970). Now concern rests on the possible warming associated with increased atmospheric CO_2. Current General Circulation Models predict that by the year 2030, summer temperatures may be 1.4°C higher than today; winter temperatures may be 1.5-2.1°C warmer; winter precipitation may be 5% greater and there could be a significant increase in the frequency of very warm years, although there may be no change in summer precipitation (e.g. CCIRG, 1991). As the climate changes, so also may climate variability (Rind *et al,* 1989), with a greater frequency of 'extreme events'.

The possible effects of such changes in the climate of the UK on indigenous vegetation have been listed by Grime (1990). These may include:

- A shifting of the growing season in the south towards autumn, winter and spring, with a quiescent phase often occurring in summer.

- Conspicuous changes in the relative abundance of various constituents in familiar vegetation types.
- A higher level of flowering, seed and spore production.
- Species which at their northern limit in England or southern Scotland will begin to expand northwards.
- Species currently restricted to south-facing slopes in northern Britain will begin to colonise other aspects.
- Expansion to higher altitudes will begin to occur in many lowland species.
- Plants of northern distribution in Europe may begin to retreat from the southern extremities of their ranges in Britain.
- Northern species may retreat from lower altitudes in southern Britain.
- Species which flourish under Mediterranean conditions may enter into Britain.
- Many rare plants, particularly those in which small populations now occupy cool, continuously damp refugia on isolated north-facing slopes, will be particularly threatened.
- Vegetation changes will proceed in 'spurts' and extreme years will be of key significance.
- The effects of climate change will depend upon present and future policies of land-use.

Long-term data-sets, such as the Bibury data-set, are valuable tools for testing some of the assertions made above.

1.3 AIMS OF THE STUDY

The study described here had a number of aims:

1. To up-date the investigation of plant/weather relationships in the Bibury road verges by incorporating vegetation data from surveys carried out in 1993 and 1994.

2. To widen the scope of the initial investigation by incorporating new meteorological and climatological variables.

3. To interpret the ecological behavior of species from the past records and deduce the relative importance of likely determining climatic factors.

4. To test and verify, under controlled conditions, selected plant/weather relationships detected in the analysis of the field records.

The thesis consists of two parts. Part 1 describes the analysis of the field records collected at Bibury. Part 2 is an account of an experiment devised to verify selected plant/weather relationships and to establish possible mechanisms for observed responses to weather.

CHAPTER 2: THE SITE CHARACTERISTICS, HISTORY AND THE VEGETATION RECORDS AT BIBURY

2.1 INTRODUCTION

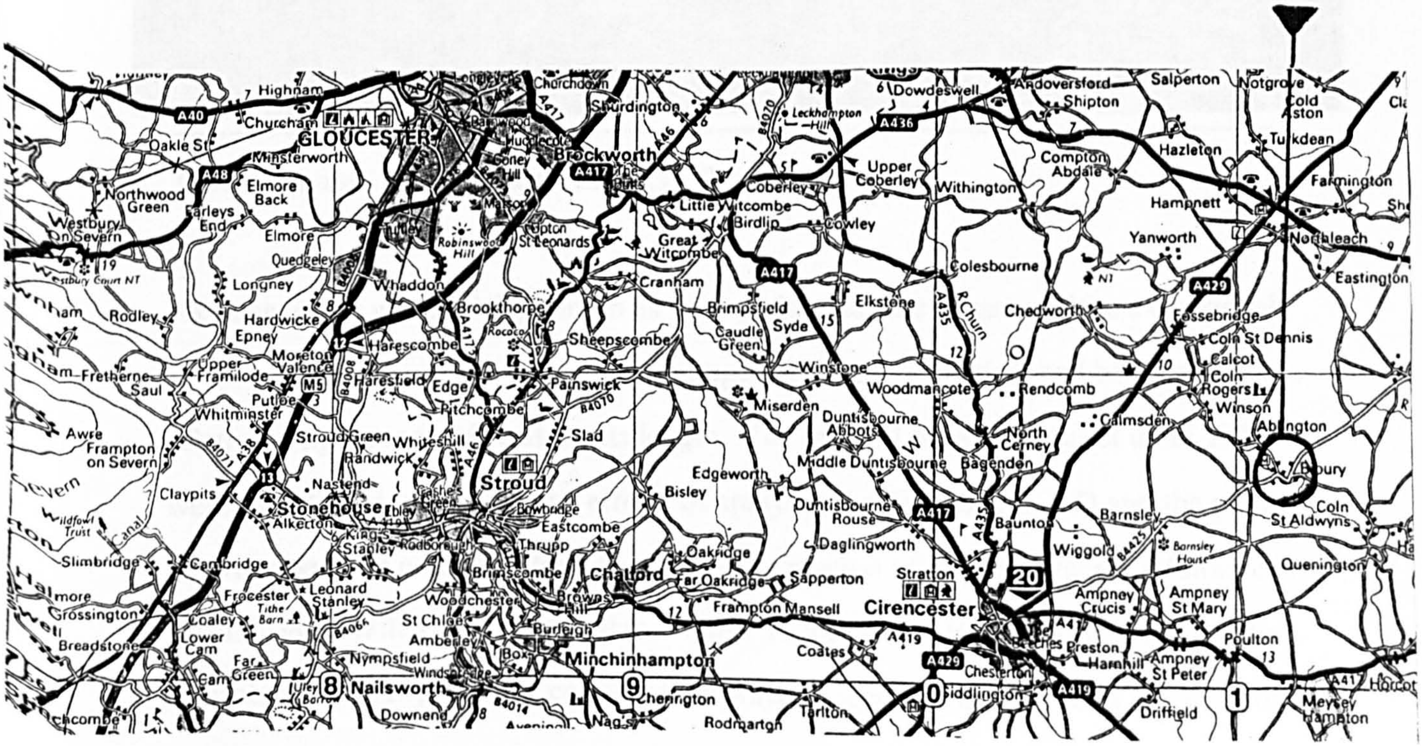
This chapter contains information on the site at Bibury, the design of the field experiment, the method of collecting vegetation records, and details of previous work conducted on the Bibury data-set.

2.2 THE FIELD SITE

2.2.1 Location

The records are collected annually from eight permanent plots set out in roadside-verge vegetation. The experimental plots lie in wide verges along part of Akeman Street, near Bibury, Gloucestershire, in the Cotswolds (Figures 2.1 & 2.2 and Plate 2.1). The altitude of the site is approximately 140m. The surrounding area is predominantly arable farmland.

Figure 2.1. The Location of Bibury.



2.2.2 History of the Site

The verges fall alongside the line of an ancient Roman road. There is evidence that at least part of the verges may have been subject to some disturbance in the past. Visual evidence indicates some re-alignment of the line of the road from its original course (A. J. Willis, pers. comm.). This suggests that a proportion of the vegetation (in which lie experimental plots 7 & 8) may be of greater antiquity than the rest (Figure 2.2).

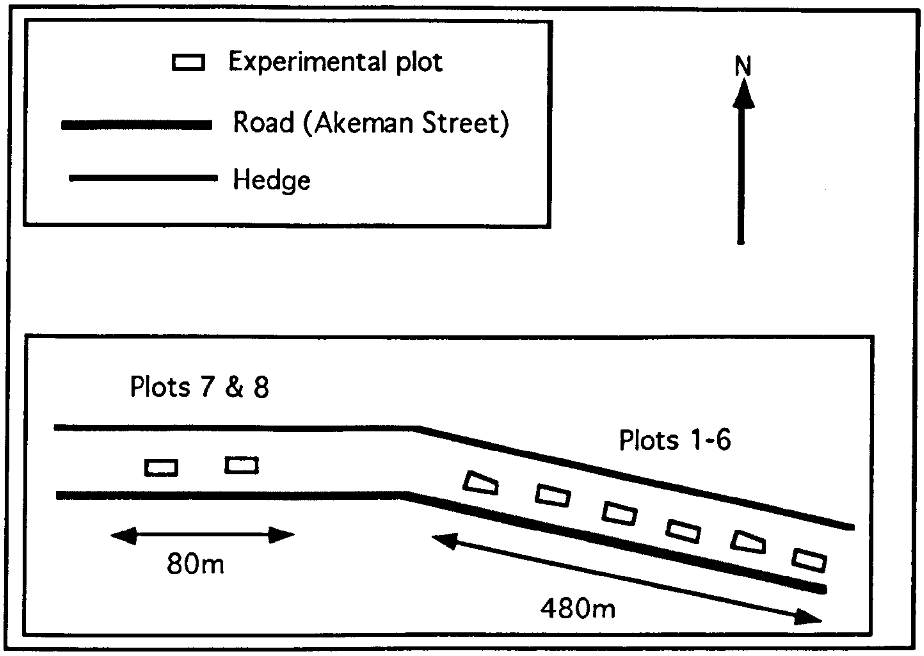
Plate 2.1. The wide verges of Akeman Street

2.2.3 Layout of the Experimental Plots

Akeman Street was initially chosen as an experimental site because of the exceptional width of its road verges, the apparent homogeneity of its vegetation, and because of the relatively light road traffic along its length. The original experiments, set up in 1958, were established to monitor the effects of spraying the herbicide 2, 4-D and the plant growth regulator maleic hydrazide onto the vegetation of the road verges (Yemm & Willis, 1962; Willis & Yemm, 1966; Willis, 1970; Willis, 1972; Willis, 1988). The controls of these experiments consist of unsprayed vegetation in eight plots, each about

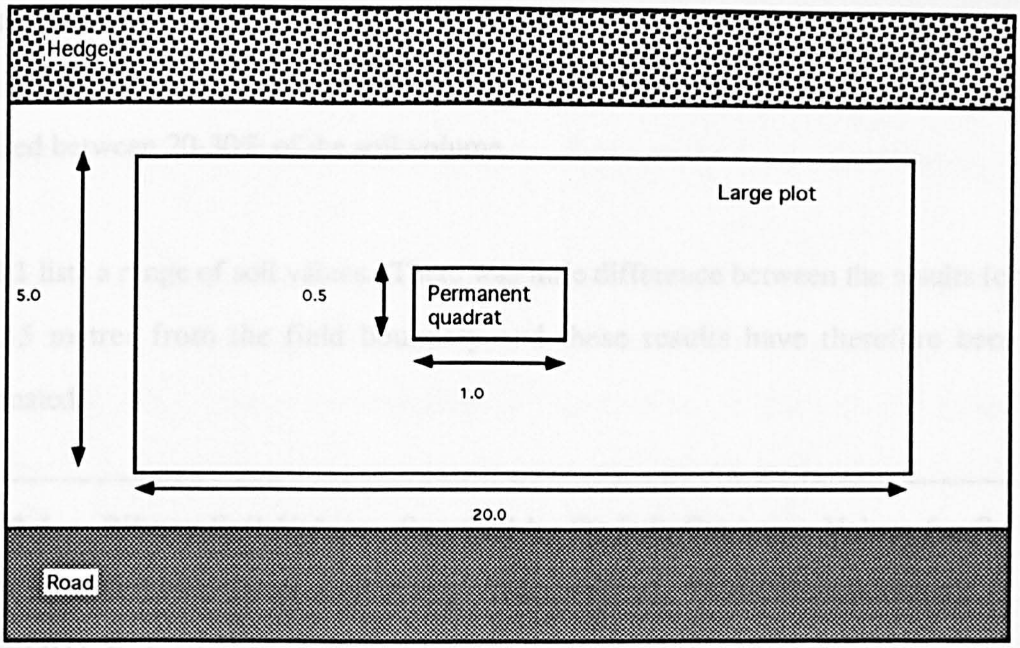
20 m long and 3.3 - 5.5 m wide. It is the data from these untreated control plots that is used in subsequent Chapters to investigate plant/weather relationships. Six of the plots (plots 1-6) form controls to the maleic hydrazide and mixed spray treatments, and two of the plots (plots 7 & 8) form controls to the 2, 4-D treatments.

Figure 2.2. The Siting of the Experimental Plots. Not to scale



Within each large plot is embedded a smaller permanent quadrat. The permanent quadrat, whose position is located by wooden posts flush with the ground surface, is sited centrally within the plot as a whole, about 2.0 m from the roadside edge of the large plot (see Figure 2.4). Each control plot is separated from the other control plots by three other plots of equal size: one plot which received the 2, 4-D treatment, one which received the maleic hydrazide treatment, and one which received a mixture of the two chemicals.

Figure 2.3 The Layout and Dimensions of an Experimental Plot. Dimensions are in metres.



2.2.4 Geology and Soil Type

A detailed soil survey was carried out on site by Dr J. S. Conway of the Royal Agricultural College, Cirencester in July 1994. Soil samples were taken from the eight Bibury plots. For each plot, samples were taken 1 metre from the road edge, immediately adjacent to the monitored quadrat, and from within the adjoining fields, at distances of 5 and 15 metres from the field margins. All samples were tested by routine analytical techniques (MAFF) for pH, plant available potassium, phosphorus and magnesium, E.D.T.A extractable copper, lead and zinc, organic matter, total (i.e. organic nitrogen, and soil texture. The results discussed below are taken from the report prepared by Dr. Conway.

The parent material of the Bibury area is primarily Oolitic limestone. The depth of the soil varies between 300mm and 800mm and pH values lie within the range of 7.5-7.9. These high pH values are attributed to the presence of about 20-30% limestone fragments in the topsoil. However, values obtained from soil samples collected in July 1993 and analysed at Sheffield (using a hand-held pH meter and a thick soil/de-ionised water paste) gave lower values (within the range 7.0 - 7.1). All the soils are of a clay texture (35-38% clay) with typical organic matter status of 3-5%. Limestone fragments comprised between 20-30% of the soil volume.

Table 2.1 lists a range of soil values. There was little difference between the results for 5 and 15 metres from the field boundary and these results have therefore been amalgamated.

Table 2.1 **Bibury Soil Values.** Supplied by Dr J. S. Conway. Values for P, K, Mg, Ca, Zn and Pb are expressed as mg l^{-1} (dry weight). Values for soil organic matter (SOM), N, sand, silt and clay are expressed as percentages (dry weight).

	pH	P	K	Mg	Cu	Zn	Pb	SOM	N	Sand	Silt	Clay
Road Side												
Min	7.7	9	210	73	1.7	12.5	16.1	3.4	0.15	38	24	16
Mean	7.9	13.5	328	94	85	32.7	21.1	5	0.19	48	27	24
Max	8	19	420	133	292	108.2	32.7	6.3	0.22	58	38	38
Field Margin												
Min	7.9	15	265	49	2.1	3	5.3	2	0.15	22	28	34
Mean	8	18	315	59	3.3	3.9	9.7	3.1	0.10	30	33	37
Max	8.1	22	375	81	5.8	5.1	14.5	3.8	0.13	38	38	40
Field Soil												
Min	7.9	19	285	41	1.9	3.6	4.1	2.9	0.15	18	34	34
Mean	8	26.5	369	64	2.9	4.7	6	3.4	0.17	26	36	38
Max	8.1	38	460	95	5.1	5.9	7.6	4.1	0.10	32	38	44

Potassium and phosphorus occur in greater concentration in the field than on the roadside, possibly because of fertiliser residues. Soil organic matter (SOM) is higher in the permanently vegetated roadside verges where there is no removal of plant litter. The decrease in magnesium concentration in the field probably reflects the abstraction of magnesium by crops without replacement by the farmer in the form of fertiliser.

However, lead contamination from vehicle exhausts is apparent in the roadside soil (although this is relatively slight) and zinc and copper contamination is high in places. In plots 6, 1, 4 and 5, copper contamination is considerable; in places it is at values which may be considered toxic to crops in plots 4 and 5. Zinc contamination is high in plot 4. The high concentration of copper and zinc by the road is possibly a result of deposition from car exhaust fumes. Plots 4 and 5 occur at a bend in the road and may be particularly susceptible to contamination as cars move around the bend at speed (A. J. Willis, pers. comm).

2.2.5 Climate

Hunt *et al.* (1993), using data from a sufficiently representative site near the experiment (RAF Lyneham), characterised the climate of the area. Monthly means of daily maximum temperature, minimum temperature and mean temperature, and monthly means of total rainfall and sunshine were averaged to produce six-monthly seasonal means. A summary of weather variables is shown in Table 2.2.

Table 2.2. Mean values for weather variables over the period 1958-1992. From Hunt *et al.*, (1993). Winter refers to the months September - February, Summer refers to the months March - August.

Variable	**Minimum**	**Mean**	**Maximum**
Summer mean of monthly mean of daily maximum temperature. °C	13.90	15.12	17.00
Winter mean of monthly mean of daily maximum temperature. °C	6.90	10.03	11.80
Summer mean of monthly mean of daily minimum temperature. °C	5.40	6.74	8.00
Winter mean of monthly mean of daily minimum temperature. °C	0.90	3.84	5.40
Summer mean of monthly total rainfall. mm	26.40	55.06	74.06
Winter mean of monthly total rainfall. mm	38.50	64.17	101.00
Summer mean of monthly total sunshine. h	126.30	172.80	214.20
Winter mean of monthly total sunshine. h	61.30	82.27	105.60

2.3 VEGETATION

2.3.1 Classification

The vegetation of the Bibury road verges is fairly typical neutral grassland, that is grassland lacking in any pronounced calcicole or calcifuge element (Tansley 1939), although some calcicoles are present. Under the National Vegetation Classification (Rodwell, 1992), such grasslands are included within the broad category of Mesotrophic Grasslands. Specifically, the Bibury verges can be classified as belonging to the grassland community type referred to as *Arrhenatheretum elatioris* (MG1). *Arrhenatheretum* are grassland communities, developed mainly on well structured and freely draining loams in which coarse-leaved tussock grasses predominate. Two grass species that are characteristically dominant of *Arrhenatheretum,* namely, *Arrhenatherum elatius* and *Dactylis glomerata,* are major components of the vegetation at Bibury, however, the other characteristic grass of the *Arrhenatheretum*, *Holcus lanatus*, is scarce in the plots. The large Umbellifers, *Anthriscus sylvestris* and *Heracleum sphondylium*, are the most conspicuous herbs. Other tall herbs at Bibury include *Cirsium arvense*, *Urtica dioica* and *Centaurea nigra*.

Although the roadside verges were chosen as an experimental site partly because of the uniformity of their vegetation, some variation is present. A distinction can be made between plots 1-6 and plots 7-8. This variation corresponds with, although is not necessarily a result of, the possible different-aged stands shown in Figure 2.2. The vegetation in plots 1-6 tends towards the more vigorous, less diverse *Festuca rubra* and *Urtica dioica* sub-communities (MG1a and MG1b respectively) while the vegetation in plots 7 and 8, at the western end of the experimental site, in what might be the more ancient part of the verge, becomes more typical of the *Centaurea nigra* sub-community (MG1f). Herbs such as *Hypericum perforatum*, *Primula veris*, *Knautia arvensis*, *Centaurea nigra*, *Galium verum*, *Centaurea scabiosa* and *Achillea millefolium* provide much flowering interest and there is a general increase in abundance of *Festuca rubra* and decrease in abundance of *Arrhenatherum elatius* and *Dactylis glomerata*.

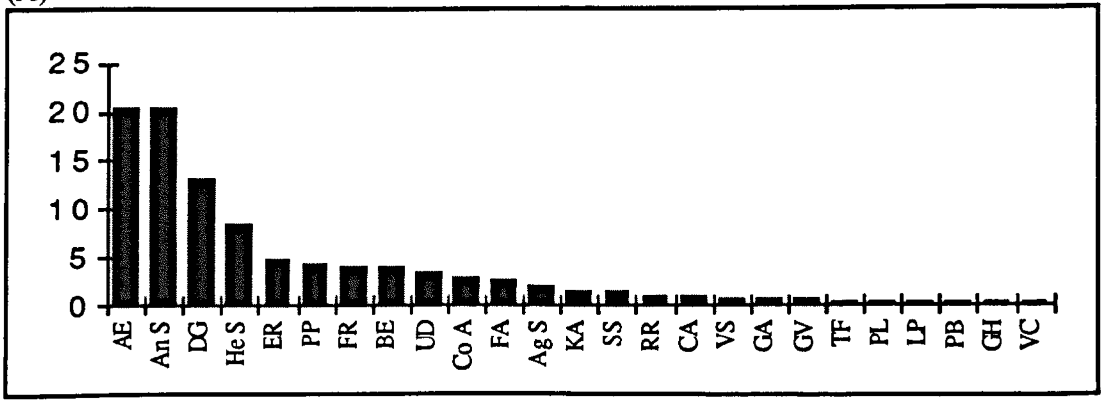
The vegetation on the site achieves a complete cover, with only traces of bare ground apparent. Amounts of ground litter are generally low in summer; however, large amounts of standing dead material can be expected to persist over the winter. Two mosses are continually present: *Brachythecium rutabulum* and *Eurhynchium praelongum*., but low in biomass, and other mosses are rare.

While there are no particularly rare or infrequent species present in the Bibury road verges, the vegetation is notable for being typical of ungrazed or lightly managed semi-natural grassland on neutral soils throughout lowland Britain. It is not without visual interest, particularly in spring and summer, with a succession of showy species from cowslips and buttercups in spring through billowing cow parsley in early summer to field scabious, St John's Wort and the knapweeds in mid-late summer.

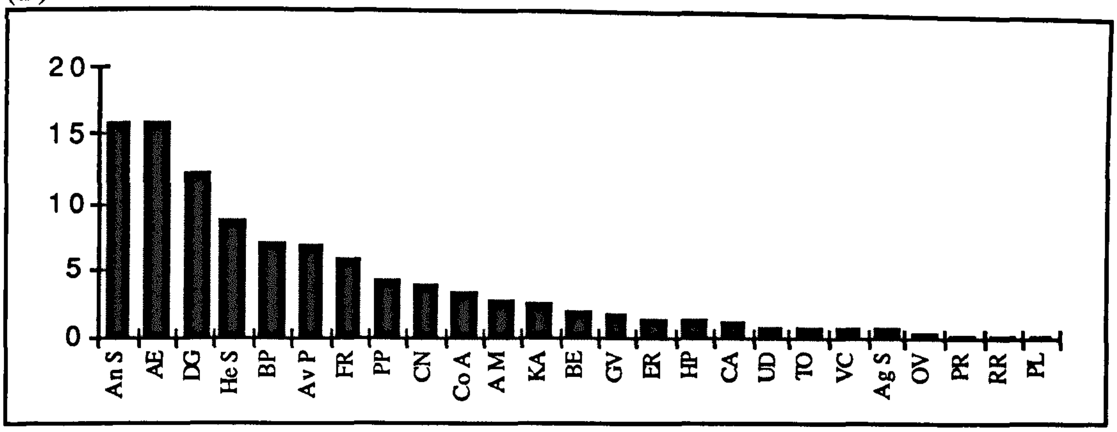
Figures 2.4 (A) and (B) illustrate the percentage contribution of the 25 most abundant species in plots 1-6 and 7-8 to the total biomass of those plots. The values are means for the period 1958-1994. Plots 1-6 are clearly dominated by four species, *Arrhenatherum elatius, Anthriscus sylvestris, Dactylis glomerata,* and *Heracleum sphondylium,* with other components of the vegetation making a minor contribution to the total. In plots 7-8, the same four species are also the most abundant; however they do not dominate the vegetation to the same extent.

Figure 2.4 The percentage contribution of the 25 most common species in plots 1-6 and 7-8. Y axis = % Contribution. (A) = Plots 1-6. B = Plots 7-8. AM = *Achillea millefolium;* AE = *Arrhenatherum elatius;* AgS = *Agrostis stolonifera;* AnS = *Anthriscus sylvestris;* Av P = *Avenula pubescens;* BE = *Bromopsis erecta;* BP = *Brachypodium pinnatum;* CA = *Cirsium arvense;* CN = *Centaurea nigra;* Co A = *Convolvulus arvensis;* CL = *Cruciata laevipes* DG = *Dactylis glomerata;* ER = *Elytrigia repens;* FA = *Festuca arundinacea;* FR = *Festuca rubra;* GA = *Galium aparine;*GH = *Glechoma hederacea;* GV = *Galium verun;* He S = *Heracleum sphondylium;* HP = *Hypericum perforatum;* KA = *Knautia arvensis;* LP = *Lolium perenne;* OV = *Odontites verna;* PB = *Phleum bertolonii;* PL = *Plantago lanceolata;* PP = *Poa pratensis;* PR = *Potentilla reptans;* RR = *Ranunculus repens;* Ru S = *Rumex* sp; SS = *Stachys sylvatica;* TO = *Taraxacum officinale* agg., TR = *Trifolium repens;* UD = *Urtica dioica;* VC = *Veronica chamaedrys,* VS = *Vicia sativa.*

(A)



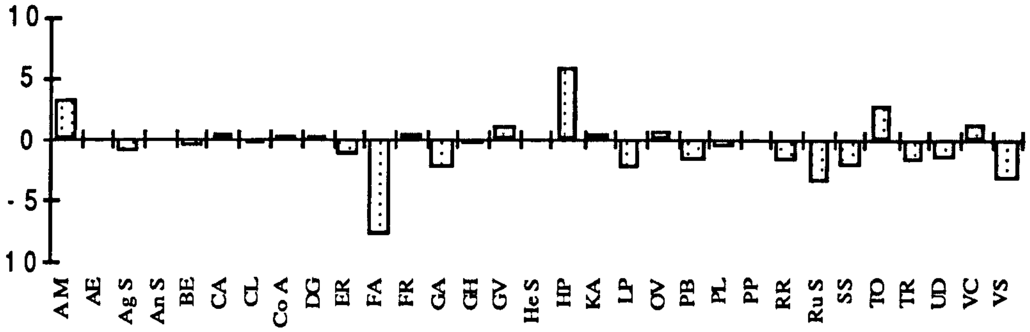
(B)



In Figure 2.5, the ratio of the percentage of the total shoot biomass that individual species occupy in plots 7-8 to the percentage they occupy in plots 1-6 is shown. Species that occupy a greater proportion of the total shoot biomass in plots 7-8 than plots 1-6 are mainly those typical of more open, less productive swards, or shorter turf, such as *Achillea millefolium, Festuca rubra, Hypericum perforatum* , *Odontities verna* and *Taraaxcum officinale*.agg. Species which occupy a greater proportion of the total shoot biomass in plots 1-6 than 7-8 tend to be vigorous grasses such as *Festuca arundinacea* and *Elytrigia repens,* or typical tall herbs of productive grasslands, such as *Urtica dioica* and *Rumex* spp.

The evidence presented above strongly suggests that the vegetation of plots 1-6 is rather more productive and less diverse than that of plots 7-8.

Figure 2.5 The ratio of the percentage of the total vegetation shoot biomass occupied by species in plots 7-8 to that occupied in series 1-6. Y axis = log (N) of the ratio of the mean values from the period 1959-1994. A positive value indicates that the species occupies a greater proportion of the total biomass in plots 7-8 than it does in plots 1-6. Abbreviations follow Figure 2.5.



2.3.2 Management and Disturbance

A characteristic feature of *Arrhenatheretum* is that it is an ungrazed grassland type (Rodwell, 1992), and this is true of Bibury. A metre-wide strip adjacent to the road is mown in late spring to maintain visibility and the rest of the verge is usually 'topped' with a flail mower in November each year at a height of approximately 0.5 metre. Although the dense nature of the sward inhibits establishment of woody plants, some scrub encroachment is apparent on areas adjacent to the monitored plots. This is controlled as and when appropriate by hand cutting.

In some years horses are ridden behind the plots adjacent to the hedge. The horses rarely leave the track. Occasionally tractors and other heavy vehicles run into the edge of the large plots adjacent to the road but there is no evidence that they have entered the quadrat area. Probably the greatest disturbance the plots receive is during the annual intensive summer vegetation survey.

2.4 THE ANNUAL VEGETATION SURVEY

2.4.1 Field Recording

Recording takes place annually in the third week of July. The recording method is explained fully in Willis *et al.* (1959) and Yemm & Willis (1962). For each plot two types of estimate are obtained. The smaller permanent quadrat is examined in detail. In the larger plot a more general estimate is made, providing information on less common species not found in the quadrat. Only data collected from the permanent quadrats are used in this thesis. The permanent quadrat in each plot is marked by wooden posts, into which could be fitted a wire grid (1.0 x 0.5 m) divided into eight subsections each of dimension 250 x 250 mm. Each subsection was scored separately by subjective estimation of 'relative bulk'. The total above ground-biomass in each subsection was given a score of ten. Each species occurring in that subsection was then given a score out of ten (after allowances had been made for bare ground and litter), according to the proportion of the total above-ground biomass that the species occupied. For example, if a species was estimated to occupy half the above-ground biomass in a subsection it was given a score of five. Species occupying less than 5% of the total bulk of the vegetation were scored as 'traces', and in calculating average results all traces were arbitrarily assessed as 1%.

In order to obtain comparative estimates of the total bulk of the vegetation of the plots a subjective estimate of the volume of living plant material in each of the subsections is made by reference to a standard volume (a cylinder of 10mm diameter and 150mm in height). The mean of the eight scores for each subsection is calculated to give a whole quadrat score.

The estimates of above-ground biomass have been compared with destructive samples, for which the fresh weight and the dry weight were determined, taken periodically over the length of the long-term study. No significant difference ($P < 0.05$) was found between the destructive and non-destructive estimates of biomass or the destructive and non-destructive estimates of relative abundance.

2.4.2 Conversion of the field records to biomass scores

In effect the field scores are estimates of the percentage contribution of individual species to the total biomass. These field scores were converted to biomass values by means of calibrations derived periodically from small destructive samples of mixed vegetation from the control plots. Bulk scores were converted to biomass values using the formula: 1 Bulk Unit (field estimate) = 5.9g (dry weight) of plant material (A. J. Willis, pers. comm.). It was then a straight-forward procedure to allocate biomass values to individual species using the field scores by calculating the relevant percentage of the total biomass for each species. The data were now in the form of biomass per unit area. All biomass values were standardised to grams per square metre and transformed to logarithms before any further analysis.

2.4.3 Flat-Trending and de-Trending of the data

Although over a hundred taxa have been recorded from the Bibury road verges, only 41 species are sufficiently well represented to be included in the work presented here, as well as bare ground and litter. As stated in the next chapter, the meteorological variables used in the analyses showed no significant long-term trends. However, several of the taxa included in the analysis did show significant trends in mean log shoot biomass over time. In the absence of any comparable meteorological trends this non-stationarity had to be removed statistically before climatic correlations could be attempted. The data for those taxa which did exhibit long-term increases or decreases in log biomass were 'de-trended' by calculating the residuals (observed values minus fitted values) about the fitted thirty-seven-year linear regression of log biomass on time.

The plant data were then replaced by those residuals. Those taxa which showed no significant increase or decrease in log biomass over time were 'flat-trended'. This was done by calculating the residuals about the thirty-seven-year mean of log biomass for each individual species, with residuals replacing the original data, as above. Those species which showed significant long-term trends over the period 1958-1994 are listed in Table 2.3.

2.4.4 Functional Types

In addition to using individual taxa in the analyses presented here, species were also grouped into functional types, *sensu* Grime (1974). Species were classified according to Grime *et al.* (1988). The mean untransformed biomass values for individual species were totalled for each functional type and then transformed to logarithm. The functional classification for the Bibury species is shown in Table 2.3. A full explanation of these functional types is given in Appendix 1.

2.5 PREVIOUS BIBURY WORK

As mentioned above, an initial analysis of the Bibury field records was carried out by Dr Rod Hunt of the NERC Unit of Comparative Plant Ecology, University of Sheffield. While much of that work is described later in the thesis, two aspects are not dealt with in detail. These are a) genome size and response to weather at Bibury, and b) extreme events.

2.5.1 Genome Size.

Genome size has been suggested as a useful predictor of plant response to temperature during the main phase of shoot expansion in the spring (Grime & Mowforth, 1982). Differences in genome size in cool temperate regions coincide with differences in the timing of shoot growth. A mechanism explaining variation in DNA amount, cell size and length of the cell cycle as a response of climatic selection has been proposed (Grime & Mowforth, 1982). Species of low nuclear DNA amount are thought to be dependent on growth through current cell divisions whereas in high DNA plants growth appears to depend more upon expansion of cells divided and stored in a preceding phase. Cell division is a particularly temperature-sensitive component of growth.. High DNA species are likely to be capable of growth under cool conditions in late winter and early spring; cell expansion can proceed at lower temperatures than cell division. However, the short cell cycle associated with small genomes is predicted to confer a greater capacity to respond to warmer conditions for those species with smaller genomes. Cool conditions in the early growing season are therefore predicted to favour large genome species, while warm periods during the early growing season are predicted to favour small genome species. The nature of the recording method at Bibury means that it is difficult to test these hypotheses using the Bibury data-set. The above-ground biomass of small genome species, as recorded in July, is likely to be affected by many factors, such as summer drought, in addition to spring temperature. However, small genome species are likely to be highly responsive to year-to-year variations in climate because of their short cell cycle and indeterminate growth. As such they are likely to show greater yearly variation in shoot biomass than high DNA species. Tests carried out on the Bibury data-set do indeed show that small DNA species do tend to show increased variation in shoot biomass (Grime *et al.*, 1994).

The genome size of Bibury species, where known, is included in Table 2.3.

2.5.2 Responses to Extreme Events at Bibury

It was noted in Chapter 1 that the frequency of extreme events is likely to increase as a consequence of global climate change and that such events may be a major driving force of vegetation change. Long-term studies, such as that at Bibury study are of great value in testing the possible responses of vegetation to such events. In closed vegetation, e.g. at Bibury, it is possible that events such as the droughts of 1975 and 1976 cause structural changes that make the vegetation temporarily invasible. A striking increase in the abundance of *Anthriscus sylvestris* was observed (Figure 2.6) in 1976 and 1977. It is possible that drought damage to the dominant species (*Dactylis glomerata* and *Arrhenatherum elatius*) enabled *Anthriscus* to benefit from the brief relaxation of dominance (Grime *et al.*, 1994). *Anthriscus* produces a large crop of large seeds and is able to colonise vegetation gaps (Thompson & Baster, 1992).

Figure 2.6 Mean biomass of *Anthriscus sylvestris* from plots 1-6, 1959-1993. X axis = year. Y axis = Shoot biomass (g m^{-2}).

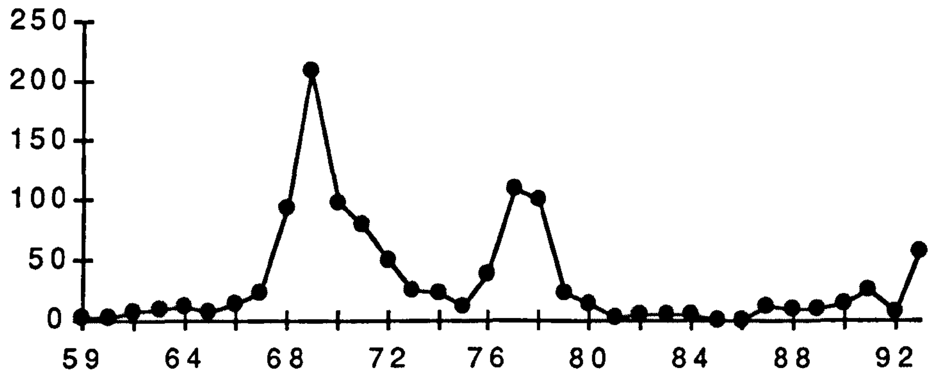


Table 2.3 The status, strategic classification, and DNA amount of common Bibury species. Status 1-6 and status 7-8 refer to the status of species in plots 1-6 and 7-8 respectively over the period 1959-1994. D = Decreasing. I = Increasing. No entry indicates no significant increasing or decreasing trend over the period. A dash indicates that the species does not occur in those plots. For a full description of CSR strategies refer to Appendix 1. DNA values are taken from Hunt *et al.* (1993).

	Status 1-6	Status 7-8	CSR Classification	2C DNA Amount (pg)
Bare ground	D	D		
Litter	D	D		
Achillea millefolium			CR/CSR	15.3
Agrostis stolonifera		D	CR	7.0
Anisantha sterilis		-	R/CR	6.7
Anthriscus sylvestris	I		CR	4.2
Arrhenatherum elatius	I		C/CSR	16.0
Avenula pubescens		-	S/CSR	10.1
Brachypodium pinnatum	-	D	SC	2.5
Bromopsis erecta		D	SC/CSR	22.6
Centaurea nigra	-	D	S/CSR	3.7
Cirsium arvense	D	I	C	3.1
Convolvulus arvensis	D		CR	3.2
Cruciata laevipes	D		CSR	
Dactylis glomerata			C/CSR	8.7
Elytrigia repens	D	D	C/CR	24.2
Festuca arundinacea	I		CSR	
Festuca rubra		D	CSR	13.9
Galium aparine	D		CR	2.6
Galium verum	I		SC/CSR	3.9
Glechoma hederacea	D	D	CSR	1.7
Heracleum sphondylium		D	CR	3.8
Hypericum perforatum	-	D	CSR	1.2
Knautia arvensis	I		CSR	9.8
Lolium perenne	I	I	CR/CSR	9.9
Odontites verna	I	I	R/CSR	
Phleum bertolonii	I		CSR	
Plantago lanceolata	I	I	CSR	2.4
Poa pratensis	D	D	CSR	10.8
Poa trivialis			CR/CSR	
Potentilla reptans			CR/CSR	
Ranunculus repens	I	I	CR	22.4
Rumex sp			CSR	3.3
Stachys sylvatica	D		C/CR	1.6
Taraxacum officinale		I	R/CSR	2.6
Tragopogon pratensis	-		CR/CSR	
Trifolium pratense		I	CSR	1.3
Trifolium repens			CR/CSR	3.1
Trisetum flavescens		-	CSR	4.7
Ulmus glabra			SC	2.1
Urtica dioica	D	D	C	3.1
Veronica chamaedrys			S/CSR	3.1
Vicia sativa	I		R/CSR	9.4
Viola hirta			S	

CHAPTER 3 CLIMATE AND VEGETATION RELATIONSHIPS: INDIVIDUAL WEATHER VARIABLES

3.1 Introduction

3.2 The First Bibury Analysis (1958-1992)

3.2.1 Methods

3.2.2 Results 1958-1992
- (i) Significance of the results
- (ii) Plant-Weather Relationships
- (iii) Plant Functional Types and Weather

3.2.3 Problems with the first analysis of the Bibury data.

3.3 The Second Bibury Analysis (1959-1994)

3.3.1 Methods

3.3.2 Results
- (i) Plant-Weather Relationships
- (ii) Plant Functional Types and Weather

3.4 Discussion

3.1 INTRODUCTION

The principal aim of the analysis of the Bibury field records presented in this thesis was to establish whether relationships could be detected between climate and plant performance in the vegetation of the road verges, and, if so, to what extent these relationships may occur. As has been shown in Chapter 2, detailed records of year-on-year fluctuations in above-ground biomass are available for 42 of the most common species at Bibury, together with estimates of litter and bare ground, and these records can be amalgamated into composite groupings to represent different functional types, life histories, or any other desired categories.

One of the most straight-forward methods for investigating whether relationships exist between the performance of these species or species groupings over any given time-period is to compare the biological time-series with meteorological time-series over the same period and look for statistically significant correlations. This basic approach has been adopted for a number of long-term studies, perhaps most notably in the work of Watt in studies of grassland in Breckland (Watt, 1971), and has also been used for studies of animal population dynamics and weather, for example with butterflies (Pollard, 1988). It is also the method used in the first major analysis of the Bibury field records (Hunt *et al.* 1992, Grime *et al.* 1994).

The first Bibury analysis compared plant performance with a range of basic meteorological variables over the period 1958-1992. The results of this analysis are briefly discussed below. In 1994/1995 the analysis was carried out again, for several reasons:

1. To bring the analysis up to date.
2. To gain more detailed information on plant/climate relationships.
3. To correct a basic flaw in the original analysis.

Firstly, the methods and a summary of the results of the first Bibury analysis, performed in 1991/92 by Dr Rod Hunt of the Unit of Comparative Plant Ecology, University of Sheffield, is presented. Secondly, the methods and results of the 1994/95 analysis are presented, and finally, both sets of results are discussed.

3.2 THE FIRST BIBURY ANALYSIS (1958-1992)

3.2.1 METHODS

The **plant data** from Bibury were converted to de-trended or flat-trended time-series as described in the previous chapter. Data from the MH and 2,4-D series were treated separately. **Meteorological data** were obtained from nearby RAF Lyneham. The following variables were used: maximum temperature (°C), minimum temperature (°C), mean temperature (°C), sunshine (h) and rainfall (mm). The data as supplied took the form of monthly means of daily maximum and minimum temperature and sunshine hours, and monthly values of total rainfall. To avoid over-complication, seasonal means were compiled from the monthly values. For this analysis, two six-monthly seasonal means were calculated: Winter (September - February) and Summer (March - August). The meteorological data showed no long-term trends and were therefore flat-trended prior to the analysis. More information on the meteorological data is given in section 3.2.3.

The residuals about the flat- or de-trended thirty-five year means of log biomass of individual species were correlated with the residuals about the 35 year means of the six-monthly meteorological variables. To account for possible lag effects in the vegetation, plant records were correlated with meteorological data in the year immediately preceding vegetation recording, with the year before that, and the year before that - lags of 0, 1, and 2 years were therefore incorporated. In each year plant records are collected in July; therefore mean values for meteorological data for the first summer were compiled from data for March - July rather than March - August. Product-moment correlations were tested for significance at $P < 0.05$.

3.2.2 RESULTS 1958-1992

(i) Significance of the results

In all, 46 taxa, two different vegetation series, and 5 weather variables over a three-year period were entered into the analysis. The maximum possible number of correlations expected from a matrix of 46 x 2 x 5 x 3 is 2760. At $P < 0.05$, this data-set might be expected to yield 138 correlations purely by chance. In fact, 150 were observed, 10% more than expected. Moreover, the distributions of correlations per taxon was markedly different from that expected: more taxa than expected had no correlations at all, fewer taxa than expected had one or two correlations each, and more than expected had five or more correlations. Such evidence suggests markedly non-random weather-plant relationships in the Bibury road verges (Hunt *et al.* 1992).

(ii)Plant-Weather Relationships

Full results are given by Hunt *et al.* (1992), and are not reproduced here. It is clear, however, that some species correlate with summer weather variables and some with winter variables, some with the current year's conditions and some with those of the previous year, or even to the year before that (Hunt *et al.*1992).

This analysis, involving 46 taxa, two different vegetation series, and five weather variables over three years, required some simplification or summary of the results. This was achieved by describing the summer or winter seasons as either 'good' or 'bad', according to the predominant type of weather that they contained, and classifying taxa by their responses to such seasons. It is apparent that, although for this analysis, different weather variables were treated as independent, they are related. For example, a dry summer is also likely to be a sunny summer, and therefore a warm summer. By grouping weather variables into recognisable types or 'families', seasons can be typified according to the type of weather they contain. Seasons were defined anthropocentrically - those exhibiting above-average means of daily maximum temperature and/or minimum temperature, and/or daily sunshine hours, and/or below average means of monthly rainfall were defined as 'good' and the opposite as 'bad' (Hunt *et al.* 1992, Grime *et al.* 1994)

Taxa showing a positive correlation with 'good' seasons (i.e seasons exhibiting any or all of the above) can be interpreted as being promoted by such conditions; taxa with negative correlations can be interpreted as being retarded. In cases of conflict, recent periods within the time series were weighted more heavily than distant ones and where this produced no consistent result the outcome was classified as 'complex'.

The results of this summary are given in Table 3.1. There are four possible response groups: those promoted by good summers and winters and those retarded by good summers and winters. Examples of all four possible responses exist within the data set.

(iii)Plant functional types and weather

Details of primary plant functional types, and predictions of their performance with regard to weather are presented in Chapter 2. The summary of their responses between 1958 and 1992 to 'good' summers and winters is shown in table 3.2.

Table 3.1. Summary of responses to climate (from Hunt *et al.* (1992). An single asterisk indicates a response in either vegetation series 1-6 or 7 & 8. Two asterisks indicate the same response in both series. A complex effect indicates inconsistencies within the same vegetation series, or conflicting results between the two series.

	Good Summers		Good Winters		Complex effects	Few or no effects
	+	-	+	-		
Bare ground		*				
Litter						*
Achillea millefolium	*					
Agrostis stolonifera			**			
Anisantha sterilis				*		
Anthriscus sylvestris						*
Arrhenatherum elatius						*
Avenula pubescens						*
Brachypodium pinnatum	*					
Bromopsis erecta		*		*		
Centaurea nigra	*					
Cirsium arvense			**			
Convolvulus arvensis		*	*			
Cruciata laevipes						*
Dactylis glomerata		*				
Elytrigia repens						*
Festuca arundinacea				*		
Festuca rubra				*		
Galium aparine		*		*		
Galium verum				*		
Glechoma hederacea		*	*		*	
Heracleum sphondylium		**		*		
Hypericum perforatum					*	
Knautia arvensis				*		
Lolium perenne						*
Odontites verna	*					
Phleum bertolonii				*		
Plantago lanceolata	*		*			
Poa pratensis					**	
Poa trivialis						*
Potentilla reptans	*					
Ranunculus repens		*	*			
Rumex sp	*					
Stachys sylvatica	*					
Taraxacum officinale	*					
Tragopogon pratensis						*
Trifolium pratense	*		*			
Trifolium repens		**				
Trisetum flavescens		*				
Ulmus glabra				*		
Urtica dioica						*
Veronica chamaedrys		*		*		
Vicia sativa	*		*			
Viola hirta			*			

Table 3.2 Summary of responses of primary plant functional types to climate. (from Hunt *et al.* (1992)).

	Good Summers		Good Winters		Complex effects	Few or no effects
	+	-	+	-		
C		*	*			
S	*					
R	*					
CR						*
CS			*			
CSR			*			
(SR n/a)						

3.2.3 Problems with the first analysis of the Bibury data.

Although the first Bibury analysis provided an initial picture of plant-weather relationships in the Bibury road verges, a number of problems with the details of the techniques employed became apparent. These problems were:

1. **Six-month seasonal averages.** Plant performance was correlated against six-month seasonal means for weather data: September to February for Winter and March to August for summer. While these means may allow very general statements to be made about plant/weather relationships, a more detailed analysis, using three-month means might add extra information. Certain species may have critical periods of the year in which they are particularly sensitive to weather and these may not be revealed by the use of six-month means alone. A further reason for carrying out a more detailed analysis is that the experiments described in the second part of this thesis required information on species relationships with weather variables over shorter periods than six months.

2. **'Good' winters and summers.** As described above, good seasons were defined as those seasons which exhibited above-average means of daily maximum

temperature and/or daily minimum temperature and/or daily sunshine hours and/or below average means of monthly rainfall. The implicit assumption is that temperature is positively correlated with sunshine and negatively correlated with rainfall. While this is clearly logical for summer (hot summers also tend to be relatively sunny and dry), it does not necessarily hold for winter. Winters exhibiting above average temperatures (i.e mild winters) would logically show the converse: being wetter and cloudier than cold winters. To establish precise relationships between weather variables at different seasons, weather variables from RAF Lyneham were correlated with each other for the period 1958 to 1994 for autumn, winter, spring, summer, and for autumn and winter combined and spring and summer combined.

The results are shown in Table 3.3 and do not match the simple model of 'good' winters and summers. In summer, maximum temperature is positively correlated with sunshine and negatively correlated with rainfall. However in winter both maximum temperature and minimum temperature are positively correlated with rainfall. In autumn, sunshine is positively correlated with maximum temperature, but there is no significant correlation between temperature and rainfall. In spring, maximum temperature is positively correlated with sunshine and negatively correlated with rainfall. On the other hand, minimum temperature is negatively correlated with sunshine.

The results indicate that winter and summer show clear and consistent relationships, both positive and negative, between the various weather variables. However, spring and autumn appear to share the characteristics of each and are in some ways transitional between the absolutes of summer and winter. In spring, above average sunshine hours tend to be associated with higher daytime temperatures (maximum temperature) and lower nighttime temperatures (minimum temperatures). This is consistent with fine weather in spring being associated with warm days and frosty nights.

Table 3.3 Correlation matrices for weather variables from RAF Lyneham for the period 1958 - 1994 for autumn, winter, spring, summer, and for autumn and winter combined and spring and summer combined. Seasonal mean weather variables are compiled from mean daily maximum temperature, mean daily minimum temperature, mean daily sunshine hours and mean monthly rainfall values. P = positive correlation, N = negative correlation. *P<0.05, **P<0.01, ***P<0.001.

AUTUMN

	MAX	MIN	SUN	RAIN
MAX	▨	P***	P**	
MIN	▨	▨		
SUN	▨	▨	▨	N***
RAIN	▨	▨	▨	▨

WINTER

	MAX	MIN	SUN	RAIN
MAX	▨	P***		P*
MIN	▨	▨		P*
SUN	▨	▨	▨	N***
RAIN	▨	▨	▨	▨

SPRING

	MAX	MIN	SUN	RAIN
MAX	▨	P***	P*	N*
MIN	▨	▨		
SUN	▨	▨	▨	N***
RAIN	▨	▨	▨	▨

SUMMER

	MAX	MIN	SUN	RAIN
MAX	▨	P***	P***	N***
MIN	▨	▨		
SUN	▨	▨	▨	N***
RAIN	▨	▨	▨	▨

AUTUMN & WINTER

	MAX	MIN	SUN	RAIN
MAX	▨	P**		
MIN	▨	▨		
SUN	▨	▨	▨	
RAIN	▨	▨	▨	▨

SPRING & SUMMER

	MAX	MIN	SUN	RAIN
MAX	▨	P*	P***	N**
MIN	▨	▨		
SUN	▨	▨	▨	N***
RAIN	▨	▨	▨	▨

The results for spring and summer combined reflect those of summer alone. However, for autumn and winter there are no significant relationships between temperature, rainfall and sunshine. For both spring and summer combined and for autumn and winter combined, minimum temperature shows no significant relationship with any other weather variable.

Two major conclusions can be drawn from this analysis of relationships between different weather variables:

1. A number of species have been wrongly classified in the original analysis. For example, *Anisantha sterilis* is classified as being retarded by good winters on the basis of a negative relationship with winter sunshine hours. However, according to the actual weather relationships, a negative correlation with winter sunshine hours can be interpreted as being favoured by cloudier, milder winters and the species should therefore be regarded as being promoted by good winters.

2. While the revised method of analysis produces much valuable information regarding species performance and weather, some caution must be exercised in interpreting the results, particularly for relationships between plant performance and weather in spring and autumn, and autumn and winter combined.

3.3 ANALYSIS OF PLANT WEATHER RELATIONSHIPS 1959-1994.

With full regard to the limitations discussed above, a second seasonal analysis of the Bibury data was performed using vegetation records up to 1994. Vegetation data from 1958 were not used because total vegetation bulk values had not been recorded for that year and therefore estimates of individual species biomass could not be made for that year.

3.3.1 METHODS

Plant scores were converted to biomass values and the time-series were de-trended or flat-trended according to the methods discussed in Chapter 2. Forty-four variables were included in the analysis: 42 plant species, bare ground and litter. The two bryophytes included in the first analysis were omitted.

Weather data were extracted from the Meteorological Office monthly weather bulletins for 1956-1991 (Meteorological Office, 1956-1991), and supplied direct from the Met Office for 1992-1994. The same variables were used as in the first analysis; however mean temperature was omitted because it did not add any additional dimension to the analysis; it being simply a function of maximum and minimum temperature. An additional variable was used: rain days. Although total rainfall for a particular period shows the total amount of rain to fall, it gives no indication of the spread of that rainfall over the period. The additional rainfall information was used to test the hypothesis that vegetation is likely to respond to the frequency of rainfall events over a period as much as to the total amount. Two possible measures of rain days could be used. Firstly, the number of days in each month with measurable rain (0.2 mm or more). This, however, represents little more than 10 minutes of normal light rainfall (Wallen 1970). Secondly, the total number of 'Wet days' in each month (those on which 1.0 mm or more rain falls). This second category was used in the Bibury analysis.

Three-monthly means of weather variables were calculated for Winter (December-February), Spring (March-May), Summer (June-August) and Autumn (September - November). Six-monthly means were also calculated as described in section 3.2.1. As in the first analysis, plant performance was compared with seasonal means of weather variables for the current year, the previous year and the year before that. For the summer of the current year, weather data from June and July only were used because vegetation recording occurs in late July and therefore August data are not relevant.

3.3.2 RESULTS

(i) Plant/Weather relationships

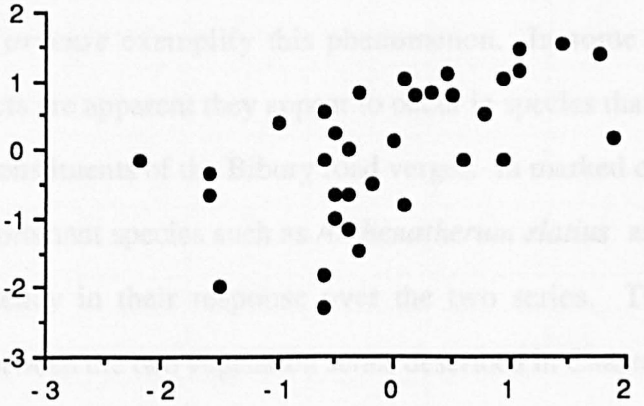
The full results of the analysis are provided in Appendix 2. Positive and negative relationships were identified for 44 Bibury taxa with five basic weather variables over three and six month periods, and for two vegetation series. Again, approximately 10% more correlations than expected to occur by chance were observed. A larger number of significant correlations were observed with respect to rain days than total rainfall. However, use of both variables provided information that was not obtained using one or the other alone.

The more detailed information obtained can be used to produce 'profiles' of individual species and their response to climate. Such a profile is illustrated for *Dactylis glomerata* in Table 3.4. The relationship between *Dactylis glomerata* and minimum temperature in spring is illustrated graphically in Figure 3.2.

Table 3.4. Weather profile for *Dactylis glomerata*. Years 0,-1 and -2 refer to the current year in which vegetation recording occurred, the previous year, and the year before that respectively. Shaded boxes indicate a significant correlation (p=0.05) between plant performance and the weather variable concerned in the season indicated. P and N refer to positive or negative correlations respectively.

	YEAR -2				YEAR -1				YEAR 0			
	AU	WI	SP	SU	AU	WI	SP	SU	AU	WI	SP	SU
MINIMUM TEMP	N	N		N							P	
MAXIMUM TEMP		N		N				N			P	
SUNSHINE				N								
RAINFALL (TOT)				P								
RAINFALL (DAYS)				P								P

Figure 3.2 The relationship between minimum spring temperature and performance of *Dactylis glomerata* (1959-1994) The time series for both minimum Spring temperatures (x-axis) and log mean biomass of *Dactylis* (y-axis) have been converted to standardised units with zero mean and unit variance. r=0.551, P<0.001.



Dactylis clearly responds to summer weather, its biomass being negatively correlated with summer temperatures and sunshine hours, and positively correlated with summer rainfall. It can therefore be classified as being retarded by 'good' summers. The species is promoted by warmer springs and would also appear to be promoted by cold winters.

Similar profiles can be constructed for all 44 taxa included in the analysis from the data in Appendix 2. Predictions of species performance based upon such profiles are tested in the second part of this thesis.

The large amount of information contained in Appendix 2 was simplified into plant responses to 'good' seasons. With reference to Figure 3.3, 'good' autumns and winters were recognised as those associated with above average values for minimum and maximum temperatures and rainfall, and below average sunshine. 'Good' springs and summers were regarded as those which are associated with above average mean values for temperature and sunshine and below average mean values for rainfall. Tables 3.5 and 3.6 list the summarised results for the Bibury series 1-6 and 7-8.

As in the first analysis, there are a number of instances where the plant/weather relationships can be described as complex; in that the same species shows different responses in the same season in the two sets of plots. *Bromopsis erecta, Festuca rubra* and *Cirsium arvense* exemplify this phenomenon. In some instances where such complex effects are apparent they appear to occur in species that could be described as subordinate constituents of the Bibury road verges. In marked contrast it is interesting to note that dominant species such as *Arrhenatherum elatius* and *Dactylis glomerata* show consistency in their response over the two series. This may be linked to differences between the two vegetation series described in Chapter 2. The vegetation in series 1-6 is less species-rich and is dominated by the robust and vigorous grasses *Arrhenatherum elatius* and *Dactylis glomerata.* It is reasonable to assume that the vegetation dynamics of such vegetation may be different from that of the more open, species-rich vegetation of series 7-8. The performance of subordinate species in series 1-6 may be affected indirectly by the performance of the dominants to a greater extent than in series 7-8. These possible differences will be discussed at greater length and tested in the second part of this thesis.

Table 3.5 Plant/Weather relationships for Bibury species: series 1-6. P = Positive correlation, N = Negative correlation.

	'Good' Autumn	'Good' Winter	'Good' Spring	'Good' Summer	'Good' Autumn & Winter	'Good' Spring & Summer
Bare ground		P			P	
Litter	P		P	P		P
Achillea millefolium			P			
Agrostis stolonifera		P	P		P	
Alopecurus pratensis	N	P			N	
Anisantha sterilis		P		P		P
Anthriscus sylvestris						
Arrhenatherum elatius	P		P			P
Avenula pubescens						
Brachypodium pinnatum						
Bromopsis erecta	P	N	N	N	N	N
Centaurea nigra						
Cirsium arvense	N	P	P	N		
Convolvulus arvensis			P			
Cruciata laevipes			P			
Dactylis glomerata		N	P	N	N	N
Elytrigia repens	N					
Festuca arundinacea	P		N	P	P	P
Festuca rubra		N	N		N	N
Galium aparine				N		N
Galium verum			N		N	
Glechoma hederacea	N	N		N	N	N
Heracleum sphondylium						
Hypericum perforatum		N				
Knautia arvensis				N		
Lolium perenne						
Odontites verna			P		N	P
Phleum bertolonii	N	P	P	P		P
Plantago lanceolata	P					
Poa pratensis	N	P			N	
Poa trivialis						
Potentilla reptans		N				
Ranunculus repens			P	N		N
Rumex sp		P				
Stachys sylvatica		P	P			
Taraxacum officinale			P	P	P	P
Tragopogon pratensis						P
Trifolium pratense			P			P
Trifolium repens				N		N
Trisetum flavescens	N					N
Ulmus glabra						
Urtica dioica						
Veronica chamaedrys		N	P			
Vicia sativa			N			P
Viola hirta			N			

Table 3.5 Plant/Weather relationships for Bibury species: series 7-8. P = Positive correlation, N = Negative correlation. * = Complex result.

	'Good' Autumn	'Good' Winter	'Good' Spring	'Good' Summer	'Good' Autumn & Winter	'Good' Spring & Summer
Bare ground		P			P	
Litter					N	
Achillea millefolium	p			P		P
Agrostis stolonifera		P	N		P	
Alopecurus pratensis						
Anisantha sterilis						
Anthriscus sylvestris				*		
Arrhenatherum elatius		P	P			P
Avenula pubescens	N	P				
Brachypodium pinnatum						
Bromopsis erecta	N		N	P	N	P
Centaurea nigra			P			P
Cirsium arvense				P		P
Convolvulus arvensis	P	P	P	P	P	
Cruciata laevipes	N	N	N			N
Dactylis glomerata		N	P	N		P
Elytrigia repens				P	P	P
Festuca arundinacea			P			
Festuca rubra	N	P	P	P	P	P
Galium aparine						
Galium verum			N			N
Glechoma hederacea		P	P			
Heracleum sphondylium	N	N	P		N	
Hypericum perforatum						
Knautia arvensis		N	P			N
Lolium perenne			N			p
Odontites verna						
Phleum bertolonii						
Plantago lanceolata		P	P	P	P	P
Poa pratensis		P	N			
Poa trivialis						
Potentilla reptans			P		N	P
Ranunculus repens	N	P	P		P	P
Rumex sp		P	P	P	P	P
Stachys sylvatica		P			p	
Taraxacum officinale		P	P	P		
Tragopogon pratensis				N		
Trifolium pratense						P
Trifolium repens	N	P				
Trisetum flavescens						
Ulmus glabra						
Urtica dioica						
Veronica chamaedrys	P	P	P		P	P
Vicia sativa		N	P	P	P	P
Viola hirta						

The second, more detailed analysis has added extra information on species performance to that reported in the first analysis. The same general conclusions can be made about species relationships with climate for both the first and second Bibury analysis. Several deep-rooted species such as *Achillea millefolium, Cirsium arvense* and *Taraxacum officinale* are promoted by 'good' summers. Such species are presumably able to tap moisture at lower levels in the soil during periods of dry weather. Other species such as *Dactylis glomerata* (fig 3.2), *Bromopsis erecta* and *Trisetum flavescens* are retarded by good summers. Some species such as *Cirsium arvense, Poa pratensis* and *Arrhenatherum elatius* may be promoted by good winters, as is the amount of bare ground (the suggested promotion of bare ground by 'good' winters is discussed in greater length in Chapter 6). Species retarded by good winters include *Festuca rubra* and *Bromopsis erecta,* as is the amount of litter.

(ii) Plant functional types and weather

As in the first Bibury analysis, the performance of primary plant functional types (*Sensu* Grime, 1974) was correlated with the same weather variables discussed in Section 3.3.1. In addition, the total vegetation biomass was also correlated with the various weather variables. The full results of this analysis are contained in Appendix 3. In all, six functional types, and total biomass in two vegetation series, were correlated with five weather variables for four seasons over three years. Forty-two significant correlations would be expected to occur by chance. Twenty-one correlations would be expected by chance for autumn and winter, and spring and summer combined. Fifty-two correlations were actually observed with individual seasons and 29 for the combined seasons.

The results in Appendix 3 have been summarised using the method described in Section 3.2.2 and are shown in Tables 3.6 and 3.7.

Table 3.6 Response of functional types to 'good' seasons for vegetation series 1-6. P and N as in Table 3.5

	'Good' Autumn	'Good' Winter	'Good' Spring	'Good' Summer	'Good' Autumn & Winter	'Good' Spring & Summer
C			P	N		N
S			P		N	P
R				P		P
CR			P			P
CS	P	N		N	N	N
CSR			N			N
ALL			P	N		N

Table 3.7 Response of functional types to 'good' seasons for vegetation series 7-8. P and N as in Table 3.5

	Good Autumn	Good Winter	Good Spring	Good Summer	Good Autumn & Winter	Good Spring & Summer
C						
S			P	P		P
R			P			
CR	N		N		N	
CS	N	P	N		P	
CSR		P		N		P
ALL		N	N	N	N	N

3.4 DISCUSSION

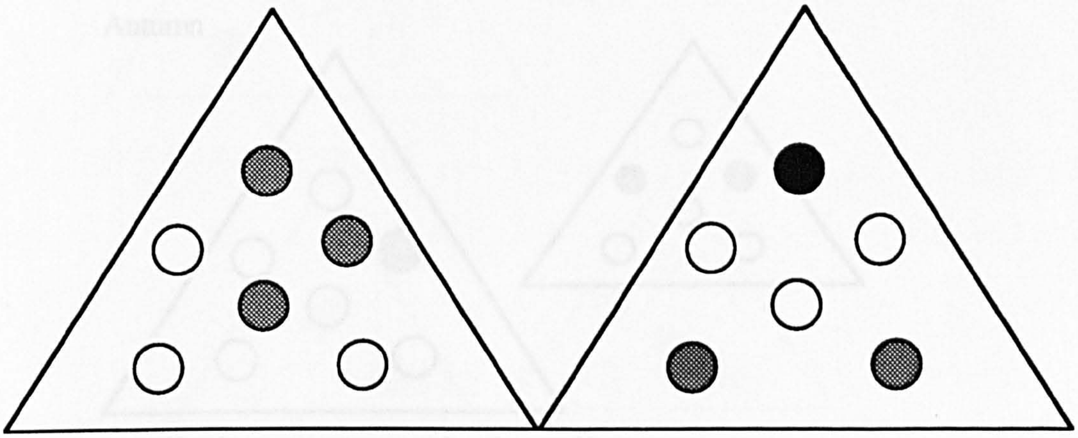
The increased number of correlations observed with weather for both individual species and functional groups in comparison with those expected to occur by chance provides clear evidence of non-random plant/weather relationships in the Bibury vegetation.

The correlations of individual weather variables with each other presented in Table 3.3 suggest that the original classification of Bibury species with respect to their weather responses at different seasons was incomplete and partially incorrect. The results from the second analysis, using data from 1959-1994, were used to compile species and functional type summaries based upon the actual relationships observed between weather variables. Although this resulted in re-classification of certain species; a similar overall pattern remained. The 1959-1994 species classification has been used as the basis for analyis of plant/weather relationships in subsequent chapters.

The original results (1958-1992) presented in Table 3.2 are depicted diagrammatically in Figure 3.3. They are based upon the triangle matrix described in Appendix 1. 'Good' (mild) winters tend to promote species conforming to the competitive strategy by effectively extending the growing season, thereby apparently allowing greater biomass production by these large, often clonal perennials. Conversely, 'good' (hot, dry) summers tend to retard the C-strategists, while at the same time promoting the ruderals and stress tolerators; both functional types which may be expected to benefit from the stress and disturbance caused by drought conditions.

Figure 3.3 Summary of responses of plant functional types to climate (1958-1992). From Hunt *et al.* (1992)

○ = No Response ◍ = Positive Response ● = Negative Response



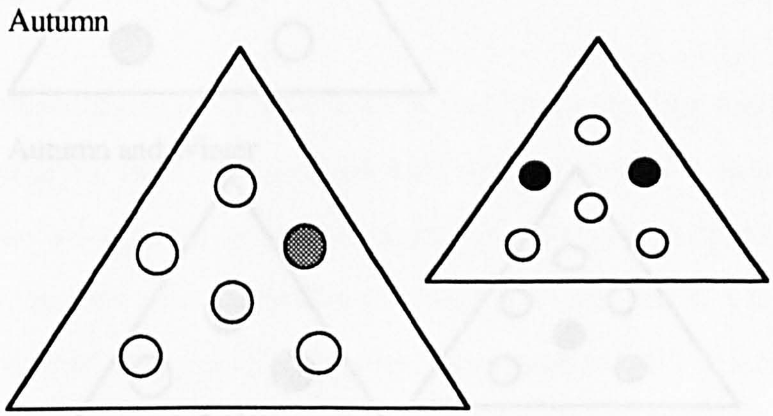
(i) 'Good' Winters

(ii) 'Good' Summers

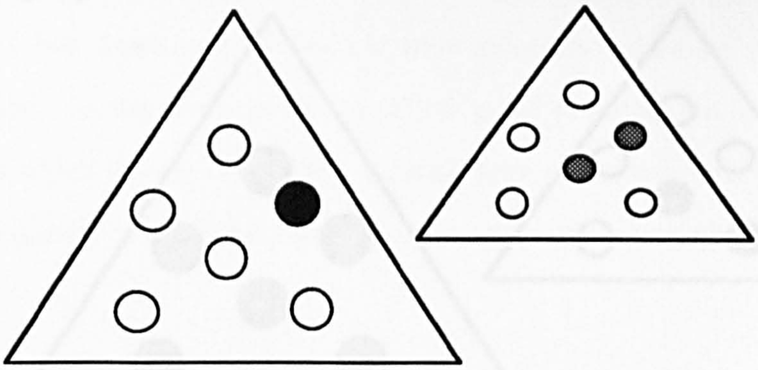
The results from the second analysis (1959-1994) shown in Tables 3.6 and 3.7 support the above model and add new information. There is no indication in this analysis of competitor strategists being promoted by 'good' winters. However, stress-tolerant species are seen to be retarded by 'good' winters and this may be as a result of competitive exclusion by the promoted competitors. Competitors are seen to be promoted by 'good', warm springs. Such species may be expected to benefit most from such favourable growing conditions in spring; again an extended growing season appears to favour competitors. Conversely, 'good' summer conditions retard competitive species. As distinct from spring, where fine weather may not necessarily be associated with moisture stress, fine weather in summer is more likely to impose unsuitable growing conditions for competitive species. Stress-tolerant species and ruderal species are still seen to be promoted by good summers. The results for individual seasons for both vegetation series are shown in Figure 3.4.

Figure 3.4 The response of Plant Functional Types to Climate in Individual Seasons for Vegetation Series 1-6 and 7-8 Large triangles show results for vegetation series 1-6. Small triangles show results for vegetation series 7&8.

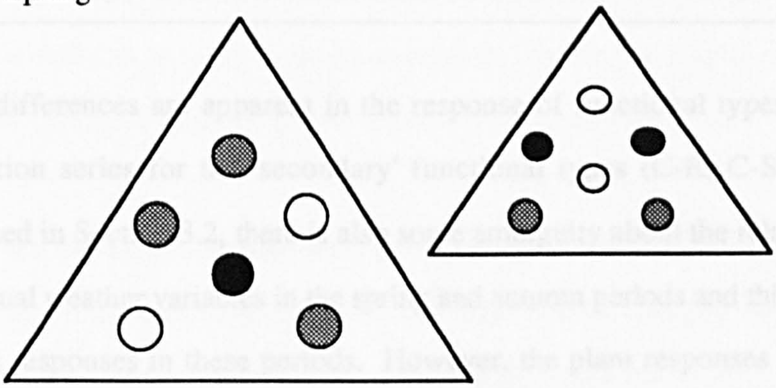
○ = No Response ◍ = Positive Response ● = Negative Response



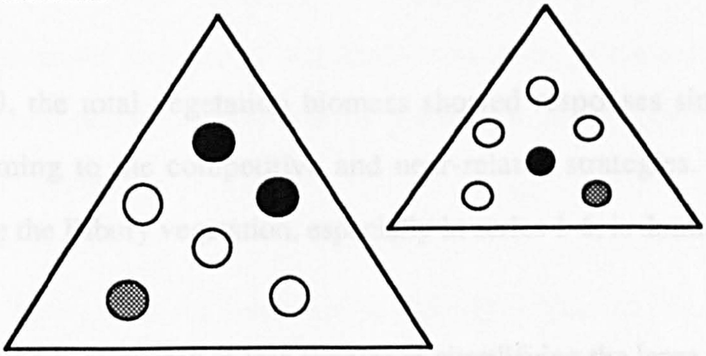
Winter



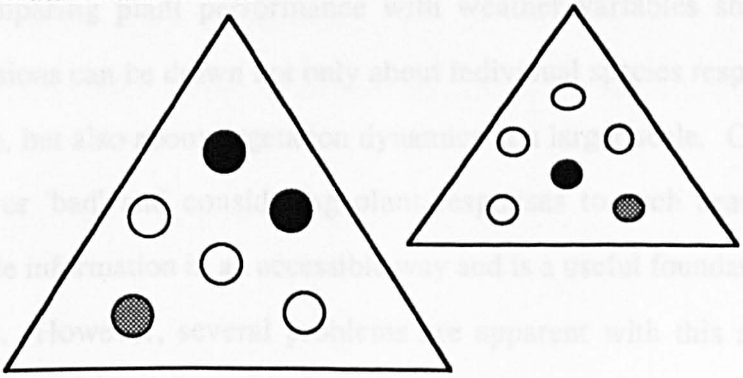
Spring



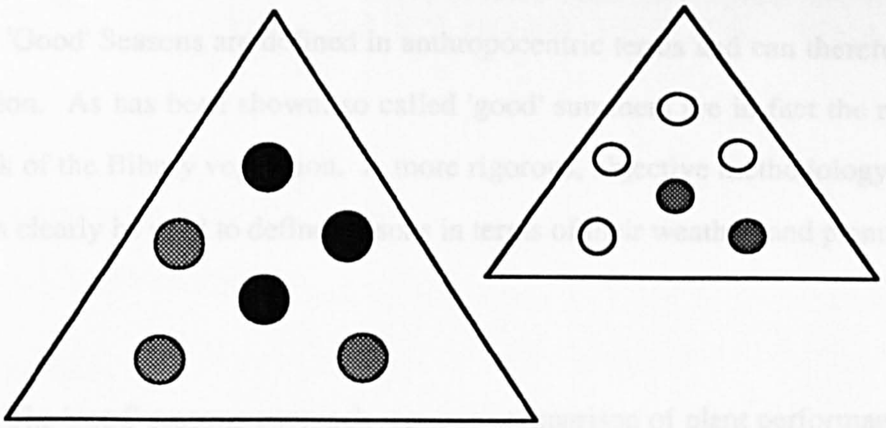
Summer



Autumn and Winter



Spring and Summer



Some differences are apparent in the response of functional types between the two vegetation series for the 'secondary' functional types (C-R, C-S and C-S-R). As discussed in Section 3.2, there is also some ambiguity about the relationships between individual weather variables in the spring and autumn periods and this is reflected in the species responses in these periods. However, the plant responses for the winter and spring and summer periods support the original model shown in figure 3.3.

Overall, the total vegetation biomass showed responses similar to those of plants conforming to the competitive and near-related strategies. This is not surprising because the Bibury vegetation, especially in series 1-6, is dominated by such plants.

The methods discussed in this chapter of simplifying the large amount of data obtained by comparing plant performance with weather variables show that meaningful conclusions can be drawn not only about individual species responses to weather and climate, but also about vegetation dynamics at a larger scale. Classifying seasons as 'good' or 'bad' and considering plant responses to such seasons provides much valuable information in an accessible way and is a useful foundation for more detailed studies. However, several problems are apparent with this approach that justify enquiry into other methods of classifying plant response to weather and which can be used to build upon the foundation presented in this chapter. These problems include:

1. 'Good' Seasons are defined in anthropocentric terms and can therefore lead to confusion. As has been shown, so called 'good' summers are in fact the reverse for the bulk of the Bibury vegetation. A more rigorous, objective methodology is needed that can clearly be used to define seasons in terms of their weather, and plant responses to it.

2. The 'good' seasons approach requires comparison of plant performance with at least five different weather variables to produce meaningful results. A system would be desirable that can be used to define seasons with fewer variables.

3. As has been demonstrated, the 'good' seasons approach does not necessarily accord with the meteorological facts. The relationships between weather variables that provide the theoretical basis for this approach are not in reality very clear and appear to hold to a statistically significant level only in summer. Weather relationships in spring and autumn are ambiguous and appear transitional between summer and winter. A more robust definition of seasons is needed that accords more directly with observed weather variables.

4. Biological time series are invariably subject to auto-correlation (Legendre, 1993), a statistical phenomenon that potentially reduces the significance of relationships observed between different time-series. A rigorous analysis of plant/weather relationships needs to account for auto-correlation.

All of these problems are addressed in Chapter 4.

CHAPTER 4. PLANT/WEATHER RELATIONSHIPS IN THE BIBURY ROAD VERGES: WEATHER TYPES

4.1 INTRODUCTION

A number of shortcomings in the 'good' and 'bad' seasons approach to classifying species' response to weather were identified in Chapter 3. These included a lack of clear, statistically significant relationships between weather variables at certain times of the year, a reliance on a large number of weather variables for the complete analysis, and a lack of clearly defined, rigorous terms for defining weather in different seasons.

A method that classifies weather in different seasons simply and which has real meteorological meaning would be preferable. An approach that, rather than considering individual weather variables, deals instead with the large-scale weather systems that dictate the characteristics of those individual weather variables would also be desirable. The weather types approach provides such a basis. Good summers (hot, dry, sunny summers) can be clearly equated with a predominance of settled or anti-cyclonic weather in such summers. Good winters (mild, wet, cloudy) can be clearly equated with a lack of settled or anti-cyclonic weather in such seasons. A method that provides a quantifiable measure of anti-cyclonic or other weather types in a given season would allow a more objective classification of species' responses to climate. An additional advantage is that seasons defined in precise meteorological terms would have greater value in predicting vegetation response to changing climate.

One previous study has used such an approach. Aebisher *et al.* (1988) compared the relationship between abundance of organisms at different trophic levels in the Atlantic Ocean over the period 1955 - 1987 with the annual frequency of Westerly weather. Striking similarities were apparent between the frequency of westerly weather and biological abundance, although no causal mechanisms were suggested or put forward.

The work described in this chapter investigates the possibilities of applying such an approach to the Bibury data-set, and the advantages and disadvantages of the technique in relation to the 'good' season approach is discussed.

4.1.2 Weather types

Much of the character of the British weather and climate is related to the direction, nature and persistence of the wind direction. Different wind directions produce different types of weather, which vary in character according to the season (Musk, 1988).

The weather of Britain can be classified into different weather types according to wind direction. A weather type is a definable entity that often lasts for several days whilst the weather undergoes variations typical of the succession of airmasses and depression tracks occurring with that prevailing wind direction and general type of weather sequence or spell (Lamb, 1964). Weather types may persist for a period of time and help shape the character of individual seasons (Musk 1988). The weather on almost any day can be classified according to a weather type or hybrids between compatible weather types.

Twenty-seven weather types have been identified in all and these are usually condensed into seven major weather types: five are directional (westerly, north-westerly, northerly, easterly and southerly) and two are used when a synoptic system dominates the region (anticyclonic and cyclonic). Hybrids between the different types are possible and are recognised when two or three of the types defined above are combined. Examination of daily synoptic charts for the British Isles enables individual days to be classified according to these weather types. Lamb's classification of daily circulation patterns over the British Isles has been used extensively in studies of the climate of the British Isles (Jones and Kelly 1982). The scheme is to a certain extent subjective, but has recently been compared with an objective classification scheme based upon mean sea-level pressure and the two schemes were found to be highly correlated (Jones *et al.* 1993). A study of the frequency of the different weather types over the hundred year period 1871-1971 showed that the anticyclonic and westerly types occurred on approximately 50% of all days, while two days out of three are either westerly, cyclonic or anticyclonic (Lamb 1972).

Because, as shown above, anticyclonic, cyclonic and westerly weather types largely define the character of the weather of the UK, these three types were selected for the analysis described in this chapter. Descriptions of the three types are given below, taken from Lamb (1964):

Anticyclonic type Weather mainly dry with light winds. Thunder, however, often occurs in summer. Usually warm in summer, cold or very cold in winter; mist or fog frequent in autumn.

Cyclonic type Depressions centred over, or frequently passing across, the British Isles. Mainly wet or disturbed weather, with very variable wind directions and strengths. Both gales and thunderstorms may occur. Usually mild in autumn and early winter; cool or cold in spring; cool or cold in summer.

Westerly type Sequences of depressions and ridges of high pressure travelling east across the Atlantic and farther east. Weather in the British Isles generally unsettled or changeable, usually with most rain in northern and western districts and brighter weather in the south and east. Cool in summer, mild in winter with frequent gales.

These descriptions suggest that the weather effects of the anticyclonic type (dry in all seasons, cold in winter, warm in summer) are opposed to the weather effects of the cyclonic and westerly types (wet in all seasons, cool in summer, mild in winter). The two opposites also correspond very closely to the concept of 'good and bad seasons' described in the previous chapter. The effect of the different weather types on the weather at Bibury is investigated in Section 4.2.3.

4.2 METHODS

4.2.1 Vegetation Data

Time-series for the 44 Bibury taxa used in the second Bibury 'good' season analysis were de-trended or flat-trended according to the methods described in Chapter 2, section 3.3.1.

4.2.2 Meteorological Data

Meteorological data were obtained from the Climate Research Unit, University of East Anglia. The data were supplied as numbers of days per month for each of the 27 Lamb weather types. The full list of weather types is given in table 4.1

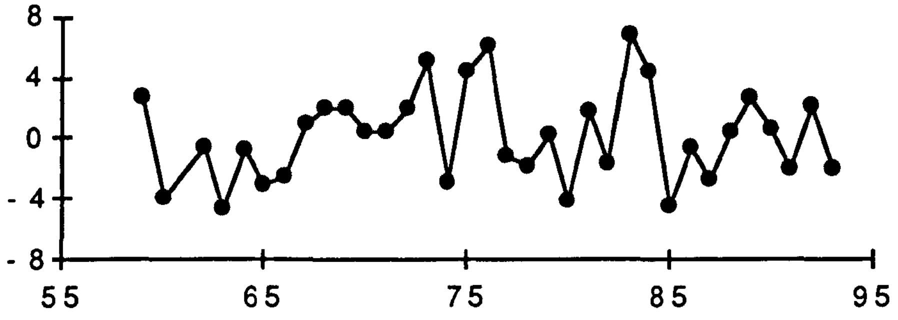
Table 4.1 List of Lamb weather types (from Jones & Keddy 1982)

A,
ANE
AE
ASE
AS
ASW
AW
ANW
AN
NE
E
SE
S
SW
W
NW
N
C
CNE
CE
CSE
CS
CSW
CW
CNW
CN
Unclassifiable

Data were supplied for every day from 1956 to 1993. Monthly totals were calculated for each of the major weather types (the five directional types: Westerly (W), North-westerly (NW), Northerly (N), Easterly (E) and Southerly (S), and the two synoptic types: Anticyclonic (A) and Cyclonic (C)), using Lamb's standard accounting procedures, where a hybrid type counts equally to each of the major types (Jones &

Keddy 1982). For example ASW counts one-third to each of A, S, and W, whereas AS counts one-half to each of A and S. Monthly frequencies for the anti-cyclonic, cyclonic and westerly types were calculated in this way. Seasonal mean frequencies were then compiled for winter, spring, summer and autumn, and for autumn and winter combined and spring and summer combined. The meteorological data were 'flat-trended' and the residuals around their long-term means were used in the analysis with plant performance. An example of one of the meteorological time series is shown in figure 4.1.

Figure 4.1 Flat-trended time series for the frequency of anticyclonic weather in summer (June-August) for 1959-1993. Y-axis = residuals about the long-term mean frequency (number of days per month) of anticyclonic weather in summer. X-axis = year.



4.2.3 Weather types and individual weather variables

The frequency of Lamb weather types for the British Isles at different seasons were compared with weather variables from RAF Lyneham to investigate the effects of the large scale weather types on the local weather at Bibury. The results of this analysis are given in table 4.2.

Table 4.2 Correlations between Lamb weather types and individual weather variables from RAF Lyneham over the period 1959-1993. P = positive correlation. N = negative correlation. Significance: * P<0.05, ** P<0.01, ***P<0.001.

(i) Anticyclonic type

	SUMMER	AUTUMN	WINTER	SPRING	AUTUMN & WINTER	SPRING & SUMMER
Minimum Temperature						
Maximum Temperature	P***			P**		P***
Rainfall	N**	N***	N**	N***	N***	N**
Sunshine	P***	P**		P***	P*	P***
Westerly	N*			N*		N*
Cyclonic	N*	N***	N*	N*	N***	N**

(ii) Westerly type

	SUMMER	AUTUMN	WINTER	SPRING	AUTUMN & WINTER	SPRING & SUMMER
Minimum Temperature			P***		P**	
Maximum Temperature	N*		P***		P***	
Rainfall			P*			
Sunshine						
Cyclonic						

(iii) Cyclonic type

	SUMMER	AUTUMN	WINTER	SPRING	AUTUMN & WINTER	SPRING & SUMMER
Minimum Temperature						
Maximum Temperature						N**
Rainfall	P**	P***	P**	P*	P***	P***
Sunshine	N*	N**			N*	N**

Anti-cyclonic weather is negatively correlated with rainfall in every season, and with sunshine in autumn, spring and summer. It is also positively correlated with temperature in spring and summer. It is negatively correlated with westerly weather in spring and summer, and with cyclonic weather throughout the year.

Westerly weather is positively correlated with temperature in winter and negatively correlated in summer. Westerly weather is also positively correlated with rainfall in winter.

Cyclonic weather is positively correlated with rainfall throughout the year, and negatively correlated with sunshine, and negatively correlated with temperature in spring and summer.

A high frequency of anticyclonic weather in summer can clearly be associated with 'good' summers (hot, dry, sunny summers) and a high frequency in winter is associated with 'bad' winters (dry, and therefore colder, winters). A high frequency of westerly and cyclonic weather is clearly associated with 'good' winters (mild, wet winters) and 'bad' summers (cold and wet).

Both cyclonic and westerly weather are negatively correlated with anticyclonic weather. Between them they can account for both 'good' winters and 'bad' summers. The relationship between individual weather variables and the frequency of both cyclonic and westerly weather combined is shown in Table 4.3. The combined frequency contains all the relationships demonstrated by westerly weather alone, and most of the relationships demonstrated by cyclonic weather alone. The combined index accounts for both 'good' winters and 'bad' summers, and is negatively correlated with anticyclonic weather throughout the year.

Table 4.3. Correlations between the frequency of westerly and cyclonic weather combined and individual weather variables from RAF Lyneham over the period 1959-1993. P = positive correlation. N = negative correlation. Significance: * P<0.05, ** P<0.01, ***P<0.001.

	SUMMER	AUTUMN	WINTER	SPRING	AUTUMN & WINTER	SPRING & SUMMER
Minimum Temperature			P***		P**	
Maximum Temperature	N**		P***	N*	P*	N**
Rainfall	P*	P*	P***	P*	P***	P**
Sunshine	N*	N*				N*
Anticyclonic	N***	N***	N***	N***	N***	N***

4.2.4 Correlation of plant performance and weather types.

De-trended or flat-trended time-series of mean log above-ground biomass for 44 Bibury taxa were correlated with flat-trended data for the anticyclonic, cyclonic, westerly, and westerly and cyclonic types combined for the period 1959-1993 (weather type data were not available for 1994). Correlations were tested at the P=0.05 level. However, for this analysis, full account was taken of temporal autocorrelation. Autocorrelation, and the procedures used to account for it, are described below.

4.2.5 Autocorrelation

Autocorrelation is a very general property of ecological variables, and of all variables observed along time-series. Most ecological observations, both spatial and temporal, are not totally independent of their neighbours. In classical statistical testing, one degree of freedom is counted for each independent observation. However, the problem with autocorrelated data is their lack of independence, i.e. the value of a variable in year *n* is statistically correlated with its value in year *n* +1 (Wigley *et al.* 1985, Legendre, 1993). Therefore corrections have to be made for the number of degrees of freedom that can be counted (Legendre, 1993). Many of the perennial species at Bibury could be expected to show some autocorrelation - i.e. their biomass in one year may have some effect on their biomass in the following year.

The vegetation data used in the Bibury analyses are in the form of residuals around flat-trended or de-trended means. If weather types is present in the residuals it is usually a sign that the original data were autocorrelated. A simple statistic, the Durbin-Watson statistic can be used to test for autocorrelated residuals (Wigley *et al.* 1985). Caution is advised if the value of the Durbin-Watson statistic indicates a statistically significant degree of autocorrelation in the residuals. The Durbin-Watson statistic is:

$$DW = \frac{\Sigma(e_t - e_{t-1})^2}{\Sigma e^2}$$

Where e_t is residual value at time t and e_{t-1} is the residual value at time -1 (Pindyck & Rubinfeld 1981). The significance of the Durbin-Watson statistic can be obtained from standard tables (Pindyck & Rubinfeld 1981).

The time-series for each Bibury species was examined for the presence of autocorrelation using the Durbin-Watson test. The results of the test are shown in Table 4.2. Approximately 75% of all taxa in series 1-6 exhibit statistically significant autocorrelation and approximately 50% in series 7-8. In series 1-6 in particular, the dominant species tend to exhibit autocorrelation. The difference between the two series may be a result of the greater diversity of series 7-8, and a lesser degree of dominance of the vegetation by a few vigorous species.

Table 4.2 **Bibury taxa that do not exhibit statistically significant autocorrelation (1959-1994) in series 1-6 and series 7-8.**

Series 1-6	Series 7-8
Cruciata laevipes	Anthriscus sylvestris
Knautia arvensis	Brachypodium pinnatum
Lolium perenne	Bromopsis erecta
Odontites verna	Cirsium arvense
Phleum bertolonii	Convolvulus arvensis
Poa pratensis	Cruciata laevipes
Rumex sp	Festuca rubra
Taraxacum officinale	Galium aparine
Trifolium pratense	
Trisetum flavescens	Heracleum sphondylium
Viola hirta	Lolium perenne
	Odontites verna
Bare ground	Phleum bertolonii
Competitors	Poa pratensis
	Rumex sp
	Taraxacum officinale
	Tragopogon pratensis
	Trifolium pratense
	Trifolium repens
	Veronica chamaedrys
	Vicia sativa
	Bare ground
	Litter
	Total Biomass
	Ruderals
	Competitive ruderals

In those cases where the degree of weather types present in the vegetation time-series was not found to be statistically significant at P = 0.05, the plant data were compared with the meteorological data using the methods described in Chapter 3. However, where autocorrelation was found to be statistically significant, the number of degrees of freedom that could be used for testing correlations between plant performance and weather was calculated using the formula of Quenouille (Hays *et al.* 1993) Quenouille's formula calculates the effective number of independent observations (*E*) where:

$$E = N/(1 + 2r_1r'_1 + 2r_2r'_2)$$

where N is the number of points in each of the two series, r_1 and r'_1 are the lag-one autocorrelations of the two series and r_2 and r'_2 are the lag-two autocorrelations of the two series. The significance of correlations between plant biomass and meteorological variables was then estimated using Fisher's Z test (Freund 1988).

4.3 RESULTS

4.3.1 Bibury taxa and weather types

The results of the analysis for the 44 Bibury taxa and weather types are presented in full in Appendix 4. Seasonal summaries of these results are shown in Tables 4.3 and 4.4. The indices of anticyclonic and cyclonic weather accounted for the majority of the responses of taxa to seasonal weather. The index for cyclonic and westerly combined added some extra information. The index of westerly weather produced conflicting results. As explained below, the frequencies of anticyclonic, cyclonic, and cyclonic and westerly weather types combined produce results that agree closely with the 'good' seasons approach: results for these three weather type indices are presented below.

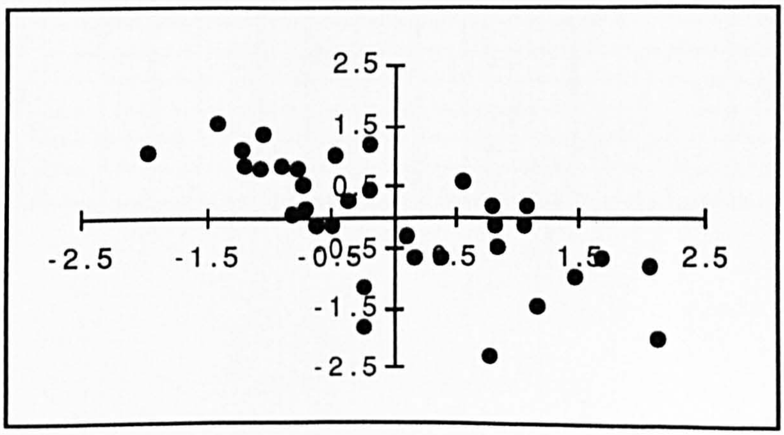
As with individual weather variables, it is possible to build species/weather-type response profiles from the information in Appendix 3. Such a profile is illustrated in Table 4.3 An example of a relationship between *Dactylis glomerata* and a seasonal weather type is shown in Figure 4.2.

Table 4.3. Weather-type response profile for *Dactylis glomerata*. Years 0,1 and 2 refer to the current year in which vegetation recording occurred, the previous year, and the year before that respectively. Shaded boxes indicate a significant correlation (p=0.05) between plant performance and the weather type concerned in the season indicated. P and N refer to positive or negative correlations respectively.

	YEAR 2				YEAR 1				YEAR 0			
	AU	WI	SP	SU	AU	WI	SP	SU	AU	WI	SP	SU
ANTICYCLONIC			N	N			N	N	P	P		
CYCLONIC				P								
CYCLONIC AND WESTERLY			P	P								

D.glomerata exhibits a negative relationship with anticyclonic conditions in summer and a positive relationship with cyclonic, and cyclonic and westerly combined. This corresponds with *D.glomerata* being retarded by 'good' summers, *D.glomerata* is promoted by anticyclonic conditions in autumn and winter. This may be linked with the winter vernalisation requirement of *D.glomerata* for maximum flowering. (Beddows 1959).

Figure 4.2. Performance of *Dactylis glomerata* and the frequency of anticyclonic weather in spring and summer (lag -2). X axis = Frequency of anticyclonic weather. Y axis = log biomass *D.glomerata*. Both time series have been converted to standard units (zero mean, unit variance). r = -0.664



4.3.1.1 Significance of the Results

44 Bibury taxa were used in the analysis. However, of these 44, 36 occur in series 1-6 and 38 occur in series 7-8. For the analysis of the performance of taxa with the frequency of weather types in different seasons, 4 seasons were considered over a period of 3 years. Three weather type indices were used. Therefore the total number of possible correlations is (36 x 4 x 3 x 3) + (38 x 4 x 3 x 3) = 2664. At $P = 0.05$ the expected number of correlations would be 133. The actual number observed was 153.

For autumn and winter, and spring and summer combined, the total number of correlations is (36 x 2 x 3 x 3) + (38 x 2 x 3 x 3) = 1332. At $P = 0.05$ the expected number of correlations would be 67. 77 were actually observed.

In both cases more significant correlations were observed than might be expected to occur purely by chance. As with the analysis using individual weather variables, this suggests markedly non-random relationships between the performance of taxa and the frequency of the weather types concerned.

Table 4.4 Correlations Between 44 Bibury Taxa and Weather types for series 1-6. (1959-1993) A = anticyclonic weather, C = cyclonic, CW = cyclonic & westerly. P = Positive correlation, N = negative correlation ($P<0.05$).

	AUTUMN			WINTER			SPRING			SUMMER			AUTUMN & WINTER			SPRING & SUMMER		
	A	C	CW	A	C	CW	A	C	CW	A	C	CW	A	C	CW	A	C	CW
B.G							P	N	N							P		
Litter				P						N								
Ach mil														N				
Agr sto														N				
Alo pra				P									P	N				
Ani ste											N	N					N	N
Ant syl																		
Arr ela																		
Ave pub																		
Bra pin																		
Bro ere							N		P	N	P	P				N	P	P
Cen nig																		
Cir arv	P		N															
Con arv																		
Cru lae				P							P	P	P		N	N		P
Dac glo									P	N		P				N		P
Ely rep																		
Fes aru		P								P						P		
Fes rub											P	P						P
Gal apa																		
Gal ver					N							P						P
Gle hed					N	N			N							N		P
Her sph																		
Hyp per					N													
Kna arv					N						P	P		P				
Lol per																		
Odo ver								N					P	N				
Phl ber													P			P		
Pla lan											P	P						
Poa pra				P														
Poa tri																		
Pot rep																		
Ran rep	P		N						P							N		P
Rum sp										P	N	N	N			P	N	N
Sta syl																		
Tar off							N	N				P						
Tra pra																		
Tri fla	N	P	P									P					P	P
Tri pra												P						
Tri rep								P										
Ulm gla								N			N							
Urt dio											N	N						
Ver cha								P		N	P							
Vic sat	P							P			P	P					P	
Vio hir																	P	

Table 4.5 Correlations Between 44 Bibury Taxa and Weather types for series 7-8. (1959-1993) A = anticyclonic weather, C = cyclonic, CW = cyclonic & westerly. P = Positive correlation, N = negative correlation (P<0.05).

	AUTUMN			WINTER			SPRING			SUMMER			AUTUMN & WINTER			SPRING & SUMMER		
	A	C	CW	A	C	CW	A	C	CW	A	C	CW	A	C	CW	A	C	CW
B.G		P			P		P	N								P		N
Litter													P					
Ach mil								N				N					N	N
Agr sto																		
Alo pra									P									
Ani ste																		
Ant syl																		
Arr ela					P	P		N										
Ave pub	N	P						P										
Bra pin					N													
Bro ere					N					P			P					
Cen nig				P	N			N	P								N	
Cir arv				P	P						N					P		N
Con arv	N	P					P			P					P			
Cru lae							N									N		
Dac glo	N							P				P	P	N				P
Ely rep										P						P		
Fes aru																		
Fes rub	P	N														P		
Gal apa				N			P											P
Gal ver													N	P				
Gle hed																		
Her sph				P	N	N		P					P		N	P		
Hyp per																		
Kna arv																		
Lol per				P				P	P									
Odo ver																	P	
Phl ber	P		N															
Pla lan		P		P						N		P						
Poa pra																		
Poa tri																		
Pot rep				P								P	P	N				
Ran rep				P														
Rum sp																		
Sta syl																		
Tar off							P		N				P	N				
Tra pra		N						N	N								N	
Tri fla																		
Tri pra	P							N										
Tri rep																	P	
Ulm gla								N										
Urt dio																		
Ver cha		N	N		N	P	P	N	N	P						P	N	N
Vic sat				P									P					
Vio hir								P										

There are 27 instances where taxa show a relationship with both cyclonic weather and with cyclonic and westerly weather combined in a given season. In all but two, the sign of that relationship is, not unsurprisingly, the same. In the same way that anticyclonic weather is negatively correlated with both cyclonic weather, and cyclonic and westerly combined, where taxa show a relationship between both anticyclonic weather and/or cyclonic or cyclonic and westerly combined, the signs of those relationships are opposite. Table 4.5 is a contingency table that summarises the signs of the relationships in tables 4.3 and 4.4.

Table 4.6 Contingency Table of the Relationship Between Plant Performance and Weather types. A = Anticyclonic Weather. C = Cyclonic Weather. CW = Cyclonic and Westerly Weather Combined. + = Positive Relationship. - = Negative Relationship. 0 = No Relationship. The numbers refer to the number of occurrences of the particular combination of variables in tables 4.3 and 4.4 in a given season. $P<0.001$ (X^2)

	A +	A -	A 0
C and/or CW +	1	13	35
C and/or CW -	22	1	27
C and/or CW 0	27	5	0

Every Bibury taxon shows a relationship with one of the weather types in either series 1-6 or 7-8. There are 94 occurrences of taxa which show a relationship with either anticyclonic weather or cyclonic and/or cyclonic and westerly weather combined. There are 37 occurrences of taxa showing a relationship with both in a given season. Where taxa do show a relationship with both in a given season, in all but two cases the signs are opposite i.e. a positive relationship with anticyclonic weather can be equated with a negative relationship with cyclonic and/or cyclonic and westerly weather.

It has been shown clearly that not only are anticyclonic, and westerly and cyclonic weather types opposed to each other in meteorological terms, but that the responses of taxa to the different weather types are also opposite. It is therefore possible to define these responses in given seasons in terms of their relationship with increased anticyclonicity (decreased cyclonicity and/or westerliness) or decreased anticyclonicity (increased cyclonicity and/or westerliness). For example, taxa which show a positive relationship with increased frequency of anticyclonic weather and/or a negative relationship with increased frequency of cyclonic weather are classified as exhibiting a positive relationship with increased anticyclonicity. Tables 4.6 and 4.7 summarise the response of taxa to increased anticyclonicity and/or decreased cyclonicity and westerliness.

Table 4.7 **The response of taxa to seasonal anticyclonicity, series 1-6.** P = Positive Correlation, N = Negative Correlation. ($P<0.05$).

	AUTUMN	WINTER	SPRING	SUMME R	AUTUMN & WINTER	SPRING & SUMMER
B.G			P			P
Litter		P		N		
Ach mil					P	
Agr sto					P	
Alo pra		P			P	
Ani ste				P		P
Ant syl						
Arr ela						
Ave pub						
Bra pin						
Bro ere			N	N		N
Cen nig						
Cir arv	P					
Con arv						
Cru lae		p		N	P	N
Dac glo			N	N		N
Ely rep						
Fes aru	N			P		P
Fes rub				N		N
Gal apa						
Gal ver		P		N		
Gle hed		P	P			N
Her sph						
Hyp per		P				
Kna arv		P		N	N	
Lol per						
Odo ver			P		P	
Phl ber					P	P
Pla lan				N		
Poa pra		P				
Poa tri						
Pot rep						
Ran rep	P		N			N
Rum sp				P	N	P
Sta syl						
Tar off			N	N		
Tra pra						
Tri fla	N			N		N
Tri pra				N		
Tri rep			N			
Ulm gla			P	P		
Urt dio				P		
Ver cha			N	N		
Vic sat	P		N	N		N
Vio hir						N

Table 4.8 The response of taxa to seasonal anticyclonicity, series 7-8. P = Positive Correlation, N = Negative Correlation. ($P<0.05$).

	AUTUMN	WINTER	SPRING	SUMMER	AUTUMN & WINTER	SPRING & SUMMER
B.G	N	N	P			P
Litter					P	
Ach mil			P	P		P
Agr sto						
Alo pra						
Ani ste						
Ant syl						
Arr ela		N	P			
Ave pub	N		N			
Bra pin		P				
Bro ere		P		P	P	
Cen nig		P	P			P
Cir arv		P		P		P
Con arv	N		P	P	N	
Cru lae			N			N
Dac glo	N		N	N	P	N
Ely rep				P		P
Fes aru						
Fes rub	P					P
Gal apa		N	P			N
Gal ver					N	
Gle hed						
Her sph		P	N		P	P
Hyp per						
Kna arv						
Lol per		P	N			
Odo ver						N
Phl ber	P					
Pla lan	N	P		N		
Poa pra						
Poa tri						
Pot rep		P		N	P	
Ran rep		P				
Rum sp						
Sta syl						
Tar off			P		P	
Tra pra	P		P			P
Tri fla						
Tri pra	P		P			
Tri rep						N
Ulm gla			P			
Urt dio						
Ver cha	P	P	P	P		P
Vic sat		P			P	
Vio hir			N			

4.3.2 Plant functional types and weather types

The time-series for the plant functional types described in Chapter 2 were compared with the weather types time-series. The plant time-series were flat-trended or de-trended as appropriate. Those time-series not exhibiting statistically significant autocorrelation (Table 4.2) were correlated directly with weather type data. For other functional types, the formula of Quenouille (Section 4.2.5) was used to estimate the significance of the correlations. The full results are given in Appendix 5. The results are summarised in Tables 4.8 and 4.9, and converted to response to seasonal anticyclonicity in Tables 4.10 and 4.11.

4.3.2.1 Significance of the results

In all, six functional types and total biomass, in two vegetation series, were correlated with three weather types and four seasons over three years. Twenty-six significant correlations would be expected to occur by chance at $P = 0.05$. Thirteen correlations would be expected by chance for autumn and winter, and spring and summer combined. Thirty-three correlations were actually observed with individual seasons and 19 for the combined seasons.

Table 4.9 Correlations between plant functional types and weather types for series 1-6. (1959-1993) A = anticyclonic weather, C = cyclonic, CW = cyclonic & westerly. P = Positive correlation, N = negative correlation (P<0.05).

	AUTUMN			WINTER			SPRING			SUMMER			AUTUMN & WINTER			SPRING & SUMMER		
	A	C	CW	A	C	CW	A	C	CW	A	C	CW	A	C	CW	A	C	CW
C									P		P	P				N	P	P
S											P			N				
R										P	N	N						N
CR									P									
CS		P								N	P	P				N	P	P
CSR											P	P					P	P
TOTAL BIOMASS									P		P	P					P	

Table 4.10 Correlations between plant functional types and weather types for series 7-8. (1959-1993) A = anticyclonic weather, C = cyclonic, CW = cyclonic & westerly. P = Positive correlation, N = negative correlation (P<0.05).

	AUTUMN			WINTER			SPRING			SUMMER			AUTUMN & WINTER			SPRING & SUMMER		
	A	C	CW	A	C	CW	A	C	CW	A	C	CW	A	C	CW	A	C	CW
C					P													
S				P	N			N	P								N	
R	P		P															
CR								P										
CS										N								
CSR																		
TOTAL BIOMASS																		

Table 4.11 Plant functional type response to seasonal anticyclonicity, Series 1-6. P = Positive Correlation, N = Negative Correlation. (P<0.05).

	AUTUMN	WINTER	SPRING	SUMMER	AUTUMN & WINTER	SPRING & SUMMER
C			N	N		N
S				N	P	
R				P		P
CR			N			
CS	N			N		N
CSR				N		N
TOTAL BIOMASS			N	N		N

Table 4.12 Plant functional type response to seasonal anticyclonicity, Series 7-8. P = Positive Correlation, N = Negative Correlation. (P<0.05). * = conflicting results between the different weather types.

	AUTUMN	WINTER	SPRING	SUMMER	AUTUMN & WINTER	SPRING & SUMMER
C		N				
S		P	*			P
R	*					
CR			N			
CS				N		
CSR						
TOTAL BIOMASS						

4.4 DISCUSSION

4.4.1 Individual Taxa and Weather types

As with the analysis of Bibury taxa and individual weather variables, there are some contradictions between the two vegetation series. *Festuca rubra, Bromopsis erecta, Taraxacum officinale* and *Veronica chamaedrys* exhibit different responses in the same season between the two vegetation series. As discussed in chapter 3, the varying species responses may be a result of differences in the nature of the vegetation in the two series.

A similar pattern emerges between the response of the Bibury taxa to the different weather types and their response to individual weather variables and 'good' and 'bad' seasons. The amount of bare ground is positively correlated with high anticyclonicity in spring and summer and negatively correlated in autumn and winter. As may be expected, hot, dry, drought conditions in summer appear to open gaps in the vegetation, whereas milder, wetter winters reduce the amount of bare ground, presumably as a result of the extended growing season promoting lush growth. Associated with this increase in biomass is an increase in the amount of litter following mild winters - increased litter is also observed following wet cool summers.

As with the 'good and bad seasons' approach, robust, potentially-preductive perennials (i.e competitors *sensu* Grime, 1974) such as *Dactylis glomerata* are retarded by high anticyclonicity in summer. This is particularly apparent in series 1-6. Other robust species, such as *Bromopsis erecta,* are promoted by mild winters. Deep-rooted perennial species such as *Achillea millefolium, Convolvulus arvensis* and *Centaurea nigra* are promoted by high anticyclonicity in summer - these species are presumably able to tap into reserves of moisture at lower levels in the soil during summer drought conditions.

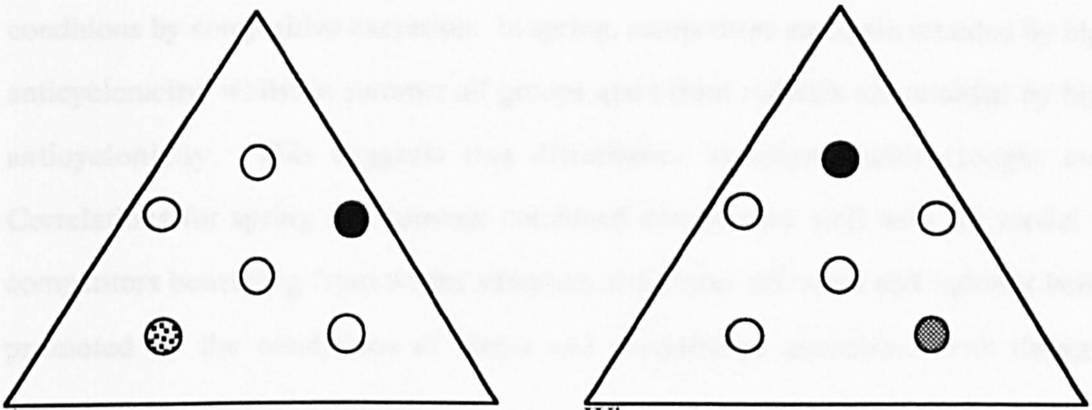
4.4.2 Plant Functional Types and Weather types.

The relationship between the performance of plant functional groups and seasonal anticyclonicity is shown diagrammatically in figure 4.2.

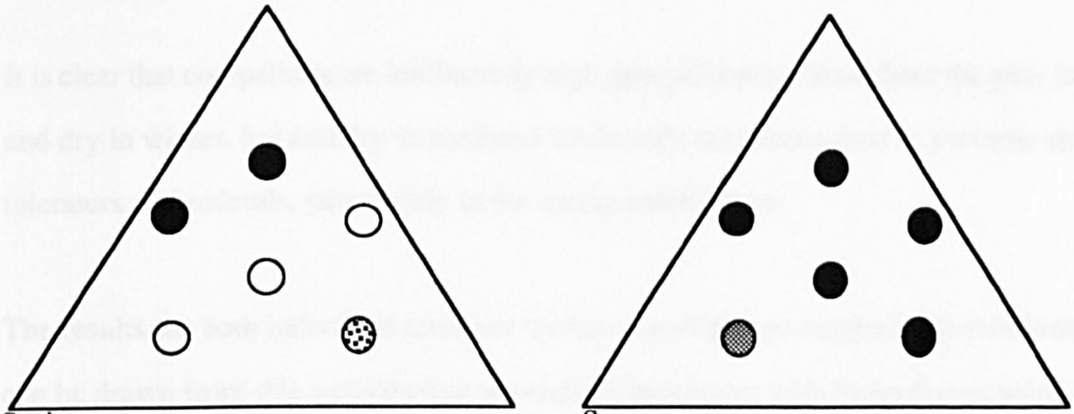
Table 4.13. The relationship between the performance of plant functional groups and seasonal anticyclonicity.

○ = No Response ◍ = Positive Response ● = Negative Response

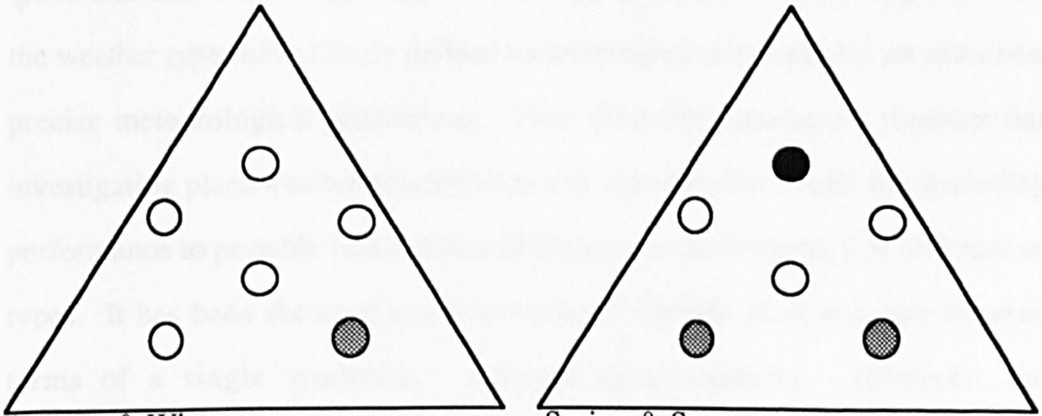
⊛ = Conflict between different weather-types



Autumn Winter



Spring Summer



Autumn & Winter Spring & Summer

The correlations of taxa with weather types agree closely with those of individual weather variables. The diagrammatic representations shown in Figure 4.2 are similar to those shown in Figure 3.4. Competitors are inhibited by high winter anticyclonicity whilst stress-tolerators are promoted. This fits well with the model of competitors benefiting from mild wet winters and stress-tolerators being retarded under such conditions by competitive exclusion. In spring, competitors are again retarded by high anticyclonicity, whilst in summer all groups apart from ruderals are retarded by high anticyclonicity. Tbis suggests that disturbance associated with drought may Correlations for spring and summer combined accord very well with the model of competitors benefiting from wetter summers and stress-tolerators and ruderals being promoted by the conditions of stress and disturbance associated with drought conditions in spring and summer.

It is clear that competitors are inhibited by high anticyclonicity throughout the year (cold and dry in winter, hot and dry in summer) while such conditions tend to promote stress tolerators and ruderals, particularly in the spring and summer.

The results for both individual taxa and for functional groups suggest that conclusions can be drawn from this analysis that are entirely consistent with those drawn using the 'good and bad' season approach. In contrast to the good season approach however, the weather types have clearly defined meteorological meaning and are associated with precise meteorological phenomena. They therefore represent a rigorous basis for investigating plant/weather relationships and also provide a basis for predicting plant performance to possible future seasonal changes in the frequency of different weather types. It has been shown that it is possible to classify plant response to weather in terms of a single syndrome: seasonal anticyclonicity. However, seasonal anticyclonicity, while being an objective measure, must still be inferred from three individual weather type indices. The possibility of using a single, higher level index, the relative position of the Gulf Stream off the east coast of the United States (which may have an underlying role in determining the relative frequencies of different weather types over the UK), is discussed in Chapter 5. A more detailed comparison of the results from the good seasons and weather type approaches is presented in Chapter 6.

CHAPTER 5 PLANT/WEATHER RELATIONSHIPS IN THE BIBURY ROAD VERGES: RELATIONSHIPS TO THE POSITION OF THE GULF STREAM

5.1 INTRODUCTION

Evidence has been presented in Chapters 3 and 4 of markedly non-random relationships between climate and vegetation in the Bibury road verges. These relationships have been demonstrated with what might be called 'first order' and 'second order' meteorological variables. First order variables include individual variables such as rainfall and temperature, and second order variables include the large-scale weather patterns that determine the frequency of the first order variables. Evidence is presented in this Chapter that links plant performance with a 'third order' variable that may in some way be responsible, at least partly, for the frequency and pattern of the second order variables. The third order variable considered is the latitudinal position of the Atlantic Gulf Stream. Preliminary results of this work, and an initial discussion of those results have been published previously (Willis *et al.* 1995). However, a more comprehensive discussion, and presentation of previously unpublished results, are included here.

5.1.1 Oceanic influences on climate and their biological implications.

The generation of weather systems is greatly influenced, if not determined, by the close association between atmospheric and oceanic processes (Gamble 1994). In particular, sea surface temperature has been shown to be directly correlated with weather patterns (Cushing and Dickson, 1976). For example, it has been clearly demonstrated that oscillations in sea surface temperatures caused by El Nino, the periodic reversal of winds and ocean currents in the Pacific, are strongly linked to rainfall in Zimbabwe (Cane *et al.* 1994). Maize yield in Zimbabwe, although highly correlated with rainfall, was found to be even more strongly correlated with sea surface temperatures in the equatorial Pacific Ocean, despite the great distance involved. Although no causal mechanism was proposed, this work demonstrates a striking relationship between oceanic processes, terrestrial weather systems and the performance of a biological system.

El Nino has long been known to be a large component of natural inter-annual climate variability in the tropics and subtropics (Rosenzweig 1994). It has also been suggested that changes in the strength of the Gulf Stream ocean current in the Atlantic Ocean may be a potentially significant source of climatic variation (Burroughs 1992). The work of Arnold Taylor (Plymouth Marine Laboratory) and colleagues appears to show, 'beyond all doubt', that this is indeed the case (Gamble 1994). Taylor and Stephens (1980) and Taylor *et al.* (1992) demonstrated that variation in the position of the 'North Wall' of the Gulf Stream as the current moves east-northeast away from the coastline of the USA is closely correlated with fluctuations in the abundance of copepods in the Eastern Atlantic and North Sea. The correlations were simultaneous and showed no obvious time-lags. This therefore implies that transport processes in the North Atlantic current system, whose currents require several months to cross the ocean, are less likely to explain the connection than are atmospheric circulation processes (Taylor *et al.* 1992). Oceanic mixed layer plankton populations are susceptible to the passage of weather systems. It is suggested that the Gulf Stream effects can be related to changes in the eastward trajectories of pressure systems across the Atlantic (Taylor 1995) Decreases or increases in the prevalence of storms affect the time of onset of the stratification which, in turn, controls the timing of the spring bloom (Gamble 1994). Similar relationships between plankton abundance and the latitudinal position of the Gulf Stream have been demonstrated for the freshwater Lake Windermere (George and Taylor 1995).

Relationships between fluctuations in oceanic currents, weather patterns and the performance of biological systems have much predictive potential in the context of possible global climate change. In the light of the relationships that had been demonstrated between fluctuations in oceanic currents and Zimbabwean crop yields, and abundance of plankton in the North Atlantic, the Bibury data-set was used to test whether any relationships could be established between oceanic processes and the dynamics of terrestrial semi-natural vegetation. This work was approached with some caution, given the greatly increased complexity of terrestrial vegetation and the external and internal factors determining plant performance, compared to the relatively simple systems of a crop monoculture or planktonic community.

5.1.2 Questions

The investigation presented in this Chapter attempts to answer three main questions:

- If relationships can be demonstrated between the relative position of the Gulf Stream and plankton abundance in the North Atlantic and Lake Windermere, can relationships be demonstrated also with the performance of terrestrial semi-natural vegetation?

- If such relationships do exist, what is the meteorological mechanism that may explain those relationships? It is beyond the scope of this thesis to provide an explanation in detailed physical, atmospheric or climatic terms. The approach adopted here is simply to compare Gulf Stream position with the frequency of first and second order meteorological variables and to draw conclusions from any correlations observed.

- If relationships are detected between Bibury species, functional groups or total vegetation biomass and the relative position of the Gulf Stream, are such relationships comparable and consistent with the relationships described in Chapters 3 and 4? This final question is discussed at length in Chapter 6.

5.2 METHODS

5.2.1 Gulf Stream Data

The Gulf Stream separates from the coast of North America near Cape Hatteras and then travels eastwards across the North Atlantic, becoming the North Atlantic current (Taylor and Stephens 1980). Figure 5.1 illustrates the position of the 'North Wall' of the Gulf Stream off the coast of the United States and plate 5.1 is a satellite image of sea surface temperatures in the western Atlantic.

Figure 5.1 The progress of the Gulf Stream across the North Atlantic

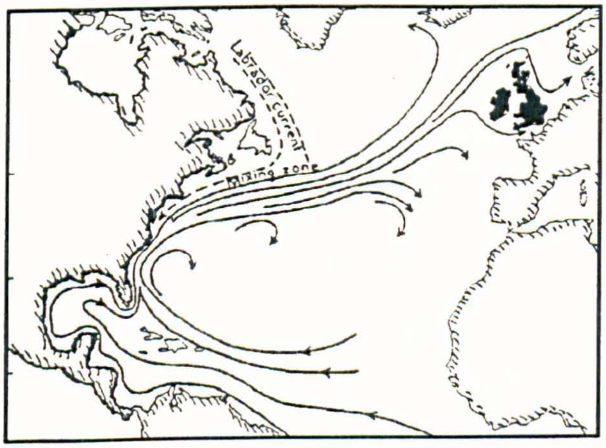
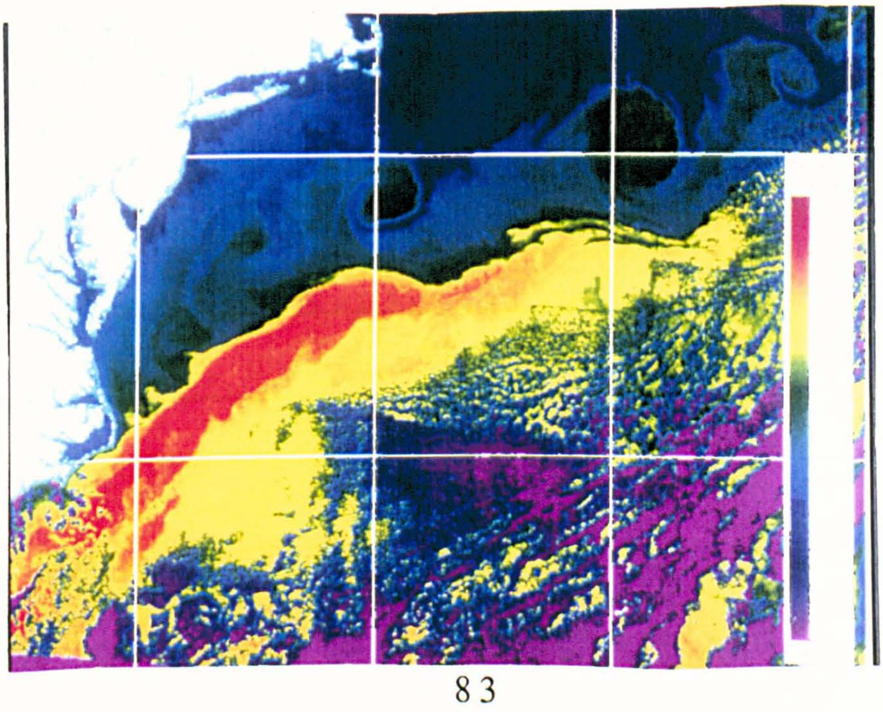
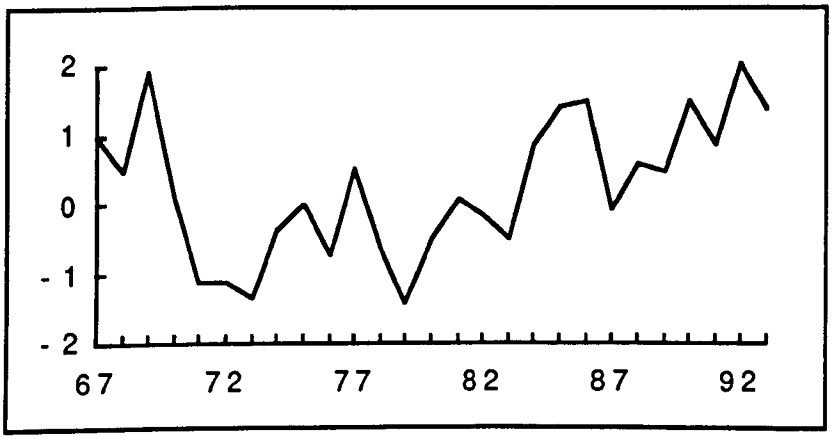


Plate 5.1 A Satellite Image of Sea Surface Temperatures in the Atlantic Ocean.



The relative position of the North Wall of the Gulf Stream shows year-on-year fluctuation; in some years being further north, in other years being further south. The data used in the analysis described below were supplied by Dr. Arnold Taylor of the Plymouth Marine Laboratory. The data were taken from the monthly charts published successively in the periodicals 'The Gulf Stream Monthly Summary', 'Gulf Stream' and 'Oceanic Monthly Summary'. The latitude of the north wall was read from the charts at longitudes 79°W to 65°W, the seasonal cycle was removed, and an index of monthly position was constructed using principal components analysis (Taylor *et al.* 1992). The monthly values were averaged to produce three month and six month seasonal averages for the same periods that were used for the first and second order meteorological variables discussed in Chapters 3 and 4. Data were available for the years 1966, when records were first collected, to 1993. A positive value of the Gulf Stream Northerliness Index indicates a northerly position of the north wall of the Gulf Stream relative to its long-term average position, and a negative value indicates a southerly position relative to its long-term average. The time-series for the Gulf Stream Northerliness index for autumn and winter is shown in Figure 5.2.

Figure 5.2 Standardised time-series (zero mean, unit variance) for the Gulf Stream Northerliness index in Autumn and Winter. Y axis = Gulf Stream Northerliness index, x axis = Year.



5.2.2 Comparison of Gulf Stream Position with first and second order meteorological variables.

To establish what relationships may exist, if any, between Gulf Stream Northerliness and meteorological variables over the UK, the Gulf Stream index was compared with the time-series for the first and second order weather variables described in the two preceding Chapters. There is some evidence that the relationship between Gulf Stream position and plankton abundance in the North Atlantic has weakened in the late 1980s and early 1990s, implying a break-down in previously strong relationships between Gulf Stream position and weather patterns (Arnold Taylor, personal communication). Meteorological variables were therefore compared with Gulf Stream position for 20 years (1966-1986), 25 years (1966-1991) and 27 years (1966-1993) to allow for any diminution in relationships that may have occurred. To gain as much information as possible, comparisons were made between Gulf Stream position and the raw values of the meteorological variables, and also their natural logarithms (log values of minimum temperature were not available because of negative values in the raw data). Comparisons were made for individual months and also for three-monthly, six-monthly and annual means. For compatibility with other analyses in this thesis, autumn is defined as September, October and November, Winter as December, January and February, and so on. The annual mean, being a mean of the four seasonal means, runs from the autumn of the previous year to the summer of the current year, and is therefore comparable with weather in the 12 months preceding the annual Bibury field recording.

It is clear that the mechanism linking Gulf Stream position and terrestrial weather is complex. To allow as clear a picture as possible to emerge from this analysis, correlations significant at $P<0.10$ have been included with the results.

5.2.3 Comparison of Gulf Stream position with plant performance at Bibury

Gulf Stream position was compared with residuals about the long-term log mean biomass (% cover in the case of bare ground) of 44 Bibury taxa for the period 1966-1993. The Bibury time-series were flat-trended or de-trended using the methods described in Chapter two. The meteorological time-series were the same as those described in Chapters 3 and 4. Correlations were corrected to account for the presence of autocorrelation in the Bibury time-series where necessary, as described in section 4.2.5. Correlations were taken to be statistically significant at $P<0.05$.

5.3 RESULTS

5.3.1 Comparison between Gulf Stream position and meteorological variables.

The results of the comparison for individual meteorological variables and Gulf Stream position for each month of the year are presented in table 5.1. There is some evidence that for a number of variables, relationships were apparent in the time series for 20 and 25 years that were not apparent for the 27 year time series, and in some cases the significance of the relationship was higher for the shorter time period. However, most relationships were detectable using the 27 year time series.

Table 5.1. Correlation Matrix for individual weather variables and Gulf Stream position for each month of the year. Min = Minimum Temperature, Max = Maximum Temperature, Rain = Rainfall and Sun = Sunshine. LN refers to the natural log of the raw meteorological data. 20 = the 20 year period from 1966-1986, 25 = the 25 year period from 1966-1991 and 27 = the 27 year period from 1966-1993. P = Positive correlation, N = Negative correlation. ** P<0.01, * P<0.05, No star = P<0.10.

	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL
MIN 20	P**											
MIN 25	P**							P				
MIN 27	P**							P				
MAX 20	P**											
LN MAX 20	P**											
MAX 25	P**											
LN MAX 25	P**											
MAX 27	P**											
LN MAX 27	P*											
RAIN 20												
LN RAIN 20												
RAIN 25												
LN RAIN 25	N*					P						
RAIN 27												
LN RAIN 27	N*					P						
SUN 20	P*											
LN SUN 20	P*											
SUN 25	P*						P*					
LN SUN 25	P*						P*					
SUN 27	P*						P*					
LN SUN 27	P*						P					

A clear and consistent pattern emerges from these results. The weather in August appears to be strongly linked to Gulf Stream position. A relatively northerly position for the north wall of the Gulf Stream is associated with above average minimum and maximum temperatures and sunshine and below average rainfall. These results (log comparisons for the 27 year period only, and only those relationships significant at P<0.05) were reported by Willis *et al.* (1995), along with results for mean atmospheric pressure at sea level, which also showed a positive correlation in August. Above average temperatures and sunshine, and below average rainfall in a summer month, can be equated with anticyclonic conditions, as shown in Chapter 4. The above average mean sea level pressure associated with a northerly position for the Gulf Stream in

August is consistent with this. Above average sunshine is also associated with a northerly Gulf Stream position in February. However, there are hints of a positive relationship with rainfall in January.

Table 5.2 contains the results of the seasonal analysis of individual weather variables with Gulf Stream position.

The results for seasonal and annual means are not as clear-cut as for individual months. A northerly Gulf Stream is associated with warmer temperatures in winter and winter and spring combined, and with cooler temperatures in autumn and in spring. As demonstrated in Chapter 3, such conditions are more consistent with unsettled weather than settled, although the negative relationship with maximum temperature in autumn and winter combined may be more in keeping with settled weather. However, rainfall appears to be positively correlated with a northerly Gulf Stream in autumn and winter and this definitely cannot be equated with a higher incidence of settled weather. This is supported by the negative relationships between Gulf Stream position and sunshine in autumn, spring, and autumn and winter combined.

Table 5.2. Correlation Matrix for individual weather variables and Gulf Stream position for three and six month seasonal means and annual mean. Min = Minimum Temperature, Max = Maximum Temperature, Rain = Rainfall and Sun = Sunshine. LN refers to the natural log of the raw meteorological data. 20 = the 20 year period from 1966-1986, 25 = the 25 year period from 1966-1991 and 27 = the 27 year period from 1966-1993. P = Positive correlation, N = Negative correlation. ** $P<0.01$, * $P<0.05$, No star = $P<0.10$.

	Autumn	Winter	Spring	Summer	Summer & Autumn	Autumn & Winter	Winter & Spring	Spring & Summer	Year
MIN 20									
MIN 25									
MIN 27			N*						
MAX 20	N					N*			
LN MAX 20	N*					N			
MAX 25									
LN MAX 25									
MAX 27		P*	N				P*		
LN MAX 27			N*				P*		
RAIN 20									
LN RAIN 20						P			
RAIN 25						P*			
LN RAIN 25						P*			
RAIN 27									
LN RAIN 27						P			
SUN 20	N*					N*			
LN SUN 20	N*								
SUN 25									
LN SUN 25									
SUN 27			N				P*		
LN SUN 27	N		N*				P*		

Gulf Stream position was also compared with the frequency of the weather types described in Chapter 4. The results of this analysis are shown in Table 5.3.

Table 5.3. Correlation Matrix for weather types and Gulf Stream position for each month of the year. Anti = anticyclonic weather, Cyc = cyclonic weather, West = westerly weather and CW = Cyclonic and westerly weather combined. LN refers to the natural log of the raw meteorological data. 20 = the 20 year period from 1966-1986, 25 = the 25 year period from 1966-1991 and 27 = the 27 year period from 1966-1993. P = Positive correlation, N = Negative correlation. ** P<0.01, * P<0.05, No star = P<0.10.

	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL
ANTI 20												
LN ANTI 20												
ANTI 25	P					N*						N
LN ANTI 25	P					N*						
ANTI 27	P											N
LN ANTI 27	P											
CYC 20												
LN CYC 20												
CYC 25		N*									P	
LN CYC 25		N										
CYC 27											P	
LN CYC 27												
WEST 20												P
LN WEST 20												P**
WEST 25		P*										P
LN WEST 25		P*										P**
WEST 27									P			P*
LN WEST 27												P**
CW 20												
LN CW 20												
CW 25							P					
LN CW 25												
CW 27												
LN CW 27												

Anticyclonic weather is associated with a northerly Gulf Stream in August. This is consistent with the results in Table 5.1. However, the relationships with anticyclonic weather in August are significant only at P<0.1. Negative relationships are apparent between Gulf Stream position and anticyclonic weather in February and July. The negative relationship with cyclonic weather in September is consistent with the positive relationship with anticyclonic weather in August. The positive relationships with cyclonic weather are again consistent with the negative relationship with anticyclonic weather in July. Gulf Stream position exhibits striking positive relationships with westerly weather in July.

Table 5.4 contains the results of the seasonal analysis of weather types with Gulf Stream position. The results suggest a negative relationship between Gulf Stream position and anticyclonic weather in autumn and winter and over the year as a whole. This is consistent with the positive relationship with cyclonic weather over summer, autumn and winter. A negative relationship with westerly weather in winter is apparent.

Table 5.4. Correlation Matrix for weather types and Gulf Stream position for three month, six month and annual means. Anti = anticyclonic weather, Cyc = cyclonic weather, West = westerly weather and CW = Cyclonic and westerly weather combined. LN refers to the natural log of the raw meteorological data. 20 = the 20 year period from 1966-1986, 25 = the 25 year period from 1966-1991 and 27 = the 27 year period from 1966-1993. P = Positive correlation, N = Negative correlation. ** P<0.01, * P<0.05, No star = P<0.10.

	Autumn	Winter	Spring	Summer	Summer & Autumn	Autumn & Winter	Winter & Spring	Spring & Summer	Year
ANTI 20						N			N*
LN ANTI 20						N			N*
ANTI 25									
LN ANTI 25		N				N*			N*
ANTI 27						N			N*
LN ANTI 27						N*			N*
CYC 20					P*	P			
LN CYC 20					P	P			
CYC 25				P	P*				
LN CYC 25					P				
CYC 27									
LN CYC 27									
WEST 20									
LN WEST 20						N*			
WEST 25									
LN WEST 25									
WEST 27									
LN WEST 27									
CW 20									
LN CW 20									
CW 25									
LN CW 25									
CW 27									
LN CW 27									

5.3.2 Relationships between Gulf Stream Position and Bibury vegetation

The full results of the comparison between Gulf Stream Position and the performance of the 44 Bibury taxa are presented in Appendix 6. These results have been summarised using the methods described in Chapter 3.

5.3.2.1 Significance of the results

As explained in section 4.3.1.1, 36 of the 44 Bibury taxa occur in series 1-6 and 38 occur in series 7-8. For the analysis of the performance of taxa with Gulf Stream position in different seasons, 4 seasons were included over a period of three years. Therefore the total number of possible correlations is (36 x 4 x 3) + (38 x 4 x 3) = 888. At $P<0.05$, the expected number of significant correlations would be 44. Seventy-five correlations were actually observed.

For autumn and winter, and spring and summer combined, the total number of possible correlations is (36 x 2x 3) + (38 x 2 x 3) = 444. At $P<0.05$, the expected number of significant correlations would be 22. Thirty-seven were actually observed.

In both cases, therefore, a greater number of statistically significant correlations were actually observed than might be expected to occur by chance. As with the comparisons between the performance of Bibury taxa and weather variables, this suggests markedly non-random relationships between the performance of taxa and the position of the Gulf Stream.

The results for the comparison between the performance of Bibury taxa and Gulf Stream position for series 1-6 and series 7-8 are presented in Tables 5.5 and 5.6.

Selected relationships are illustrated graphically in figure 5.2.

Figure 5.2. Relationships between Gulf Stream position and performance of components of the vegetation at Bibury. A is taken from Willis *et al.* (1995) All units have been converted to standardised units (zero mean, unit variance). A. Total above-ground biomass, series 1-6 (solid line) and Gulf Stream Northerliness index in the next-to-previous spring and summer months (broken line) r = 0.489. B. *Knautia arvensis* in Bibury plots 7-8 (y axis) and Gulf Stream position in the previous autumn and winter (x axis) r = 0.64.

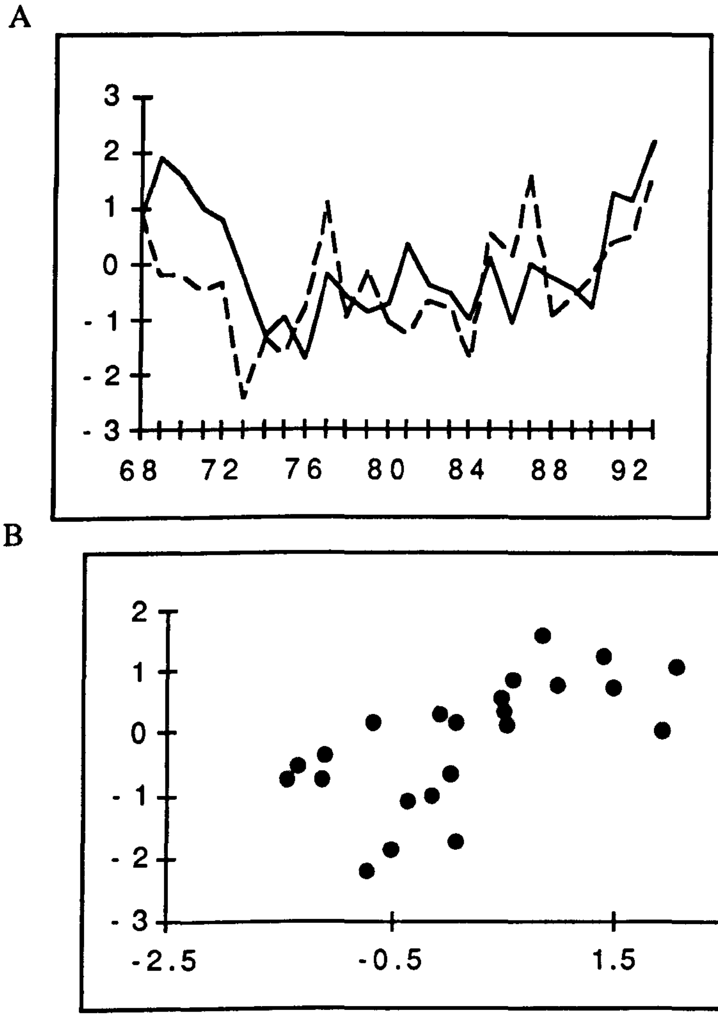


Table 5.5 Correlations between 44 Bibury taxa and Gulf Stream position for series 1-6. (1966-1993) P = Positive correlation, N = negative correlation ($P<0.05$). A positive correlation indicates an increase in above-ground biomass (or % cover in the case of bare ground) associated with a more northerly Gulf Stream position.

	Autumn	Winter	Spring	Summer	Autumn & Winter	Spring & Summer
B.G	N		N	N		N
Litter						
Ach mil			P	P		
Agr sto						
Alo pra		N	N		N	N
Ani ste	N	N			N	
Ant syl						
Arr ela						
Ave pub						
Bra pin						
Bro ere		P				
Cen nig						
Cir arv						
Con arv						
Cru lae	P	P			P	
Dac glo						
Ely rep			P			P
Fes aru	N		N		N	
Fes rub	P					
Gal apa						
Gal ver		P			P	P
Gle hed						
Her sph						
Hyp per						
Kna arv	P	P	P	P	P	P
Lol per						
Odo ver						
Phl ber				P		
Pla lan	P		P		P	P
Poa pra						
Poa tri						
Pot rep						
Ran rep						
Rum sp	N				N	
Sta syl						
Tar off		P	P	P	P	P
Tra pra	P					
Tri fla						
Tri pra						
Tri rep						
Ulm gla						
Urt dio	N					
Ver cha						
Vic sat						P
Vio hir						N

Table 5.6 Correlations between 44 Bibury Taxa and Gulf Stream Position for Series 7-8. (1966-1993) P = Positive correlation, N = negative correlation ($P<0.05$). A positive correlation indicates an increase in above-ground biomass (or % cover in the case of bare ground) associated with a more northerly Gulf Stream position.

	Autumn	Winter	Spring	Summer	Autumn & Winter	Spring & Summer
B.G	N			N		N
Litter		P		P		P
Ach mil						
Agr sto						
Alo pra						
Ani ste						
Ant syl						
Arr ela	N		N	N	N	N
Ave pub						
Bra pin						
Bro ere				N		
Cen nig		P	P			
Cir arv		N	N		N	N
Con arv	N					
Cru lae				N		
Dac glo	P					
Ely rep						
Fes aru						
Fes rub						
Gal apa						
Gal ver			N			
Gle hed						
Her sph				P		
Hyp per						
Kna arv	P	P	P		P	P
Lol per						
Odo ver						
Phl ber						
Pla lan		P				
Poa pra		N				
Poa tri						
Pot rep		P	P			P
Ran rep						
Rum sp		P		P		P
Sta syl	N			N		
Tar off						
Tra pra						
Tri fla						
Tri pra						
Tri rep						
Ulm gla						
Urt dio						
Ver cha	P			N		
Vic sat		P		P		
Vio hir			N			

5.3.3 Comparison between Gulf Stream position and performance of plant functional types, and the total vegetation biomass.

The full results of this analysis are listed in Appendix 7.

5.3.3.1 Significance of the results.

Six functional types were included in the analysis. For the comparison between the performance of plant functional types and Gulf Stream position in different seasons, four seasons were considered over a period of three years, for the two vegetation series. Therefore the total number of possible correlations is 6 x 4 x 3 x 2 = 144. At P<0.05, the expected number of significant correlations would be 7. 9 were actually observed.

For autumn and winter, and spring and summer combined, the total number of possible correlations is 6 x 2 x 3 x 2 = 72. At P<0.05, the expected number of significant correlations would be 4. 5 were actually observed.

In both cases, more correlations were actually observed than might be expected to occur by chance alone, although the number of observed correlations were only marginally greater than the expected. Tables 5.7 and 5.8 present a summary of the results.

Table 5.7 Comparison between Gulf Stream Position and plant functional groups and total above ground vegetation biomass for series 1-6. P = Positive Correlation, N = Negative Correlation. A positive relationship indicates an increase in biomass associated with a more northerly position of the Gulf Stream.

	Autumn	Winter	Spring	Summer	Autumn & Winter	Spring & Summer
C						
S						
R	N			N		
CR						
CS		P	P			
CSR						
TOTAL BIOMASS		P		P	P	P

Table 5.8 Comparison between Gulf Stream position and plant functional groups and total above ground vegetation biomass for series 7-8. P = Positive Correlation, N = Negative Correlation. A positive relationship indicates an increase in biomass associated with a more northerly position of the Gulf Stream.

	Autumn	Winter	Spring	Summer	Autumn & Winter	Spring & Summer
C						
S		P	P			
R						
CR	N	N	N			N
CS						
CSR						
TOTAL BIOMASS						

5.4 DISCUSSION

5.4.1 Comparison Between Gulf Stream Position and Meteorological Variables.

The results do not suggest a consistent relationship between Gulf Stream position and the frequency of weather variables throughout the year. Previous work on the relationship between Gulf Stream Northerliness and meteorological variables also indicates a variable pattern. Taylor (1995) compared Gulf Stream Northerliness with changes in atmospheric pressure and cyclone numbers over the Atlantic and around the British Isles. Comparisons were made for winter, spring, summer and autumn. In most cases, relationships detected using these variables were too weak to be statistically significant. However, spring and autumn appeared to be associated with an increase in atmospheric pressure and a decrease in cyclone numbers; while during summer and winter, a decrease in atmospheric presure and increase in cyclone numbers was observed. In summer and autumn, winds associated with a more northerly Gulf Stream tended to have a southerly component, indicating warmer conditions (Taylor, 1995).

Different metoerological variables were employed in this thesis to compare Gulf Stream position with weather. Rather than comparing the simple number of cyclones with Gulf Stream northerlines in any given season, here the number of days of cyclonic or anticyclonic weather in a given season was used. Variables such as temperature and rainfall were used in addition to mean sea level pressure. However, a similar pattern emerges from this analysis to that described by Taylor.

There are clear indications of a positive relationship between a more northerly Gulf Stream and an increase in anticyclonic weather in late summer and autumn (increased sea level pressure and anticyclonic weather in August, negative correlation with cyclonic weather in September).

However, in other months (January, February, April, June and July) there are suggestions of a negative relationship between Gulf Stream position and anticyclonic weather (positive relationships with westerly and cyclonic weather and rainfall, as well as negative relationships with anticyclonic weather).

A northerly Gulf Stream therefore appears to be associated with fewer cyclones in autumn, and increased numbers in summer and winter (although there is no evidence of reduced numbers in spring).

Over the year as a whole, a clear negative relationship with anticyclonic weather emerges.

A further method of establishing the effect of Gulf Stream position on terrestrial weather is to compare the relationships between Gulf Stream position and plant performance, and the relationship between those same plants and weather variables. The remainder of this chapter, and Chapter 6, will be devoted to this.

5.4.2 Relationships between Gulf Stream position and Bibury vegetation

Willis *et al* (1995) concluded that any changes in the overall productivity of the Bibury vegetation and the performance of certain individual species 'are mediated through changes in the frequency of anticyclonic weather. By implication, the latter act through variations in rainfall and temperature at critical periods which effectively extend or reduce the growing season'

The results presented in this thesis are more extensive than those given by Willis *et al.* (1995), which discussed prelimonary results for the 24 most common Bibury species in series 1-6. Of these 24 species, ten showed a positive relationship between above-ground biomass and a northerly Gulf Stream, three species showed a negative relationship, and ten species showed no relationship. It was notable that two out of the three species showing a negative relationship were annuals, while only one out of the ten species showing a positive relationship was an annual. Two out of the three species exhibiting a negative relationship tend to be restricted to moist or shaded habitats while none of those species exhibiting a positive response are so restricted (Table 5.9).

Table 5.9 Gulf Stream relations, life history and habitat affinity of the major Bibury species (from Willis *et al* 1995). Ecological data from Grime *et al* (1988)

Species	Relationship with Gulf Stream Northerliness	Life History	Restricted to moist or shaded habitats?
Ach mil	Positive	Perennial	No
Agr sto	Positive	Perennial	No
Bro ere	Positive	Perennial	No
Dac glo	Positive	Perennial	No
Ely rep	Positive	Perennial	No
Fes rub	Positive	Perennial	No
Gal ver	Positive	Perennial	No
Kna arv	Positive	Perennial	No
Pla lan	Positive	Perennial	No
Vic sat	Positive	Annual	No
Ani ste	Negative	Annual	No
Gal apa	Negative	Annual	Yes
Urt dio	Negative	Perennial	Yes
Ant syl	None	Biennial	Yes
Arr ela	None	Perennial	No
Cir arv	None	Perennial	No
Con arv	None	Perennial	No
Fes aru*	None	Perennial	No
Her sph	None	Biennial	Yes
Poa pra	None	Perennial	No
Ran rep	None	Perennial	Yes
Sta syl	None	Perennial	Yes
Tri fla	None	Perennial	No

**Festuca arundinacea* is listed in this table as exhibiting no relationship with Gulf Stream position. The species is listed in Table 5.5 as showing a negative relationship with Gulf Stream position. This difference can be accounted for by a difference in assessing the significance of correlations for species which exhibit autocorrelation. The significance of correlations for species listed in table 5.5 was extracted from published tables. The significance for correlations listed in Table 5.9 was determined exactly using Fisher's Z test (section 4.2.5). The negative correlation for *F.arundinacea* lies on the borderline of significance following correction for autocorrelation.

These associations and relationships were interpreted in terms of species' phenologies and drought tolerance:

"Species favoured by northerly tracks (of the Gulf Stream) include robust, perennial grasses (*Bromopsis erecta, Dactylis glomerata, Elytrigia repens* and *Festuca rubra*). At Bibury, and across Western Europe, these grow rapidly in early spring and are major contributors to community biomass. The similarly responsive dicotyledons (*Achillea millefolium, Galium verum, Knautia arvensis, Plantago lanceolata* and *Vicia sativa*) have relatively later phenologies and fairly deep root systems. Species declining in biomass with Gulf Stream Northerliness (*Anisantha sterilis, Galium aparine* and *Urtica dioica*) are more heterogeneous ecologically, but are either annuals and/or have field distributions associated with damp or shaded locations where water relations may be important.

"The circumstantial evidence is that variation in Gulf stream position is associated with changes in the relative abundance of components of the vegetation. Because these differ in phenology and rooting depth, moisture supply seemed to be implicated, though the precise mechanism is unclear " (Willis *et al.* 1995).

The additional results presented in this chapter both support and bolster the above interpretation and also allow a mechanism to be suggested for Gulf Stream/vegetation relationships. However, the nature of that mechanism is rather different to that implied by Willis *et al.* (1995).

The interpretation outlined above suggests, in part, that those species favoured by a northerly Gulf Stream are robust species with some degree of summer drought tolerance, while those species retarded by a northerly Gulf Stream are predominantly species of damp or shaded habitats or annuals, both of the latter may be susceptible to prolonged summer drought.

The relationships between meteorological variables and Gulf Stream position in August and September add some weight to this explanation. However, the more detailed investigation into Gulf Stream/weather relationships described in section 5.3 suggests a rather more complicated pattern than that suggested by Willis *et al.* (1995), with a northerly Gulf Stream tending to be negatively correlated with anticyclonic weather in summer and winter, and over the year as a whole. .

If a northerly Gulf Stream may actually be associated with more unsettled conditions in summer and winter, a different interpretation may be made of the results in Table 5.9 and Tables 5.5 and 5.6. Those species which are promoted by a northerly Gulf Stream tend to exhibit, at least to some extent, the competitive strategy (being robust, fast-growing perennials). While many of the species, such as *Dactylis glomerata*, may indeed possess some degree of drought tolerance, they are also the species that are best able to respond positively to conditions more favourable to plant growth. Those species which are retarded by a northerly Gulf Stream may exhibit, at least in part, the ruderal strategy (being annuals). They are therefore more likely to respond positively to any disturbance to the vegetation caused by summer drought associated with a more southerly Gulf Stream. This interpretation is consistent with the other analyses presented in this thesis which suggest that competitive species tend to be retarded by hot summers and cold winters, and by a high frequency of anticyclonic weather. The revised interpretation does not alter the validity of the statements made by Willis *et al.* (1995) and quoted above, but it does suggest an additional explanation for them.

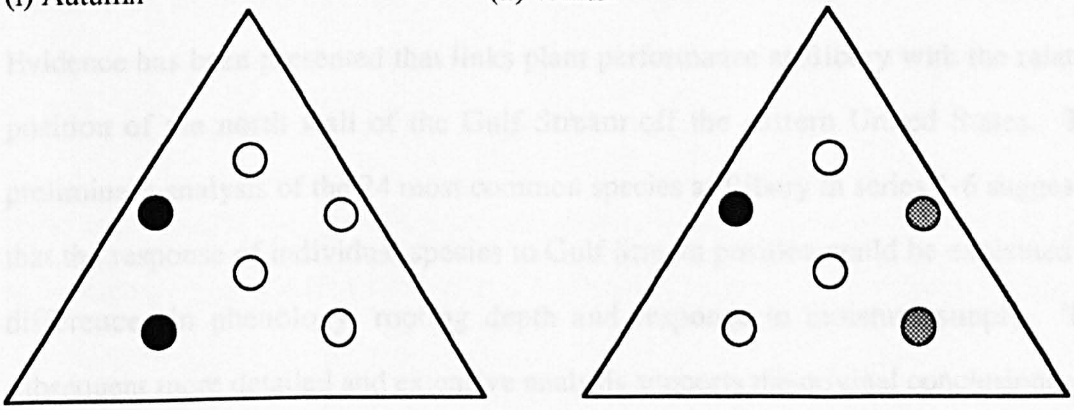
In short, the Bibury results are consistent with an interpretation that equates a northerly Gulf Stream with unsettled weather in winter and summer (mild winters and cool, wet summers) and settled weather in late summer and autumn.

5.4.3 Plant Functional Types, Total Vegetation Biomass, and Gulf Stream Position

The response of the six plant functional types represented at Bibury are shown diagrammatically in Figure 5.4. The results lend support to the interpretation offered above. The total vegetation biomass is positively correlated with Gulf Stream position. As shown in Chapters 3 and 4, the total vegetation biomass tends to increase following cooler, unsettled summers. Ruderal species are retarded by a northerly Gulf Stream. Again, as has been shown in Chapters 3 and 4, ruderal species tend to be retarded by unsettled conditions and promoted by a high frequency of anticyclonic weather in summer.

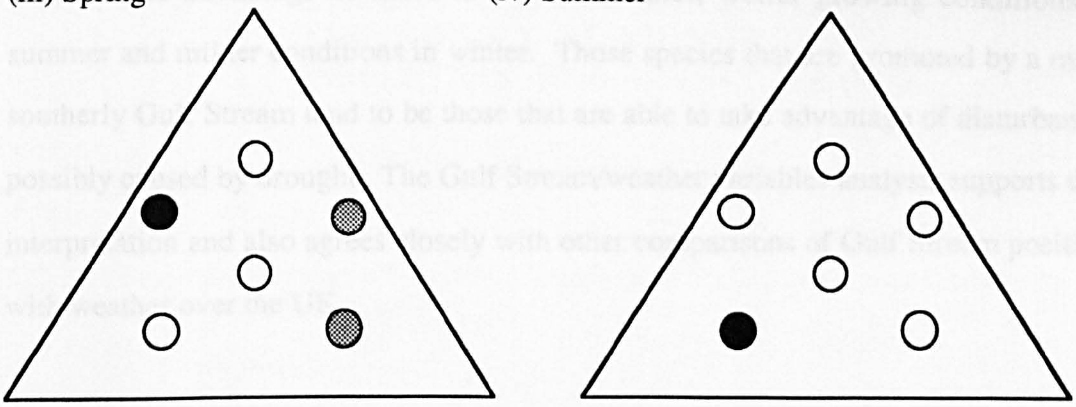
Figure 5.4 The Relationship Between the Performance of Plant Functional Types and Gulf Stream Northerliness. A full explanation of the triangle diagram is given in Appendix 1.

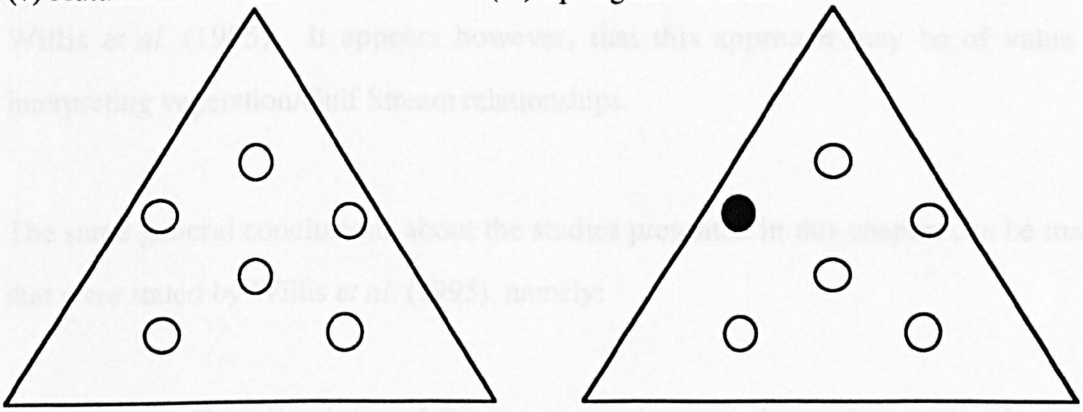
○ = No Response ▨ = Positive Response ● = Negative Response



(i) Autumn

(ii) Winter


(iii) Spring (iv) Summer


(v) Autumn and Winter (vi) Spring and Summer

5.4.4 Conclusions

Evidence has been presented that links plant performance at Bibury with the relative position of the north wall of the Gulf Stream off the eastern United States. The preliminary analysis of the 24 most common species at Bibury in series 1-6 suggested that the response of individual species to Gulf Stream position could be explained by differences in phenology, rooting depth and response to moisture supply. The subsequent more detailed and extensive analysis supports the original conclusions and broadly maintains the plant groupings (vigorous early growing grasses, deep rooted dicotyledons, and annual species) described in the original analysis. While moisture supply remains the most plausible explanation for changes in the relative abundance of components of the vegetation, an additional mechanism has been proposed to explain the observed results. The interpretation of the results of the second analysis rests on suggesting that those species are promoted by a more northerly Gulf Stream are best able to take advantage of more favourable, cooler, wetter growing conditions in summer and milder conditions in winter. Those species that are promoted by a more southerly Gulf Stream tend to be those that are able to take advantage of disturbance, possibly caused by drought. The Gulf Stream/weather variables analysis supports this interpretation and also agrees closely with other comparisons of Gulf Stream position with weather over the UK.

Discussion of plant functional type responses to Gulf Stream position was omitted from Willis *et al.* (1995). It appears however, that this approach may be of value in interpreting vegetation/Gulf Stream relationships.

The same general conclusions about the studies presented in this chapter can be made that were stated by Willis *et al.* (1995), namely:

"a) The overall productivity of Bibury vegetation and the performance of certain individual species are both linked indirectly to Gulf Stream displacements, and b) such changes are mediated through changes in the frequency of anticyclonic weather. By implication, the latter act through variations in rainfall and temperature at critical periods which effectively extend or reduce the growing season."

If the interpretation suggested above is correct, it should be possible to compare plant response to Gulf Stream position with plant response to individual weather variables and weather types and find similarities. Such a comparison is presented in Chapter 6.

CHAPTER 6. CLIMATE/PLANT RELATIONSHIPS IN THE BIBURY ROAD VERGES: SYNTHESIS AND CONCLUSIONS

6.1 Introduction

In previous chapters it has been demonstrated that non-random relationships exist between plant performance in the Bibury road verges, and three orders of meteorological variables: individual weather variables, such as sunshine and rainfall; weather types and seasonal anticyclonicity; and Gulf Stream northerliness.

In this chapter the similarities between vegetation response to the three levels of meteorological variables are explored. In particular, three questions generated by results in previous chapters are investigated:

1. Can vegetation response to settled and unsettled conditions described in Chapter 3 can be equated with vegetation responses to seasonal anticyclonicity, described in Chapter 4?

2. It has been noted in previous chapters that the response of plant functional types to weather variables tends to remain constant throughout the year i.e. Competitors tend to respond negatively to anticyclonic conditions in summer and in winter. Can a similar constant response be detected for individual taxa?

3. Can comparisons be made between the response of Bibury taxa to Gulf Stream northerliness and the response of Bibury taxa to the frequency of anticyclonic weather over the growing season which will shed light on the possible relationship between Gulf Stream northerliness and plant performance?

6.2 Comparison between vegetation response to settled and unsettled seasons and seasonal anticyclonicity

6.2.1 Methods

To avoid the problems discussed in Chapter 3 over the use of the terms 'good' and 'bad' to describe the weather in particular seasons, henceforth 'good' and 'bad' summers will be referred to as settled and unsettled summers respectively, and 'good' and 'bad' winters will be referred to as unsettled and settled winters respectively.

The responses of taxa to settled seasons and seasonal anticyclonicity for autumn, winter, spring, summer, and autumn and winter combined, and spring and summer combined, taken from Chapters 3 and 4 are listed in Tables 6.1 and 6.2. For those instances where taxa exhibited a response to both settled seasons and seasonal anticyclonicity, the sign of that response was compared. To allow a wider understanding of underlying relationships between different meteorological variables, those relationships which, although significant at $P< 0.05$ under standard correlation procedure, are not significant because of autocorrelation, have been included in the tables. Such relationships are shown in brackets in Tables 6.1 and 6.2. The distribution of positive and negative responses was assessed using a Chi Squared Test.

Table 6.1 **Comparison of the response of Bibury taxa to settled weather and seasonal anticyclonicity for Series 1-6.** P = Positive response, N = Negative response.

	Settled Weather						Anticyclonicity					
	Au	Wi	Sp	Su	A+W	S+S	Au	Wi	Sp	Su	A+W	S+S
Bare Ground		N			N				P			P
Litter	N		P	P		P		P		N		
Ach mil			P					P			P	
Agr sto		N	P		N						P	
Alo pra	P	N			P			P			P	
Ani ste		N		P		P				P	P	
Ant syl										(P)		
Arr ela	N		P			P						
Ave pub												
Bra pin												
Bro ere	N	P	N	N	P	N			N	N	N	
Cen nig												
Cir arv	P	N	P	N			P					
Con arv			P									
Cru lae			P					(P)		N	P	N
Dac glo		P	P	N	P	N		P	N	N		N
Ely rep	P											
Fes aru	N		N	P	N	P	N			(P)		P
Fes rub		P	N		P	N				N		N
Gal apa				N								
Gal ver			N		P			P		N		N
Gle hed	P	P		N	P	N		P	P	P		N
Her sph												
Hyp per		P						P				
Kna arv				N				P		N	N	
Lol per												
Odo ver			P		P	P	N		P		P	
Phl ber	P	N	P	P		P					P	(P)
Pla lan	N									N		
Poa pra	P	N			P			P				
Poa tri												
Pot rep		P										
Ran rep			P	N		N	P		N			N
Rum sp		N								P	(N)	P
Sta syl		N	P									
Tar off			P	P	N	P			P	N		
Tra pra						P						
Tri fla	P					N	N			N		N
Tri pra			P			P				N		
Tri rep				N		N			N			(N)
Ulm gla									P			
Urt dio										P		(P)
Ver cha			P						N	N		(N)
Vic sat			N			P	P		N	N		N
Vio hir			N									

Table 6.2 Comparison of the Response of Bibury Taxa to Settled Weather and Seasonal Anticyclonicity for Series 7-8. P = Positive response, N = Negative response.

	Settled Weather						Anticyclonicity					
	Au	Wi	Sp	Su	A+W	S+S	Au	Wi	Sp	Su	A+W	S+S
Bare Ground		P			N		N	N	P			P
Litter					P						P	
Ach mil	N			P		P			P	P		P
Agr sto		N	N		N			P				
Alo pra									N			
Ani ste												
Ant syl												
Arr ela		N	P			P		N	P	(P)		
Ave pub	P	N					N		N		(P)	
Bra pin								P				
Bro ere	P		N	P	N	P		P		(P)	(P)	
Cen nig			P			P		P	P			P
Cir arv				P		P		P		P		P
Con arv	N	N	P	P	N		N		P	P	N	
Cru lae	P	P	N			N			N			(N)
Dac glo		P	P	N		P	N		N	N	P	N
Ely rep				P	N	P				P		P
Fes aru			P								N	
Fes rub	P	N	P	P	N	P	P					(P)
Gal apa								(N)	(P)			N
Gal ver			N			N	(N)				N	
Gle hed		N	P		N	P						
Her sph	P	P	P		P			P	N		P	(P)
Hyp per											(N)	
Kna arv		P	P			N		(P)				N
Lol per			N			P		P	N			
Odo ver												N
Phl ber							P					
Pla lan		N	P	P	N	P	N	P		N		
Poa pra		N	N									
Poa tri												
Pot rep			P		P	P		P		P	(P)	N
Ran rep	P	N	P		N	P		P				
Rum sp		N	P	P	N	P						
Sta syl		N			N							(P)
Tar off		N	P	P					P		(P)	
Tra pra				N			P		P			
Tri fla												
Tri pra						P	(P)		P			
Tri rep	P	N										N
Ulm gla									P			
Urt dio												
Ver cha	N	N	P		N	P	P		P	P		P
Vic sat		P	P	P	N	P		P			(P)	
Vio hir									N			

6.2.2 Results

For each individual season there were more instances of taxa exhibiting the same response to settled weather and high anticyclonicity than the opposite response. The results for autumn, winter, spring and summer are amalgamated in Table 6.3. The number of occurrences of taxa exhibiting the same response to settled weather and high anticyclonicity is twice that of the number of occurrences of opposite responses. This difference is significant at P = 0.014.

Table 6.3 Contingency table comparing the response of Bibury taxa to seasonal anticyclonicity and settled conditions in autumn, winter, spring and summer. Numbers refer to the number of occurrences of the particular combination of responses in Tables 6.1 and 6.2

	Seasonal Anticyclonicity	
	+	-
Settled +	22	10
Settled -	9	16

A similar pattern is evident with the results for autumn and winter combined and spring and summer combined. The number of occurrences of taxa exhibiting the same response to settled conditions and high anticyclonicity is almost four times that of the number of occurrences of opposite responses. This difference is significant at P = 0.003.

Table 6.4 Contingency table comparing the response of Bibury taxa to seasonal anticyclonicity and settled conditions in autumn and winter combined, and spring and summer combined. Numbers refer to the number of occurrences of the particular combination of responses in Tables 6.1 and 6.2

	Seasonal Anticyclonicity	
	+	-
Settled +	14	4
Settled -	2	8

6.2.3 Discussion

It is clear that the two indices of seasonal weather conditions are comparable. Vegetation response to seasonal anticyclonicity can indeed be equated with its response to settled or unsettled conditions.

6.3 Comparison of the response of Bibury taxa to weather throughout the year.

6.3.1 Methods

The data for spring and summer combined and autumn and winter combined in Tables 6.1 and 6.2 were used to compare the response of individual taxa to weather throughout the year. The number of taxa which showed the same or opposite responses to settled weather or high anticyclonicity in the two periods of the year was assessed using a Chi-Squared test.

6.3.2 Results

The results of the comparisons are shown in Tables 6.5 and 6.6.

Table 6.5 Contingency table comparing the response of Bibury taxa to seasonal anticyclonicity in autumn and winter combined, and spring and summer combined Numbers refer to the number of occurrences of the particular combination of responses in Tables 6.1 and 6.2

	Autumn and Winter	
	+	-
Spring and +	5	9
Summer -	8	2

The difference between the observed distribution and that which might be expected to occur by chance is significant at P = 0.04. A greater number of occurrences was found of taxa which exhibit opposite responses than the same response.

Table 6.6 Contingency table comparing the response of Bibury taxa to settled weather in autumn and winter combined, and spring and summer combined Numbers refer to the number of occurrences of the particular combination of responses in Tables 6.1 and 6.2

	Autumn and Winter	
	+	-
Spring and +	2	11
Summer -	4	0

There are insufficient entries in the table to enable a Chi-Squared test to be performed. However, again there is a greater number of occurrences of which exhibit opposite responses than the same response.

6.3.3 Discussion

It is clear from Tables 6.5 and 6.6 that in the majority of cases where taxa exhibit a response to both settled weather and high anticyclonicity in both autumn and winter, and spring and summer, the response tends to be opposite between the two combined seasons. This is in contrast to the more constant response of plant functional types throughout the year.

A similar phenomenon in which the behavior of individual species is in contrast to the behavior of aggregated groups occurs within the Park Grass Experiment (Silvertown 1980) where despite some notable changes in the species composition of the experimental plots, the ratios of the biomass of three separate guilds (grasses: legumes:'other species') has remained at equilibrium within the plots since 1900. However, in the Park Grass Experiment, the three guilds were found to be positively correlated with each other *within* plots, whereas at Bibury this is not necessarily the case.

6.4 Comparison between vegetation response to seasonal anticyclonicity and Gulf Stream position

6.4.1 Methods

It was noted in Chapter 5 that previous studies on the relationship between Gulf Stream position and the weather over the UK indicated that a more northerly Gulf Stream is associated with reduced cyclone numbers in spring and autumn, and increased numbers in winter and summer. The new comparisons between Gulf Stream northerliness and terrestrial weather variables reported in Chapter 5 broadly support this view, although no evidence was found of reduced cyclone numbers or increased atmospheric pressure in spring.

If such relationships do exist it would be reasonable to assume that the response of taxa at Bibury to a more northerly Gulf Stream may be reflected in associated relationships between those same taxa and different meteorological variables. In this section such comparisons are made. Unfortunately the number of occurrences of taxa showing responses to Gulf Stream northerliness and the different meteorological variables in the same season was too low to allow statistical analysis. To determine underlying patterns, two comparisons are made; one general and one detailed.

Firstly, in Tables 6.7 and 6.8, the response of taxa to Gulf Stream northerliness has been compared with seasonal anticyclonicity in autumn and winter combined and in spring and summer combined. Because the sign of response to Gulf Stream northerliness remained constant over different seasons for all Bibury species within the two vegetation series (with one exception), each taxon has been given a single general classification according to its response to Gulf Stream northerliness. This allows a broad analysis to be carried out, although responses in individual seasons are not identified.

Secondly, a more detailed comparison is shown in Tables 6.9 - 6.12. In these tables, the response of taxa to Gulf Stream northerliness is compared directly with response to seasonal anticyclonicity or settled or unsettled weather for each season.

6.4.2 Results

The response of taxa to Gulf Stream northerliness and different meteorological variables is compared in Tables 6.7 - 6.12.

Table 6.7. Summary of the responses of Bibury taxa to Gulf Stream position and seasonal anticyclonicity for vegetation series 1-6. Gulf = Gulf Stream northerliness index. P = Positive correlation, N = Negative correlation. Entries in brackets indicate correlations not significant after correction for autocorrelation, but significant under standard correlation procedure at P<0.05.

	GULF	ANTICYCLONICITY					
		Aut	Win	Spr	Sum	Au+Wi	Sp+Su
Bare Ground	N			P			P
Litter			P		N		
Ach mil	P		P			P	
Agr sto	P					P	
Alo pra	N		P			P	
Ani ste	N				P	P	
Ant syl					(P)		
Arr ela							
Ave pub							
Bra pin							
Bro ere	P			N	N	N	
Cen nig							
Cir arv		P					
Con arv							
Cru lae	P		(P)		N	P	N
Dac glo	(P)		P	N	N		N
Ely rep	P						
Fes aru	N	N			(P)		P
Fes rub	P				N		N
Gal apa	N						
Gal ver	P		P		N		N
Gle hed	(P)		P	P	P		N
Her sph							
Hyp per			P				
Kna arv	P		P		N	N	
Lol per							
Odo ver		N		P		P	
Phl ber	P					P	(P)
Pla lan	P				N		
Poa pra			P				
Poa tri							
Pot rep							
Ran rep		P		N			N
Rum sp	N				P	(N)	P
Sta syl							
Tar off	P			P	N		
Tra pra	P						
Tri fla		N			N		N
Tri pra	(P)				N		
Tri rep	(P)			N			(N)
Ulm gla				P			
Urt dio	N				P		(P)
Ver cha	(P)			N	N		(N)
Vic sat	P	P		N	N		N
Vio hir	N						

Table 6.8. Summary of the responses of Bibury taxa to Gulf Stream position and seasonal anticyclonicity for vegetation series 7-8. Gulf = Gulf Stream northerliness index. P = Positive correlation, N = Negative correlation. Entries in brackets indicate correlations not significant after correction for autocorrelation, but significant under standard correlation procedure at $P<0.05$.

	GULF	ANTICYCLONICITY					
		Au	Wi	Sp	Su	Au+Wi	Sp+Su
Season							
Bare Ground	N	N	N	P			P
Litter	P					P	
Ach mil				P	P		P
Agr sto	(N)		P				
Alo pra				N			
Ani ste							
Ant syl							
Arr ela	N		N	P	(P)		
Ave pub	(N)	N		N		(P)	
Bra pin			P				
Bro ere	N		P		(P)	(P)	
Cen nig	P		P	P			P
Cir arv	N		P		P		P
Con arv	N	N		P	P	N	
Cru lae	N			N			(N)
Dac glo	P	N		N	N	P	N
Ely rep					P		P
Fes aru						N	
Fes rub		P					(P)
Gal apa			(N)	(P)			N
Gal ver	N	(N)				N	
Gle hed	(P)						
Her sph	P		P	N		P	(P)
Hyp per	(P)					(N)	
Kna arv	P		(P)				N
Lol per			P	N			
Odo ver							N
Phl ber		P					
Pla lan	P	N	P		N		
Poa pra	N						
Poa tri							
Pot rep	P		P		P	(P)	N
Ran rep	(P)		P				
Rum sp	P						
Sta syl	N						(P)
Tar off				P		(P)	
Tra pra		P		P			
Tri fla							
Tri pra	(P)	(P)		P			
Tri rep							N
Ulm gla				P			
Urt dio	(P)						
Ver cha		P		P	P		P
Vic sat	P		P			(P)	
Vio hir	N			N			

Table 6.9. Summary of the responses of Bibury taxa to Gulf Stream position and seasonal anticyclonicity for vegetation series 1-6. P = Positive correlation, N = Negative correlation. Entries in brackets indicate correlations not significant after correction for autocorrelation, but significant under standard correlation procedure at $P<0.05$.

	Anticyclonicity				Gulf Stream			
	Au	Wi	Sp	Su	Au	Wi	Sp	Su
B.G			P		N		N	N
Litter		P		N				
Ach mil		P					P	P
Agr sto								
Alo pra		P				N	N	
Ani ste				P	N	N		
Ant syl				(P)				
Arr ela								
Ave pub								
Bra pin								
Bro ere			N	N		P		
Cen nig								
Cir arv	P							
Con arv								
Cru lae		(P)		N	P	P		
Dac glo		P	N	N				
Ely rep							P	
Fes aru	N			(P)	N		N	
Fes rub				N	P			
Gal apa								
Gal ver		P		N	(P)	P		
Gle hed		P	P	P			(P)	(P)
Her sph								
Hyp per		P						
Kna arv		P		N	P	P	P	P
Lol per								
Odo ver	N		P					
Phl ber								P
Pla lan				N	P		P	
Poa pra		P						
Poa tri								
Pot rep								
Ran rep	P		N					
Rum sp				P	N			
Sta syl								
Tar off			P	N		P	P	P
Tra pra					P			
Tri fla	N			N				
Tri pra				N	(P)			
Tri rep			N					
Ulm gla			P					
Urt dio				P	N			
Ver cha			N	N	(P)			
Vic sat	P		N	N				
Vio hir								

Table 6.10. Summary of the responses of Bibury taxa to Gulf Stream position and seasonal anticyclonicity for vegetation series 7-8. P = Positive correlation, N = Negative correlation. Entries in brackets indicate correlations not significant after correction for autocorrelation, but significant under standard correlation procedure at P<0.05.

	Anticyclonicity				Gulf Stream			
	Au	Wi	Sp	Su	Au	Wi	Sp	Su
B.G	N	N	P		N			N
Litter						P		P
Ach mil			P	P				
Agr sto		P			N			
Alo pra			N					
Ani ste								
Ant syl								
Arr ela		N	P	(P)	N		N	N
Ave pub	N		N					
Bra pin		P						
Bro ere		P		(P)				N
Cen nig		P	P			P	P	
Cir arv		P		P		N	N	
Con arv	N		P	P	N			
Cru lae			N		(N)			N
Dac glo	N		N	N	P	(P)	(P)	
Ely rep				P				
Fes aru								
Fes rub	P							
Gal apa		(N)	(P)					
Gal ver	(N)						N	
Gle hed					(P)		(P)	(P)
Her sph		P	N					P
Hyp per						(P)		(P)
Kna arv		(P)			P	P	P	(P)
Lol per		P	N					
Odo ver								
Phl ber	P							
Pla lan	N	P		N		P		
Poa pra						N		
Poa tri								
Pot rep		P		P	(P)	P	P	
Ran rep		P						
Rum sp						P		P
Sta syl					N	(N)		N
Tar off			P			(P)		
Tra pra	P		P					
Tri fla								
Tri pra	(P)		P					
Tri rep								
Ulm gla			P					
Urt dio								
Ver cha	P		P	P	P			N
Vic sat		P				P		P
Vio hir			N				N	

Table 6.11. Summary of the responses of Bibury taxa to Gulf Stream position and settled weather for vegetation Series 1-6. P = Positive correlation, N = Negative correlation. Entries in brackets indicate correlations not significant after correction for autocorrelation, but significant under standard correlation procedure at P<0.05.

	Settled Season				Gulf Stream			
	Au	Wi	Sp	Su	Au	Wi	Sp	Su
B.G		N			N		N	N
Litter	N		P	P				
Ach mil			P				P	P
Agr sto		N	P					
Alo pra	P	N				N	N	
Ani ste		N		P	N	N		
Ant syl								
Arr ela	N		P					
Ave pub								
Bra pin								
Bro ere	N	P	N	N		P		
Cen nig								
Cir arv	P	N	P	N				
Con arv			P					
Cru lae			P		P	P		
Dac glo		P	P	N				
Ely rep	P						P	
Fes aru	N		N	P	N		N	
Fes rub		P	N		P			
Gal apa				N				
Gal ver			N		(P)	P		
Gle hed	P	P		N			(P)	(P)
Her sph								
Hyp per		P						
Kna arv				N	P	P	P	P
Lol per								
Odo ver			P					
Phl ber	P	N	P	P				P
Pla lan	N				P		P	
Poa pra	P	N						
Poa tri								
Pot rep		P						
Ran rep			P	N				
Rum sp		N			N			
Sta syl		N	P					
Tar off			P	P		P	P	P
Tra pra					P			
Tri fla			P					
Tri pra				N	(P)			
Tri rep	P							
Ulm gla								
Urt dio					N			
Ver cha		P	P		(P)			
Vic sat			N					
Vio hir			N					

Table 6.9. Summary of the responses of Bibury taxa to Gulf Stream position and settled seasons for vegetation series 7-8. P = Positive correlation, N = Negative correlation. Entries in brackets indicate correlations not significant after correction for autocorrelation, but significant under standard correlation procedure at P<0.05. An asterisk indicates conflict between the response of taxa to individual weather variables.

	Settled Season				Gulf Stream			
	Au	Wi	Sp	Su	Au	Wi	Sp	Su
B.G		N			N			N
Litter						P		P
Ach mil	N			P				
Agr sto		N	N		N			
Alo pra								
Ani ste								
Ant syl				*				
Arr ela		N	P		N		N	N
Ave pub	P	N						
Bra pin								
Bro ere	P		N	P				N
Cen nig			P			P	P	
Cir arv				P		N	N	
Con arv	N	N	P	P	N			
Cru lae	P	P	N		(N)			N
Dac glo		P	P	N	P	(P)	(P)	
Ely rep				P				
Fes aru			P					
Fes rub	P	N	P	P				
Gal apa								
Gal ver			N				N	
Gle hed		N	P		(P)		(P)	(P)
Her sph	P	P	P					P
Hyp per						(P)		(P)
Kna arv		P	P		P	P	P	(P)
Lol per			N					
Odo ver								
Phl ber								
Pla lan		N	P	P		P		
Poa pra		N	N			N		
Poa tri								
Pot rep			P		(P)	P	P	
Ran rep	P	N	P					
Rum sp		N	P	P		P		P
Sta syl		N			N	(N)		N
Tar off		N	P	P		(P)		
Tra pra				N				
Tri fla								
Tri pra	P	N						
Tri rep								
Ulm gla								
Urt dio								
Ver cha	N	N	P		P			N
Vic sat		P	P	P		P		P
Vio hir							N	

6.4.3 Discussion

6.4.3.1 General relationships between Gulf Stream position and seasonal anticyclonicity

Table 6.13 compares the response of Bibury Taxa to Gulf Stream northerliness and seasonal anticyclonicity for autumn, winter, spring and summer.. Each cell displays the number of occurrences of each particular combination in Tables 6.7 and 6.8. The response to Gulf Stream northerliness is therefore the general classification, as shown in Tables 6.7 and 6.8.

Table 6.13 Comparison of the response of Bibury Taxa to Gulf Stream northerliness for autumn, winter, spring and summer.

AUTUMN	Anticyclonicity	
Gulf Stream northerliness	+	-
+	2	0
-	2	5

WINTER	Anticyclonicity	
Gulf Stream Position	+	-
+	13	4
-	0	2

SPRING	Anticyclonicity	
Gulf Stream Position	+	-
+	4	6
-	5	3

SUMMER	Anticyclonicity	
Gulf Stream Position	+	-
+	2	8
-	13	0

This comparison supports, in part, the suggestions made in Chapter 5 that in autumn a northerly Gulf Stream is associated with an increased frequency of anticyclonic weather, while in summer, a more northerly Gulf Stream is associated with more unsettled conditions. However, in this analysis, a northerly Gulf Stream also appears to be associated with an increased frequency of anticyclonic weather in winter, while in spring there is a tendency towards a northerly Gulf Stream to be associated with less settled conditions. These results suggest an affinity between the response of taxa to Gulf Stream northerliness in autumn and winter, and in spring and summer.

Table 6.14, partly taken from Willis *et al.* (1995) and discussed in detail in Chapter 5, is reproduced below with the addition of information on taxa responses to seasonal anticyclonicity (significant at $P<0.05$ after correction for autocorrelation).

Table 6.14 Relationship to Gulf Stream Position, Seasonal Anticyclonicity, Life History and Habitat Affinity of the Major Bibury Species. Ecological data from Grime *et al.*(1988)

Species	Relationship with Gulf Stream northerliness	Life Span	Moist or shaded habitats	Frequency of Anti -cyclonic weather in spring & summer	Frequency of Anti-cyclonic weather in autumn & winter
Ach mil	Positive	Perennial	No	-	P
Agr sto	Positive	Perennial	No	-	-
Bro ere	Positive	Perennial	No	N	-
Dac glo	Positive	Perennial	No	N	-
Ely rep	Positive	Perennial	No	-	-
Fes rub	Positive	Perennial	No	N	-
Gal ver	Positive	Perennial	No	N	-
Kna arv	Positive	Perennial	No	-	P
Pla lan	Positive	Perennial	No	-	-
Vic sat	Positive	Annual	No	N	P
Ani ste	Negative	Annual	No	P	P
Fes aru	None	Perennial	No	P	-
Gal apa	Negative	Annual	Yes	-	-
Urt dio	Negative	Perennial	Yes	P	-
Ant syl	None	Biennial	Yes	-	-
Arr ela	None	Perennial	No	-	-
Cir arv	None	Perennial	No	-	-
Con arv	None	Perennial	No	-	-
Her sph	None	Biennial	Yes	-	-
Poa pra	None	Perennial	No	-	-
Ran rep	None	Perennial	Yes	N	-
Sta syl	None	Perennial	Yes	-	-
Tri fla	None	Perennial	No	N	-

Taxa are classified in Table 6.14 according to their response to Gulf Stream northerliness. An attempt was made in Chapter 5 to explain the responses of the most common Bibury species to Gulf Stream northerliness in terms of life span and whether or not they were restricted to moist or shaded habitats. This was partially successful in that a cohesive explanation could be given for those common taxa which showed a relationship with Gulf Stream position, but it did not explain why the remaining taxa showed no relationship with Gulf Stream position.

A much clearer and more comprehensive explanation is suggested in Table 6.10 by comparing response to Gulf Stream position with response to spring and summer anticyclonicity. All but three of the common species showing a positive response to Gulf Stream northerliness also show a negative response to spring and summer anticyclonicity. Three out of the four species showing a negative response to Gulf Stream northerliness show a positive response to spring and summer anticyclonicity (including *Urtica dioica* which previously did not appear to fit with the other negative Gulf Stream species). In all but two cases, where species show no relationship with Gulf Stream northerliness they also show no relationship with spring and summer anticyclonicity.

No clear link between Gulf Stream northerliness and anticyclonicity in autumn and winter were apparent for these common Bibury species.

The results of this analysis support the hypothesis that the relationship between Gulf Stream northerliness and terrestrial weather varies over the year. However there are a number of shortcomings to the method of analysis adopted here. Firstly, the comparisons between Gulf Stream northerliness and anticyclonicity are not direct. A single response to Gulf Stream northerliness has been assigned to each taxa for the whole year regardless of whether that taxa actually exhibited a response in all seasons. Secondly, the different responses in autumn and winter and spring and summer may simply reflect the finding in section 6.3 that taxa tend to exhibit opposite responses to weather in these two periods of the year.

6.4.3.2 Detailed comparison of Gulf Stream northerliness, seasonal anticyclonicity and settled weather for individual seasons.

This analysis allows direct comparisons to be made between the response of taxa to Gulf Stream northerliness and seasonal anticyclonicity, and settled and unsettled weather. As mentioned above, the number of occurrences of taxa showing responses to Gulf Stream northerliness and the meteorological variables in the same season was too low to allow statistical analysis. Table 6.15 compares Gulf Stream northerliness with seasonal anticyclonicity.

Table 6.15 Comparison of Gulf Stream northerliness and seasonal anticyclonicity in autumn, winter, spring and summer. The numbers in the cells refer to the number of occurrences of the particular combination of responses in Tables 6.9 and 6.10. Figures in brackets refer to the total number of occurrences, including those not significant after correction for autocorrelation, but significant under standard correlation procedure at $P<0.05$.

		Gulf Stream northerliness			
		+	-		
Anticyclonicity	+	1	0	6(8)	2
	-	1	3	0	0
		Autumn		Winter	
		2(3)	2	0(1)	1(2)
		0(1)	1	2	0
		Spring		Summer	

These comparisons again support the hypothesis that a northerly Gulf Stream is associated with an increased frequency of anticyclonic weather in spring and autumn, and a decreased frequency in summer. However, as in the analysis described in section 6.4.3.1, a northerly Gulf Stream in winter also appears to be associated with an increased frequency of anticyclonic weather.

Table 6.16 compares Gulf Stream northerliness with the frequency of settled weather in autumn, winter, spring and summer.

Table 6.16 Comparison of Gulf Stream northerliness and settled weather in autumn, winter, spring and summer. The numbers in the cells refer to the number of occurrences of the particular combination of responses in Tables 6.11 and 6.12. Figures in brackets refer to the total number of occurrences, including those not significant after correction for autocorrelation, but significant under standard correlation procedure at $P<0.05$.

Gulf Stream northerliness

Settled weather	+	-
+	2(3)	0(1)
-	2	0

Autumn

Settled weather	+	-
+	6(7)	0
-	2(3)	1(2)

Winter

Settled weather	+	-
+	5(7)	1
-	0	3

Spring

Settled weather	+	-
+	4	1
-	1(2)	0

Summer

The results of this analysis for autumn and summer are not as clear as that those for seasonal anticyclonicity. However, a northerly Gulf Stream in spring appears to be associated with a higher frequency of settled weather, as it also appears to be in winter.

From the results presented in this chapter, it appears that a northerly Gulf Stream can be equated with higher frequencies of anticyclonic weather in autumn, winter and spring, and reduced frequencies in summer. Apart from the winter relationships, these agree with previous findings by Taylor (1995). It must be stressed, however, that these conclusions are not based on statistically significant relationships (in common with those of Taylor). In this thesis it has been demonstrated that relationships exist between Gulf Stream position, terrestrial weather, and the performance of biological systems. However, it is apparent that extensive further work is needed to establish the mechanisms that lie behind the observed relationships

In Willis *et al.*(1995) it was suggested that those taxa which exhibited a positive response to a more northerly Gulf Stream tend to be robust, vigorous perennials capable of early growth and some drought tolerance. In this thesis it is suggested that, in addition, taxa which respond positively to a northerly Gulf Stream tend to be those which are also favoured by more unsettled conditions in summer. The two explanations are by no means mutually exclusive. Indeed, robust perennials, may show drought tolerance in late summer and autumn *and* have the ability to respond positively and gain competitive advantage from favourable conditions earlier in the growing season (such as wet weather in early-mid summer and/or warm, sunny weather in spring).

6.5 A model of plant functional types and weather

The results of the correlations between plant functional types and weather variables are shown in Tables 6.17 and 6.18

Table 6.17 **Comparison of the response of plant functional types and the total shoot biomass to settled weather and seasonal anticyclonicity for series 1-6.** P = Positive response, N = Negative response.

	Settled Weather						Anticyclonicity					
	Au	Wi	Sp	Su	A+W	S+S	Au	Wi	Sp	Su	A+W	S+S
C			P	N		N			N	N		N
S			P		P	P				N	P	
R				P		P				P		P
CR			P			P			N			
CS	N	P		N	P	N	N			N		N
CSR			N			N				N		N
ALL			P	N		N			N	N		N

Table 6.18 **Comparison of the response of plant functional types and the total shoot biomass to settled weather and seasonal anticyclonicity for series 7-8.** P = Positive response, N = Negative response.

	Settled Weather						Anticyclonicity					
	Au	Wi	Sp	Su	A+W	S+S	Au	Wi	Sp	Su	A+W	S+S
C								N				
S			P	P		P		P	*			P
R			P				*					
CR	P		N		P				N			
CS	P	N	N		N					N		
CSR		N		N		P						
ALL		P	N	N	P	N						

The results of correlations between individual Bibury Taxa and weather variables suggest much variation in taxon response, whereas a more or less coherent picture emerges from the results of correlations between plant functional type and weather variables.

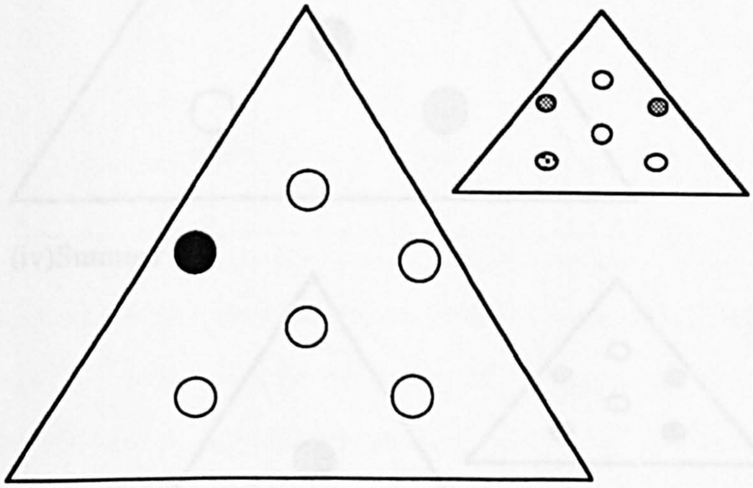
Figure 6.1 summarises plant functional type responses to weather. The figure amalgamates information from functional type response to seasonal anticyclonicity and to individual meteorological variables.

Figure 6.1 Plant functional type response to weather. The figure amalgamates information on functional type responses to seasonal anticyclonicity and individual weather types. A positive response indicates a positive response to high anticyclonicity and/or settled weather. The large triangles represent results from vegetation series 1-6. The small triangles represent results from vegetation series 7-8.

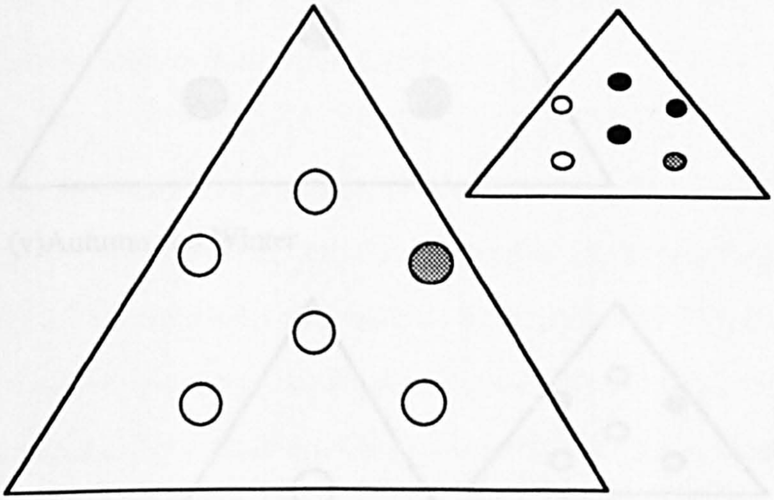
○ = No Response ◍ = Positive Response ● = Negative Response

▨ = Conflict between different weather-types

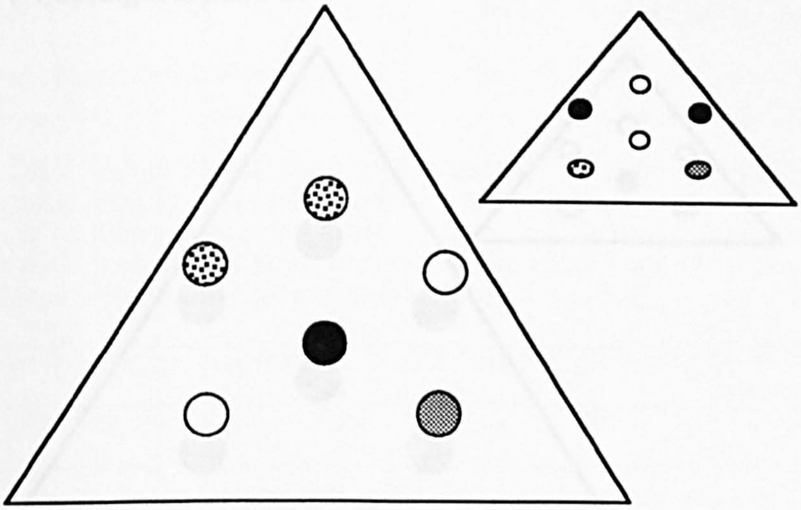
(i)Autumn



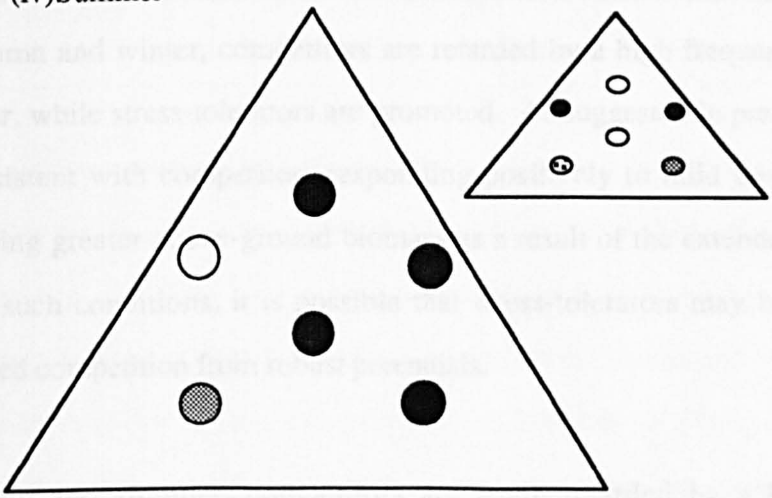
(ii)Winter



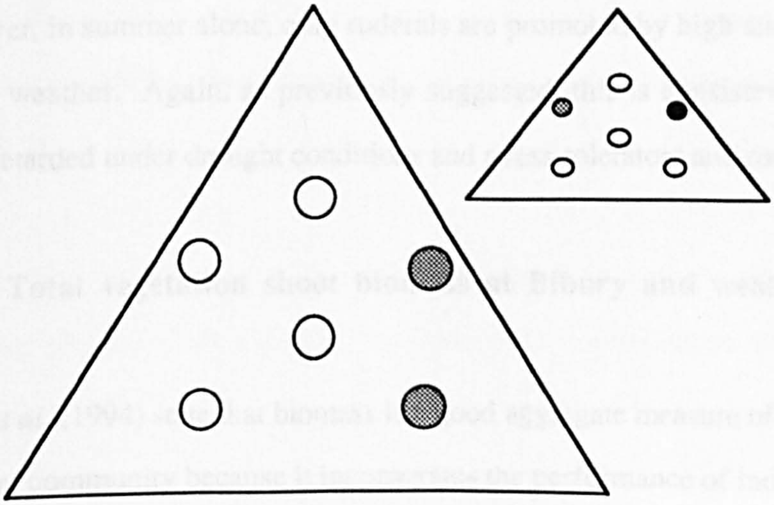
(iii)Spring



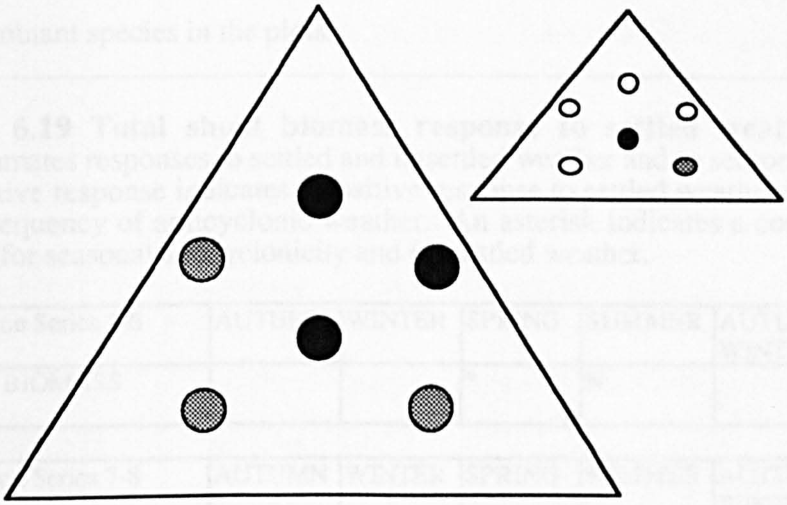
(iv)Summer



(v)Autumn and Winter



(vi)Spring and Summer



In autumn and winter, competitors are retarded by a high frequency of anticyclonic weather, while stress-tolerators are promoted. As suggested in previous chapters, this is consistent with competitors responding positively to mild unsettled winters and producing greater above-ground biomass as a result of the extended growing season. Under such conditions, it is possible that stress-tolerators may be retarded through increased competition from robust perennials.

In spring and summer, competitors are again retarded by a high frequency of anticyclonic weather, while both ruderal species and stress-tolerators are promoted. However, in summer alone, only ruderals are promoted by high anticyclonicity and/or settled weather. Again, as previously suggested, this is consistent with competitors being retarded under drought conditions and stress-tolerators and ruderals advantaged.

6.6 Total vegetation shoot biomass at Bibury and weather

Dodd *et al*. (1994) state that biomass is a good aggregate measure of the performance of the plant community because it incorporates the performance of individual species and guilds. It is also a measure of plant community performance that allows comparison between the performance of different plant communities, despite differing species composition. And it is also a comparable measure to the yield of agricultural crops. However, it is a measure that, at Bibury, is largely determined by the performance of the dominant species in the plots.

Table 6.19 Total shoot biomass response to settled weather. The table amalgamates responses to settled and unsettled weather and to seasonal anticyclonicity. A positive response indicates a positive response to settled weather and/or a relatively high frequency of anticyclonic weather. An asterisk indicates a conflict between the results for seasonal anticyclonicity and for settled weather.

Vegetation Series 1-6	AUTUMN	WINTER	SPRING	SUMMER	AUTUMN & WINTER	SPRING & SUMMER
TOTAL BIOMASS			*	N		N

Vegetation Series 7-8	AUTUMN	WINTER	SPRING	SUMMER	AUTUMN & WINTER	SPRING & SUMMER
TOTAL BIOMASS		P	N	N	P	N

In both series, total plant biomass is reduced by a high frequency of anticyclonicity or settled weather in spring and summer. This can be equated directly with the findings of Silvertown *et al.*(1994), that rainfall over the growing season is positively correlated with productivity in the Park Grass plots. It is reasonable to assume that the performance of the vegetation in spring and summer at Bibury can also be linked directly to moisture supply. In plots 1-6, total biomass is negatively correlated with anticyclonicity in spring, but positively correlated with settled weather. This conflict may result from robust perennial species, such as *Dactylis glomerata* being promoted by warm temperatures in early spring, but being retarded by drought in late spring (see Chapter 3).

The total vegetation biomass is promoted by high anticyclonicity in winter in plots 7-8. This may partly reflect a higher incidence of stress-tolerators and ruderals in these plots.

6.7 Weather and the amount of bare ground

Table 6.20 contains the combined results for the response of bare ground to settled weather.

Table 6.20 The response of bare ground to settled weather. The table amalgamates responses to settled and unsettled weather and to seasonal anticyclonicity. A positive response indicates a positive response to settled weather and/or a relatively high frequency of anticyclonic weather. An asterisk indicates a conflict between the results for seasonal anticyclonicity and for settled weather.

All Series	AUTUMN	WINTER	SPRING	SUMMER	AUTUMN & WINTER	SPRING & SUMMER
BARE GROUND	N	N	P		N	P

As might be expected, a high frequency of settled weather in spring and summer promotes the amount of bare ground. This supports the well-established finding that spring and summer droughts increase the number of gaps in grassland swards (e.g Buckland 1994). It might also be expected that a high frequency of settled weather in autumn and winter would also create bare ground. However, the opposite is suggested here. The negative response of bare ground to high anticyclonicity is actually observed in plots 7-8: the same plots in which high anticyclonicity in winter promotes total vegetation biomass.

6.8 Weather and the amount of litter

Table 6.21 contains the combined results for the response of bare ground to settled weather.

Table 6.21 The response of litter to settled weather. The table amalgamates responses to settled and unsettled weather and to seasonal anticyclonicity. A positive response indicates a positive response to settled weather and/or a relatively high frequency of anticyclonic weather.

All Series	AUTUMN	WINTER	SPRING	SUMMER	AUTUMN & WINTER	SPRING & SUMMER
LITTER	N	P	P	*	P	P

As might be expected, a high frequency of settled weather increases the amount of litter. Spring and summer drought would be expected to increase the amount of dead material on the ground surface. The amount of litter in the system also increases following a settled winter. This result is more difficult to explain. The promotion of litter following a settled winter is most pronounced in plots 7-8. In these plots, the amount of bare ground is reduced following a settled winter, while the total above ground biomass increases. Both of these consequences of a settled winter are compatible with increased litter. A number of major components of the vegetation, such as *Heracleum sphondylium* and *Dactylis glomerata* are promoted following a settled winter (it is noted in the second part of this thesis that most British grasses require winter chilling for maximum flowering and that this may explain why cold winters promote some major grasses at Bibury). It is probable that promoted growth of dominant species in plots 7 & 8 following a cold winter may result in reduced bare ground and increased litter in these plots. Heavy flowering after cold winters might cause culms and seeds to be a major sink, effectively starving vegetative growth and causing vegetative dieback.

6.9 A Model of vegetation response to weather at Bibury.

Overall, settled, hot, dry summers appear at Bibury to decrease the total productivity of the vegetation, promote the amount of litter and bare ground in the system, reduce the above-ground biomass of competitors, and promote ruderals. Unsettled, mild winters appear to promote competitors and retard stress-tolerators, as well as reducing the amount of litter. In plots 7-8, settled winters appear to be associated with increased total biomass and an associated reduction in the amount of bare ground.

Experimental tests of the relationships between vegetation performance and weather at Bibury shown by the analysis of the field records are considered in the second part of this thesis.

PART TWO: EXPERIMENTAL TESTING OF CLIMATE/VEGETATION RELATIONSHIPS IN THE BIBURY ROAD VERGES

CHAPTER SEVEN Experimental Manipulation of Synthesised Plant Communities

7.1 INTRODUCTION

In Part One it was shown that the performance of individual taxa, plant functional types and the total vegetation biomass could be linked to the frequency of first, second and third order meteorological variables. As stated in Chapter One, the Bibury data-set provides one of the most comprehensive and consistent data-sets available to ecologists who wish to study the links between weather and terrestrial ecosystems.

For the results of this study to have wider application, it must be shown that the plant/weather relationships described for the Bibury verges can be repeated elsewhere. If this can be done, it would be reasonable to assume that the behaviour of individual taxa at Bibury is representative of their behaviour in other systems. This would then lead to the testable hypothesis that the system at Bibury is representative of other *Arrhenatheretum* grasslands and possibly of aspects of other temperate grasslands in general. If the results for plant functional types could be repeated then it might well be assumed that the results may have implications for systems other than grasslands.

One method by which a wider application might be established would be to demonstrate similarities between the results at Bibury and those for other published studies - for example at Bibury the productivity of the vegetation is reduced by hot dry springs and summers and this finding is comparable with the results from the analysis of the Park Grass experiment (Silvertown *et al.*, 1994). A drawback to this approach is that the results from field-based studies are based upon systems that have many factors influencing them apart from weather. It is therefore extremely difficult to establish the precise effect of different weather variables on plant performance. It is also impossible to distinguish the direct effects of weather on species' performance and those mediated through competition.

An alternative approach is to conduct manipulative experiments on plant communities, artificially altering climatic factors and measuring the effects on plant performance. This approach allows the effects of climate to be separated more easily from other environmental factors. Such experiments can be carried out in the field on existing plant communities (Buckland, 1994) and have the advantage of being based upon real systems subject to the full range of environmental influences, only a small number of which are manipulated. However, such techniques are costly in terms of equipment, need constant recording, a power source and protection against vandalism or disturbance and, as such, are not suitable for the field site at Bibury. An alternative approach is to create artificial plant communities and to manipulate these under controlled conditions. Synthesised plant communities allow precise control of initial species composition while having some similarieties with a functioning natural system to remain. This was the approach adopted for the Bibury experiment.

7.1.1 The Bibury Experiment

A large scale experiment was set up, at The University of Sheffield Experimental Garden at Tapton, Sheffield. The aim of the experiment was to establish whether the plant/weather relationships that were apparent from the analysis of the field records could be repeated under controlled conditions. Simple plant communities were created using species selected according to their response to weather at Bibury. Climatic factors were manipulated and the effect on plant biomass was measured.

7.2 EXPERIMENTAL DESIGN

The experimental unit was a simple synthesised plant community in a movable container. The containers used had to be sufficiently deep to allow adequate root development and sufficiently wide to allow plants to spread and interact, and yet not too large to prevent transport to treatment sites. The chosen containers were hard plastic 'bag bins' (supplied by Plysu Housewares Ltd, Bedford), rigid enough to keep their shape. These had a diameter of 450 mm and allowed a rooting depth of 600 mm.

7.2.1 Experimental Treatments

It was shown in Chapter 3 how the year was divided into two six-month periods for the original analysis of the field records: winter and summer. Taxa were classified according to their response, positive or negative, to settled or unsettled weather conditions in these two periods. Experimental treatments were needed that reflected this division.

Space and time constraints meant that a single treatment only could be used to account for the responses of taxa in either winter or summer. It was assumed at the start of the experiment that two major climatic factors could account mainly for vegetation productivity throughout the year: temperature and moisture supply. Further, it was assumed that, over the winter months, the primary limit on plant growth is temperature, while in summer the primary limit is moisture supply. Treatments were therefore devised which manipulated temperature over the winter and which manipulated moisture supply over the summer. The chosen treatments were: warming at the level of the soil surface in winter and spring; a severe late spring frost; and a severe summer drought.

7.2.2 Plant Selection

At the commencement of the project information was available only from the original Bibury analysis described in Chapter Three and it was on the basis of this that species were selected. Four main considerations were taken into account when selecting species to be included in the experiment:

1. The selected species should be common Bibury species, and when grown together should be representative of the vegetation at Bibury.

2. The selected species should, between them, have exhibited significant positive and negative responses to settled and unsettled conditions in winter and summer.

3. The selected species should be easily grown and propagated.

4. The selected species should be, at least initially, compatible, with no one species likely to out-compete all others completely.

The minimum number of species that could be included in the experiment was 4: one for each possible response to temperature and moisture in winter and spring. It was decided to restrict the maximum number of species included so that vegetation recording could be simplified and competitive interactions between the species included could develop to the full. In accordance with point 1, the desired vegetation structure was a matrix of grasses with gaps for dicotyledons. It was decided also that one of the dominant Bibury grasses had to be present: *Dactylis glomerata* or *Arrhenatherum elatius*. *Arrhenatherum* was not suitable, however, because of point 4. The other four species chosen were *Achillea millefolium, Cirsium arvense, Festuca rubra* and *Poa pratensis*. The basis upon which they were selected is shown in Table 7.1.

Table 7.1 The Response of the Five Species Included in the Bibury Experiment. + indicates a positive response to unsettled winters or settled summers, and - indicates a negative response.

	Unsettled Winter		Settled Summer	
	+	-	+	-
Achillea millefolium			•	
Cirsium arvense	•			•
Dactylis glomerata		•		
Festuca rubra		•		
Poa pratensis				•

All three grasses occur in close association at Bibury (Plate 7.1), while the two herbs are among the 25 commonest species in the Bibury plots. More detailed characteristics of the five selected species are reviewed later in this Chapter.

7.2.3 Plant Collection

It was decided to collect vegetative plant material from the Bibury field site and use this to create synthesised plant communities, rather than sowing a mix of seed into the bins. Such a technique has several advantages. It allows precise control over the number of propagules for each species included, as well as enabling an exact record to be kept of the initial planting position of each propagule in the synthesised community. It also means that the material used in the experiment came directly from the Bibury site and was drawn from the population of individuals which had successfully established in the vegetation. The experimental containers would be inoculated with soil microorganisms direct from the field site if rooted plants are dug from the site. Finally, by planting vegetative material directly, a considerable head start could be gained over sowing seed.

Plants were collected from the road verges at Bibury on April 3rd and 4th, 1992. Plant collection points were situated near and around the perimeter of the control plots - plants were not removed from the interior of the plots themselves. Turves approximately 20 x 20 cm in area and approximately five cm deep were dug, each containing specimens of *Poa, Achillea, Dactylis* or *Festuca*. *Poa* and *Achillea* tended to occur in mixed vegetation and many other species occurred in these turves. The turves containing *Festuca* and *Dactylis* tended to include fewer other species. Representative examples of all the species were collected from throughout the study area. Strong shoots of *Cirsium* were removed from the vegetation, attached to a section of rhizome As much of the rhizome as possible was extracted from the soil. All the plants and turves were placed in large plastic bags as soon as they had been dug up prior to transport by car to Sheffield.

Sufficient material for *Poa, Festuca, Dactylis* and *Achillea* was collected to plant up the Tapton experiment during this first expedition. However in early April there were not enough emerged shoots of *Cirsium* to collect and therefore a second collecting trip was made on May 25th 1992. *Cirsium* plants were collected in the manner described above and were transported back to Sheffield where they were planted immediately. In addition further turves containing *Festuca, Poa, Achillea* and *Dactylis* were collected - the plants in these turves were intended to be 'back-ups' should any of the original plants fail to establish.

The collected turves were placed in uncovered cold frames at the University Experimental garden at Tapton and watered daily as required.

7.2.4 Preparation of the Experimental Containers

The black plastic 'bag bins' were converted to plant containers by the drilling of 15 drainage holes of five mm diameter in the base of each bin. To enable easy transport of the bins, two wooden 'runners' of dimension 40 x 40 x 300 mm were attached to the base of each bin with steel bolts. The runners were fixed in parallel at approximately 250 mm apart. This raised each bin above ground level and allowed the prongs of a trolley to be inserted beneath each bin. At the top of each bin an incurving rim was removed.

Each bin was filled with several layers of growing media. The base of each bin was covered with a 30 mm layer of gravel to aid efficient drainage. A layer of nylon mesh was placed on top of the gravel to separate it from the material above. The rest of the bin was filled with layers of sand and soil.

For reasons of cost and convenience, sand was used to fill approximately two thirds of each bin. Builders sand (supplied by C.Paget & Co., Sheffield) was used in the experiment. Simple chemical analyses were carried out on sand samples prior to use in the experiment. pH and concentrations of sodium, iron and calcium were measured. 20g of air-dried sand were mixed with 40 ml of de-ionised water. For pH measurement the soil/water mix was shaken and left to stand for 30 minutes. pH was then read with a hand-held pH meter, buffered at pH 7.0. For Ca, Na and Fe concentrations the sand/water mixes were shaken for two hours, filtered and the filtrate stored in plastic bottles. Na content was measured using flame emission photometry with sodium chloride solution as a standard, and Ca and Fe were measured using atomic absorption spectrophotometry, with calcium nitrate and ferric nitrate solutions as standards. Three samples were used for each test. The results are shown in table 7.2.

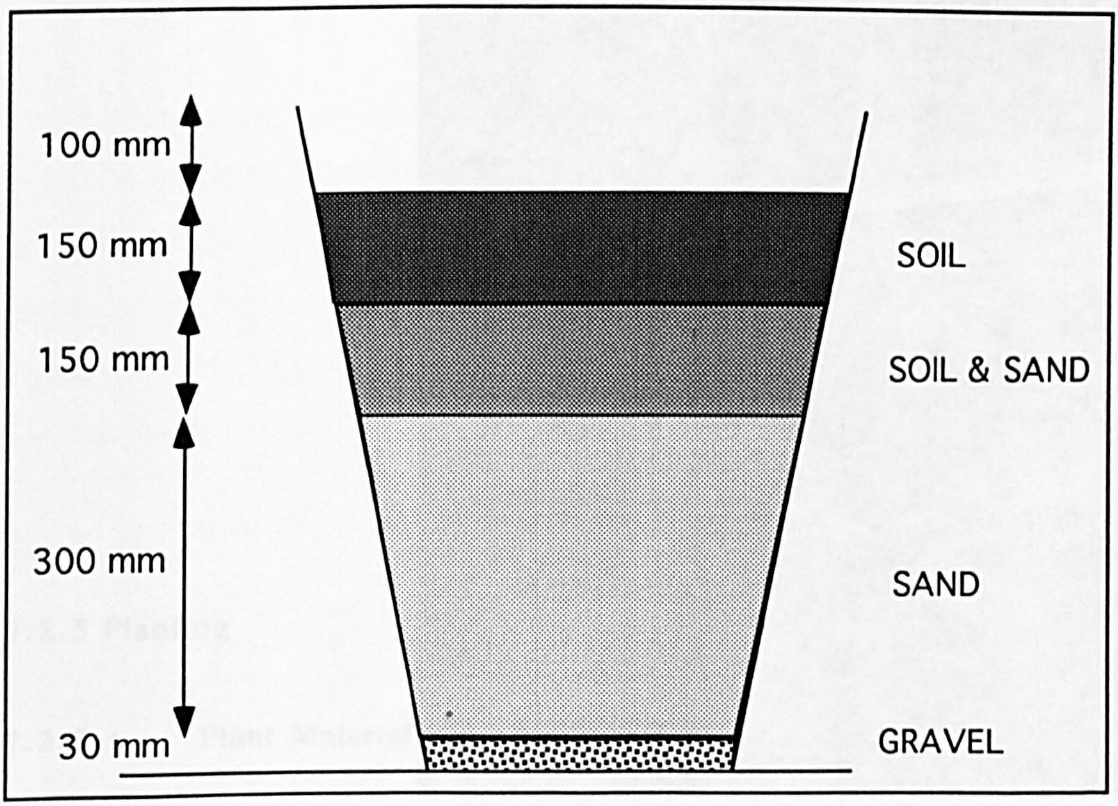
Table 7.2 **Sand Analysis.** Figures are mean values.

Na (μg/ml)	Ca (μg/ml)	Fe (μg/ml)	pH
6.8	30.5	8.6	6.3

The soil used in the experiment was topsoil from an agricultural field - the soil was surplus soil (pH 6.5) from a previous climate manipulation experiment (Hillier *et al.* 1994) that had been stored under plastic sheeting at Tapton for two years.

The bins were filled according to the scheme shown in Figure 7.2. A 300 mm layer of sand was placed above the gravel. Above this was a 150 mm layer of sand and soil mixed in equal measure, and above this was a 150 mm layer of pure topsoil. Top soil was used in the upper layers of the profile, not so much to recreate exactly the soil type at Bibury, but rather to provide a suitable medium for initial plant establishment. An unfilled rim of 100 mm was left at the top of each bin to contain the spread of plants within each bin.

Figure 7.2. The Contents of an Experimental Bin. The drawing is not to scale.



The bins were filled with the growing media in March 1992 and left to stand for two weeks before planting to allow the contents to settle.

Five replicates were used for each of the five species and the mixture for each of the four treatments and the control. A total therefore of 150 bins was included in the experiment.

The bins were placed in a sheltered, open sunny position, on an area of hard standing, in front of a south-facing wall. (Plate 7.1) The bins were sited in a grid of four rows, each containing 50 bins (the additional 50 bins were used for a different experiment). Treatments and contents were randomly assigned to each bin at the start of the experiment, prior to planting. In the winters of 1992/3 and 1993/4 each bin was randomly assigned a new position within the grid of four rows of 50 bins.

Plate 7.1 Experimental Layout. The bins were placed in four rows, each containing 50 bins.

7.2.5 Planting

7.2.5.1 Plant Material

Uniformly-sized units of the five species were prepared for planting, using either number of shoots, length of rhizome, or turf cores as the criteria for standardisation.

i) *Achillea millefolium*. The turves containing the *Achillea* plants also contained many other species. Clonal sections of *Achillea* were carefully removed from the turf, retaining as much soil as possible on the roots. Each plant used in the experiment had two growing shoots.

ii) *Dactylis glomerata*. Each tuft was split into sections, each with two or three shoots and associated roots.

iii) *Festuca rubra*. *Festuca* was collected in dense single-species turves. Cores of 30 mm x 30 mm were cut from these turves by trowel.

iv) *Poa pratensis*. Again, 30 mm x 30 mm cores were taken from turves containing *Poa*. Any species other than *Poa* were removed from the cores. Each core contained between three and five tillers of *Poa*.

v) *Cirsium arvense*. 100 mm sections of rhizome, each with an associated aerial shoot, were planted.

The fresh weights, immediately prior to planting, of a randomly selected sample of ten units of each species, apart from *Cirsium*, are shown in Table 7.2. *Cirsium* units were not weighed because these were collected during hot weather at the end of May and it was imperative that they were planted as soon as they were brought to Sheffield. The figures also include the weight of attached soil on the plant roots and therefore some variation is to be expected.

Table 7.2 Mean Fresh Weights of Vegetation Units Immediately Prior to Planting.

Species	*Achillea*	*Dactylis*	*Festuca*	*Poa*
Mean Weight	2.31	6.85	28.75	11.32
Standard Error	0.25	1.30	2.90	2.17

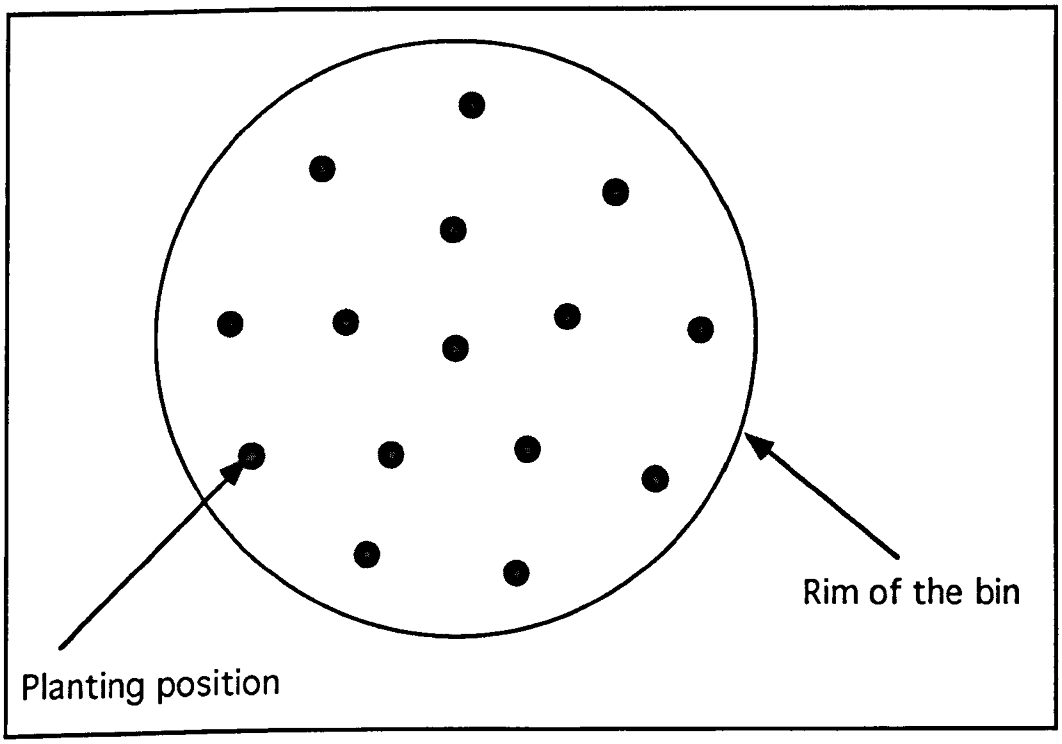
Prior to planting all units of plant material for each species were mixed to prevent individuals of the same clone being planted in the same bin.

7.2.5.2 Planting Arrangement

One of the aims of the experiment was to distinguish between the direct effects of experimental treatments on plant performance and those mediated through competition, by growing plants in both mixture and monoculture. Mahmoud & Grime (1976) and Austen *et al.* (1988) suggested that an additive experimental design, in which the density of a species in mixture is equal to its density in monoculture, was more satisfactory than a substitutive design in which the density of a species in mixture is a fraction of its monoculture density. This is because differences in yield between monocultures and mixtures can not be interpreted unequivocally as resulting from competition if the densities also vary. This view has been upheld by Snaydon (1991 & 1994). An additive design was therefore chosen for the Bibury experiment.

Three individual units of each species were planted in a replicate. Therefore each monoculture bin contained three individuals and each mixture bin contained 15. A standardised planting method was used to plant the bins. A template was made which located 15 planting positions for a bin, arranged in an outer ring of nine positions, an inner ring of five, and a central position (Figure 7.2).

Figure 7.2 The Standard Template for Assigning Planting Positions in a Bin.



Each position was given a number. Each planting unit was randomly assigned a number between one and 15, and planted in the appropriate position.

7.2.5.3 After-care

(i) Gap Filling During the first week of June any plants that had failed to establish were replaced by reserve plants.

(ii) Watering Once the bins had been planted up they were watered every day for one week, and again every day during hot dry weather and every three days or so otherwise. This continued until the middle of June. For the rest of the summer the bins were not watered at all during wet periods, but were watered frequently during hot dry periods. Watering ceased after mid September. The same pattern of watering was repeated in 1993 and 1994.

(iii) Weeding Seedlings germinated from the stored topsoil almost immediately. The most frequent species germinating were *Urtica dioica, Cirsium palustre* and *Agrostis stolonifera.* The bins were weeded regularly to remove unwanted plants while still at the seedling stage. Weed problems were greater in the monoculture bins where there was a relatively large proportion of bare soil. Some unwanted species were also introduced with the plants brought from Bibury. Particular problems included *Agrostis stolonifera* intimately mixed with Festuca and some *Arrhenatherum elatius* with *Dactylis.*

(iv) Feeding Fertiliser was added to the bins in the first week of June in 1993 and 1994. Fertiliser was not added earlier so as not to influence treatments carried out in the spring. Nitrogen was added at a rate of 80kg/ha (Hydrofertilisors Ltd 52 Regular - NPK 20:10:10). The granular fertiliser was spread evenly over the soil surface of the bin and the bins were then well watered.

(v) Cutting

The vegetation was cut back in the last week of November of 1992, 1993 and 1994. Plants were cut level with the rim of the bins, leaving approximately 100 mm still standing. By this time of the year much of the vegetation had died back. The litter was removed.

The vegetation in the bins was cut back for several reasons:

- A mass of decaying vegetation resting on the soil surface over winter might have an impeding effect on growth in the following spring.

- To ease the application of any winter treatments.

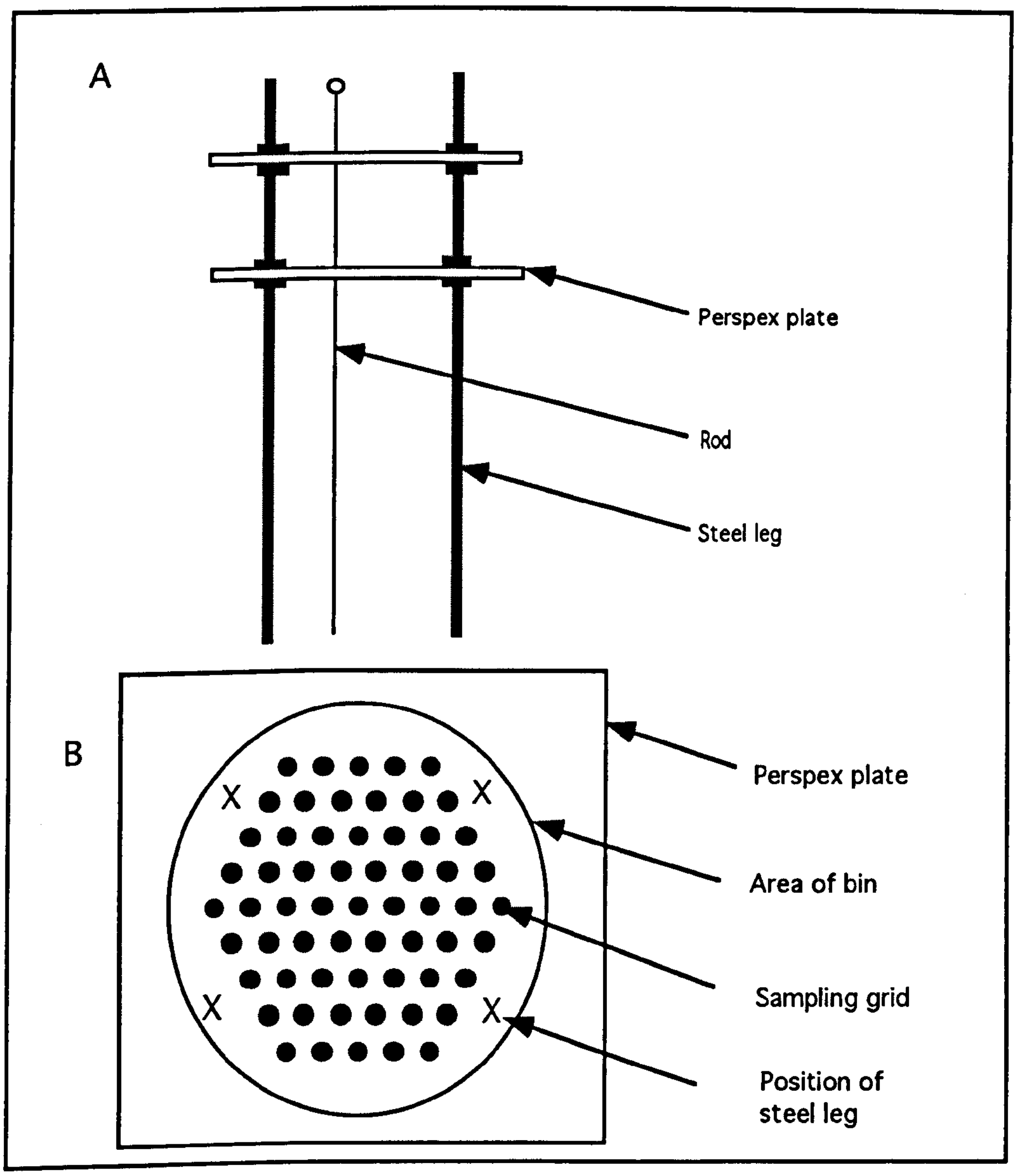
- To mirror the situation in the field at Bibury, where the verges are cut back in the autumn. At Bibury only the tallest vegetation is removed to aid visibility, apart from a thin strip along the very edge of the road which is cut short. However, because of the reasons given above, it was felt that cutting the vegetation back to a low level in the bins was justified.

7.2.6 Monitoring

The point quadrat was chosen as the main technique to monitor the performance of the plants in the bins - it is a non-destructive method that causes minimal disturbance to the vegetation. It has been demonstrated that, provided an adequate number of pins are recorded, the proportions of hits on the different species corresponds closely to the their relative contributions to the total weight of the shoot material (Greig-Smith 1983). The measurements are therefore directly comparable to the field records at Bibury, which also estimate shoot biomass.

A point quadrat frame was built that would fit the experimental bins. Two perspex plates were attached by nuts to four threaded steel legs. A grid of 5 mm diameter holes was made in each perspex sheet. The holes were 50 mm apart in the rows and the rows were 50 mm apart. A total of 61 holes were used. The legs of the frame were spaced so as to rest against the sides of a bin when the frame was placed over it. The holes in the two perspex plates were perfectly aligned so that a pin (a metal welding rod) could be directed to a specific part of a bin by being dropped through the appropriate holes. The construction of the quadrat frame and the distribution of holes are shown in Figure 7.3.

Figure 7.3 The Construction of the Point Quadrat Frame. A. The Frame. B. A Plan View of the Perspex Sheet, Showing the Distribution of Holes. Each hole is 50 mm apart in the rows and each row is 50 mm apart.



The major point quadrat surveys of all the bins in 1993 and 1994 were carried out in August. Other point quadrat surveys were carried out also, as detailed in subsequent Chapters. In each case, the total number of hits for each species at each point was recorded. In some instances, the number of hits at particular heights was noted and this enabled a height profile of the vegetation structure to be constructed. The amount of bare ground and litter was also surveyed.

The height of the vegetation was monitored throughout the growing season by measuring foliage height, flowering height, and length of longest leaf. Three measurements were made of each characteristic in each replicate, totalling 15 measurements for each treatment.

For the dicots, the mean number of shoots per replicate was recorded for each treatment. For all species flowering performance was assessed, both by counting the mean number of inflorescences and by collecting seed and fruits.

The incidence of insect infestations and fungal diseases was also recorded.

7.2.7 Statistical Analysis

The aim of the experiments described in the following chapters was to assess the effect of the various treatments on plant performance. No information was needed on the effect of the treatments relative to each other, but purely on the performance of the plants in the treated replicates compared to that in the untreated controls. For each treatment therefore, t tests were used to assess whether mean values for treated replicates were significantly different from mean values for controls.

7.2.8 Summary of the Experimental Design

Five species were included in the experiment. They were grown in large containers (plastic 'bag bins'), either by themselves (monoculture) or together (mixture). Five experimental treatments were used (including untreated controls). Each bin was taken to be an experimental replicate. Five replicates for each species and the mixture were assigned to each treatment. A total of 150 bins were therefore used.

7.3 PLANT GROWTH

A point quadrat survey was carried out on all the replicates in October 1992, after one full growing season to provide base-line information before any treatments were imposed. Analysis of variance was performed on the results and no significant difference was found between the mean number of hits for each species between replicates, for both the mixtures and monocultures. It is therefore reasonable to assume that any subsequent differences between replicates result from to the treatments imposed.

At the end of the first growing season in the monocultures, *Festuca, Poa* and *Cirsium* had spread to fill the available space within the bin. *Dactylis* had formed large clumps with tall arching foliage, although the clumps remained in their three original planting positions. The plants of *Achillea* had formed many new rosettes, although again the original planting positions were still apparent.

The mixture replicates quickly became dominated by *Dactylis*. *Festuca* and to a lesser extent *Achillea* had spread but were largely restricted to their original planting positions. The three *Cirsium* plants in each replicate produced no extra shoots in the first season. *Poa* weaved between the other species. The effect of competition on the five species in mixture can be simply assessed by calculating the 'relative yield' of the different species - the ratio of yield in mixture to that in monoculture (Austin *et al.* 1988). The mean relative yields of the five species for the control replicates is shown in Table 7.3.

Table 7.3 Relative Yield of the Experimental Species in the Control Replicates.

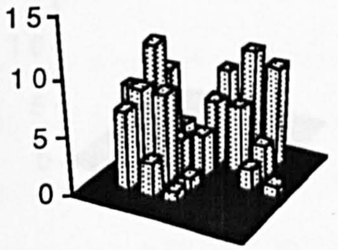
Achillea	*Cirsium*	*Dactylis*	*Festuca*	*Poa*
0.096	0.106	0.771	0.470	0.179

Dactylis is clearly the dominant species, little affected by competition compared to the other species. It has been suggested that *Dactylis* is able to compete effectively in mixture both above ground as a result of its relatively tall tillers and below ground through an extensive root system (van den Bergh & Elberse, 1970). The two forbs in the system were both greatly affected by competition.

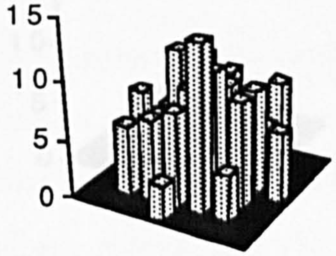
Sample results from the point quadrat survey in August 1994 are shown diagrammatically in Figures 7.4 and 7.5. In monoculture *Achillea* can still be seen to occupy distinct positions within the bin. In mixture the yield of the two forbs is strikingly reduced and their spread is restricted. *Festuca* and *Dactylis* dominate the mixture. *Poa* has been forced to occupy gaps within the vegetation and around the edge of the bin.

Figure 7.4 Diagrammatic Representation of Point Quadrat Results for Representative Control Monoculture Replicates. Each column represents a point on the sampling grid. The y axis represents the number of hits at each sampling point.

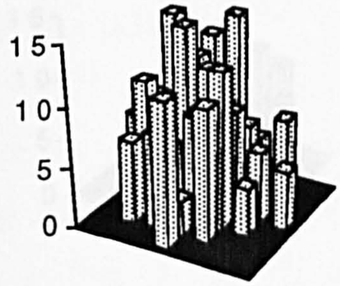
Achillea



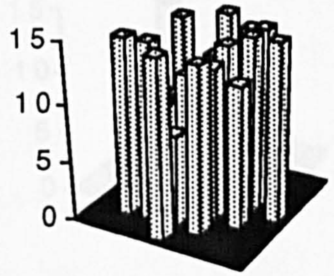
Cirsium



Dactylis



Festuca



Poa

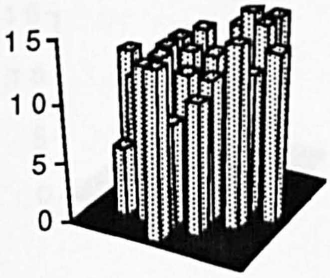
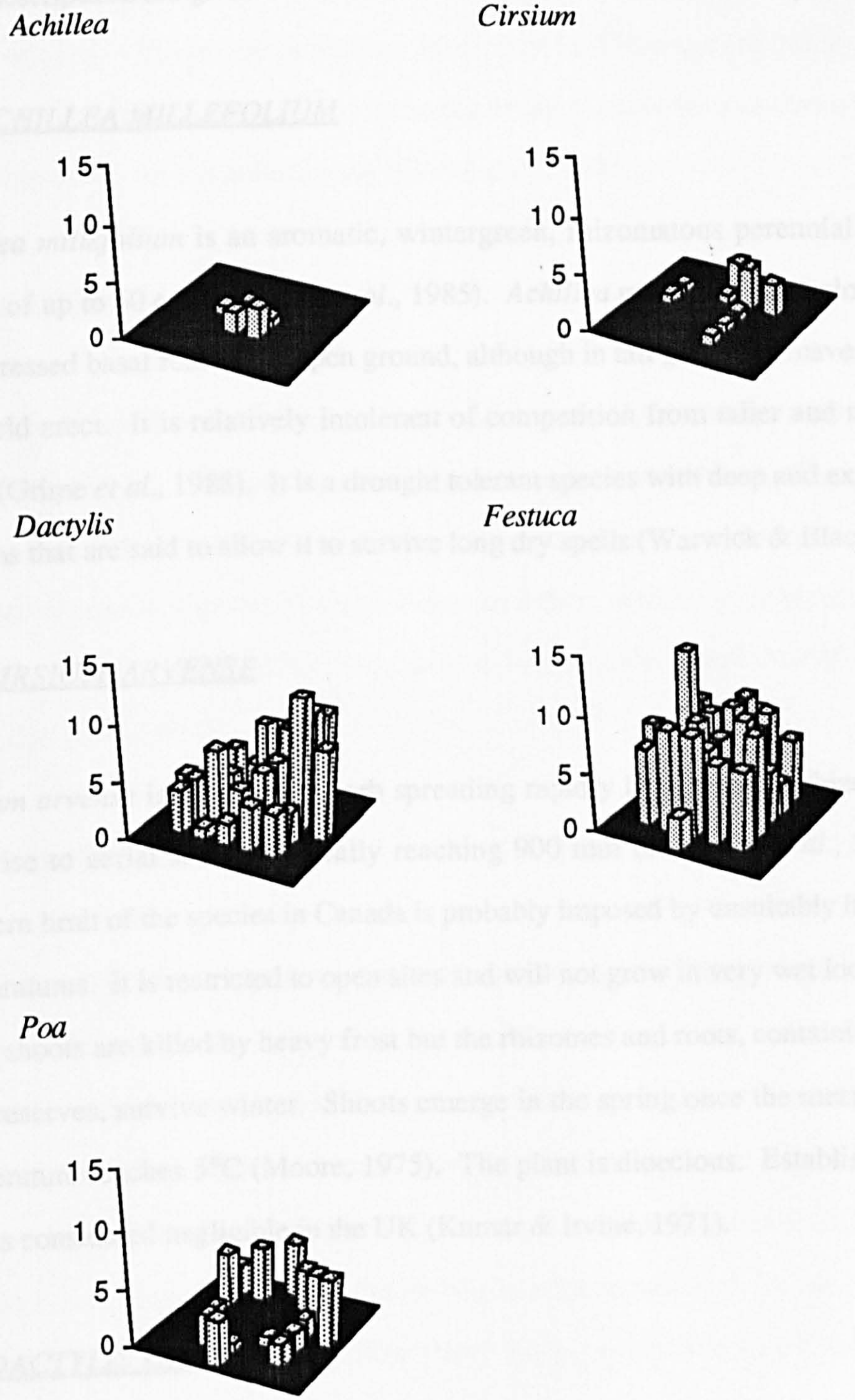


Figure 7.5 Diagrammatic Representation of Point Quadrat Results for a Representative Control Mixture Replicate. Each column represents a point on the sampling grid. The y axis represents the number of hits at each sampling point.



7.4 PLANT PROFILES

Brief descriptions are given below of the five species included in the experiment.

(i) *ACHILLEA MILLEFOLIUM*

Achillea millefolium is an aromatic, wintergreen, rhizomatous perennial reaching a height of up to 60 cm (Clapham *et al.*, 1985). *Achillea* may form large clonal patches of adpressed basal rosettes in open ground, although in tall grassland leaves are longer and held erect. It is relatively intolerant of competition from taller and more robust herbs (Grime *et al.*, 1988). It is a drought tolerant species with deep and extensive root systems that are said to allow it to survive long dry spells (Warwick & Black, 1982).

(ii) *CIRSIUM ARVENSE*

Cirsium arvense is a perennial herb spreading rapidly by horizontal rhizomes which give rise to aerial shoots, typically reaching 900 mm (Clapham *et al.*, 1985). The southern limit of the species in Canada is probably imposed by unsuitably high summer temperatures. It is restricted to open sites and will not grow in very wet locations. The aerial shoots are killed by heavy frost but the rhizomes and roots, containing abundant food reserves, survive winter. Shoots emerge in the spring once the mean weekly air temperature reaches 5°C (Moore, 1975). The plant is dioecious. Establishment from seed is considered negligible in the UK (Kumar & Irvine, 1971).

(iii) *DACTYLIS GLOMERATA*

Dactylis glomerata is a coarse, tussock-forming perennial grass with erect or spreading culms (Beddows, 1959). Typically it can reach 1.4 m in height (Hubbard, 1984). Growth can occur throughout the year - leafy shoots are produced in the winter when temperatures rise above 5°C. Growth is most active during April and May, with a second peak in July. Vegetative propagation does not normally occur. The species requires a period of vernalisation for maximum flowering. Late spring frosts can injure the developing inflorescences and can also cause leaf damage (Beddows, 1959). In neglected grasslands, *Dactylis* may form relatively massive tussocks which may exert local dominance on less robust herbs (Grime *et al.*, 1988).

(iv) *FESTUCA RUBRA*

Festuca rubra is a perennial rhizomatous grass typically growing to 0.9 m in height (Hubbard, 1984). The species can form extensive clonal stands (Harberd, 1961). *Festuca rubra* often forms a non-flowering understory beneath *Arrhenatherum elatius* in roadside vegetation (Grubb, 1982): it occurs at Bibury in this way in places. However, *F.rubra* is able to coexist effectively with *A.elatius* under conditions of low fertility (Berendse *et al.*, 1992).

(v) *POA PRATENSIS*

Poa pratensis is a wintergreen, perennial rhizomatous grass, typically reaching 0.9 m in height (Hubbard, 1984). In roadside vegetation the species tends to occur in longer vegetation that is not frequently disturbed (Davies, 1938). It rarely dominates vegetation but is widespread as a minor component (Grime *et al.*, 1988). In a comparative study of five co-existing grasses, *Poa pratensis* was found to have the earliest phenology and tolerance of low soil temperatures early in the year. It was suggested that this early phenology may partly explain its survival as a minor component of productive vegetation (Veresoglou & Fitter, 1984).

7.5 PREDICTED RESPONSES TO EXPERIMENTAL TREATMENTS

The five species were originally selected on the basis of the first Bibury analysis. However, since the beginning of the project additional analyseses have been carried out, as described in Chapters Three and Four, enabling more detailed plant/weather profiles to be built. Summary profiles for the five species are shown below, taken from the appendices, together with predicted responses to the experimental treatments. These predicted responses are compared with the actual responses in the following chapters.

It is apparent that, in some instances, responses are different for the two vegetation series in the same season. As described in Chapter Two, the vegetation in series 1-6 is less species-rich and more productive than that in series 7-8. The synthesised plant communities in the bins bear greater resemblance to the vegetation in series 1-6, being dominated by *Dactylis* with other species as subordinates. In the case of conflict between the two series, priority is therefore given to plant/weather relationships in plots 1-6. Where no relationship is found in a particular season for plots 1-6, predictions will be based on relationships in series 7-8.

Because all the plots at Bibury contain mixed vegetation, predictions can only be made for the responses of plants in mixture. Where differences exist between the responses of plants in mixture and in monoculture to the various treatments imposed, these will demonstrate those effects which were a direct result of the treatment, and those which may be mediated through competition. Where the response of a species to a given treatment is the same in monoculture and in mixture the effect of the treatment could be said to be direct. However, where the response in mixture and monoculture is different then the effect of that treatment could be said to be mediated through competiion.

(i) *ACHILLEA MILLEFOLIUM*

Table 7.4 Plant/Weather Profile for *Achillea millefolium.* P = positive relationship, N = negative relationship.

SERIES 1-6	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp			P			
Min Temp						
Rain (mm)						
Rain (days)						
Sun						
Anticyclonicity					P	

SERIES 7-8	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp				P		
Min Temp						
Rain (mm)						
Rain (days)	P			N		N
Sun						
Anticyclonicity			P	P		P

Achillea was selected for the experiment because of its positive response to settled springs and summers. This is reflected in both weather profiles. The positive relationship with spring temperature and autumn rainfall suggests a possible positive response to winter and spring warming.

Predictions: Positive response to drought.

(ii) *CIRSIUM ARVENSE*

Table 7.5 Plant/Weather Profile for *Cirsium arvense.* P = positive relationship, N = negative relationship.

SERIES 1-6	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp		P		N		
Min Temp	N			N		
Rain (mm)			N			
Rain (days)	N			P		
Sun	P		P			
Anticyclonicity	P					

SERIES 7-8	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp						
Min Temp						P
Rain (mm)				N		
Rain (days)				N		
Sun						
Anticyclonicity		P		P		P

Cirsium was originally selected for the experiment because of its negative response to settled summers and positive response to unsettled winters. This is reflected in the profile for series 1-6. The positive response to winter temperature suggests a positive response to the warming treatment. The positive response to summer rain, and negetative relationships with temperature in summer suggest a negative response to the drought treatment.

In the more open, less productive conditions of plots 7-8, *Cirsium* shows a positive relationship with summer temperature and anticyclonicity and a negative relationship with summer rainfall, indicating that the species is promoted following settled summers under such conditions.

Predictions: *Cirsium* will show a positive response to winter warming. *Cirsium* will respond negatively to the drought treatment.

(iii) *DACTYLIS GLOMERATA*

Table 7.6 Plant/Weather Profile for *Dactylis glomerata*. P = positive relationship, N = negative relationship.

SERIES 1-6	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp		N	P	N		N
Min Temp		N	P	N		P
Rain (mm)				P		
Rain (days)				P		P
Sun				N		
Anticyclonicity			N	N		N

SERIES 7-8	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp			P			
Min Temp			P		N	
Rain (mm)						
Rain (days)				P		
Sun		P				
Anticyclonicity	N		N	N	P	N

Dactylis was originally selected for the experiment because of its positive response to settled winters. This is still apparent in both series. This suggests that cold, dry winters will promote *Dactylis*. However, in both series a positive response to warm springs is shown, suggesting a positive response to spring warming. Both series also suggest a negative response to settled summers.

Predictions: Negative response to summer drought. Positive response to spring warming and therefore negative response to spring frost. Possible negative effects of winter warming.

(iv) *FESTUCA RUBRA*

Table 7.7 Plant/Weather Profile for *Festuca rubra.* P = positive relationship, N = negative relationship.

SERIES 1-6	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp			N		N	
Min Temp		N			N	
Rain (mm)			P			
Rain (days)						P
Sun						
Anticyclonicity				N		N

SERIES 7-8	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp		P	P	P		
Min Temp				P	P	P
Rain (mm)	N			N		
Rain (days)						
Sun						
Anticyclonicity	P					P

Festuca was originally selected for the experiment as a result of a negative response to unsettled winters. This response is still apparent for series 1-6 (a positive response to settled winters). The species also shows a negative response to warm springs. The species also exhibits a negative response to settled summers in series 1-6. However, *Festuca* has opposite responses in series 7-8, indicating that in more open, less productive conditions it may be promoted by warm winters and springs and benefit from warm dry summers.

Predictions: *Festuca* will be retarded by the spring warming treatment. *Festuca* will be retarded by the summer drought.

(V) POA PRATENSIS

Table 7.8 Plant/Weather Profile for *Poa pratensis*. P = positive relationship, N = negative relationship.

SERIES 1-6	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp						
Min Temp						
Rain (mm)	N					
Rain (days)						
Sun		N			P	
Anticyclonicity		P				

SERIES 7-8	AUT	WIN	SPR	SUM	AUT & WIN	SPR & SUM
Max Temp			N			
Min Temp						
Rain (mm)						
Rain (days)						
Sun	N	N			N	
Anticyclonicity		N	N			

Poa was originally selected for the experiment because of a negative response to settled springs and summers. This is still apparent in the response to settled springs in series 7-8. It appears that *Poa* responds positively to settled winters in series 1-6 (despite the negative relationship with winter sunshine). However, in series 7-8, *Poa* appears to be retarded by settled winters.

Predictions: *Poa* will be retarded by the summer drought. *Poa* will respond negatively to winter warming.

A summary of the predicted species responses is shown in Table 7.9.

Table 7.9 Summary of predicted responses to experimental treatments.

	Warming	Drought	Water
Achillea		+	-
Cirsium	+	-	
Dactylis	-/+	-	+
Festuca	-	-	+
Poa	-	-	+

These predicted responses form the hypotheses that are tested in the rest of the thesis. If the predicted responses of individual species are matched by their actual responses then much credibility can be attached to the analysis of Bibury field records and the results could justifiably be given the wider application alluded to in the introduction to this Chapter.

7.5.2 Predictions based upon 2C Nuclear DNA Content.

As explained in Chapter Two, 2C nuclear DNA content has been suggested as a possible predictor of a plant's response to winter and spring weather. While the five species were selected purely on the basis of their response to weather at Bibury, they also show a wide spread of DNA values (see Table 2.3). Species with a low DNA value may be advantaged by warm winter weather but may also be susceptible to severe late frosts (Macgillivray 1994).

Predictions: Species with low nuclear DNA values will respond positively to the warming treatment, but may be damaged by the frost treatment.

CHAPTER EIGHT: SIMULATION OF A MILD WINTER AND A WARM SPRING

8.1 INTRODUCTION

The aim of this treatment was to simulate the effects on vegetation of a mild winter and an early spring: in effect to increase the length of the growing season. It was decided that, as with the other treatments imposed, simulation of an extreme year would yield more useful results than gentle application of the treatment. No temperature control system was installed - the aim being to drive the system forward by a large increase in temperature, rather than to achieve a consistent warming to a standard value above ambient, although, in practice, this is what is likely to happen with a constant heat input.

Two separate warming treatments were applied. In the winter and spring of 1993, five replicates of each species monoculture were warmed, along with five mixture replicates. In the spring of 1994, a further 20 mixture replicates were warmed. These mixture bins, which were being used for a separate experiment, were planted at the same time as all the other bins and had been treated in exactly the same way as the controls throughout 1993.

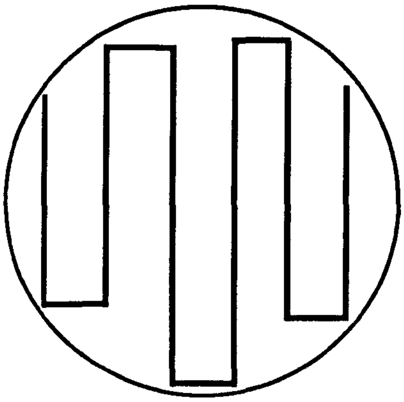
8.2 METHODS

A method was required which would raise the air temperature around the plants growing in the bins, but would not alter other micro-climate variables, such as rainfall and wind speed; which would limit disturbance to the plants; and which would not prevent access to the plants by insects Placing cloches or transparent tents over the bins was ruled out as altering too many weather variables in addition to temperature. Burying electrical soil warming cables as advocated by, for example, Van Cleve *et al.* (1990), would cause disturbance to the system and also creates unrealistic soil temperature profiles (Hillier *et al.*, 1994). A more appropriate method for relaticely short turf, involves applying warming at the soil surface (Hillier *et al.*, 1994, Buckland, 1994). This was the method employed in the experiment, using electrical soil warming cables to apply heat at the soil surface.

8.2.1 Installation of heating cables

The cables used (Camplex, Ltd) were three metres long - a single cable was used in each bin. The cables were pegged, in parallel rows, to the soil surface with short lengths of galvanised wire. Rows were spaced eight centimetres apart (Figure 3.1). The cable was laid directly on the soil surface.

Figure 8.1 The Arrangement of a heating cable in each warmed bin.



8.2.2 Arrangement of the bins

To enable safe and efficient wiring, it was necessary to group the bins in five separate blocks, with one replicate of each of the five monocultures and one mixture replicate in each block. The bins remained in this position throughout the remainder of the period of treatment. The bins were arranged such that three of the treatment blocks remained among the main mass of bins. However, because of limitations of space, two new blocks had to be made a short distance away, in a similar, open site. A complete set of control replicates (five monocultures and one mixture) were moved adjacent to each treatment block. All the cables from the bins in a single block were connected to the 240V power supply via a sealed, waterproof junction box.

8.2.3 Monitoring and control

The temperatures of the heated and control bins were monitored continuously throughout the treatment period. Recordings were made at the soil surface and the treated and control bins were read simultaneously.

It was inevitable that, when using a heating cable grid, temperature gradients would develop between the rows of cable. For example, Table 8.1 shows temperatures recorded on April 8th 1993. The figures are mean values taken from three replicates recorded simultaneously of each monoculture and mixture. The control (ambient) temperature is a mean of values recorded in a single replicate of each monoculture and a mixture.

Table 8.1 Mean temperatures (°C) at different distances from the heating cables, recorded on April 8th 1993. Figures in brackets are standard errors.

Species	Distance from cable (cm)			
	0	1	2	Mid point between cables
Festuca	16.67 (0.39)	15.5 (0.13)	13.33 (0.15)	12.83 (0.01)
Achillea	17.17 (0.58)	14.25 (0.11)	12.67 (0.01)	13.00 (0.13)
Dactylis	18.5 (0.81)	17.33 (0.34)	13.33 (0.15)	13.33 (0.01)
Poa	18.0 (0.15)	17.67 (0.15)	14.33 (0.6)	13.00 (0.13)
Cirsium	14.7 (0.2)	14.7 (0.01)	13.67 (0.3)	12.33 (0.08)
Mixture	18.8 (0.34)	15.3 (0.3)	13.3 (0.15)	12.33 (0.08)
Control				8.54 (0.14)

The aim of the treatment was to achieve an increase in temperature of between 4 and 6 °C at the mid point between the cables. This was achieved throughout the warming period, as shown in table 8.2.

Table 8.2 Mean mixture and control (ambient) temperatures (°C) at different times throughout the treatment period. Figures in brackets are standard errors.

Date	Mixture	Control	Difference from Control
1st Mar	6.17 (0.27)	0.00 (0.00)	6.17
15th Mar	14.33 (0.33)	8.50 (0.76)	5.83
8th Apr	12.33 (0.08)	8.54 (0.14)	3.79
6th May	20.50 (0.29)	15.67 (0.67)	4.83

The bins were placed in their warming blocks in early February 1993. The cables were placed in the bins in mid-February and the power connected on February 26th. January and February 1993 were relatively mild, with little frost. However, on the 27th February a sharp cold snap occurred, lasting for several days, with severe overnight frost and snow. The heated bins escaped this cold period.

During dry periods it was necessary to water the heated bins on a regular basis - warming at the soil surface would otherwise lead to drying out of the upper layer of soil in the bins. All the other bins were also watered along with the heated bins. Watering was carried out as and when required for the remainder of the warming period.
The cables were switched off on May 24th 1993.

8.2.4 Warming 1994

Only the bins in the second experiment were warmed - therefore less space was required and all bins could be treated in the same area. Five blocks of four replicates were distributed along the main mass of bins. Cables were placed in the bins and connected as in 1993.

The positions of all the bins were 're-randomised' during the second and third weeks of December 1993 and heating cables placed in the bins in the third week of December.

The cables were switched on January 28th 1994. Watering was again carried out as and when required. The cables were again switched off on May 24th.

8.2.5 Measurements

A number of different measurements were made to assess the response of the plants during the warming period. The **mean height of the vegetation** was recorded throughout the period. Three measurements were made for each species in each replicate bin, and means were calculated from the resulting 15 measurements. In the case of *Dactylis* and *Achillea,* where the three individual clones could still be recognised within each replicate, a maximum height value was recorded for each clone. For the other species, which had spread to fill the bins, three height measurements were made at random within the bin.

The **mean length of longest leaf** was also recorded. This was particularly important for the rosette or clump-forming species (*Achillea*, young *Cirsium* and *Dactylis*), for which, initially, growth occurred laterally as expanding leaves, rather than as upward extension. Again, where individual clones could be recognised a measurement was made from each, otherwise three random measurements were made. In addition, for the two forbs, the **mean number of shoots** was recorded, as was the flowering performance of all species. The number of inflorescences produced was counted for all species, and the total seed weight was determined for the grasses. A point quadrat survey was carried out within one month of the end of the warming treatment, and again in October 1993, May 1994 and August 1994.

For those replicates warmed in 1994, point quadrat surveys were carried out in March, April and May to enable calculation of growth rates in response to warming, in addition to measurements of heights and numbers of shoots. Point quadrat results were expressed in either absolute terms for the mixtures and monocultures, or in relative terms for the mixtures. The mean percentage of the total vegetation shoot biomass that a given species occupied was regarded as indicating the competitive 'success' of that species following treatment.

8.3 RESULTS

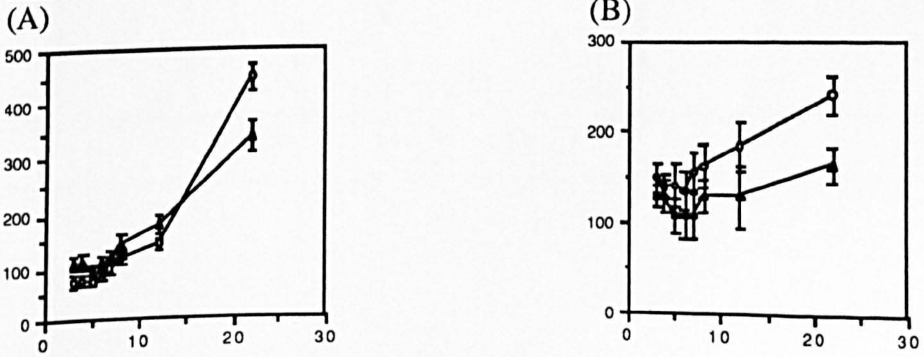
8.3.1 *ACHILLEA MILLEFOLIUM*

Heights

Monocultures: The warmed plants were significantly taller than the control plants (P<0.05) throughout the warming period, apart from weeks seven and eight, when there was no significant difference between the heights of the control plants and the warmed plants. However, measurements taken in the first week of August show that the control plants had overtaken the warmed plants and were now significantly taller (P<0.01).

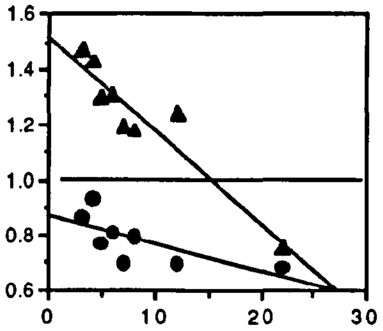
Mixtures: Throughout the warming period there was no significant difference between the mean heights of the warmed plants and the control plants. Again, measurements taken in the first week of August revealed that the control plants had overtaken the warmed plants and were now significantly taller (P<0.01).

Figure 8.2. *Achillea* Mean Heights Throughout the Warming Treatment for Warmed and Control Plants. x-axis = weeks from the start of the warming treatment. y-axis = height (mm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



The ratio of the heights of the plants in the controls and warmed replicates is shown in Figure 8.3. The warmed monoculture plants are initially stimulated but steadily lose their advantage over the growing season. Although the warmed mixture plants do not show any initial stimulation, they too exhibit a steady decline over the growing season.

Figure 8.3 The Ratio of the Height of Warmed Plants to Control Plants. Triangles = Monocultures. ($P<0.001$) Circles = Mixtures. ($P<0.05$) X axis = Weeks after start of warming treatment. Y axis = Ratio.

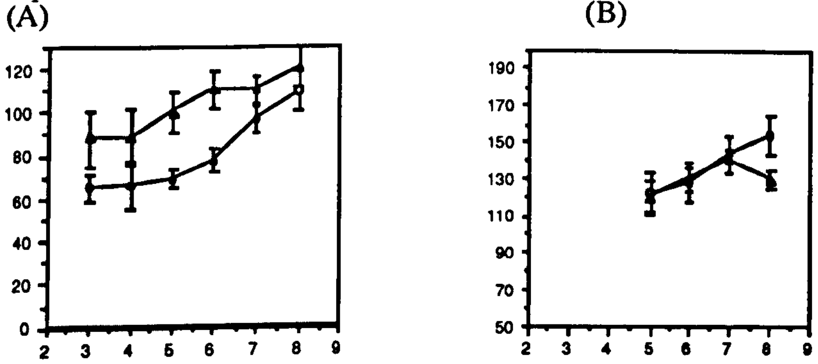


Mean length of longest leaf

Monocultures: Initially the mean lengths of the longest leaf of the warmed plants were significantly greater than those of the control plants (e.g. $P<0.001$ in week five). However this gap was closed and two months after the start of warming there was no significant difference between the two sets of plants.

Mixtures: Until week seven the mean lengths of the longest leaf of the warmed and control plants were closely similar . However, in week eight, the mean length of the longest leaf of the control plants was greater than in the warmed plants ($P=0.1$).

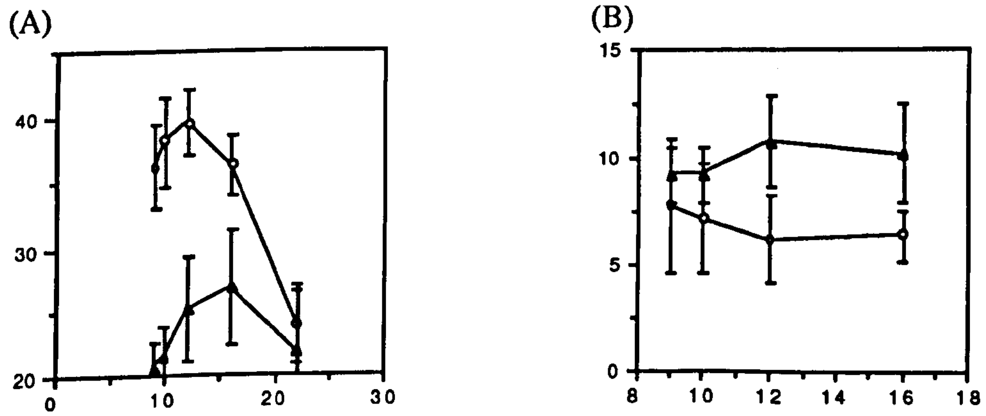
Figure 8.4. ***Achillea*** **Mean Length of Leaf Throughout the Warming Treatment for Warmed and Control Plants.** x-axis = weeks from the start of the warming treatment. y-axis = Length (mm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Mean number of shoots

Initially there was no significant difference between the mean number of shoots produced by the warmed plants and the control plants. However, by week twelve, the mean number of shoots in the warmed bins was significantly less than in the control ($P<0.05$). A possible reason for this reduction is increased snail and slug herbivory in the warmed bins.

Figure 8.5. ***Achillea*****: Mean Number of Shoots per Replicate Throughout the Warming Treatment for Warmed and Control Plants.** x-axis = weeks from the start of the warming treatment. y-axis = Number of shoots. (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Flowering

Two different measures were made of the flowering performance of *Achillea*: the mean number of corymbs per replicate on 26th August 1993, and the total number of individual capitula produced over the whole season (Table 8.3). In both cases, the flowering performance of the warmed plants was significantly lower than the controls (P<0.05).

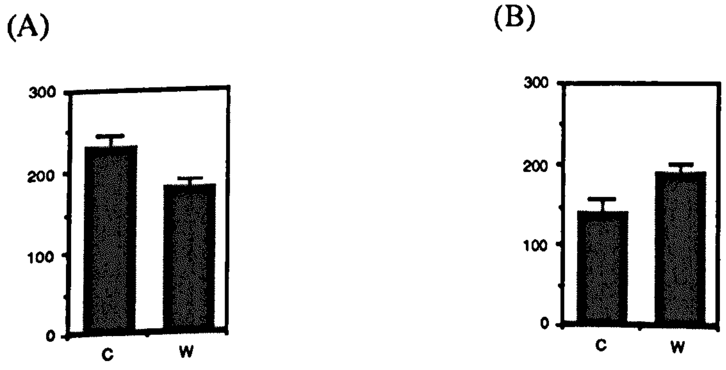
Table 8.3 Flowering performance of *Achillea millefolium*.

	Mean number of corymbs, 26th August 1993		Mean number capitula produced over the season	
	Control	Warm	Control	Warm
Number	23.8	8.2	419	70.4
SE	4.81	3.18	140	42.0
Probability	0.03		0.04	

Vegetation Measurements in 1994

The mean heights, number of shoots and flowering performance of the plants warmed in 1993 were recorded in the first week of June 1994. Plants of *Achillea* were by now present in only three out of the five warmed replicates. The mean values for the mixture plants are values for plants in the three replicates. No significant difference was found between the warmed and control plants for number of shoots and flowering. However the mean height of the plants in the warmed replicates was significantly less for the monocultures, but significantly greater for the mixtures. (Figure 8.6)

Figure 8.6 Mean Height of *Achillea* Plants in June 1994. A Monocultures (P = 0.03) B Mixtures (P = 0.04) Y axis = height (mm). Bars represent standard errors.



Shoot biomass (point quadrat survey)

Monocultures There was no significant difference between the warmed and control replicates throughout the sampling period.

Mixtures Again, no significant difference was recorded between the control and warmed plants.

Table 8.4 Shoot biomass of *Achillea millefolium*. Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
June 1993	Control	Warm
Mean	100.0	104
SE	16.0	6.6
Probability	0.80	
October 1993		
Mean	108.6	96.4
SE	47.8	19.4
Probability	0.81	
August 1994		
Mean	174.5	242.6
SE	52.4	28.2
Probability	0.295	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
June 1993	Control	Warm	Control	Warm
Mean	15.0	15.0	2.7	2.6
SE	3.8	5.5	0.8	1.0
Probability	1.00		0.94	
October 1993				
Mean	10.4	7.2	1.5	0.9
SE	4.2	2.6	0.6	0.3
Probability	0.53		0.39	
May 1994				
Mean	4.8	1.8	1.9	0.9
SE	1.7	1.2	0.5	0.7
Probability	0.19		0.29	
August 1994				
Mean	7.8	6.8	1.27	0.99
SE	2.8	4.3	0.5	0.6
Probability	0.849		0.732	

Herbivory

Achillea, more than any of the other species in the bins, was susceptible to insect herbivory. Two insects were involved: aphids and froghoppers.

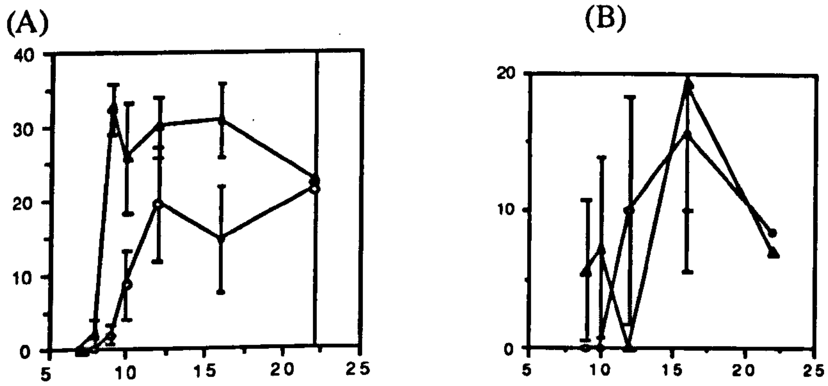
Aphids

Monocultures Aphids were first noticed on the warmed plants during the last week of April. Because the main experiment was set up to investigate the effect of warming on plants, detailed monitoring of insects was not undertaken before May. However, the difference between the warmed and unwarmed plants was so striking that insect monitoring was carried out regularly from then on.

Throughout the remainder of the warming period and on to the end of June, the warmed plants consistently supported more aphids than the controls. On every monitoring occasion, apart from that in the 2nd week of May, this difference was significant at $P<0.05$. Aphid infestation occurred both earlier and to a greater degree on the warmed plants. Monitoring later in the summer (9th August) showed no significant difference in aphid numbers between the two sets of plants.

Mixtures Aphids were first recorded on the warmed mixture plants during the first week of May. During this week and the second week of May no aphids were observed on the control plants. However, differences between the warmed and control plants were not significant throughout the period, mainly because *Achillea* plants were small in the mixtures and therefore supported relatively few insects.

Figure 8.7. ***Achillea*****: Percentage of Shoots infested with Aphids.** x-axis = weeks from the start of the warming treatment. y-axis = Percentage of shoots. (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Aphids in 1994

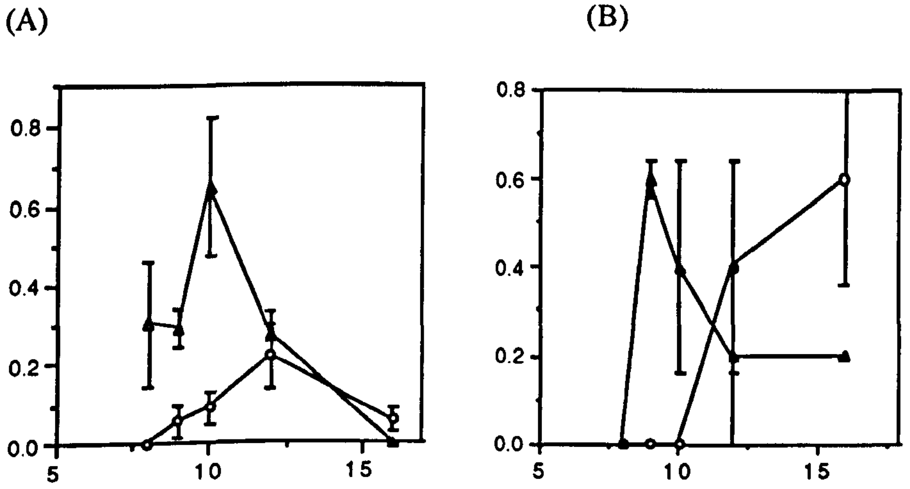
A separate set of mixture replicates was warmed in the late winter and spring of 1994. No aphids were observed on either the warmed or control plants over the warming period. In fact, no aphids were observed on the plants until the first week of June - around a month later than 1993. The difference in the time of appearance of aphids in 1994 may be due to the colder winter and spring of 1994 compared to 1993. The mean maximum temperature over the period February to May was 0.5°C lower in 1994 than in 1993 (Bibury data).

Froghoppers

Monocultures Froghoppers, *Philaneus spumaris,* were first noticed in 1993 on the warmed plants in the last week of April. The insects first appeared on the control plants in the first week of May. Insect populations on the control plants built to a peak in the last week of May, before falling in June. The populations on the warmed plants followed a similar pattern but reached their peak some two weeks earlier, and at a higher number. Froghopper numbers were significantly greater on the warmed plants than on the controls for the first three weeks of May (P<0.05).

Mixtures Froghoppers appeared two weeks earlier on the warmed plants than the controls. Insect numbers reached a peak on the warmed plants in the second week of May, but by the end of May mean numbers on the control plants were greater than on the warmed plants. However, as with the aphids, insect numbers were low on the mixture plants and differences between the warmed and control plants were not significant at any time.

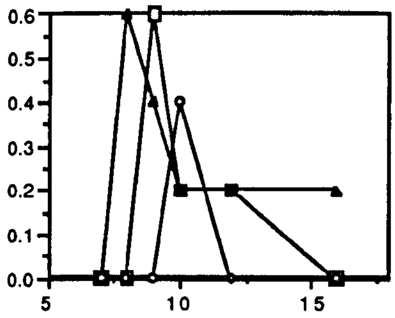
Figure 8.8. ***Achillea*****: Mean Number of Insects per Replicate.** x-axis = weeks from the start of the warming treatment. y-axis = Number of Insects. (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Froghoppers in 1994

Froghopper numbers recorded on the mixture plants showed a similar pattern in 1994 to 1993. An initial peak is followed by a decline in numbers. However, the peak in 1994 occurred a week later than in 1993, again possibly reflecting the cooler winter and spring. Figure 8.9 shows the results for the warmed plants in 1994 and 1993, together with the controls for 1994. The peak in froghopper numbers for the control plants occurred a week later than on warmed plants.

Figure 8.9. ***Achillea*: Mean Number of Insects per Replicate (Mixture).** x-axis = weeks from the start of the warming treatment. y-axis = Number of insects.. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants in 1993. Squares = Warmed plants in 1994



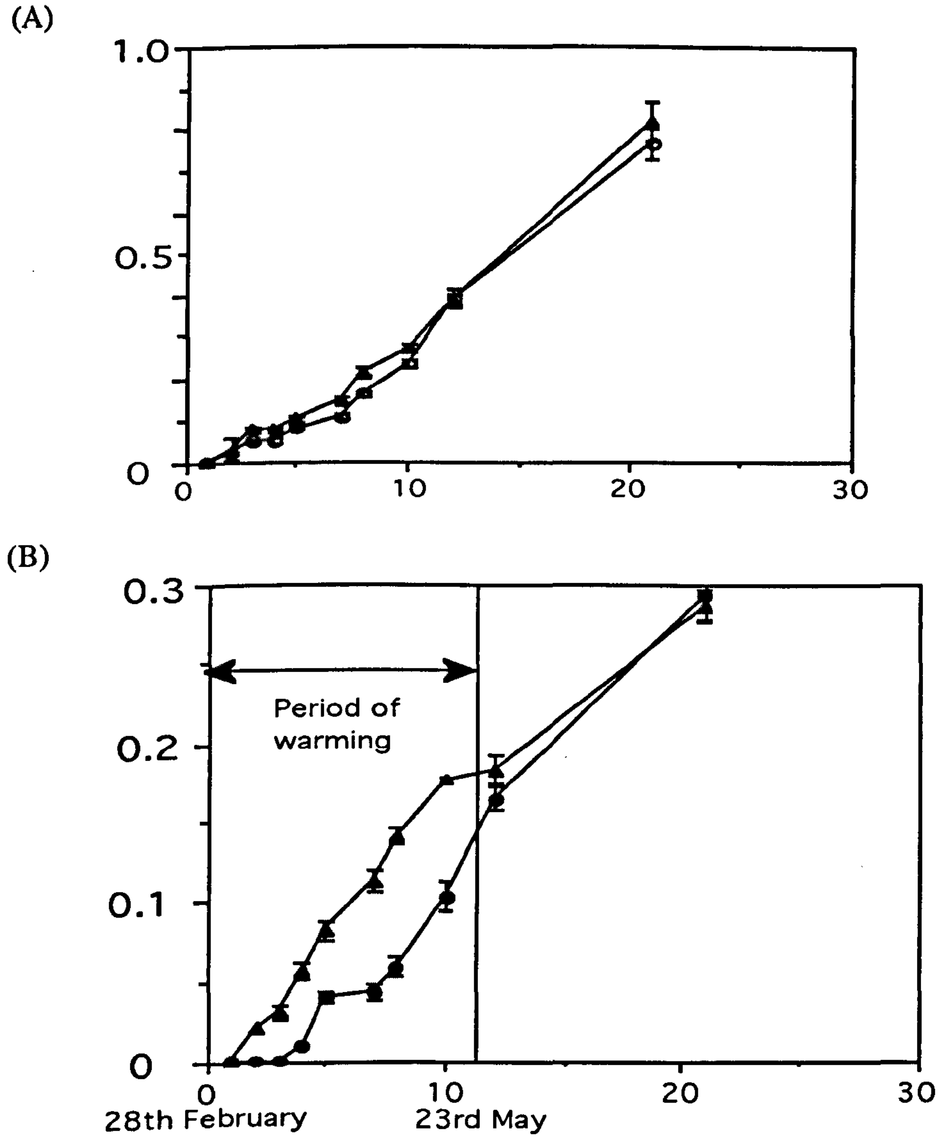
8.3.2 *CIRSIUM ARVENSE*

Heights

Monocultures Throughout the warming period the mean height of the warmed plants was significantly greater than the controls ($p<0.01$). By the end of May, however, there was no significant difference between the two sets of plants. The convergence in height between the warmed and control plants coincides with the end of the warming treatment.

Mixtures As with the monocultures, the warmed plants were significantly taller throughout the whole of the warming period ($P<0.001$). At the end of May, however, once warming ceased, no significant difference was found between the two sets of plants, and measurements in the first week of November again showed no significant difference.

Figure 8.10. ***Cirsium*** **Mean Heights Throughout the Warming Treatment for Warmed and Control Plants.** x-axis = weeks from the start of the warming treatment. y-axis = height (m). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.

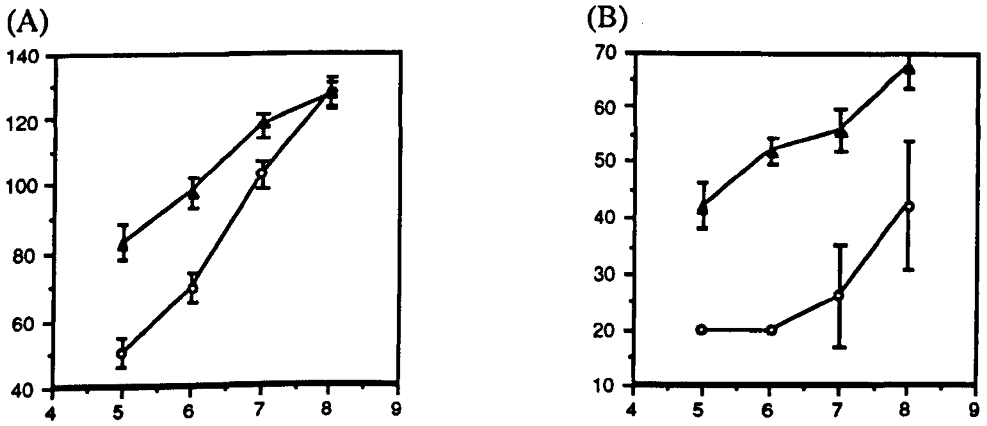


Length longest leaf

Monocultures Measurements taken throughout April showed that the mean length of the longest leaves of the warmed plants was significantly greater during the first and second weeks ($P<0.001$) and the third week ($P<0.01$). However, by the end of April no significant difference was found between the two sets of plants.

Mixtures Measurements taken throughout April showed that the mean length of the longest leaves of the warmed plants was significantly greater than the controls ($P<0.001$).

Figure 8.11. *Cirsium* Mean Length of Longest Leaf Throughout the Warming Treatment for Warmed and Control Plants. x-axis = weeks from the start of the warming treatment. y-axis = Length of longest leaf (cm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.

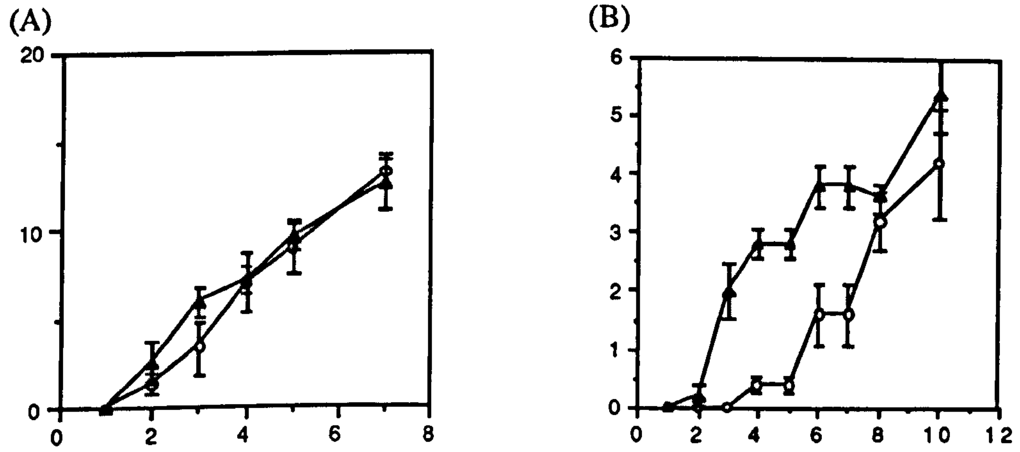


Number of shoots

Monocultures In 1993 the first *Cirsium* shoots appeared in the warmed bins in the second week of March. However, the first new shoots appeared in the control monocultures a few days after those in the warmed. Throughout the warming period, and subsequently, there was no significant difference between the number of shoots produced by both sets of plants.

Mixtures In 1993 the first *Cirsium* shoots appeared in the warmed bins during the second week of March. Shoots did not appear in the control bins until two weeks later. From this time until the first week of May there were significantly more *Cirsium* shoots in the warmed bins ($P<0.01$). However, after the first week of May there were no significant differences between the two sets of plants.

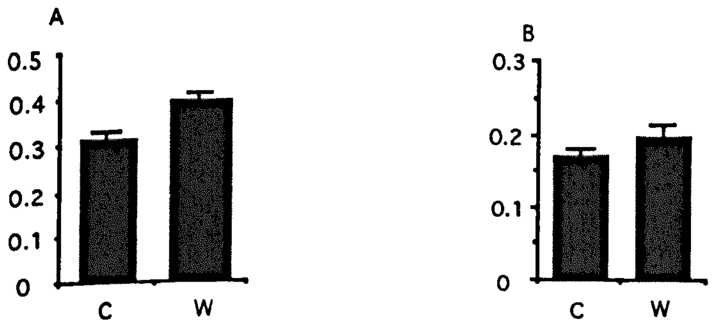
Figure 8.12. *Cirsium* Mean Number of Shoots Throughout the Warming Treatment for Warmed and Control Plants. x-axis = weeks from the start of the warming treatment. y-axis = Number of shoots. (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.

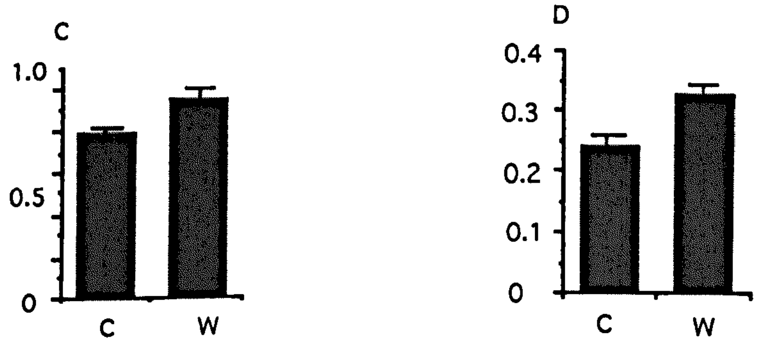


Vegetation Measurements in 1994

The mean height, number of shoots and number of flowers were recorded twice in 1994, firstly at the end of May and secondly at the end of August. No significant difference between the controls and the plants warmed in 1993 was found in either instance for mean number of shoots or number of flowers. However in both instances the mean height of the warmed plants was significantly greater for the warmed plants in both mixture and monoculture.

Figure 8.13. *Cirsium* Mean Heights for Warmed and Control Plants in May and August 1994. Y-axis = height (m). (A) Monoculture, May. (B) Mixture, May (P= 0.002) (C) Monoculture, August (D) Mixture, August (P= 0.003) Bars represent standard errors.





Warming of second set of replicates in 1994

A second set of mixture plants was warmed in 1994; but the treatment commenced one month earlier than in 1993. Measurements of the number of shoots produced and their heights gave results similar to those obtained in 1993. However, the first shoots appeared in the warmed replicates in the third week of February, three weeks earlier than in 1993. Shoots appeared at the same time in the controls in both 1994 and 1993.

Shoot biomass (point quadrat survey)

No significant difference was found between the shoot biomass of the warmed and control plants, either in mixture or monoculture in 1993. A survey in May 1994 of the mixtures again showed no significant difference between the two sets of plants, although, as can be seen from the figures, *Cirsium* as yet contributed only a small percentage to the total shoot biomass. Again in August 1994, no significant difference was found between the two treatments.

Table 8.4 Shoot biomass of *Cirsium arvense* Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
June 1993	Control	Warm
Mean	225.0	209.0
SE	30.0	18.0
Probability	0.10	
October 1993		
Mean	213.6	199.8
SE	22.6	24.7
Probability	0.69	
August 1994		
Mean	367.6	346.8
SE	16.8	15.1
Probability	0.38	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
June 1993	Control	Warm	Control	Warm
Mean	24.0	23.0	4.3	4.3
SE	3.4	2.6	0.7	0.6
Probability	0.8		0.94	
October 1993				
Mean	22.6	17.4	3.41	2.47
SE	1.9	1.8	0.5	0.3
Probability	0.08		0.15	
May 1994				
Mean	1.2	2.4	0.5	0.3
SE	0.8	1.0	0.1	0.2
Probability	0.37		0.63	
August 1994				
Mean	19.4	20.6	3.0	3.2
SE	8.2	4.4	0.8	0.3
Probability	0.81		0.88	

Herbivory

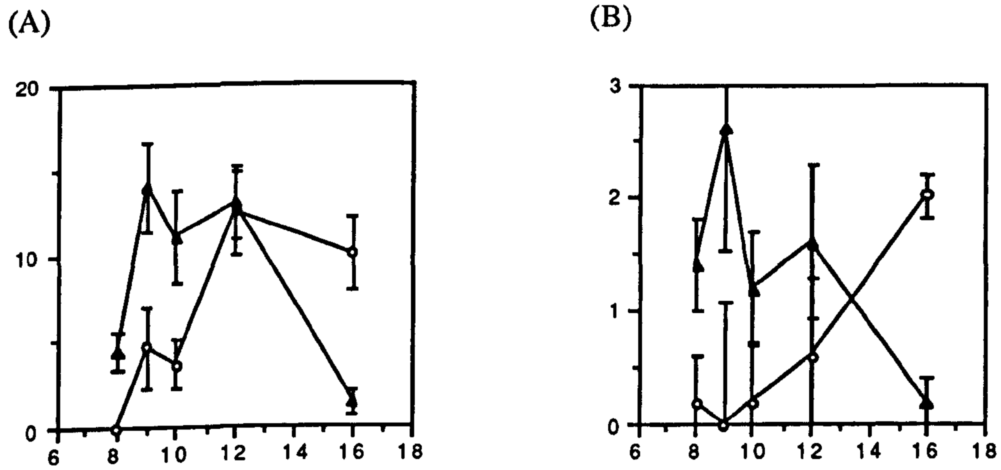
Froghoppers

Unlike *Achillea*, *Cirsium* was not susceptible to aphid herbivory. However, it was prone to infestation with froghoppers.

Monocultures Insects were first observed on the control plants during the first week of May 1993. Numbers reached a peak during the last week of May, and subsequently declined. However, warmed plants were already infested by the last week of April. In the first week of May, insect numbers were at their highest on the warmed plants, three weeks before the peak on the control plants. Insect numbers on the warmed plants remained steady before sharply declining during June.

Mixtures Similar patterns were apparent in the mixture replicates as for the monocultures. Insect numbers on the warmed plants reached a peak in the first week of May and subsequently declined. However, by the end of the recording period at the end of June, insect numbers on the controls had still not reached the maximum attained on the warmed plants.

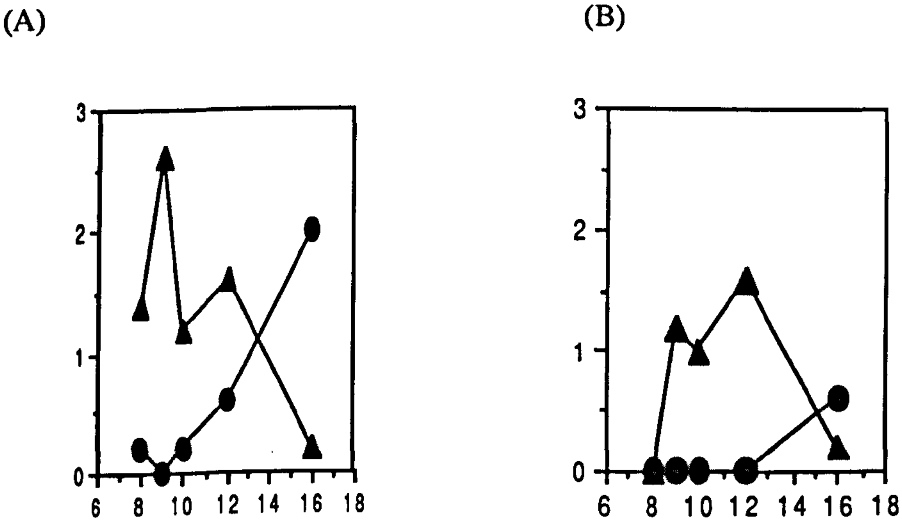
Figure 8.14. ***Cirsium*: Mean Number of Insects per Replicate.** x-axis = weeks from the start of the warming treatment. y-axis = Number of Insects. (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Froghoppers in 1994

A separate set of mixture replicates was warmed in 1994, and the number of froghoppers occurring on the plants was monitored throughout the warming period and on into June. The results are presented in figure 8.15, along with the corresponding results for 1993. In 1994 insects were not observed on the control plants until three to four weeks later than in 1993, again possibly reflecting the cooler conditions in spring and winter 1994. However, the pattern of insect numbers on the warmed plants was almost the same in both years, although insect numbers in 1993 were initially twice those in 1994.

Figure 8.15 ***Cirsium*** **Mixture Froghopper Numbers in 1993 and 1994.** x axis = weeks from start of warming treatment. A = 1993. B = 1994. Y axis = mean number of insects per replicate. Circles = Controls, Triangles = Warmed plants.



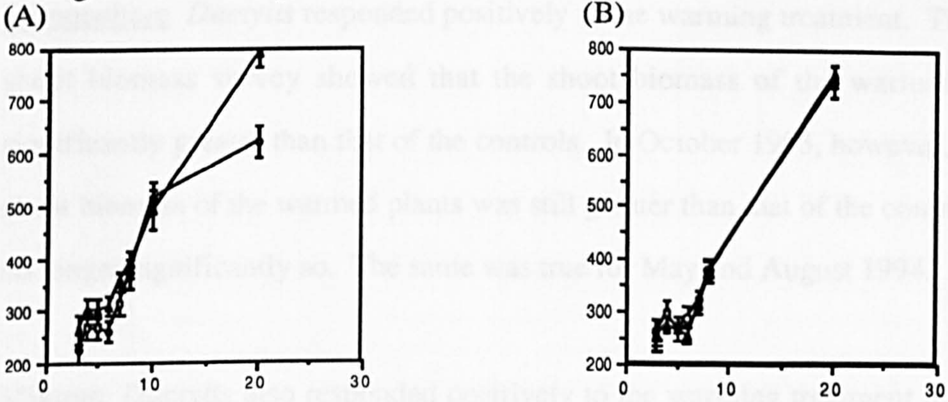
8.3.3 *DACTYLIS GLOMERATA*

Heights

Monoculture Throughout the period of warming there was no significant difference between the mean maximum height of the warmed plants and the controls. However, by the second week of August, the warmed plants were significantly taller (P<0.001).

Mixtures No significant difference was found between the warmed and control plants.

Figure 8.16. ***Dactylis* Mean Heights for Warmed and Control Plants.** x-axis = weeks from the start of the warming treatment. y-axis = height (mm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.

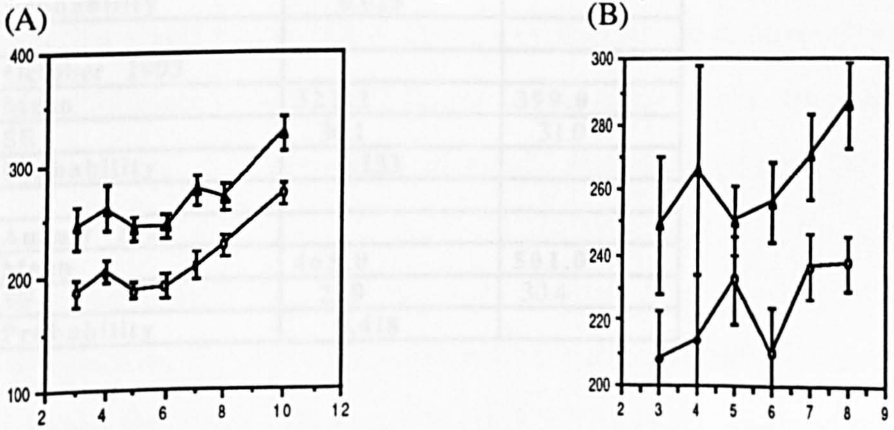


Length longest leaf

Monocultures Throughout the warming period, the mean length of the longest leaf of the warmed plants was found to be significantly longer ($P<0.01$) than the control plants.

Mixtures The mean length of the longest leaf of the warmed plants was consistently longer for the warmed plants than the controls; however, the difference was significant only from the second week of April onwards.

Figure 8.17. ***Dactylis* Mean Length of Longest Leaf for Warmed and Control Plants.** x-axis = weeks from the start of the warming treatment. y-axis = length of longest leaf (mm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Shoot biomass

Monoculture *Dactylis* responded positively to the warming treatment. The June 1993 shoot biomass survey showed that the shoot biomass of the warmed plants was significantly greater than that of the controls. In October 1993, however, the absolute shoot biomass of the warmed plants was still greater than that of the controls, although no longer significantly so. The same was true for May and August 1994.

Mixture *Dactylis* also responded positively to the warming treatment in mixture. In June 1993, the shoot biomass of *Dactylis* was significantly greater in the warmed bins, in both absolute and relative terms. From October 1993, however, although the absolute values for *Dactylis* shoot biomass were greater than the control values, they were not significantly so. In October 1993, *Dactylis* still occupied a significantly greater proportion of the total shoot biomass in the warmed replicates than in the controls. In 1994 *Dactylis* continued to occupy a proportionally greater percentage of the total shoot biomass in the warmed replicates, at a significance level of P=0.07.

Table 8.5 Shoot biomass of *Dactylis glomerata* Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
June 1993	Control	Warm
Mean	263.8	368.8
SE	24.7	21.7
Probability	0.013	
October 1993		
Mean	327.2	399.0
SE	30.1	31.0
Probability	0.133	
August 1994		
Mean	468.0	501.0
SE	23.9	30.4
Probability	0.418	

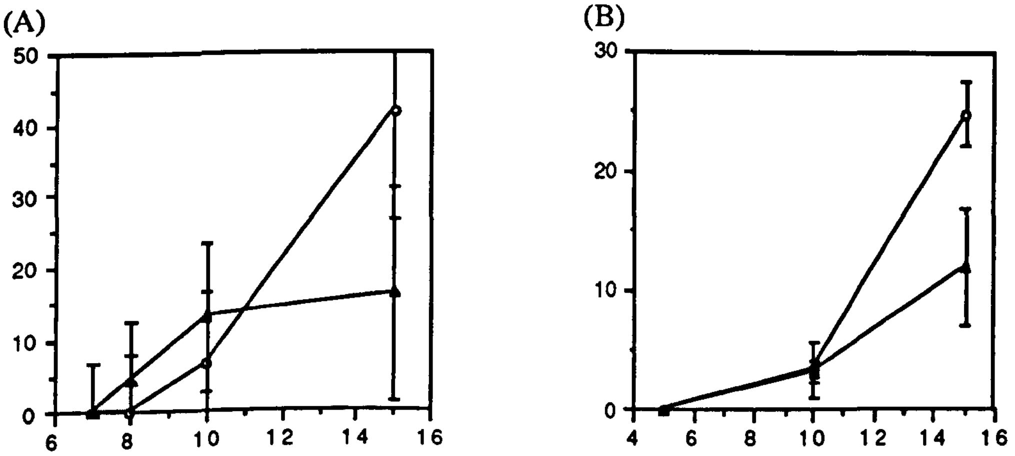
MIXTURE	Absolute shoot biomass		% of total shoot biomass	
June 1993	Control	Warm	Control	Warm
Mean	196.6	255.0	35.1	47.9
SE	19.2	12.1	2.1	3.1
Probability	0.033		0.01	
October 1993				
Mean	252.2	322.0	36.68	46.22
SE	30.55	25.4	1.6	2.0
Probability	0.117		0.006	
May 1994				
Mean	196.4	215.6	38.33	51.35
SE	47.2	13.2	5.0	3.7
Probability	0.705		0.069	
August 1994				
Mean	206.60	261.8	31.50	41.48
SE	29.8	5.0	4.1	2.2
Probability	0.105		0.065	

Flowering

During the period of warming, surveys were carried out on the mean number of inflorescences per replicate 7, 8, 10 and 15 weeks after the start of warming (first and third weeks of April, and third week of June respectively). No inflorescences were apparent in the control monocultures during weeks 7 and 8, although some were present in the warmed replicates. In week 10, inflorescences were present in the controls. The numbers were less than for the warmed replicates, although not significantly so. However, the survey carried out 15 weeks after the start of warming (third week of June) showed that the mean number of inflorescences produced by the warmed plants was significantly smaller than for the controls (P = 0.03). Warming therefore appeared to promote flowering one to two weeks earlier, although overall the mean number of inflorescences produced was smaller (Figure 8.18).

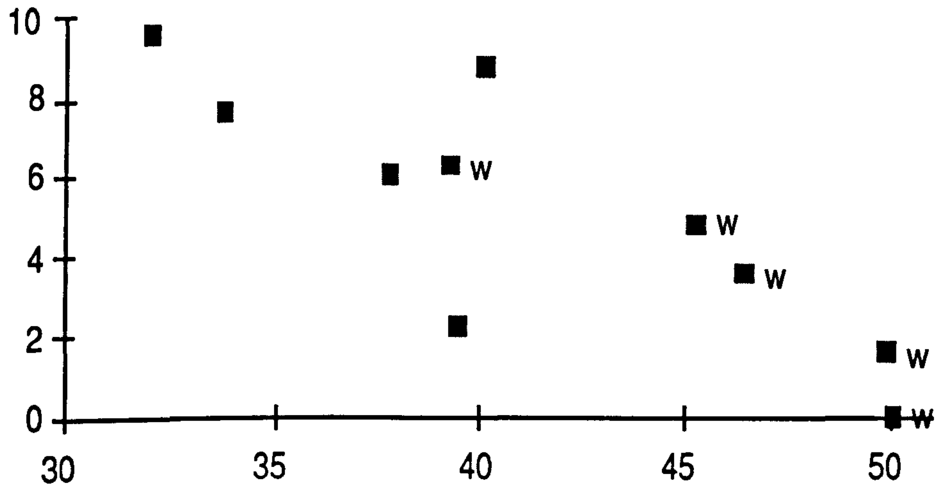
No inflorescences were apparent in the mixtures during week 8. In week 10 there was no significant difference between the mean number of inflorescences in the control and warmed replicates. However, in week 15, as in the monocultures, the number of inflorescences produced by the warmed plants was significantly smaller than that for the controls (P = 0.05)

Figure 8.18 Flowering Performance of *Dactylis*. x-axis = weeks from the start of the warming treatment. y-axis = Number of inflorescences. (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



A negative relationship was apparent between the vegetative shoot biomass of the plants and flowering performance. This could be detected for both the warmed and control replicates, and for the mixtures and monocultures separately, but was most pronounced for the warmed plants. Taking the two groups of plants together, it was clear that the controls had produced more inflorescences and less vegetative shoot biomass, and the warmed plants had produced fewer inflorescences and more vegetative shoot biomass (Figure 8.19).

Figure 8.19 **Flowering and Shoot biomass of *Dactylis*.** X axis = % of total shoot biomass occupied by *Dactylis* in mixture replicates. Y axis = total seed yield (g). Points marked W are warmed replicates, others are controls. $P<0.05$.



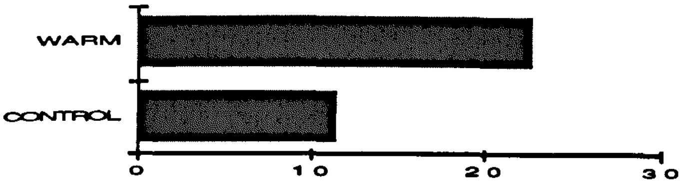
Vegetation Measurements in 1994

The mean leaf height, mean number of inflorescences, and mean inflorescence height of the plants warmed in 1993 were recorded at the end of August 1994. No significant difference was found between the warmed plants and the controls in either mixture or monoculture.

Pathogens

Dactylis is susceptible to attack by the fungal pathogen *Epichloe typhina* which causes developing inflorescences to abort (Beddows, 1959). A survey in the third week of June showed that over twice as many inflorescences aborted in the warmed replicates as in the controls.

Figure 8.18 Infection of *Dactylis* Inflorescences with *Epichloe typhina* - Monoculture Replicates X axis = mean number of infected inflorescences



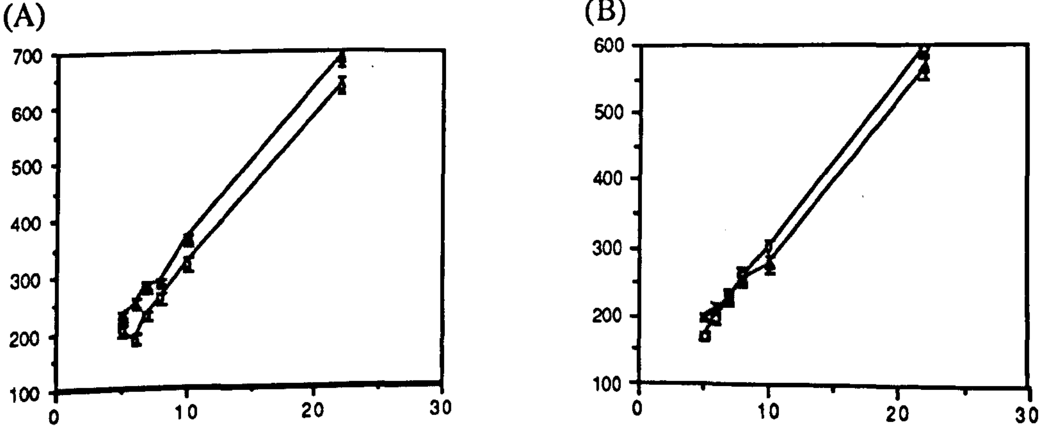
8.3.4 *FESTUCA RUBRA*

Heights

Monocultures Throughout the warming period the mean height of the warmed plants was greater than the controls, although not significantly so. However, measurements made in the second week of August showed that the warmed plants were significantly taller than the controls (P<0.01).

Mixtures Throughout the warming period and subsequently, the height of the warmed plants was smaller than in the controls. This difference was not significant during the early part of the warming period; however, by mid-May this difference was significant (P=0.01)

Figure 8.21. *Festuca* Mean Heights for Warmed and Control Plants. X axis = weeks from the start of the warming treatment. Y axis = height (mm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.

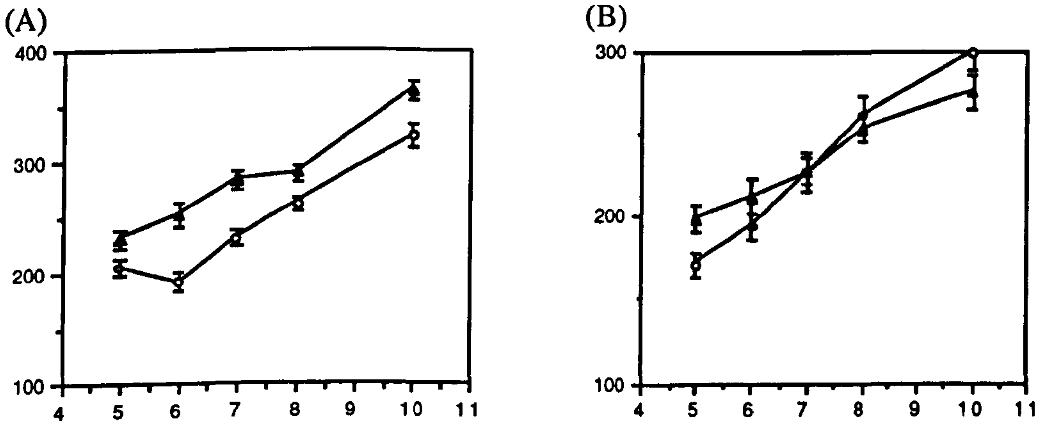


Length Longest Leaf

Monocultures Throughout the warming period the mean length of the longest leaf of the warmed plants was significantly greater than that of the controls (P=0.05, week five; P<0.001, weeks six to eight; P<0.01, week nine).

Mixtures Initially the mean length of the longest leaves of the warmed plants was significantly greater than the controls (P<0.01, week five). However, during weeks six to nine, this difference was reversed. By week ten, the mean length of the longest leaf of the controls was greater than that of the warmed plants (P=0.15).

Figure 8.22. *Festuca* Mean Length of longest leaf for Warmed and Control Plants. X axis = weeks from the start of the warming treatment. Y axis = length of longest leaf (mm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Shoot biomass

Monocultures No significant difference was found between the warmed and control plants.

Mixtures In June 1993 the mean absolute shoot biomass of the warmed plants was less than that of the controls, although not significantly so. The pattern was repeated in October 1993 and in August 1994. The proportion of the total shoot biomass occupied by *Festuca* was significantly smaller in the warmed replicates than in the control replicates in June 1993. Although the relative values were again smaller in October 1993 and in May and August 1994, the differences were no longer significant.

Table 8.6 Shoot biomass of *Festuca rubra*. Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
June 1993	Control	Warm
Mean	767	745
SE	30.8	40.8
Probability	0.67	
October 1993		
Mean	857.0	701.8
SE	48.93	53.35
Probability	0.06	
August 1994		
Mean	752.0	830.6
SE	49.8	53.7
Probability	0.314	

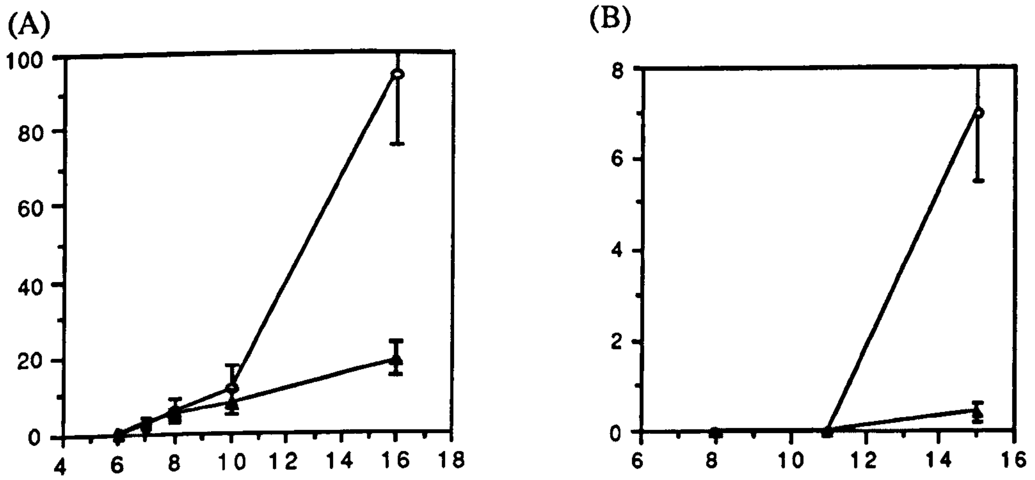
MIXTURE	Absolute shoot biomass		% of total shoot biomass	
June 1993	Control	Warm	Control	Warm
Mean	270.0	223.0	48.9	40.6
SE	28.3	23.8	1.7	2.4
Probability	0.24		0.02	
October 1993				
Mean	329.8	315.8	49.81	45.14
SE	28.8	23.9	2.77	1.06
Probability	0.72		0.15	
May 1994				
Mean	130.8	186.8	50.55	42.94
SE	23.0	19.0	7.26	1.38
Probability	0.18		0.33	
August 1994				
Mean	340.0	293.2	53.99	46.12
SE	30.0	24.4	4.3	2.0
Probability	0.256		0.138	

Flowering

Monocultures Inflorescences were first recorded in both the warmed and control replicates during week 8 (third week of April). A further survey in week 11 showed no significant difference between the two sets of plants. However, a survey in week 15 showed that the controls had now produced a significantly greater mean number of inflorescences than the controls. Warming therefore appeared to have no effect on the timing of flowering, but greatly reduced the number of inflorescences produced.

Mixtures Surveys in weeks 8 and 11 recorded no inflorescences. Recording in week 15 showed a significantly larger number of inflorescences in the control replicates than in the warmed. Again, warming did not advance flowering.

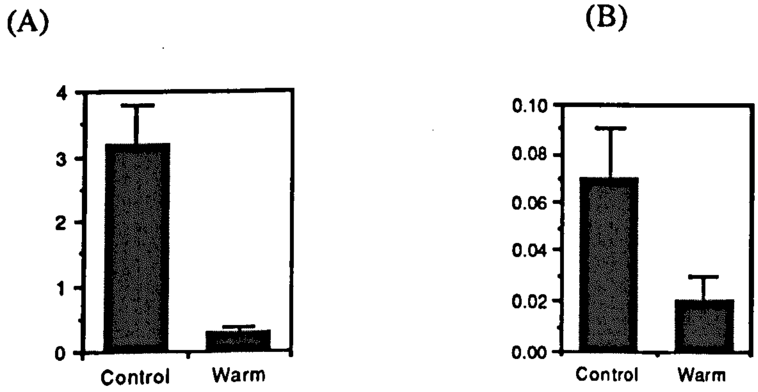
Figure 8.23. *Festuca* Mean Number of Inflorescences per Replicate Throughout the Warming Treatment for Warmed and Control Plants. x-axis = weeks from the start of the warming treatment. y-axis = Number of inflorescences. (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Yield

The mean seed yield of the monoculture control plants was significantly greater than that of the warmed plants (P=0.02). The mean yield of the mixture control plants was also greater than that of the warmed plants, however the difference was not significant (P=0.11).

Figure 8.24. ***Festuca*** **Seed Yield for Warmed and Control Plants in 1993** x-axis = weeks from the start of the warming treatment. y-axis = Seed Yield (g). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.

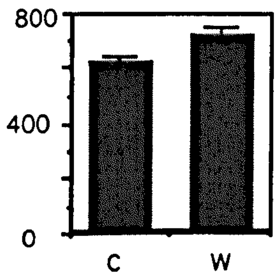


Vegetation Measurements in 1994

The mean height and mean number of inflorescences were recorded at the end of August 1994. No significant difference was found between the warmed plants and the controls in either mixture or monoculture.

The mean height of the warmed plants in monoculture was found to be significantly greater than the heights of the controls (P=0.008). No significant difference was found between any of the other parameters, in either mixture or monoculture.

Figure 8.25 Mean Height of *Festuca* Monocultures in August 1994. Y axis = Height (mm) Bars represent standard errors. P = 0.008.



A point quadrat survey was carried out in June 1994 at the end of the warming period for the second set of mixture replicates. The shoot biomass of *Festuca* was found to be significantly lower for the warmed plants than for the controls (P=0.02).

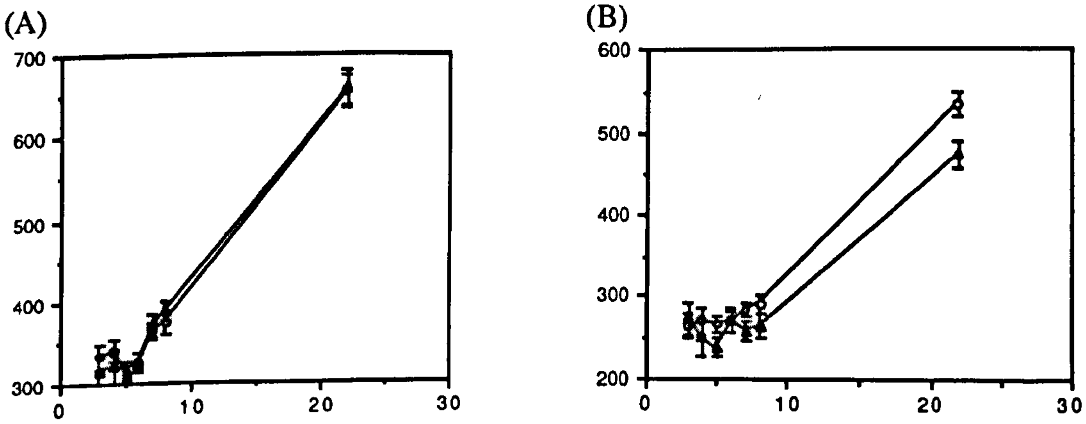
8.3.5 *POA PRATENSIS*

Heights

Monocultures Throughout the warming period there was no significant difference between the mean heights of the warmed and control plants. Measurements taken in the second week of August again showed no significant difference.

Mixtures Again, throughout the warming period there was no significant difference between the two sets of plants. However, measurements made in the second week of August showed that the mean height of the warmed plants was significantly lower than that of the controls (P=0.02).

Figure 8.26. ***Poa*** **Mean Heights for Warmed and Control Plants.** x-axis = weeks from the start of the warming treatment. y-axis = Height (mm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.

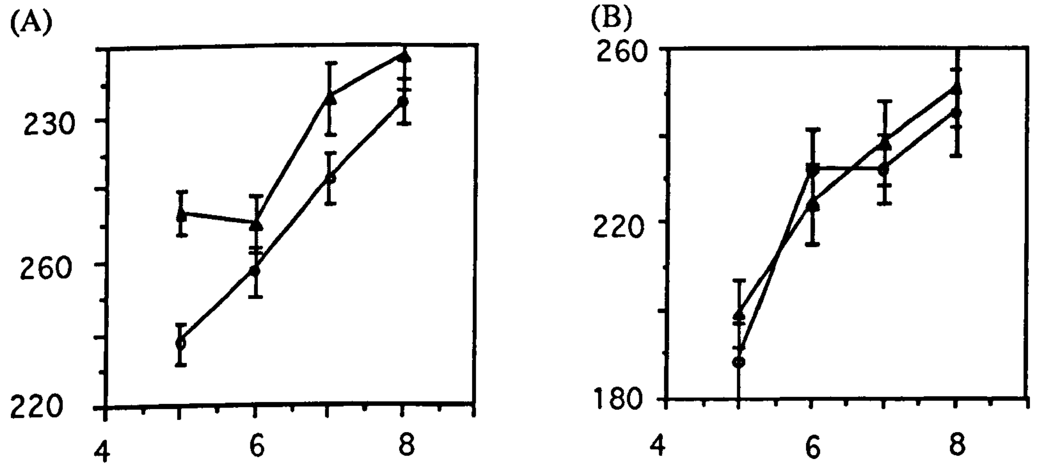


Mean length of the longest leaf

Monocultures The mean length of the longest leaf of the control plants increased at a steady rate throughout the warming period. Measurements made 5 weeks after the start of warming showed that the warmed plants appeared to have gained an initial advantage, with the mean length of their longest leaves being significantly greater than that of the controls ($P<0.001$). However, over the rest of the warming period there was no significant difference between the two sets of plants.

Mixtures Throughout the warming period there was no significant difference between the two sets of plants.

Figure 8.27. *Poa* Mean Length of Longest Leaf for Warmed and Control Plants. x-axis = weeks from the start of the warming treatment. y-axis = Length of Leaf (mm). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Shoot biomass

Monocultures The survey in June 1993 showed that the shoot biomass of the two sets of plants was the same. In October 1993 and August 1994 there was again no significant difference between the two sets of plants.

Mixtures The June survey showed that the mean shoot biomass of the warmed plants was less than that of the controls in both absolute ($P<0.06$) and relative ($P<0.05$) terms. The surveys in October 1993, May 1994 and August 1994 showed that the mean shoot biomass of the warmed plants was again less than that of the controls, in both absolute and relative terms; however the differences were no longer significant.

Table 8.7 Shoot biomass of *Poa pratensis* Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
June 1993	Control	Warm
Mean	567.0	570.0
SE	39.0	33.0
Probability	0.96	
October 1993		
Mean	442.4	499.6
SE	53.9	24.4
Probability	0.55	
August 1994		
Mean	544.4	494.4
SE	35.5	41.4
Probability	0.385	

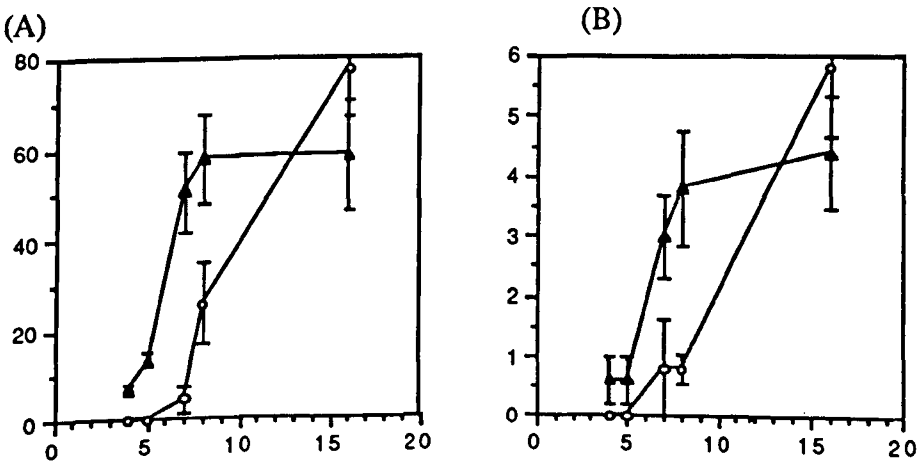
MIXTURE	Absolute shoot biomass		% of total shoot biomass	
June 1993	Control	Warm	Control	Warm
Mean	65.8	43.2	11.7	7.7
SE	7.7	6.6	1.4	1.1
Probability	0.06		0.05	
October 1993				
Mean	79.2	60.8	11.57	8.45
SE	12.0	8.3	2.0	1.0
Probability	0.24		0.19	
May 1994				
Mean	62.8	38.8	12.6	8.2
SE	14.8	12.6	3.1	2.1
Probability	0.25		0.28	
August 1994				
Mean	89.8	75.2	13.66	11.15
SE	10.5	14.11	1.5	1.9
Probability	0.430		0.331	

Flowering

Monocultures Inflorescences were first recorded in the control monocultures in the seventh week after the start of warming (third week of April). However, warming greatly advanced flowering - the first flowering survey four weeks after the start of warming found inflorescences already present in the warmed replicates. Throughout the warming period the mean number of inflorescences produced by the warmed plants was significantly more than in the controls ($P<0.001$, week seven; $P<0.05$ week eight). However a survey in the third week of June showed that, overall, the mean number of inflorescences produced by both sets of plants was not significantly different.

Mixtures The mixture plants showed a very similar pattern to the monocultures. Again, warming advanced flowering by three to four weeks, and throughout the warming period the mean number of inflorescences produced by the warmed plants was greater than in the controls, although this difference was significant only in week nine ($P<0.01$). Again, the survey in the third week of June showed that the mean number of inflorescences produced by the warmed bins was not significantly greater than the controls.

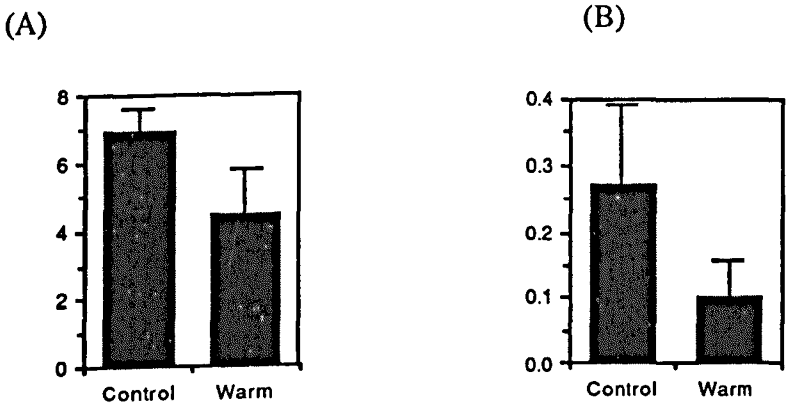
Figure 8.28. *Poa* Mean Number of Inflorescences for Warmed and Control Plants. x-axis = weeks from the start of the warming treatment. y-axis = Number of Inflorescences. (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.



Yield

The mean seed yield of the warmed plants was less than in the controls in both the monocultures and mixtures, although in both cases this difference was not significant.

Figure 8.29. *Poa* Mean Seed Yield for Warmed and Control Plants. x-axis = weeks from the start of the warming treatment. y-axis = Seed Yield (g). (A) Monoculture. (B) Mixture. Bars represent standard errors. Circles = Controls. Triangles = Warmed plants.

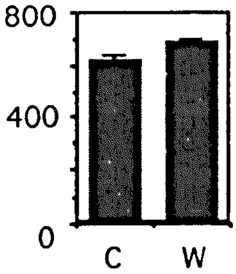


Vegetation Measurements in 1994

The mean height and mean number of inflorescences of the plants warmed in 1993 were recorded at the end of August 1994. No significant difference was found between the warmed plants and the controls in either mixture or monoculture.

The mean height of the warmed plants in monoculture was significantly greater than the heights of the controls (P=0.02). No significant difference was found between any of the other parameters, in either mixture or monoculture.

Figure 8.30 **Mean Height of *Poa* Monocultures in August 1994.** Y axis = Height (cm) Bars represent standard errors. P = 0.02.



A point quadrat survey was carried out in June 1994 at the end of the warming period for the second set of mixture replicates. The shoot biomass of *Poa* was found to be significantly lower for the warmed plants than for the controls (P=0.004).

8.4 COMPARATIVE RESULTS

8.4.1 Performance and DNA Value

In 1993 the height and length of longest leaf were recorded for each of the species in the mixtures and monocultures every week, from the end of March to the end of April. The performance of each species was calculated by finding the % increase or decrease in height or length of longest leaf of the warmed plants relative to the controls at each recording period. The results for all species over the four week period, in mixture and in monoculture, are presented in figures 8.30 and 8.31. Species' performance is plotted against the natural log of the 2C DNA value for the species. Linear regression lines have been drawn through all points and the significance of those regressions indicated.

The results for the species grown in monoculture are markedly different from those grown in mixture. No clear pattern emerges from the leaf length data for the monocultures and no regressions were significantly different.

In the mixtures, *Cirsium* consistently showed the greatest increase in height or leaf length . For both the height and leaf length data, the plants grown in mixture all showed a negative relationship between response to warming and DNA content. In all cases the relationship was significant at P=0.05. The significance of the regression statistic increased over the period of measurement. The final 'snapshot' record for leaf length showed a pattern in accordance with predictions for species response to warming and 2C DNA content. This relationship was significant at P<0.001.

Figure 8.31 The Response of the Five Species to Warming in Mixture and 2C DNA Value: Height Data. X axis = log(N) 2C DNA value. Y axis = ratio (expressed as percentage) of height of warmed plants to controls. A = Measurements from first week of April 1993. B = Second week. C = Third week. D = Fourth week.

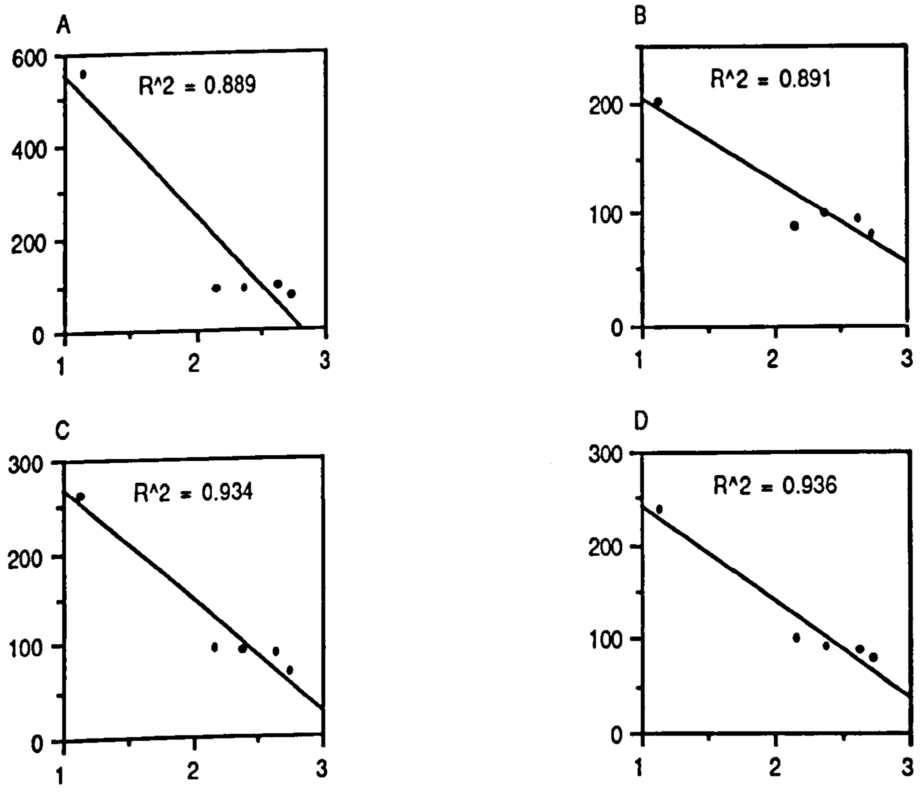
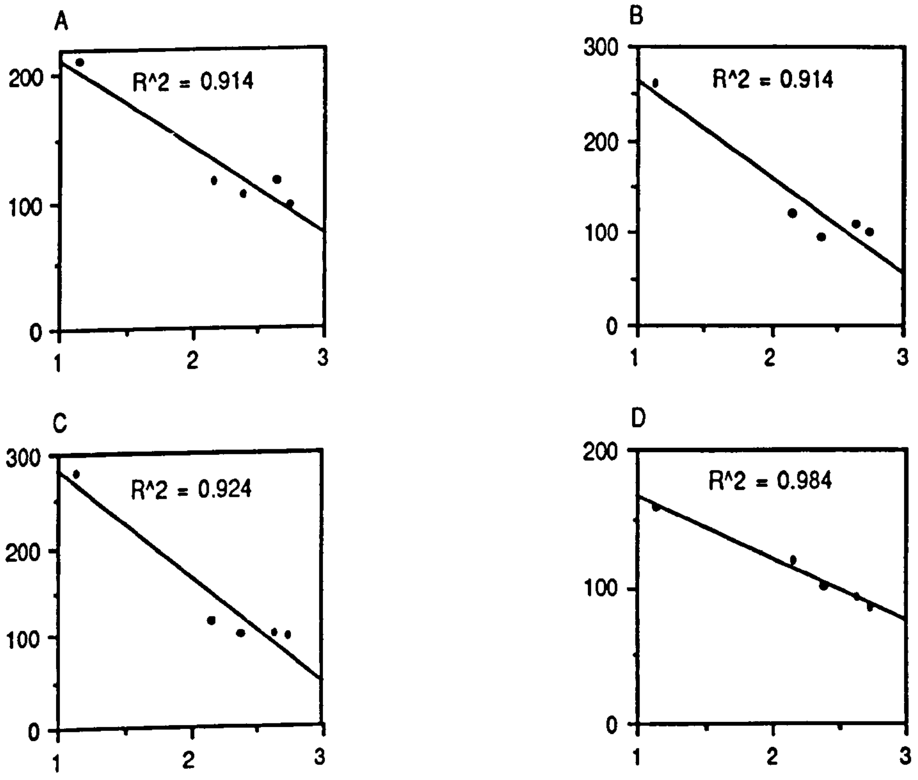


Figure 8.32 The Response of the Five Species to Warming in Mixture and 2C DNA Value: Leaf length Data. X axis = log(N) 2C DNA value. Y axis = ratio (expressed as percentage) of height of warmed plants to controls. A = Measurements from first week of April 1993. B = Second week. C = Third week. D = Fourth week.



Figures 8.31 and 8.32 demonstrate differences in plant performance over a given time period with reference to 'snapshot' measurements made at specific points during that period. An alternative approach is to calculate differences in growth rate over a given period in response to warming.

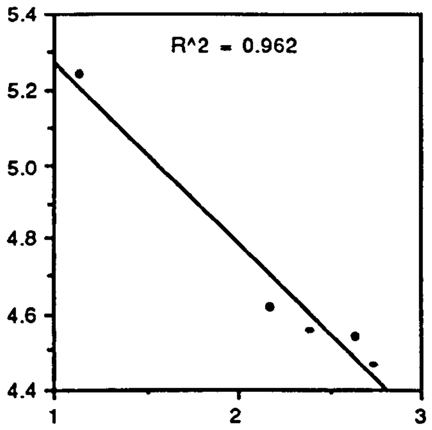
In 1994 a second set of mixture replicates were subjected to the warming treatment. A measure of the absolute growth rate of the five different species growing in mixture was obtained using point quadrat results obtained from surveys in the first week of May and the second week of June. Growth rate was estimated adapting the equation (Hunt, 1990):

$$G = (W_2 - W_1)/(t_2 - t_1)$$

where W = shoot dry weight and t = time. Shoot biomass (point quadrat value) was substituted for dry weight.

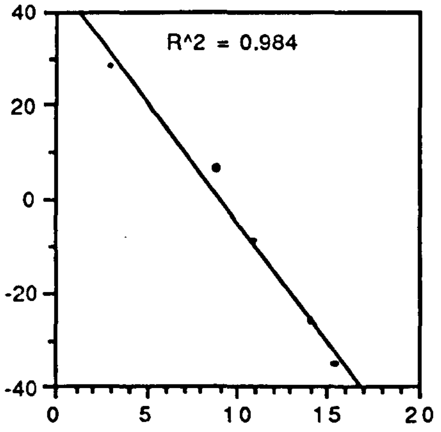
The growth rate of each species under the warming treatment is plotted against 2C DNA value in Figure 8.33 A significant negative relationship ($P<0.05$) exists. This Figure suggests that species with a lower DNA value are able to respond to a greater degree to warming than those with a higher DNA value.

Figure 8.33 The Response of the Five Species to Warming in Mixture and 2C DNA Value: Absolute Growth Rate. X axis = 2C DNA value. Y axis = Absolute growth rate.



This relationship is expressed more clearly in Figure 8.34, where the relative performance of the warmed plants compared to the controls is plotted against 2C DNA value. Plant performance is expressed as the ratio of absolute growth rate in the warmed plants to that of the controls. Again a negative relationship exists ($P=0.001$). Species with a relatively low DNA value show a positive response to the warming treatment, while those with a relatively high value show a negative response. It is striking that the results for 1994 agree with the results obtained in 1993, using a different set of replicates and a different measure of plant performance.

Figure 8.34 The Response of the Five Species to Warming in Mixture and 2C DNA Value: 'Relative' Absolute Growth Rate. X axis = log(N) 2C DNA value. Y axis = The ratio (expressed as percentage) of the absolute growth rate of warmed plants to controls.



8.4.2 Performance and Growth Rate

The relative 'performance' values obtained from measurements of plant height and leaf length gained from the 1993 warmed replicates (and shown in Figures 8.31 and 8.32) are plotted against the absolute growth rate values obtained from the warmed replicates in 1994. The relationships are shown in Figures 8.35 and 8.36. In each case a positive relationship is obtained, all significant at P=0.05. The relationship is particularly striking for plant height in week 4. Again, the results of 1993 are repeated in 1994, using different replicates.

Figure 8.35 The Response of the Five Species to Warming in Mixture: Relative Performance and Growth Rate. Height Data. X axis = Absolute Growth Rate (1994 data) Y axis = ratio (expressed as percentage) of height of warmed plants to controls (1993 data).. A = Measurements from first week of April 1993. B = Second week. C = Third week. D = Fourth week.

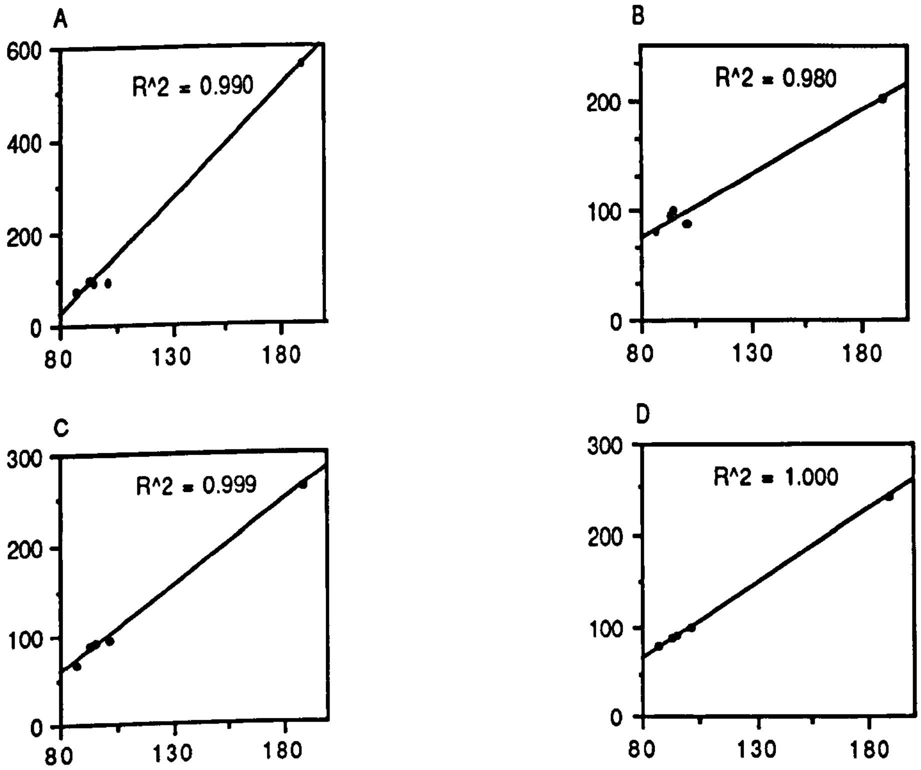
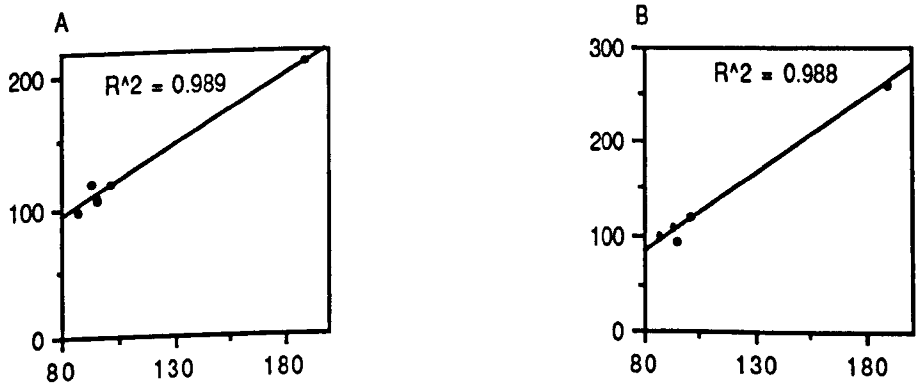
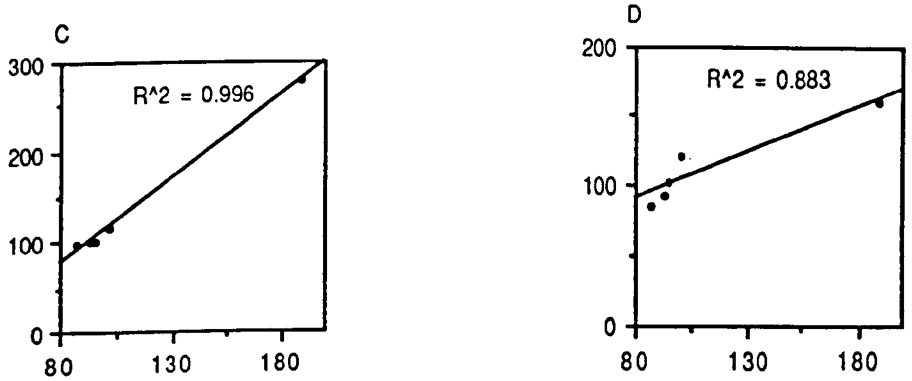


Figure 8.36 The Response of the Five Species to Warming in Mixture: Relative Performance and Growth Rate. Leaf length Data. X axis = Absolute Growth Rate (1994 data) Y axis = ratio (expressed as percentage) of leaf length of warmed plants to controls (1993 data).. A = Measurements from first week of April 1993. B = Second week. C = Third week. D = Fourth week.





8.4.3 Flowering

The effect of the warming treatment on the time of flowering was assessed in 1993. *Cirsium* and *Achillea* commenced flowering after the warming treatment was completed and the time of flowering was not significantly altered, although, as shown above, the overall flowering performance was affected.

The three grasses in the mixtures commenced flowering during the warming period, and comparison of the effect of the warming treatment on the timing of flowering reveals differences between the species. There was no apparent effect of warming on the time of flowering of *Festuca*. However, warming advanced flowering in both *Poa* and *Dactylis*, particularly in the monocultures. *Poa* was the first grass to flower in both the mixture and monoculture bins, and its flowering was also advanced to a greater degree than that of the two other species. Comparison of the flowering of *Poa* in both the warmed and control monoculture replicates with *Dactylis* and *Festuca* is shown in Figures 8.37 and 8.38. The figures clearly demonstrate the earlier flowering of the warmed *Poa* replicates compared with the *Poa* controls and the warmed and control replicates of the other two grasses.

Figure 8.37 Flowering of *Poa* and *Festuca* in Warmed and Control Replicates. X axis = Weeks after start of warming treatment. Y axis = Mean number of inflorescences per replicate. (Data from figures 8.22 and 8.27, in which error bars are shown).

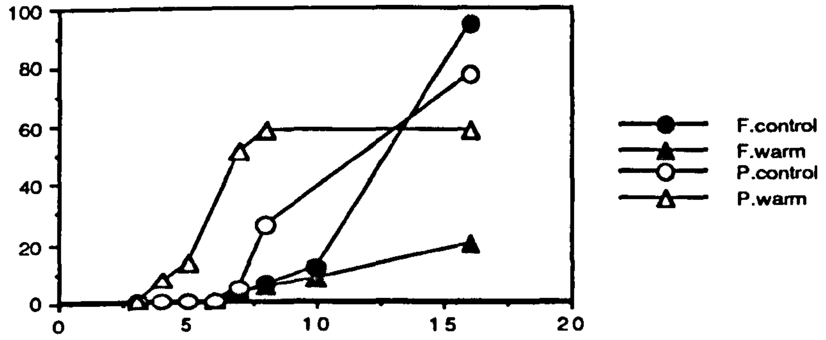
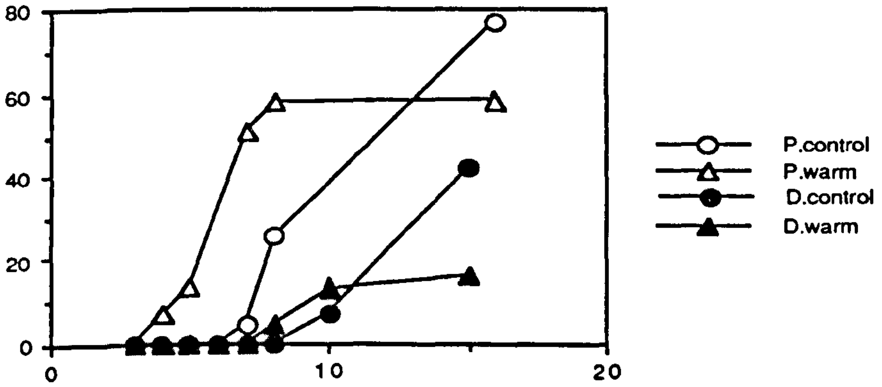


Figure 8.38 Flowering of *Poa* and *Dactylis* in Warmed and Control Replicates. X axis = Weeks after start of warming treatment. Y axis = Mean number of inflorescences per replicate. (Data from figures 8.18 and 8.27, in which error bars are shown).



8.5 DISCUSSION

8.5.1 *ACHILLEA MILLEFOLIUM*

No firm predictions were made in Chapter 7 about the performance of *Achillea* in response to the warming treatment. In the experiment *Achillea* was retarded by warming. In monoculture the plants initially responded positively to the treatment.

However, by the end of the warming period this advantage had been lost, and a range of indicators showed the warmed plants to be performing significantly less well than the controls. In mixture, by the end of the period and over the summer, a range of indicators showed the warmed plants performing more poorly than the controls.

In view of its relatively high DNA value, and large fructan reserves in its rhizomes in winter, *Achillea* may be expected to be capable of growth during cool periods (Grime *et al.*, 1988). As the plants may already have been in active growth at the start of the treatment, the initial positive response in monoculture would be expected. However, the results suggest that *Achillea* is weakened by prolonged 'forcing' at high temperature. The clear increase in susceptibility to insect herbivory may partly account for the reduced performance of the plants in both monoculture and mixture, while in mixture *Achillea* was heavily shaded by promoted *Dactylis* in the warmed replicates. As a result of this increased competition, *Achillea* was eliminated from two of the five warmed replicates by the beginning of the second growing season.

8.5.2 *CIRSIUM ARVENSE*

The predicted response of *Cirsium arvense* to the warming treatment was positive. The experimental evidence indicates that *Cirsium* did indeed respond positively and rapidly to the warming treatment, in both mixture and monoculture. While in the first season warming did not ultimately result in greater shoot biomass, the warmed plants in both mixture and monoculture were significantly taller than the controls in the second season after warming. Warming did not increase the total number of shoots produced, although it did cause shoots to emerge much earlier in the mixtures.

Cirsium arvense had the lowest 2C DNA value of all the species in the experiment. As such it may be expected to grow primarily through concurrent cell division and expansion once temperatures rise in the spring (Grime & Mowforth, 1983). A low

DNA content and associated small cell size and rapid cell cycle may also mean that *Cirsium* is able to respond rapidly to increased temperatures during cooler periods. Two results in particular suggest that *Cirsium* responds directly to increased temperatures. Firstly, the height advantage of the warmed plants in mixture in 1993 was lost once warming ceased, and secondly, the earlier warming in 1994 resulted in a corresponding earlier emergence of shoots than in 1993, even though, because of a colder winter, the shoots of the control plants actually emerged several weeks later than in 1993.

8.5.2.1 Herbivory

The warmed plants of *Cirsium*, like those of *Achillea*, suffered earlier and greater infestation with insects than the control plants. The insects infesting both *Achillea* and *Cirsium* would have been migratory and actively selected the infected plants, rather than have over-wintered on the plants and been promoted into early growth by the warming (V. K. Brown, pers. comm.). There are two possible explanations for the difference in infestation between the treated and control plants. Firstly, the insects may have been attracted to the warm conditions in the treated bins rather than the plants themselves, or secondly, the warmed plants were in some way more attractive to the migrating insects than unwarmed plants. The evidence suggests that the second possibility is more likely. A similar underlying pattern of infestation is apparent for all replicates - a build up in insect numbers to a peak and then a decline. Typically, warming advances the infestation by a number of weeks, but does not alter the underlying pattern. This suggests that the two species have particular points in their growth during which they are susceptible to infestation. The earlier growth prompted by warming advances the point at which the plants may be susceptible. The migrating insects are able to detect this, whether through a chemical message such as sap sugar content, or a visual one, such as leaf colour (V. K. Brown, pers. comm.) and settle on those attractive plants. If warming not only causes earlier infestation, but also heavier infestation, this may have negative effects on plant growth, as may have occurred with *Achillea*.

Aphid migration patterns are dependent on mean monthly temperature in late winter and spring (Clark *et al.*, 1992, Hulle *et al.*, 1994). As a result, year to year changes in winter and spring temperatures may result in yearly differences in the timing of aphid infestations. However, the results discussed above also suggest that yearly variation in weather may also affect the timing of plant susceptibility to herbivory. The food web involving aphids is complicated, making it difficult to interpret the effects of weather. As well as the condition of the food plant, the build up of predators and parasites (which have their own predators and parasites) must also be considered (Ward, 1990).

8.5.3 *DACTYLIS GLOMERATA*

Both positive and negative effects of warming were predicted for *Dactylis*. As predicted, the shoot biomass, height and leaf length of *Dactylis* were strongly promoted by the warming, in both mixture and monoculture. However, the treatment also had a pronounced negative effect on the flowering performance and subsequent seed yield of the plants. In fact, a clear negative relationship was apparent between vegetative (foliage) shoot biomass and seed yield; larger plants produced fewer inflorescences. Warming appeared to produce robust, leafier plants with fewer inflorescences. *Dactylis*, along with many other British grasses, is known to have a winter chilling requirement for maximum flowering to occur (Beddows, 1959). The plants may not have received adequate chilling to enable full flowering and instead produced greater vegetative growth. This may be one possible explanation for the negative effects of a mild winter on *Dactylis* shoot biomass evident at Bibury. Poor flowering following a mild winter may result in a lower field score during the summer survey. Also, because *Dactylis* is a clump-forming grass that relies entirely on seed to produce new plants, *Dactylis* may be under-represented in the vegetation in years following a poor seed set.

Consistent with this hypothesis is the finding in Chapter 3 that the negative effects of a mild winter on *Dactylis* are not apparent at Bibury until two years after the event.

8.5.4 *FESTUCA RUBRA*

It was predicted in Chapter 7 that *Festuca* will be retarded by warming. In monoculture, *Festuca* was in fact promoted during the treatment, although this was not reflected in increased shoot biomass subsequently. In mixture, however, *Festuca* was retarded. In the absence of competition, *Festuca* may be promoted, and is certainly not retarded, whereas in mixture it is retarded. It appears, therefore, that under competitive conditions, *Festuca* is indirectly retarded as a result of warming, perhaps as a consequence of the increased vigour of other species, such as *Dactylis*.. *Festuca* appeared to have a similar chilling requirement to *Dactylis* for maximum flowering.

8.5.5 *POA PRATENSIS*

As with *Festuca, Poa* was predicted to respond positively to warming in monoculture but negatively in mixture. The experimental results broadly support these predictions. Monoculture plants were certainly not retarded, and although generally there were no significant differences between treated and control plants, height and leaf length measurements suggested some promotion through warming. *Poa* in mixture was clearly retarded by the warming treatment. Again it would appear that *Poa* is indirectly retarded by warming through competition from other species in the mixed vegetation.

8.5.7 COMPARATIVE RESULTS

8.5.7.1 Plant performance and DNA

In Chapter 7 it was predicted that species with low nuclear DNA content may be promoted by warm winter weather, while under cooler conditions species with larger DNA values may be at an advantage.

This hypothesis is supported by the experimental results, but only for the mixture replicates. This is as expected. In mixture, the lower value DNA species (*Cirsium* and *Dactylis*) performed better under the warming treatment than under control conditions, while the higher value DNA species (*Festuca* and *Achillea*) performed less well. It is reasonable to assume that these latter species are retarded through competition with promoted low DNA species. Low DNA species may be able to respond rapidly to favourable growing conditions because of their capacity for rapid cell division, while higher value species may gain greatest advantage under cooler conditions, growing primarily through cell extension rather than division in winter and early spring (Grime & Mowforth 1983)

8.5.7.2 Performance and Growth Rate

Credibility is added to the results of the warming treatment through the results of 1993 being repeated in 1994, using a different set of replicates, and a different method of calculation of plant performance.

8.5.7.3 Flowering

The flowering of *Poa* was advanced by the warming treatment to a much greater extent than in the other two grasses. *Poa* was also the earliest grass to flower in the control replicates. The results of this experiment support other work on the effect of increased spring temperatures on flowering in grasses: those species which are earliest to flower in the year tend to flower earlier under increased temperature, while those that flower later in the season are relatively insensitive to temperature but are instead controlled by day-length (R. Booth, pers. comm.). In some species, mild winters may induce growth and generate competing sinks for photosynthate and mineral nutrients before day-length is sufficient fully to induce flowering (Heide , 1986). This may also explain the reduced flowering performance of *Dactylis* and *Festuca* following warming.

8.6 CONCLUSIONS

The predictions that were made about the response of individual species to the warming treatment were all fulfilled. *Dactylis* and *Cirsium* appeared to be promoted by the direct effect of increased temperature on growth. *Achillea, Festuca* and *Poa* appeared to be retarded by the treatment indirectly through competition, primarily with *Dactylis*, which produced a greater amount of tall, arching foliage as a result of the treatment.

The two species directly promoted by the treatment were also the two species with the lowest nuclear DNA content. Again, this fitted exactly the predictions made.

CHAPTER NINE: APPLICATION OF A LATE SPRING AIR FROST

9.1 INTRODUCTION

This chapter describes an experiment conducted to assess the response of plants in monoculture and mixture replicates to extreme low temperatures. Initially the proposed treatment was intended to achieve a continuous reduction in the temperature of the plant environment over an extended period early in the year (comparable with the warming treatment described in Chapter 8). However, while realistically simulating a cold winter, this approach had to be ruled out on the grounds of cost and technical feasibility.

A second approach aimed to simulate a short, sharp cold snap in spring. This was considered both practical, and potentially more illuminating. The effect of cold on plants is not only determined by the magnitude of the drop in temperature, but is to a large extent dependent upon the season, developmental stage and on how long the low temperature lasts. Species of temperate climates vary in their freezing tolerance from a minimum of practically none in the new spring growth to the maximum value of midwinter (Levitt, 1972). Episodic drops of temperature during spring and summer in temperate climates are therefore more dangerous for plants than periodic cold in winter because the plants are in an active state of growth (Alberch & Corcuera, 1991). Late spring frosts can cause considerable damage to plants in active growth in the field (Luken, 1990). Rapid spring growth, such as that following a period of above-average temperatures, is particularly susceptible because it is essentially unable to harden (Levitt, 1972).

A technique was devised that would impose a severe frost on the plants growing in the experimental containers at a period when the plants were in active growth. It was envisaged that the treatment would:indicate species' resistance to frost while in active spring growth. Unfortunately no direct predictions could be made about the possible effects of the treatment on individual species in the experiment from the analysis of the Bibury field records, described in Part 1. However, it was envisaged that the treatment would impose severe disturbance on the vegetation in the bins and that the resulting changes in plant performance would allow insights to be gained into the possible effects of climate-induced disturbance on the dynamics of grassland vegetation.

9.2 METHODS

9.2.1 Experimental Technique

The chosen technique was adapted from a device capable of simulating night-time air frosts in field situations, designed jointly by P. C. Thorpe and C. W. Macgillivray of the NERC Unit of Comparative Plant Ecology, University of Sheffield, and G. H Priestman of the Department of Mechanical and Process Engineering, University of Sheffield (Thorpe *et al.*, 1993). The original device was used to impose frost on 2 x 2 m areas of derelict limestone grassland (Buckland, 1994). Several modifications were therefore needed to the design to enable its use with the bins containing of the Bibury transplants.

9.2.2 Design of the Apparatus

The re-designed apparatus consisted of an insulated compartment that was placed over an experimental bin. The insulated chamber was constructed from a bin of the same dimensions as the experimental containers, in which inlet holes had been drilled. The chamber was inverted over the experimental container. Jets of cold air were generated by passing compressed air through commercially available vortex tubes. The cold air jets were mixed in an air dispersal chamber from which the cold air sank onto the plants below.

Vortex tubes are cylindrical tubes into which compressed air enters through tangential nozzles. A hot stream flows from one end of the tube through a peripheral annular exit.

The remaining gas exits as a cold stream at the other end through a circular orifice on the tube axis. The overall gas flow is controlled by the tube size and input pressure; the cold stream temperature and flow split can be controlled by adjusting the area of the hot stream exit (Thorpe *et al.*, 1993).

Compressed air was generated at 7 bars by a diesel-driven compressor unit (Atlas Copco XAS 60, Vibroplant, Rotherham, UK) and delivered through rubber pipes to a vortex tube (Model 208 25H, Meech Static Ltd, London, UK). The compressed air was first passed through an after blast cooler (to reduce the temperature of the air) and an oil filter (to protect both the treated plants and the internal working of the vortex tubes. Both the cooler and filter were hired from Vibroplant, Rotherham). The cold air output of the tube was directed into the top of the insulated chamber.

A nylon mesh screen was fixed to the inside of the chamber 200 mm from its base. The screen allowed the cold air stream to mix with ambient air and then settle onto the plants below. The chamber was insulated with a standard boiler insulation jacket (Wickes, Sheffield). The whole unit was sealed with self-adhesive parcel tape. Figure 9.1 shows the construction of the frosting apparatus in diagrammatic form.

9.2.3 Temperature Control

Temperatures were controlled automatically during operation. The compressed air supply to the vortex tubes could be switched on or off using valves. The opening and closing of the valves was determined by the temperature within the frosting chamber. Temperature probes (thermocouples) were suspended within the chamber at vegetation height (15 mm above soil level) and wired to a central control box which controlled the opening of the valves. When the chamber reached a pre-set minimum temperature, the valves were closed and the supply of compressed air shut off. This caused the temperature within the chamber to rise. However, once the temperature had again risen above the pre-set temperature the valves were opened, again forcing cold air back into the chamber.

A temperature probe attached to a hand-held digital thermometer was also suspended adjacent to the control thermocouple. Temperature readings were made every 15 minutes during operation. If the temperature in the chamber had deviated from its pre-set level, the temperature was returned manually to the desired value by standard adjustments to the vortex tubes. Finally, a third temperature probe was inserted which was attached to a data logger which produced a continuous record of temperatures throughout the operating period. Figure 9.2 illustrates the arrangement of the frosting apparatus and controls.

9.2.4 Operation of the Apparatus

Frosting was carried out in 1993 in the third week of May. A total of thirty containers were frosted (five each of the five species monocultures and five mixtures). The treatment aimed to expose the vegetation to a minimum temperature of -3.0°C for a period of three hours. The frost was applied in the early hours of the morning, between midnight and 4.00 am. Because of the noise of the compressor and the vortex tubes in operation, the treatment had to be carried out in a non-residential area. The replicates were therefore transported to a suitable site: Blackburn Meadows Water Treatment Works (Yorkshire Water), Tinsley, Sheffield. To accompany the treated replicates, thirty corresponding control replicates were also taken to the site and remained there for the duration of the treatment.

Frosting was applied to five replicates at once. Replicates were randomly assigned to each frosting event. The compressed air supply was split and fed to five vortex tubes attached to five insulated chambers. Plate 9.1 illustrates the frosting apparatus in action.

Figure 9.1 Diagrammatic Representation of the Frosting Apparatus. Not to scale

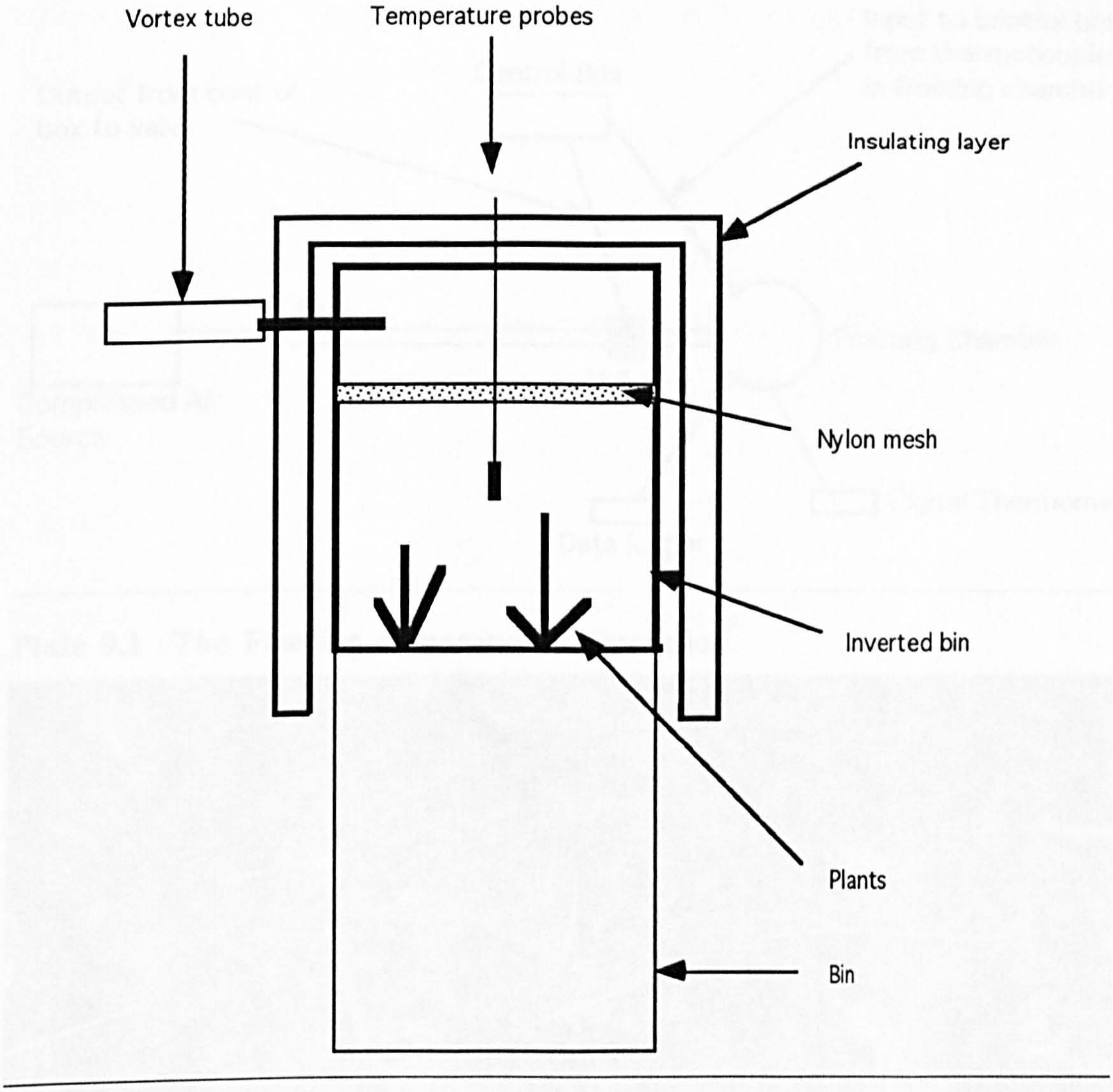


Figure 9.2 **Layout of the Frosting Apparatus and Controls.** Not to Scale.

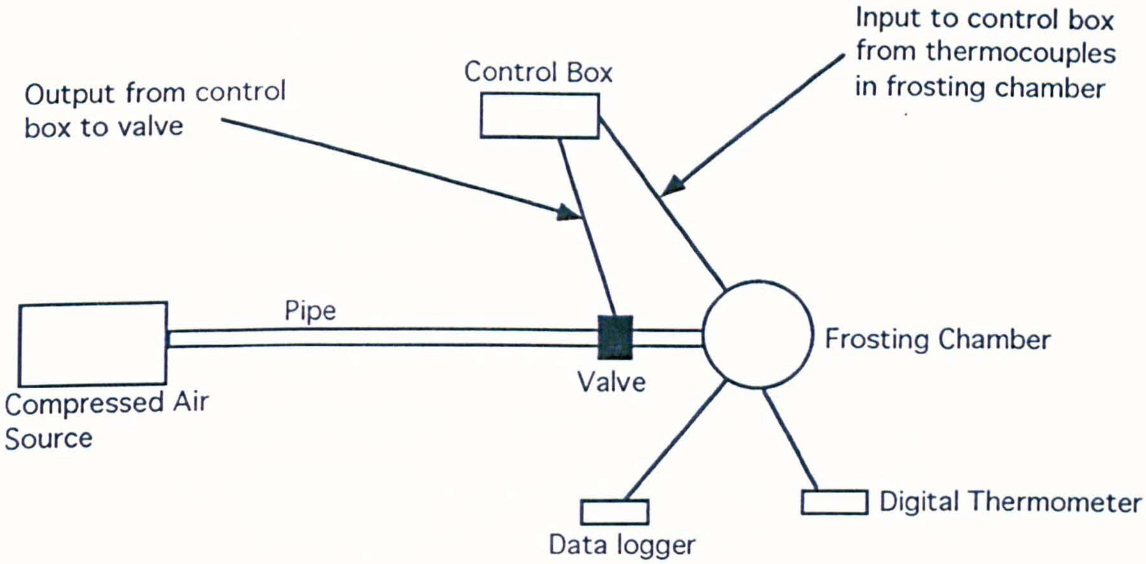
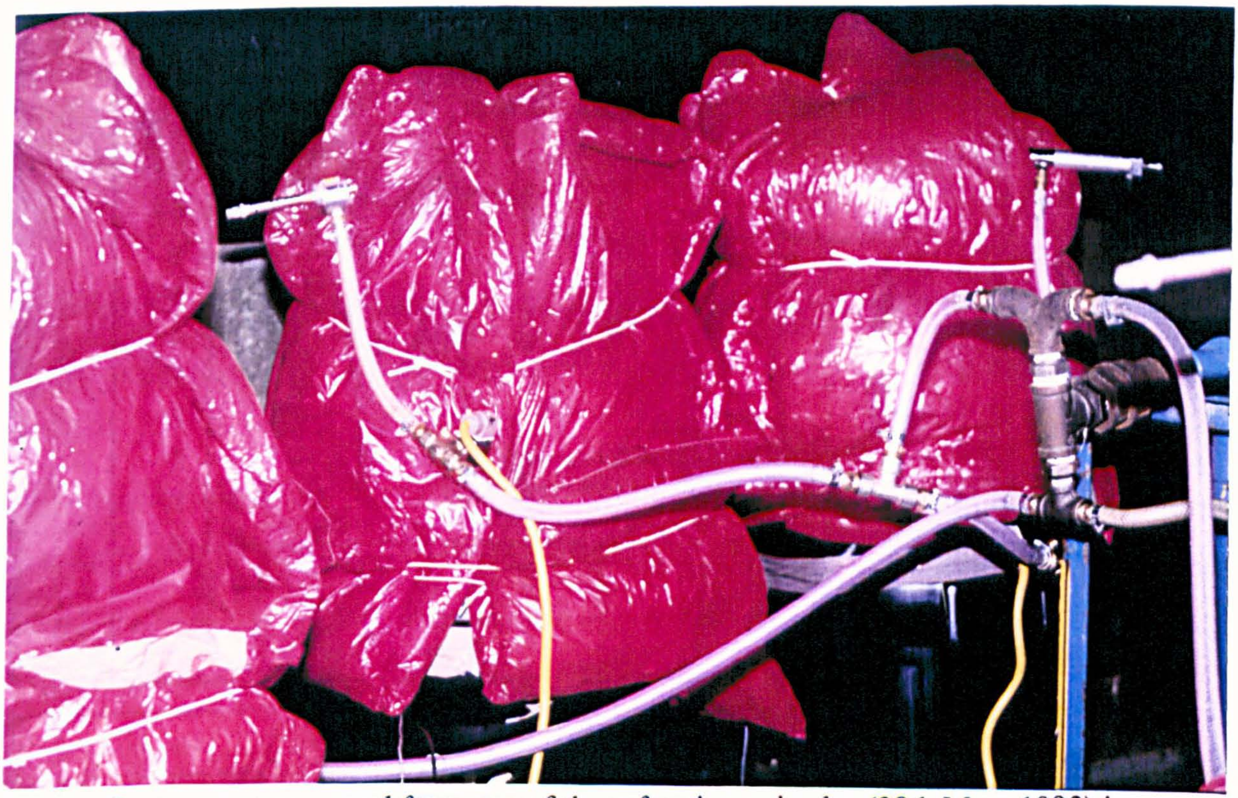
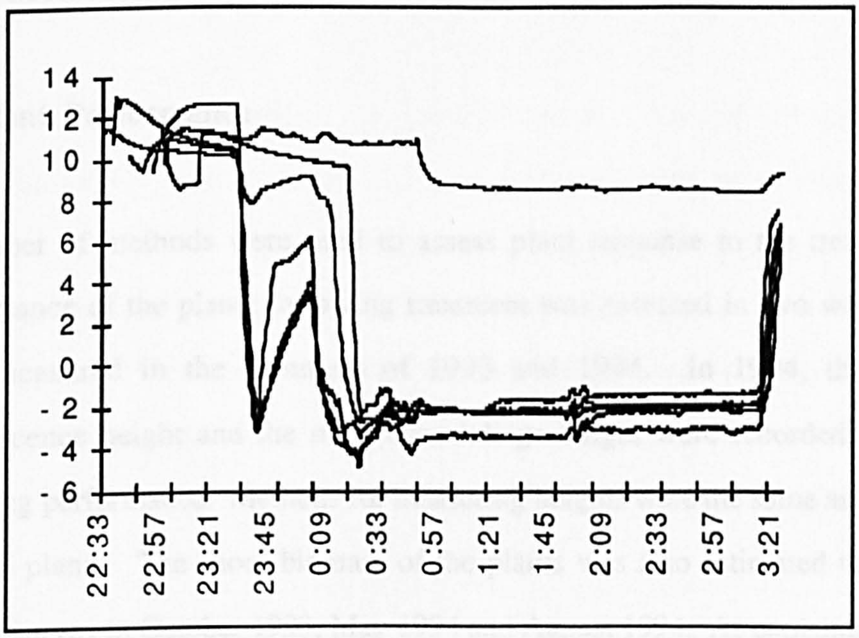


Plate 9.1 **The Frosting Apparatus in Operation.**



A sample temperature record from one of these frosting episodes (20th May, 1993) is shown in Figure 9.3. The uppermost track represents ambient temperature, recorded from a probe left in the open air. The five other tracks are from the frosted replicates. An initial rise in temperature relative to ambient is noticeable in the tracks of the treated replicates. This is associated with the placing of the chambers over the plants, and is probably caused by heat exchange from the soil to the trapped air by convection and radiation. This is followed by a period of cooling as the cold air is introduced to the chambers. In 30 minutes the temperature drops from 12°C to the desired temperature. After a short period of adjustment and stabilisation, the desired temperature is maintained to a remarkable degree. Once the treatment is completed, and the source of compressed air turned off, temperatures rapidly recover to ambient. The ambient track shows a drop of around 2°C at 00.45 am. This may be associated with a sudden drop in air temperatures, for example through a change in wind direction or decrease in cloud cover, or it may be a result of an accidental change in the position of the ambient probe.

Figure 9.3 Temperature Record for the Frosting Treatment of May 20th 1993. X axis = Time (24 hr) Y axis = Temperature (°C) Six tracks are shown, five of frosted replicates and one (uppermost) at ambient temperature..



Subsequent analysis of the temperature records showed that it had not been possible to maintain a constant minimum temperature for all the replicates. Some replicates had been exposed to much lower temperatures (the lowest being -8.7°C) while others had been exposed to minimal frosting (the highest minimum temperature being -1.1°C)

This variation initially appeared to defeat the original aim of the experiment. However, because of the random assignment of replicates to frosting on different nights, each set of replicates was exposed to a range of minimum temperatures and this enabled observations to be made on the tolerance of the different species to varying degrees of frost. An analysis of variance carried out on all the treated replicates showed that there was no significant difference between the mean minimum temperatures to which each set of replicates had been exposed.

Technical failure resulted in temperature tracks not being recorded for all five replicates on one night, and for four additional replicates over the other nights. For each set of five replicates, temperature records were available for at least three of the replicates, and in most cases four.

9.2.5 Monitoring

(i) Plant Performance

A number of methods were used to assess plant response to the treatment. The performance of the plants following treatment was assessed in two ways. Heights were measured in the summers of 1993 and 1994. In 1994, the maximum inflorescence height and the maximum foliage height were recorded, as well as flowering performance. Methods for measuring heights were the same as those for the warmed plants. The shoot biomass of the plants was also estimated through point quadrat survey in October 1993, May 1994 and August 1994. As explained in Chapter Seven, shoot biomass can be inferred from point quadrat results. Shoot biomass was evaluated in two ways: absolute shoot biomass and relative shoot biomass. Absolute shoot biomass is the actual numer of point quadrat hits recorded. Relative shoot biomass was calculated for the plants in mixture as the proportion of the total shoot biomass occupied by each species. Relative shoot biomass therefore gave an indication of the 'success' of each species in mixture. Flowering performance was also monitored.

(ii) Frost Damage

Point quadrat surveys were carried out immediately before and immediately after the treatment. Frost damage was apparent and obvious within two days of the treatment, as blackened or bleached tissue. The second point quadrat surveys were performed in the period between two and five days following the treatment.

Damage was assessed in two ways. Firstly the number of hits on undamaged, green tissue was recorded and compared with the number of hits on damaged, blackened tissue. The percentage of the total number of hits recorded as damaged gave an initial measure of frost sensitivity.

The pre-frosting survey showed that there was no significant difference between the shoot biomass of plants in the controls and the replicates to be treated. The second assesment compared the number of hits on undamaged tissue for the treated plants following frosting with the total number of hits for the controls. The degree of difference between the two sets of replicates again allowed an assessment to be made of frost sensitivity and resistance.

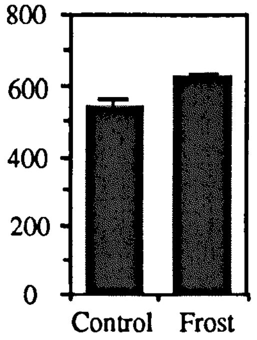
9.3 RESULTS

9.3.1 ACHILLEA MILLEFOLIUM

(i) Height: Flowering Height

Monoculture There was no significant difference between the mean heights of treated plants and control plants in August 1993. However in August 1994, the treated plants were significantly taller than the controls (P=0.001).

Figure 9.4 Achillea: Mean Maximum Height in August 1994. Y axis = Height (cm). Bars represent standard errors



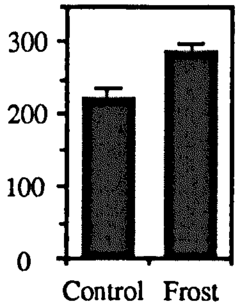
Mixture There was no significant difference between the heights of the two sets of plants at any time.

(ii) Height: Foliage

Monoculture There was no significant difference between the two sets of plants.

Mixture The foliage height of the frosted plants in mixture was significantly greater than that of the controls in August 1994 (P=0.002)

Figure 9.5 Achillea: Mean Foliage Height in August 1994. Y axis = Height (cm). Bars represent standard errors



(iii) Flowering

Two methods of estimating flowering performance were used: the number of corymbs present in August 1993 and 1994, and the total number of florets produced in 1993 (corymbs were harvested continuously and stored dry over the season and the total number of capitula counted at the end of the season). In 1993, both the number of corymbs present and the total number of capitula produced were greater for the frosted plants although not significantly so. However, in August 1994, the plants frosted in 1993 had produced significantly more corymbs ($P<0.001$).

(iv) Frost Damage: Immediate Damage

Table 9.1 Achillea Immediate Frost Damage

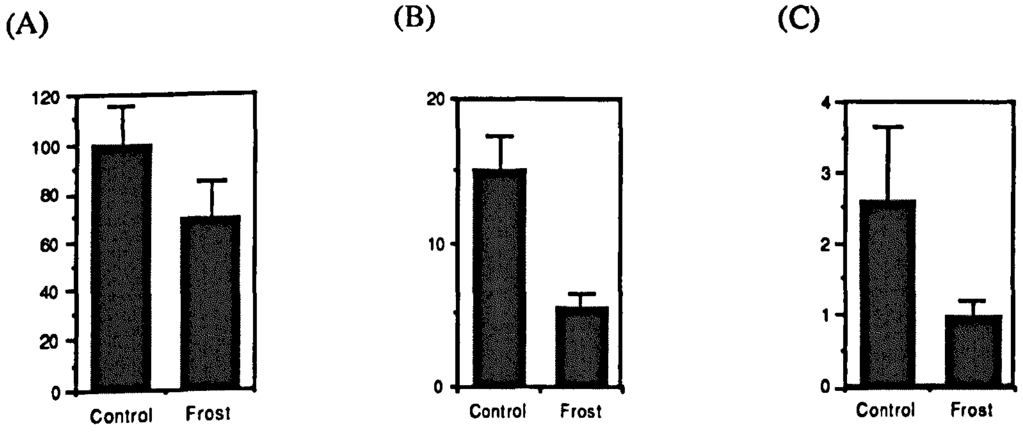
	Mean Frost Damage (%)	Standard Error
Monoculture	24	12
Mixture	38	16

(v) Frost Damage: Comparison with Controls

Monocultures The shoot biomass of the frosted plants immediately after frosting was less than the controls, although not significantly so ($P=0.2$).

Mixture Again in mixture the shoot biomass of the frosted plants immedietly after frosting was less than that of the controls in absolute terms, at a significance of P=0.056. The proportion of the total mixture shoot biomass occupied by *Achillea* after frosting was less than that of the controls, but not significantly so (P=0.146).

Figure 9.6 Achillea Frost Damage. Y axis = Number of point quadrat hits on undamaged tissue. A = Monocultures. B = Mixtures absolute value. C = Mixtures relative value. Bars represent standard errors.



(vi) Shoot biomass

Monoculture Despite initial frost damage, *Achillea* appeared to be stimulated by the treatment and by August 1994 the frosted plants were performing significantly better than the controls.

Mixture In mixture the frosted *Achillea* plants did not recover from the treatment and consistently produced less shoot biomass than the controls. In May 1994 the difference was significant, although by October there was no significant difference. It may be that competition with other plants in the bins delayed growth of the weakened *Achillea* plants in the frosted mixtures.

Table 9.2 Achillea Shoot biomass Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Control	Frost
Mean	108.6	168.8
SE	47.08	21.90
Probability	0.272	
May 1994		
Mean	217.2	339.6
SE	94.16	43.81
Probability	0.273	
August 1994		
Mean	232.33	346.8
SE	10.33	32.58
Probability	0.016	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Control	Frost	Control	Frost
Mean	10.4	2.94	1.51	0.772
SE	4.15		0.57	0.411
Probability	0.273		0.321	
May 1994				
Mean	9.6	0.8	1.88	0.189
SE	3.48	0.8	0.535	0.189
Probability	0.039		0.017	
August 1994				
Mean	15.4	6.8	1.27	0.447
SE	5.56	2.93	0.51	0.37
Probability	0.307		0.229	

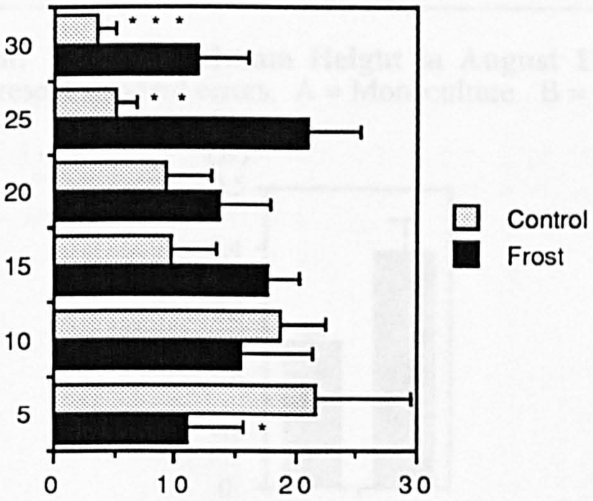
(vii) Response of Achillea to Frost

Although in monoculture *Achillea* suffered around 25% damage, it is clear that it soon recovered, and even appeared to be stimulated by the treatment. Observation of the effect of frosting on the plants revealed that *Achillea* appeared to have a protective mechanism against frost damage. Inspection of each *Achillea* shoot immediately the treatment had finished showed that the uppermost leaves of each shoot had curled in on itself and upwards apparently protecting the sensitive growing point in a sheath of enveloping foliage. The leaves unfurled over the following day to reveal an undamaged apex (Plates 9.2 & 9.3). Leaves lower down the stem were damaged. Subsequently, the plants grew strongly, but the damaged leaves did not regrow.

Plates 9.2. Frosted Achillea two weeks after treatment

A point quadrat survey was carried out in September 1993, in which the number of hits of *Achillea* at 50, 100, 150, 200, 250 and 300 mm above soil level were counted. The results are shown in Figure 9 and clearly show that compared with the controls, the frosted plants had relatively little foliage at their bases, but much more at the higher levels.

Figure 9.7 Vertical Structure of *Achillea* in Frosted and Control Monocultures. X axis = mean number of point quadrat hits. Y axis = height of survey (cm). Bars represent standard errors. The significance of any difference is indicated *** = P<0.001 **=P<0.01, * = P<0.05.



The plants in mixture, being smaller and weaker, apparently did not have the same capacity for shoot protection and were damaged to a greater extent. The weakened plants did not appear to recover fully in the mixtures.

9.3.2 CIRSIUM ARVENSE

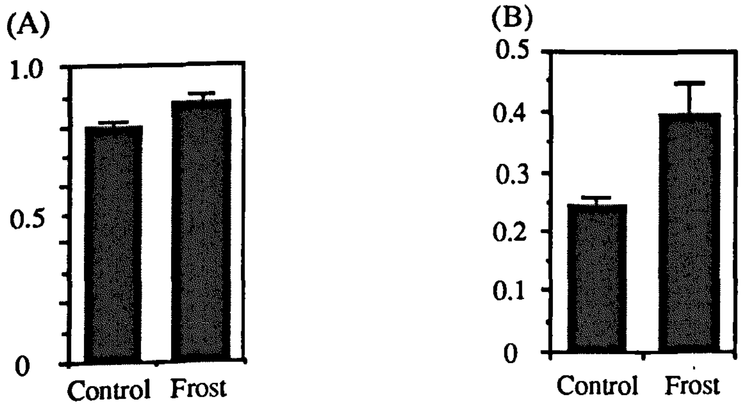
(i) Height

<u>Monoculture</u> In August 1993 there was no significant difference between the heights of the frosted and control plants. However, in August 1994, the frosted plants were significantly taller than the controls (P=0.01).

<u>Mixture</u> In both August 1993 and August 1994, the frosted plants were significantly taller than the controls (P=0.02). The mixture plants were approximately half the

height of the monoculture plants (presumably as a result of competition from vigorous robust species in the mixtures); however the increased height of the frosted plants in mixture compared to the controls following one complete growing season possibly indicates a release from that competition through damage to dominant species.

Figure 9.8 Cirsium: Mean Maximum Height in August 1994. Y axis = Height (m). Bars represent standard errors. A = Monoculture. B = Mixture



(ii) Flowering

There was no significant difference between the flowering performance of frosted and control plants.

(iii) Frost Damage Immediate Damage

Table 9.3 Cirsium Immediate Frost Damage

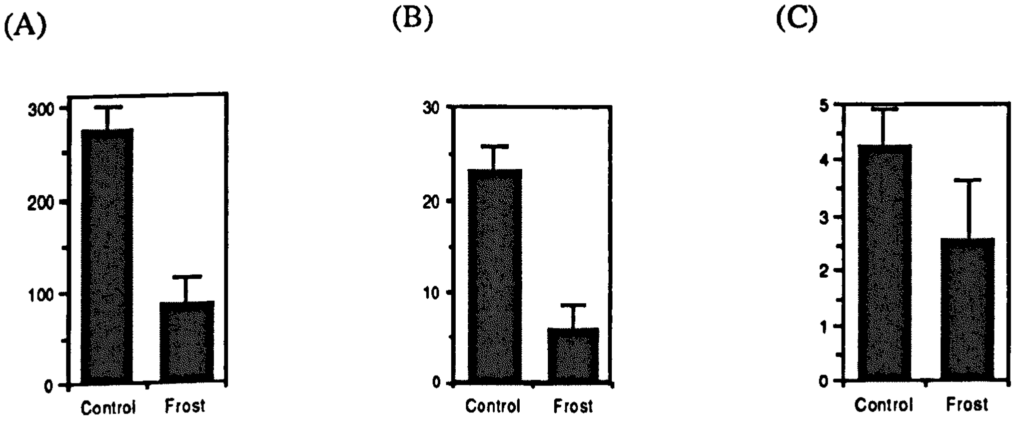
	Mean Frost Damage (%)	Standard Error
Monoculture	45	15
Mixture	62	16

(vi) Frost Damage: Comparison with Controls

Monoculture The shoot biomass of the frosted plants was significantly reduced compared to the controls immediately after frosting (P = 0.003).

Mixture Again, in absolute terms, the shoot biomass of the frosted plants was significantly lower than that of the controls (P = 0.002). However, because of general reductions in shoot biomass in all other species, the proportion of the total shoot biomass that *Cirsium* occupied in the mixtures after frosting was not significantly reduced (P = 0.211).

Figure 9.9 Cirsium Frost Damage. Y axis = Number of point quadrat hits on undamaged tissue. A = Monocultures. B = Mixtures absolute value. C = Mixtures relative value. Bars represent standard errors.



(v) Shoot biomass

Monoculture The shoot biomass of the frosted plants was consistently lower than that of the controls, and significantly so in August 1994.

Mixture In August 1993 and May 1994 the shoot biomass of *Cirsium* in the frosted replicates was lower than that of the controls although the difference was not significant. However, by August 1994, the position had reversed, and the frosted plants appeared to be performing better than the controls, although, again, the difference was not significant.

Table 9.4 Cirsium Shoot biomass Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Control	Frost
Mean	213.6	193.6
SE	22.6	28.95
Probability	0.601	
May 1994		
Mean	427.2	387.2
SE	45.32	57.91
Probability	0.6	
August 1994		
Mean	367.6	301.0
SE	16.83	24.3
Probability	0.05	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Control	Frost	Control	Frost
Mean	22.6	20.2	3.41	2.95
SE	1.88	5.67	0.49	0.73
Probability	0.698		0.62	
May 1994				
Mean	4.8	2.4	0.453	0.268
SE	1.94	1.2	0.197	0.186
Probability	0.37		0.513	
August 1994				
Mean	19.4	34.2	3.03	4.72
SE	4.21	21.65	0.77	3.01
Probability	0.521		0.599	

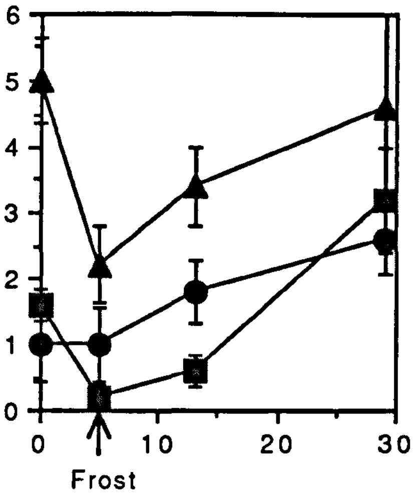
(vi) Response of Cirsium to Frost

Cirsium is clearly sensitive to the frost treatment, suffering around 50% loss in shoot biomass immediately following the treatment. However, *Cirsium* showed some recovery from this loss. In monoculture, the frosting treatment had the effect of damaging the main growing point of the plant, as well as many leaves. The plants responded by producing new shoots towards the top of the stems, which then grew rapidly. Damaged leaves further down however were not replaced. This explains how the frosted monoculture plants were eventually taller than the controls, but less shoot biomass was recorded.

The monoculture plants were around 300 mm tall when frosted. The mixture plants were only around 100 mm or less when frosted, and the effect of the treatment on these plants was to kill completely whole shoots. In this case the affected plants responded by producing new shoots at ground level from the base of the killed shoots (one, two or three replacing a single frosted shoot). Again, these new shoots grew rapidly.

In 1994 two additional sets of mixture replicates were frosted. One set received only the frosting treatment. However the other set was heated, according to the methods and timing described in Chapter 8, prior to frosting. Three sets of bins were therefore compared: the (unheated) controls, bins which received frosting only, and bins which were heated and frosted. The heated bins had produced significantly more *Cirsium* shoots at the time of frosting than either of the unheated sets of bins (P=0.001). There was no significant difference between the mean number of shoots in the two sets of unheated bins. Following frosting, both sets of frosted plants produced new shoots at ground level; three weeks after frosting the mean number of shoots in both treated replicates exceeded that of the controls.

Figure 9.10 The Response of the Cirsium in Mixture to the Frosting Treatment in 1994. X axis = days. Y axis = mean number of shoots. Circles = controls, Triangles = warmed and frosted plants, Squares = frosted only.



The results for *Cirsium* are very similar to those observed for another clonal, albeit woody, species, *Rhus typhina* (Luken, 1990). Following damage caused by a late spring frost in 1986, a high density of new shoots emerged. The 'root sprout response' of *R.typhina* was interpreted as being consistent with theories regarding apical dominance and the inhibition of bud release in other clonal tree species. For example, root sprout release may be induced by decapitation, defoliation, stem cutting or insect herbivory in *Populus tremuloides.* It would appear that removal of apical dominance in *Cirsium* through frost damage induces growth of dormant rhizomatous buds (a similar phenomenon was observed following destruction of above-ground shoot biomass of *Cirsium* during the droughting treatment, reported in Chapter 10).

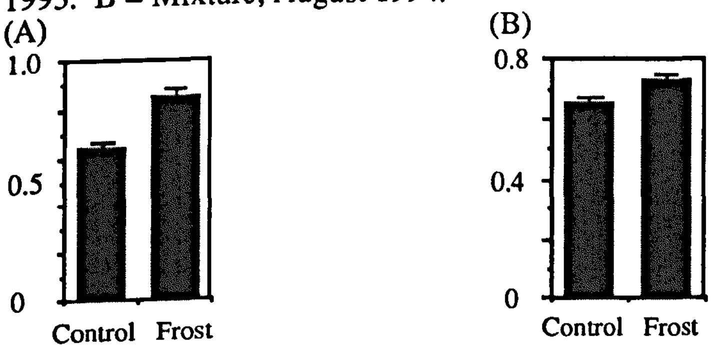
9.3.3 DACTYLIS GLOMERATA

(i) Height

Monoculture There was no significant difference in the flowering height of the two sets of replicates. However the foliage height of the frosted plants in August 1993 was significantly greater than that of the controls (P<0.001). There was no significant difference in August 1994.

Mixture Again, there was no significant difference in the flowering height of the two sets of replicates. However, in August 1994, the foliage height of the frosted plants was significantly greater than that of the controls (P = 0.02).

Figure 9.11 Height of Dactylis. Y axis = height (m). A = Monoculture, August 1993. B = Mixture, August 1994.



(ii) Flowering

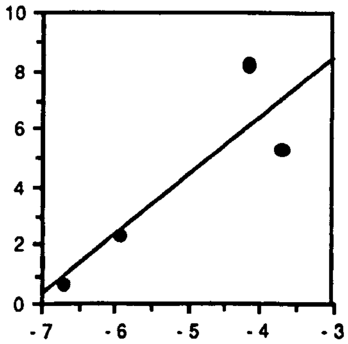
The total weight of seed produced by the plants was used to assess flowering performance in 1993. In 1994 the total number of inflorescences produced over the season was counted.

Monocultures The total seed yield was reduced for the frosted plants but the data showed high variability and the difference between the two sets of replicates was not significant. In 1994, the mean number of inflorescences produced by the plants frosted in 1993 was 5.6, and by the control plants was 10.0, but again, the difference was not significant.

Mixtures The total seed yield of the frosted plants was significantly less than that of the controls in 1993 (P=0.012). In 1994 the frosted plants on average produced more inflorescences than the controls, but the difference was not significant.

The frosting treatment occurred at the time of peak flowering of *Dactylis* in 1993. The inflorescences were clearly sensitive to frost and damaged inflorescences could be recognised easily by their bleached appearance. In the monoculture replicates 65% of all inflorescences produced were damaged while in the mixtures 85% were damaged. For individual replicates, the amount of damage and subsequent reduction in yield were closely related to the minimum temperature to which that particular replicate was subjected to during frosting (Figure 9.12). No such relationship was apparent for the monoculture replicates.

Figure 9.12 The Relationship between the Minimum Temperature Achieved During Frosting and Seed Yield: Mixture. X axis = Temperature (°C). Y axis = Yield (g) P<0.05. Only four points are shown because only four minimum temperatures were recorded.



It was suspected that the reduction in yield could be accounted for by the destruction of developing embryos by the treatment. To test this the viability of seed from frosted plants was compared to that from control plants. Seed harvested in the summer of 1993 was stored in dark, dry conditions at room temperature. Seeds were sown on damp filter paper in petri dishes: 30 seeds from each of the five monoculture and five control replicates were used. The percentage germination is shown in Table 9.

Table 9.5 The Effect of Frosting on Seed Viability

	% Germination	Standard Error
Control	74.9	4.6
Frosted	34.3	15.4

Frosting significantly reduced the viability of the affected seeds (P=0.035)

(iii) Frost Damage: Immediate Damage

Table 9.6 Dactylis Immediate Frost Damage

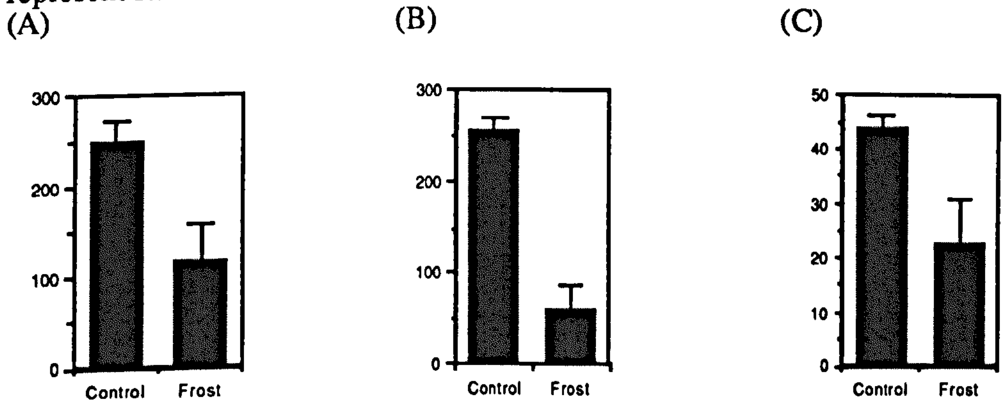
	Mean Frost Damage (%)	Standard Error
Monoculture	53	13
Mixture	67	14

(iv) Frost Damage: Comparison with Controls

Monoculture The shoot biomass of the frosted plants was significantly reduced compared to the controls immediately after frosting (P = 0.01).

Mixture Again, in absolute terms, the shoot biomass of the frosted plants was significantly lower than that of the controls (P = 0.0002). The proportion of the total shoot biomass that *Dactylis* occupied in the mixtures after frosting was also significantly reduced (P = 0.03).

Figure 9.13 Dactylis Frost Damage. Y axis = Number of point quadrat hits on undamaged tissue (Y axis for (C) = % of the total undamaged tissue). A = Monocultures. B = Mixtures absolute value. C = Mixtures relative value. Bars represent standard errors.



(v) Shoot biomass

Monoculture There was no significant difference between the shoot biomass of the treated plants and the control plants.

Mixture Again, there was no significant difference between the two sets of replicates, and indeed, by August 1994, in terms of the proportion of the total shoot biomass that was occupied by *Dactylis* in the mixtures, the two sets of replicates were identical.

Table 9.7 Dactylis Shoot biomass Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Control	Frost
Mean	**372.2**	**358.2**
SE	30.66	17.74
Probability	0.4	
May 1994		
Mean	**654.4**	**716.4**
SE	60.12	35.48
Probability	0.4	
August 1994		
Mean	**468.0**	**430.6**
SE	23.9	20.31
Probability	0.27	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Control	Frost	Control	Frost
Mean	**252.2**	**212.0**	**36.68**	**33.94**
SE	30.54	33.0	1.80	6.92
Probability	**0.397**		**0.709**	
May 1994				
Mean	**196.4**	**142.4**	**38.33**	**33.60**
SE	47.2	26.14	4.99	7.69
Probability	**0.346**		**0.620**	
August 1994				
Mean	**206.6**	**220.2**	**31.50**	**31.81**
SE	29.8	47.2	4.13	7.26
Probability	**0.81**		**0.97**	

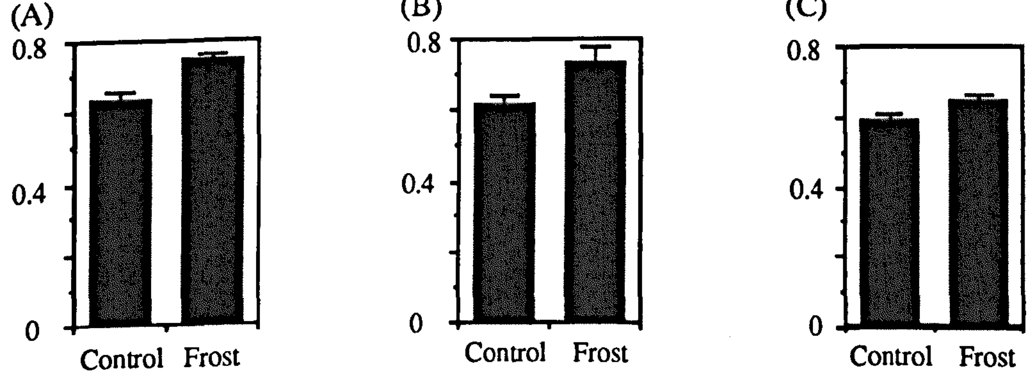
9.3.4 FESTUCA RUBRA

(i) Heights

Monoculture The frosted plants were significantly taller than the controls in August 1993 ($P<0.001$) and for both foliage and flowering height in August 1994 ($P<0.01$).

Mixture Again, the frosted plants were significantly taller than the controls in 1993 ($P=0.03$); however in 1994 there was no significant difference between the heights of the two sets of plants.

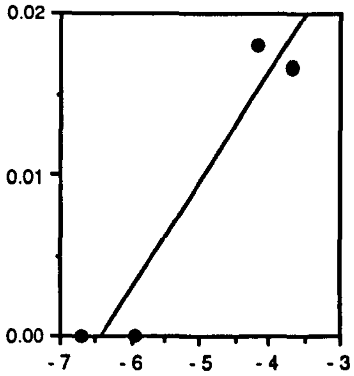
Figure 9.14 Festuca Maximum Height of Frosted Plants and Controls. Y axis = Height (m). Bars represent Standard Errors. A = Monocultures, August 1993. B = Monoculture flower heights 1994, C = Mixture heights 1993.



(ii) Flowering

There was no significant difference between the flowering performance of the frosted plants and the controls in 1993 and 1994. Visible damage to inflorescences was minimal. However, as with *Dactylis*, the seed yield of the plants in mixture was related to the minimum temperature to which the replicate was subjected during frosting, although no such relationship was apparent for the monocultures.

Figure 9.15 The Relationship Between the Minimum Temperature to which a Replicate Fell During Treatment and Seed Yield in Mixture. X axis = minimum temperature (°C). Y axis = Yield (g).



(iii) Frost Damage: Immediate Damage

Table 9.8 Festuca Immediate Frost Damage

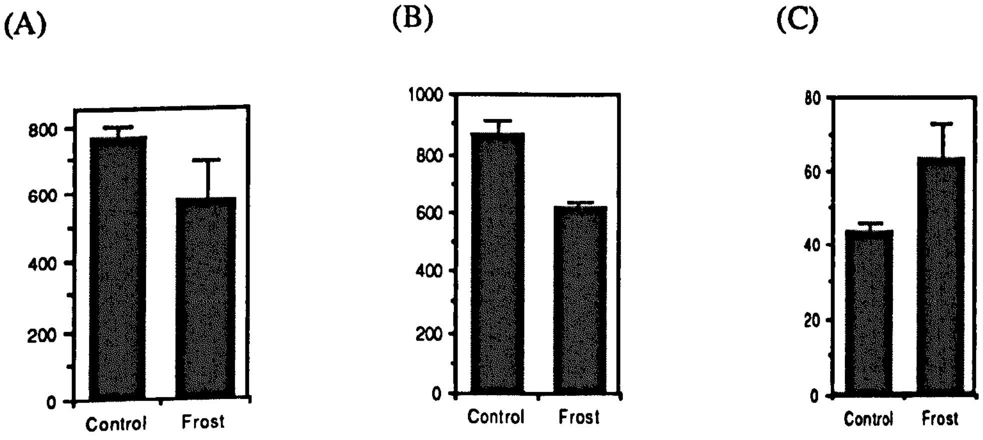
	Mean Frost Damage (%)	Standard Error
Monoculture	17	16
Mixture	25	15

(iv) Frost Damage: Comparison with Controls

<u>Monoculture</u> The shoot biomass of the frosted plants was reduced compared to the controls, but with no significant difference between the two sets of replicates (P = 0.2).

Mixture In absolute terms, the shoot biomass of the frosted plants was lower than that of the controls, but again not significantly so (P = 0.27). However, the proportion of the total shoot biomass that *Festuca* occupied in the mixtures after frosting was significantly increased (P = 0.05).

Figure 9.16 Festuca Frost Damage. Y axis = Number of point quadrat hits on undamaged tissue (Y axis for (C) = % total hits on undamaged tissue). A = Monocultures. B = Mixtures absolute value. C = Mixtures relative value. Bars represent standard errors.



(v) Shoot biomass

Monoculture There was no significant difference between the shoot biomass of the treated plants and the control plants.

Mixture Again, there was no significant difference between the two sets of replicates, and indeed, by August 1994, in terms of the proportion of the total shoot biomass that was occupied by *Festuca* in the mixtures, the two sets of replicates were identical.

Table 9.9 Festuca Shoot biomass Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Control	Frost
Mean	701.8	680.2
SE	53.35	51.23
Probability	0.778	
May 1994		
Mean	701.5	680.2
SE	53.35	24.05
Probability	0.777	
August 1994		
Mean	752.0	783.2
SE	49.81	48.01
Probability	0.665	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Control	Frost	Control	Frost
Mean	329.8	359.4	48.8	56.76
SE	28.79	51.1	2.77	1.99
Probability	0.627		0.339	
May 1994				
Mean	230.8	276.0	50.55	66.41
SE	22.93	34.3	7.25	7.69
Probability	0.306		0.167	
August 1994				
Mean	340.0	407.0	53.99	60.5
SE	29.49	55.72	4.32	1.53
Probability	0.32		0.51	

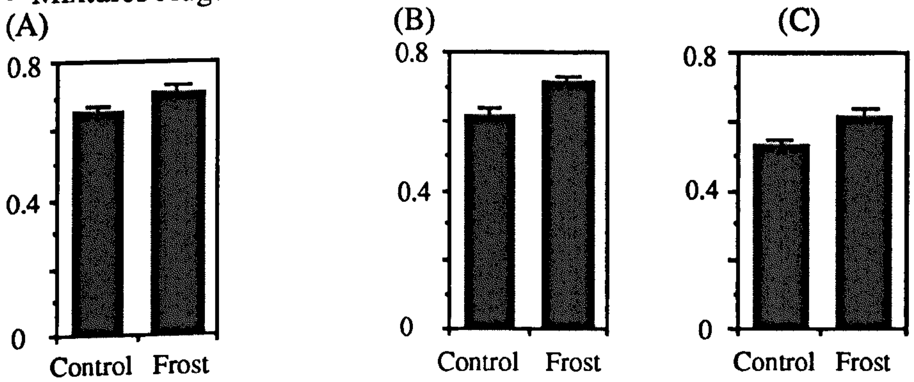
9.3.5 POA PRATENSIS

(i) Heights

Monoculture In August 1993 the mean height of the frosted plants was significantly greater than that of the controls (P=0.045). In August 1994 the foliage height was again significantly greater (P=0.004); however the inflorescence heights of the two sets of replicates were not significantly different.

<u>Mixture</u> In August 1993 the mean height of the frosted plants was significantly greater than that of the controls (P=0.009). However in 1994 there was no significant difference between the two sets of replicates.

Figure 9.17 Poa Maximum Heights Y axis = height (m). Bars represent standard errors. A = Monocultures, August 1993, B = Monocultures August 1994, C = Mixtures August 1993.



(ii) Flowering

There was no significant difference between the two sets of plants in terms of the numbers of inflorescences produced in 1994.

(iii) Frost Damage: Immediate Damage

Table 9.10 Poa Immediate Frost Damage

	Mean Frost Damage (%)	Standard Error
Monoculture	36	13
Mixture	36	16

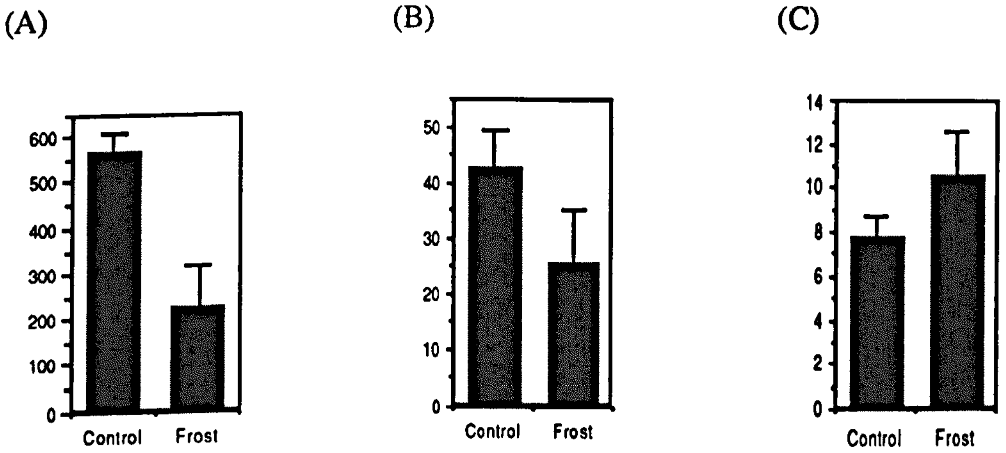
(iv) Frost Damage: Comparison with Controls

<u>Monoculture</u> The shoot biomass of the frosted plants was significantly reduced compared to the controls (P = 0.009).

<u>Mixture</u> In absolute terms, the shoot biomass of the frosted plants was lower than that of the controls, but not significantly so (P = 0.168). However, the proportion of the

total shoot biomass that *Poa* occupied in the mixtures after frosting was increased, although again not significantly so (P = 0.32).

Figure 9.18 **Poa Frost Damage.** Y axis = Number of point quadrat hits on undamaged tissue (Y axis for C = % total hits on undamaged tissue). A = Monocultures. B = Mixtures absolute value. C = Mixtures relative value. Bars represent standard errors.



(v) Shoot biomass

Monoculture The shoot biomass of the frosted plants was consistently less than that of the controls but there was no significant difference between the two sets of plants.

Mixture Initially the shoot biomass of *Poa* in the two sets of replicates was similar. However, by August 1994, the shoot biomass of *Poa* in the frosted bins was less than that of the controls (P=0.07).

Table 9.11 **Poa Shoot biomass** Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Control	Frost
Mean	442.4	360.6
SE	53.88	24.09
Probability	0.203	
May 1994		
Mean	884.8	721.2
SE	107.76	48.1
Probability	0.203	
August 1994		
Mean	544.0	504.8
SE	35.45	33.92
Probability	0.442	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Control	Frost	Control	Frost
Mean	79.2	66.4	11.57	10.02
SE	12.03	20.35	1.99	3.11
Probability	0.603		0.685	
May 1994				
Mean	62.8	27.6	12.06	6.04
SE	14.16	6.96	3.14	1.42
Probability	0.064		0.093	
August 1994				
Mean	89.8	55.4	13.65	7.80
SE	10.48	16.10	1.53	2.37
Probability	0.11		0.07	

9.4 COMPARATIVE RESULTS

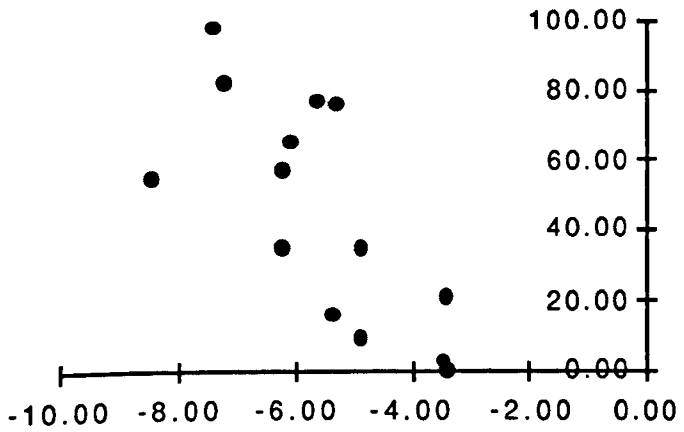
As explained in the methods section of this chapter, technical failure meant that the temperature records for all five individual replicates in a set were not available. For all replicate sets there were, however, at least three temperature records. For the comparative results discussed below three replicates have therefore been used instead of the usual five. In those cases where more than three replicates in a set had a temperature record available, the three replicates that had been subjected to the lowest minimum temperature were selected.

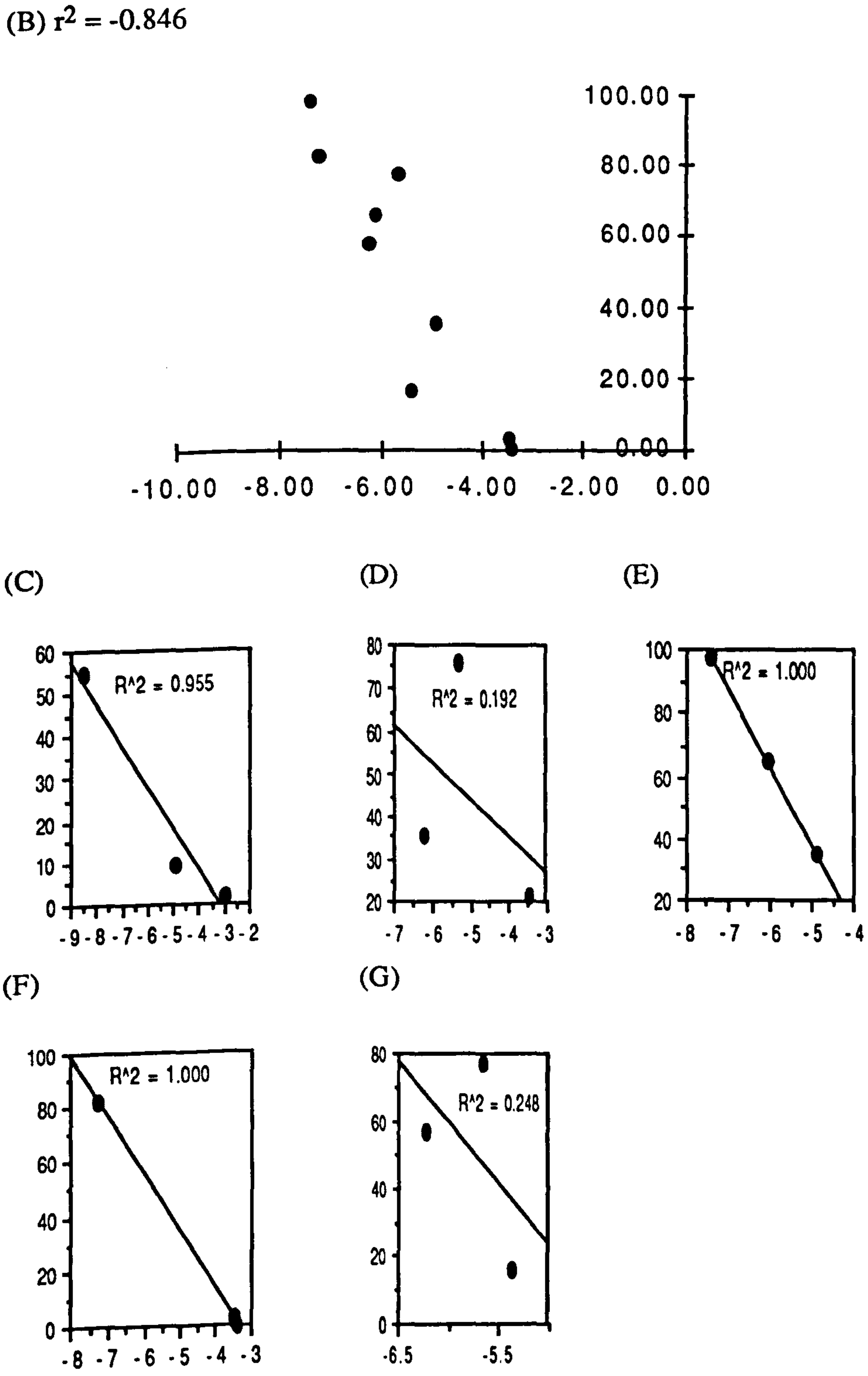
9.4.1 Temperature and Frost Damage to Grasses

Comparison of the lowest temperature to which the monoculture bins were subjected during the frosting treatment with the % damage recorded on plants immediately following frosting reveals a clear relationship between minimum temperature and frost damage: the lower the minimum temperature to which the plants were subjected the greater the damage. The relationship between frost damage and the mean minimum temperature achieved over the frosting period was not so strong, suggesting that it is not the duration of frosting that causes most damage, but the minimum temperature reached. Significant relationships were obtained for all replicates together, grasses alone, and for *Dactylis* and *Festuca.*

Figure 9.18 The Relationship Between the Minimum Temperature to which Replicates were Subjected and Damage to Plants. X axis = Minimum temperature. Y axis = % damage. A = All Replicates (P<0.01). B = Grasses (P<0.001). C = *Achillea.* D = *Cirsium.* E = *Dactylis* (P<0.001). F = *Festuca* (P<0.001). G = *Poa.*

(A) r^2 =-0.545



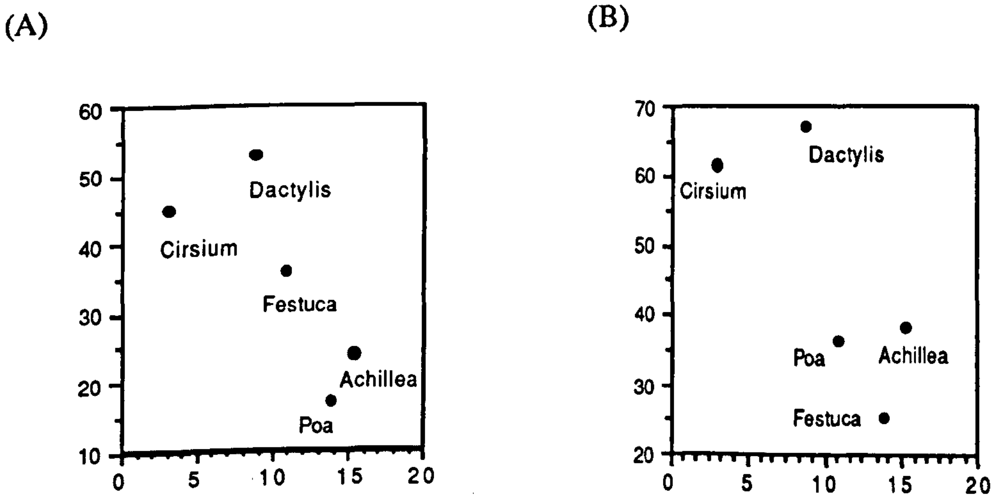

(B) $r^2 = -0.846$

Because frost damage depends on temperature, it might be supposed that differences observed between species in frost damage in the experiment may be accounted for by differences in frosting temperature experienced rather than differences in sensitivity of the plants. However an analysis of variance performed on the mean temperatures to which each of the replicates fell showed that there was no significant differences between the temperatures experienced by different species. Therefore it is reasonable to assume that observed differences can be accounted for by different sensitivities to frost.

9.4.2 DNA and Frost Damage to Grasses

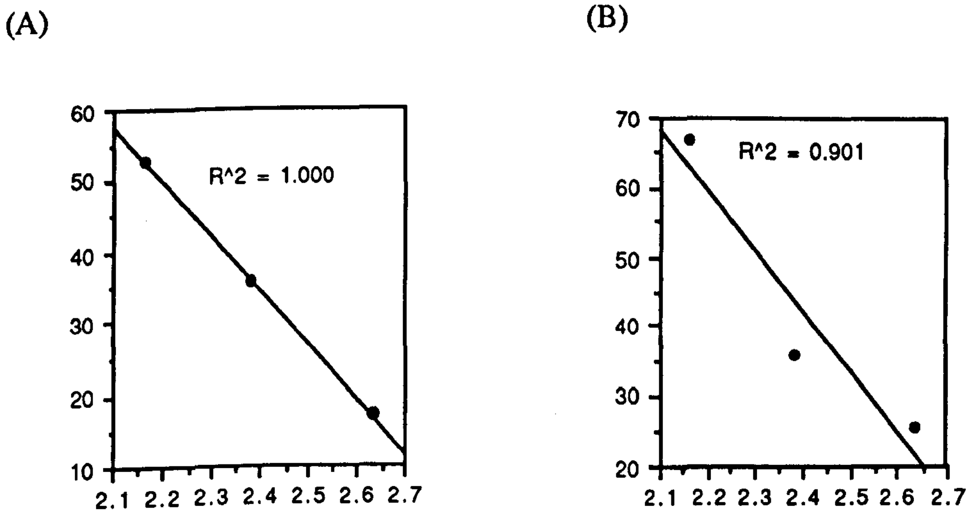
In an experiment in which turves extracted from species-rich calcareous grassland were subjected to extreme minimum temperatures in June, MacGillivray (1993) found that the % damage suffered by plants in the turves immediately after the treatment was negatively correlated with 2C DNA content. Similar results were found in the Bibury experiment. The results for all five species, in mixture and monoculture are illustrated in Figure 9.19. Although a negative relationship is apparent, there are too few points for this to have significance. However, in both cases it is clear that, if taken separately, the forbs and grasses both conform to the negative relationship, with *Cirsium* suffering more damage than *Achillea* in both cases, and the three grasses showing increasing damage with decreasing DNA content.

Figure 9.19 The Relationship between 2C DNA Content. % Damage. X axis = 2C DNA Content (pg). Y axis = % Damage. (A) = Monoculture. (B) = Mixture



In Figure 9.20 The data for grasses are plotted separately against DNA value. For both mixtures and monocultures there is a clear negative relationship between genome size and frost sensitivity.

Figure 9.20 The Relationship Between Frost Damage and 2C DNA Content for Grasses. X axis = log(N)2C DNA (pg) Content. Y axis = % Damage. (A) = Monoculture (P<0.001). (B) = Mixture



9.5 DISCUSSION

9.5.1 ACHILLEA MILLEFOLIUM

Achillea showed strikingly different responses in mixture and in monoculture. In monoculture, a range of indicators suggested that the plants were stimulated by the treatment. However in mixture, the treated plants appeared to be weakened.

It was demonstrated in Chapter 7 that *Achillea* was the weakest competitor in the control mixture replicates. In the field, the species tends not to grow in dense vigorous swards, but, rather, in more open vegetation. It may be that the damage to the plants in mixture caused by the frost treatment made them even less effective in competition with *Dactylis* and *Festuca* resulting in their reduced performance compared with the controls.

In monoculture, *Achillea* clearly exhibited the greatest resistance to frost and there was evidence of the plants possessing a protective mechanism against the treatment. *Achillea* is a species with a relatively large genome. It has been suggested that such species are able to grow in the cooler months of the year primarily through cell expansion rather than cell division. The growth of plants with a smaller genome is mainly effected through cell division, which involves greater energy expenditure than cell expansion. Plants of small genome size are therefore likely to grow later in the year than plants with a larger genome size (Grime & Mowforth, 1982) As such, species with larger genomes could be expected to have been exposed to regular spring frosts and to have acquired traits associated with frost resistance (Macgillivray & Grime 1995). The results for *Achillea* suggest that this is indeed the case.

9.5.2 CIRSIUM ARVENSE

Cirsium in both mixture and monoculture suffered a high degree of damage immediately following the treatment. This accords with field observations that *Cirsium* is particularly sensitive to late spring frosts (J. P. Grime, Pers. comm.). *Cirsium arvense* is a species with a relatively small genome; as such, according to the arguments above, would be expected to exhibit heavy frost damage.

However, in both mixture and monoculture, the plants showed rapid and effective recovery from the treatment. The monoculture plants produced new shoots from below the damaged growing points and from axillary buds, while the plants in mixture produced new shoots from ground level.

Rather than showing resistance to the treatment, and some degree of protection, as in *Achillea, Cirsium* appeared to show a degree of resilience following the treatment, rapidly responding to damage. In mixture, although much of the above ground shoot biomass of the plants was destroyed, it appears the damage stimulated the growth of buds on the rhizome. The quick growth of the new shoots may have been supported by reserves of stored carbohydrate in the extensive rhizome system of *Cirsium*. *Cirsium* has a late phenology and may therefore still have considerable reserves of carbohydrate in late spring. Growth may also be enhanced as a result of weakened *Dactylis* and *Festuca* immediately following the treatment. This is a probable explanation of the increased height of frosted thistle plants in mixture compared with control plants at the end of the growing season following frosting.

Hodgson & Grime (1989) discussed the possible implications of mild winters followed by severe spring frosts on the performance and competitive ability of sensitive plants. They particularly identified low DNA species as being particularly problematical. The results presented in this Chapter with regard to *Cirsium* that had undergone winter warming and subsequent frosting suggest that, for species such as *Cirsium*, mild winters promote earlier growth and increased shoot biomass which is susceptible to frost damage. However, recovery of the promoted plants, in this instance, was also enhanced.

Cirsium could not be said to exhibit any appreciable frost resistance. However, it did exhibit striking resilience to the treatment. As such, the predictions made in Chapter 7 have been supported by the experimental evidence.

9.5.3 DACTYLIS GLOMERATA

Dactylis showed substantial sensitivity to the treatment: 53% in monoculture and 67% in mixture. However, height and shoot biomass measurements in August 1993 showed that the plants had recovered over the summer.

While in 1994 there was no significant difference between the shoot biomass of the two sets of replicates, the treated plants were significantly taller in both mixture and monoculture, and the plants in mixture had produced more inflorescences. This indicates a possible stimulating effect of frost damage in the year following the extreme event. It is of interest to note that, while the positive relationship of *Dactylis* with spring temperatures at Bibury occurs in the current year, the negative relationship of *Dactylis* with winter temperatures relates to the previous year and the year before that.

The negative effect of the treatment on seed yield and viability corresponds with the effects of spring frosts on *Dactylis* observed in the field (Beddows, 1959).

9.5.4 FESTUCA RUBRA

Festuca exhibited relatively little damage. In fact in mixture, the relative contribution of *Festuca* to the total shoot biomass was significantly increased. However, monitoring in August 1993 and 1994 showed that this apparent competitive advantage was not maintained. As with *Cirsium*, *Festuca* appeared to gain some competitive advantage from temporary weakening of *Dactylis* following frosting.

9.5.5 POA PRATENSIS

In common with the other grasses in the experiment, the height of *Poa* was significantly increased following the treatment. However in monoculture the shoot biomass of the frosted plants was significantly less than that of the controls. In mixture, although the absolute shoot biomass of the plants was reduced, their relative contribution to the total shoot biomass increased. Surveys in August 1993 and 1994 revealed no differences between the two sets of replicates.

9.5.6 COMPARATIVE RESULTS

DNA and Frost Damage to Grasses

It was predicted in Chapter 7 that small genome species would be more sensitive to frost than high genome species. The results from the experiment support these predictions, and also agree with the results of Macgillivray (1993) who demonstrated a highly significant positive relationship between genome size and frost resistance. It was shown in Chapter 8 that a negative relationship may also exist between DNA content and response to warm weather in winter. Grime (1989) has suggested that the greater potential of small genome species to respond to warmer temperatures may result in their expansion in temperate floras in response to global warming. However MacGillivray and Grime (1995) concluded that, as a result of the potential sensitivity of small DNA species to late frost events, the potential rate of expansion of such species may be checked by the periodic occurrence of spring cold snaps. In effect, their potential responsiveness to global warming could be curtailed by the continued occurrence of late frosts. Further, they suggested that genome size may be a useful predictor of frost resistance, and as such can be incorporated into models of vegetation response to climate change.

The results presented in this Chapter suggest that these statements may be premature. MacGillivray and Grime base their assertion on the results obtained from a point quadrat survey carried out immediately after a frosting treatment. As with the results from the Bibury experiment, a negative relationship is found between DNA content and sensitivity to frost. However, this relationship alone may not be sufficient to predict vegetation response to frost. In addition, account must be taken of the ability of individual species to recover from frost damage. The results presented in this Chapter suggest that some species that are most susceptible to frost damage may also be those that are best able to recover rapidly from it.

9.6 CONCLUSIONS

Some striking results were apparent from the survey carried out following the frosting treatment. The results suggest that the weakening of *Dactylis*, the dominant species in the mixtures, allowed species such as *Cirsium* and *Festuca* to gain temporary competitive advantage. However, in most cases, surveys carried out in August 1993 and August 1994 revealed no significant difference between the two sets of replicates. It may be that a single application of the treatment was not sufficient to cause lasting damage to the plants or to shift the competitive balance in the mixtures whereas repetition of the treatment might have produced more conclusive results. Or it may be that the treatment was not sufficiently severe. However, observations of the damage suffered by plants, and of the actual frosting temperatures recorded suggest that this was not the case.

CHAPTER 10 IMPOSITION OF AN ARTIFICIAL DROUGHT

10.1 INTRODUCTION

Rainfall has been found to be strongly correlated with annual variation in the productivity of English hay meadows (Smith 1960). In the Park Grass Experiment, total rainfall over the growing season (March - August) was again found to be positively correlated with hay shoot biomass (Silvertown *et al.* 1994), and indirectly related, through that effect on shoot biomass, with species composition. It has been suggested that response to drought is a major determinant of variability (variation in shoot biomass, and by implication, species composition) in the Park Grass plots (Dodd *et al.* 1994). Similar relationships may well occur between rainfall, productivity and species composition at Bibury.

This chapter contains details of an experiment designed to test the predicted responses, based on their performance in the field at Bibury, of the selected plants subjected to severe water stress in mixture and monoculture. As with the other treatments, the method selectedwas chosen to simulate an extreme event, rather than a modest reduction in rainfall.

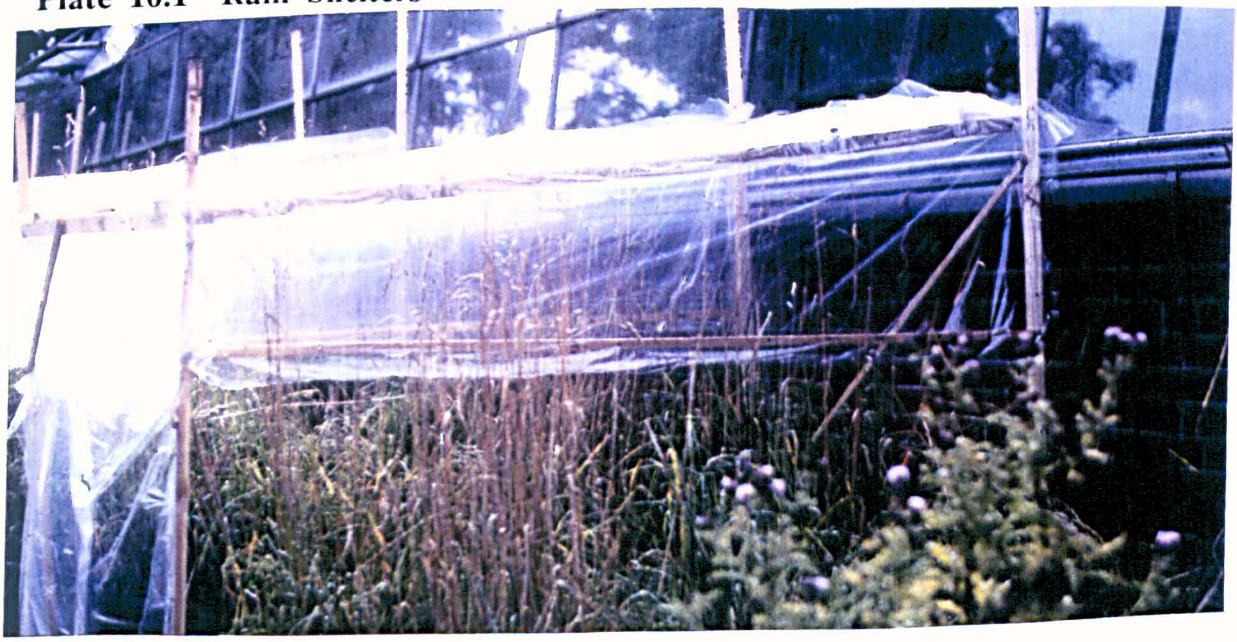
10.2 METHODS

In the first week of July, 1993, each of 150 bins was moved to a new position; all were 're-randomised' within the rows. At the same time, the replicates to be droughted were organised into five blocks, each block containing one replicate of each species in monoculture, and one mixture. Controls were assigned to each block and sited adjacent to them.

Drought was induced in stages. On July 7th, 1993 all watering of the treated bins ceased. One week later polyethylene rain shelters were constructed over each block of bins. The shelters were 1.5m high at the back, sloping to 1.3m at the front. They were 1.2m wide and 2.0m long. In the first week following construction only the roof of the shelters was covered with polyethylene. One week later the sides of the shelters were partially clad with polyethylene, leaving the sides open to 1.0m to allow free ventilation. The shelters were fully constructed by July 28th. Plate 10.1 shows the completed shelters in position. The shelters remained in place for four weeks.

A set of mixture and monoculture bins were watered continuously throughout the period that water was withheld from the droughted bins. Water was applied to these bins every two days. A single moisture block was positioned in these bins at a depth of 150mm. The performance of the plants in the droughted bins was compared with the performance of the plants in the watered bins.

Plate 10.1 Rain Shelters



10.2.1 Monitoring

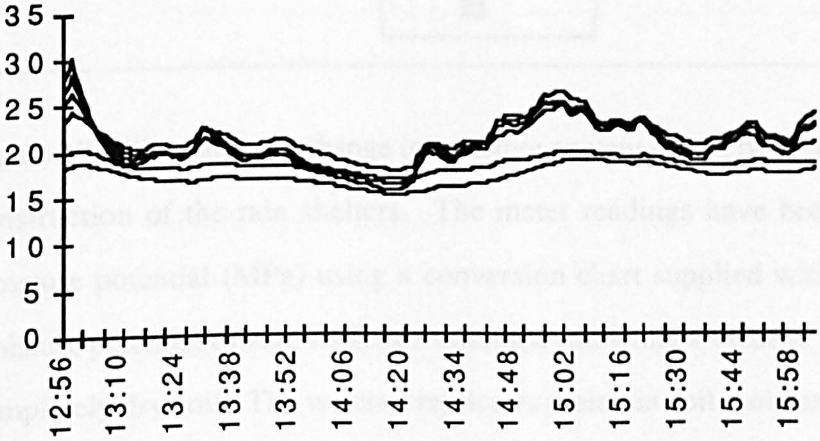
10.2.1.1 The Treatment

Measurements were made on the effects of the rain shelters on temperature and light at mean canopy height, and on the effects of the treatment on soil moisture.

Light was measured using a hand-held light meter. Five alternate recordings under and outside the shelter were made for each shelter. The mean % reduction in light was calculated for each shelter, and the mean of these values was then calculated. The mean value to which light was reduced under the shelters was 85.6% (standard error 3.3).of the no shelter control readings.

Temperatures were recorded using thermocouples placed amongst the vegetation in treated and control replicates. The thermocouples were connected to a data-logger. A sample temperature record is shown in Figure 10.1. The temperature under the shelters was some 2°C higher than ambient. This did not raise concern because the treatment aimed to simulate a prolonged hot, dry period.

Figure 10.1 Temperature Record for Droughted and Watered (Ambient) Bins Over a Three Hour Period, August 1993. The lower two tracks are ambient temperature. X axis = Time (24hrs). Y axis = Temperature (°C).



Soil moisture was recorded using commercially available gypsum moisture blocks (ELE International Ltd, Hemel Hempstead), which consist of the gypsum blocks within which are embedded two lengths of plastic coated wire. Soil moisture is recorded by attaching the two loose ends of the wire to a resistance meter. The blocks were inserted into the bins at the appropriate levels as they were being filled with soil and sand in the spring of 1992. One block was placed at the interface of the soil and soil/sand layers (150mm below the surface), one was placed centrally in the sand layer (300mm below surface) and the final block was placed at the base of the sand layer (600mm below the surface).

Figure 10.2 Positioning of moisture blocks within experimental bins
Each block is attached to wire which protrudes from the soil surface and can be attached to a resistance meter. The upper block is 150mm below the soil surface, the middle block is 300mm and the lower block 600mm. Not to scale.

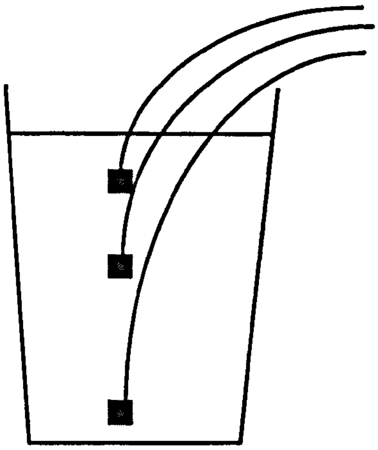
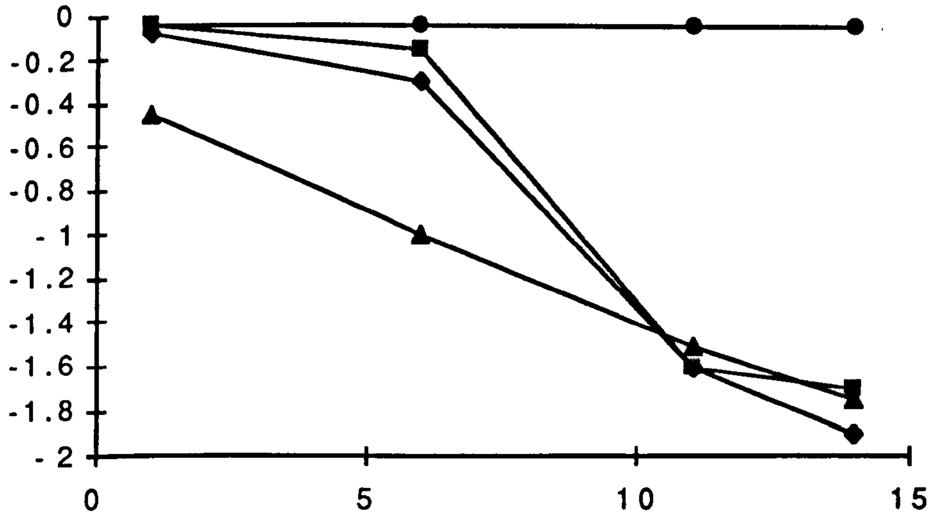


Figure 10.3 illustrates the change in moisture content over a two week period following construction of the rain shelters. The meter readings have been converted to soil moisture potential (MPa) using a conversion chart supplied with the meter. A soil moisture potential of zero indicates saturated soil while a value of minus two indicates completely dry soil. The watered replicates maintain soil moisture potentials close to zero throughout the monitoring period indicating constantly moist conditions. Readings from blocks 150mm below the surface of the droughted bins show a consistent decrease in moisture content at this level over the monitoring period. Readings from the blocks at greater depth in the droughted bins indicate an initial reservoir of moisture at these lower levels. However in the later stages the bins appear to be evenly dry throughout their depth.

Figure 10.3 Moisture Profile of Droughted and Watered Replicates. X axis = days from start of construction of rain shelters. Y axis = Mean soil moisture potential (MPa). Circles = Watered bins (150mm below surface) Triangles = Droughted bins (150mm below surface. Diamonds = Droughted bins (300mm below surface) Squares = Droughted bins (600mm below surface).



10.2.1.2 Plant Performance

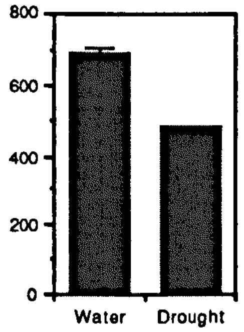
A number of measures of plant performance were used. Heights were measured in August 1993 and August 1994. The methods used for measuring heights were the same as those for the warmed plants, described in Chapter 8. Flowering performance was assessed by counting the mean number of inflorescences produced per replicate. Point quadrat surveys were carried out in October 1993 and August 1994. Shoot biomass was evaluated in two ways: absolute shoot biomass and relative shoot biomass. Absolute shoot biomass is the actual number of point quadrat hits recorded. Relative shoot biomass was calculated for the plants in mixture as the proportion of the total shoot biomass occupied by each species. Relative shoot biomass therefore gave an indication of the degree of dominance attained in the mixture for each species.

10.3 RESULTS

10.3.1 TOTAL SHOOT SHOOT BIOMASS

The total shoot shoot biomass of the droughted mixtures (the total number point of quadrat hits for all species) was significantly less than that of the watered mixtures in August 1993 (P < 0.001). In 1994, however, there was no significant difference between the two sets of replicates.

Figure 10.4 Comparison of the total shoot biomass of the droughted and watered mixtures in 1993. Y axis = Number of point quadrat hits. Bars represent standard errors.

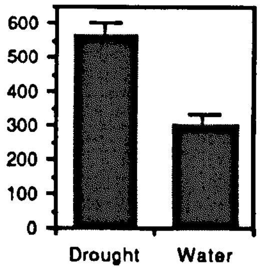


10.3.2 ACHILLEA MILLEFOLIUM

(i) Heights

Monoculture In 1993 the mean maximum (flowering) height of the droughted plants was significantly greater than that of the controls (P<0.001). In 1994 the mean leaf height of the droughted plants was again greater (P<0.001), although there was no significant difference between the mean inflorescence height of the two sets of plants.

Figure 10.5 The Mean Maximum Height of the Droughted and Watered Plants in Monoculture in August 1993 Y axis = Height (mm). Bars represent standard errors.



Mixture In 1993 and 1994 there were insufficient plants growing in the droughted replicates to enable mean heights to be compared.

(ii) Flowering

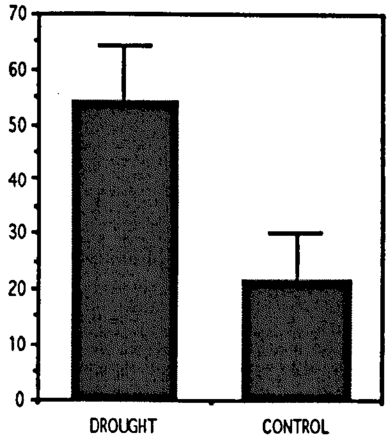
Monocultures Flowering performance was measured in two ways in 1993: the number of corymbs present in August 1993 and the total number of capitula produced in 1993 (corymbs were harvested at the end of the season and the total number of capitula counted). In both cases the flowering performance of the droughted plants exceeded that of the watered plants, although the difference was not significant (P=0.13 and 0.057 for corymbs and capitula respectively).In 1994 the number of capitula present in August were counted. Again there was no significant difference between the two sets of plants.

Mixtures No flowering occurred in the mixture replicates.

(iii) Herbivory

Aphid herbivory on the monoculture plants was assessed in August 1993 by counting the number of shoots of *Achillea* that were infested with insects. A significantly greater proportion of shoots of the droughted plants were infested compared to the controls, indicating a greater susceptibility to herbivory of the droughted plants.

Figure 10.6 Aphid infestation of *Achillea* in monoculture. Data collected on August 9th 1993. Y axis = mean % of shoots infested with aphids.



(iv) Shoot biomass

Monocultures In 1993 the shoot biomass of the droughted plants was greater than that of the watered plants. In 1994 the shoot biomass of the droughted plants was again greater than that of the watered plants (P=0.09).

Mixtures In 1993, in both absolute and relative terms the shoot biomass of the droughted plants was less than that of the watered plants, although not significantly so. However in 1994 the differences were significant and *Achillea* was virtually eliminated from the mixtures.

Table 10.1 **Achillea Shoot biomass** Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Water	Drought
Mean	88.4	126.6
SE	22.38	9.00
Probability	0.152	
August 1994		
Mean	246.4	297.4
SE	15.09	22.08
Probability	0.09	

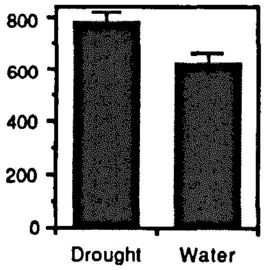
MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Water	Drought	Water	Drought
Mean	10.4	1.0	1.51	0.20
SE	4.15	1.0	0.57	0.20
Probability	0.059		0.062	
August 1994				
Mean	7.8	0.2	1.27	0.032
SE	2.8	0.2	0.51	0.032
Probability	0.026		0.041	

10.3.3 CIRSIUM ARVENSE

(i) Heights

Monocultures In 1993 the droughted plants were significantly taller than the watered plants. In 1994 there was again no significant difference between the two sets of plants.

Figure 10.7 The Mean Height of the Droughted and Watered Plants in Monoculture in August 1993. Y axis = Height (mm). Bars represent standard errors.

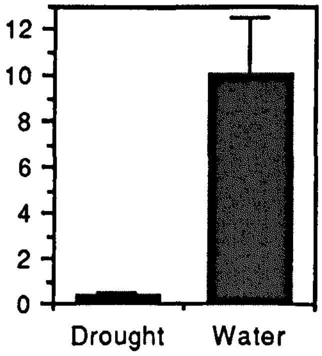


Mixtures In August 1993 *Cirsium* had shrivelled and was not present in sufficient quantity for measurements to be made. In 1994 there was no significant difference between the two sets of plants.

(ii) Flowering

A survey of the number of flowers present on the monoculture plants in mid August 1993 showed that the droughted plants had produced significantly fewer flowers than the watered plants. There was no significant difference between the two sets of monoculture plants in 1994. Plants in mixture did not flower.

Figure 10.8 Flowering Performance of Monoculture Plants in August 1993 Y axis = Mean number of flowers. Bars represent standard errors.



(iii) Number of Shoots

A survey of emergent shoots in the monoculture replicates was made in December 1993. Emergent shoots took the form of short rosettes up to 20mm in height. The five droughted replicates contained respectively two, ten, one, one and zero emergent shoots. No watered replicates contained any shoots. None of the other *Cirsium* monoculture replicates contained any shoots. Although the droughted replicates contained many more shoots than the controls, the difference between the two sets of plants was not significant.

(iv) Shoot biomass

Monoculture In 1993 the shoot biomass of the droughted plants was greatly reduced compared to the watered plants. However, in 1994 there was no significant difference between the two sets of replicates.

Mixture In 1993, *Cirsium* was eliminated above ground by the treatment in the droughted replicates. In 1994, however, the shoot biomass of the droughted plants was less than that of the watered plants, but the difference was not statistically significant.

Table 10.2 Cirsium Shoot biomass Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Water	Drought
Mean	217.6	14.2
SE	4.8	12.5
Probability	<0.001	
August 1994		
Mean	363.2	369.6
SE	10.24	3.95
Probability	0.576	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Water	Drought	Water	Drought
Mean	13.4	0	1.94	0
SE	1.81	0	0.27	0
Probability	<0.001		<0.001	
August 1994				
Mean	11.8	9.4	2.36	1.39
SE	3.121	4.68	0.65	0.68
Probability	0.681		0.337	

10.3.4 DACTYLIS GLOMERATA

(i) Heights

Monoculture There was no significant difference between the two sets of plants in 1993 or 1994.

Mixture There was no significant difference between the two sets of plants in 1993 or 1994.

(ii) Flowering

There was no significant difference between the flowering performance of the plants in mixture and monoculture, in 1993 and 1994.

(iii) Shoot biomass

Monoculture The shoot biomass of the droughted plants was significantly less than that of the watered plants in 1993. In 1994 the droughted plants still had a lower shoot biomass (P=0.06).

Mixture Again in mixture in 1993 the shoot biomass of the droughted plants was significantly less than that of the watered plants in absolute terms. Despite this reduction, the shoot biomass of *Dactylis* remained high. The proportion of the total biomass that *Dactylis* occupied was not significantly different from that of the watered plants. In 1994 there was no significant difference between the two sets of replicates.

Table 10.3 Dactylis Shoot biomass Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Water	Drought
Mean	369.0	235.8
SE	25.36	27.16
Probability	0.007	
August 1994		
Mean	471.8	387.0
SE	23.99	31.0
Probability	0.062	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Water	Drought	Water	Drought
Mean	259.0	171.4	44.48	36.43
SE	28.31	15.4	5.2	2.97
Probability	0.026		0.68	
August 1994				
Mean	315.0	239.0	40.55	38.6
SE	37.36	12.84	6.94	2.25
Probability	0.56		0.79	

10.3.5 FESTUCA RUBRA

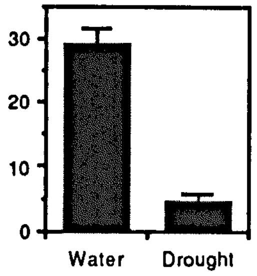
(i) Heights

There was no significant difference between the two sets of replicates in either 1993 or 1994, in mixture and in monoculture.

(ii) Flowering

There was no significant difference between the two sets of replicates in monoculture in 1993 or 1994. In mixture in 1994, the watered plants produced a significantly greater number of inflorescences than the droughted plants (P = 0.02).

Figure 10.9 The Flowering Performance of Watered and Droughted plants in Mixture in August 1994 Y axis = Mean number of inflorescences per bin. Bars represent standard errors.



(iii) Shoot biomass

Monoculture The shoot biomass of the droughted plants was significantly smaller than that of the watered plants in 1993. However, in 1994 the shoot biomass of the droughted plants was greater, although not significantly so.

Mixture There was no significant difference between the shoot biomass of the two sets of plants in 1993. However, in 1994, the shoot biomass of the droughted plants was significantly greater than the watered plants. In 1993 and 1994, *Festuca* occupied a greater proportion of the total shoot biomass in the droughted bins than in the watered bins: approximately 60% in both years in the droughted bins as compared to approximately 40 and 45% in the watered bins in 1993 and 1994 respectively.

Table 10.4 **Festuca Shoot biomass** Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Water	Drought
Mean	763.6	519.8
SE	32.38	44.57
Probability	0.002	
August 1994		
Mean	759.6	906.0
SE	20.06	78.21
Probability	0.107	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Water	Drought	Water	Drought
Mean	302.0	262.2	44.89	57.97
SE	39.05	12.10	5.27	3.36
Probability	0.359		0.07	
August 1994				
Mean	221.6	346.6	41.33	57.21
SE	43.81	29.03	7.72	3.39
Probability	0.045		0.096	

10.3.6 POA PRATENSIS

(i) Heights

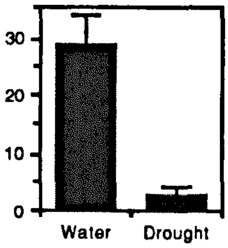
There was no significant difference between the two sets of replicates in either 1993 or 1994, in mixture and in monoculture.

(ii) Flowering

Monoculture Flowering of *Poa* had ceased in 1993 prior to the treatment. In 1994 the droughted replicates produced fewer inflorescences than the watered plants (P=0.07).

Mixture Flowering of *Poa* had ceased in 1993 prior to the treatment. In 1994 the droughted plants produced significantly fewer inflorescences than the watered plants (P = 0.02).

Figure 10.10 The Flowering Performance of Poa in Mixture in 1994 Y axis = Mean number of inflorescences produced per bin. Bars represent standard errors.



(iii) Shoot biomass

Monoculture In 1993 the shoot biomass of the droughted plants was significantly reduced compared with the watered plants. In 1994 the shoot biomass was still less, although the difference was no longer significant.

Mixture In absolute terms the shoot biomass of *Poa* in the droughted replicates was less than that of the watered plants in 1993 and 1994. In relative terms, *Poa* occupied less of the total shoot biomass in the droughted bins than in the watered bins, although the differences were not significant.

Table 10.5 Poa Shoot biomass Figures refer either to the absolute shoot biomass (number of PQ hits for the species alone), or to % of total shoot biomass (% of total number of PQ hits)

MONOCULTURE	Absolute shoot biomass	
October 1993	Water	Drought
Mean	407.8	278.2
SE	24.16	36.5
Probability	0.018	
August 1994		
Mean	532.4	450.4
SE	41.07	31.09
Probability	0.15	

MIXTURE	Absolute shoot biomass		% of total shoot biomass	
October 1993	Water	Drought	Water	Drought
Mean	99.6	46.0	14.48	9.59
SE	17.56	2.85	2.659	0.57
Probability	0.017		0.11	
August 1994				
Mean	98.8	43.2	17.5	6.95
SE	33.66	8.13	5.41	1.48
Probability	0.147		0.106	

10.4 DISCUSSION

10.4.1 ACHILLEA MILLEFOLIUM

Achillea was predicted to show a positive response to the drought treatment. This it clearly did in monoculture, appearing to perform better following the treatment than without it. *Achillea* is a deep-rooted species that is able to tap moisture at depth (Warwick & Black 1982). In monoculture the plants were presumably able to develop such an effective root system.

Achillea may also have other drought-tolerating mechanisms. It has been observed that maximum accumulation of fructans occurs in summer for a wide range of British species (Hendry, 1987). In a survey of 130 species of the Sheffield flora, only 20 species were found in which fructan formed a significant part of the reserve carbohydrate. *Achillea* was included in this list of 20. *Cirsium, Dactylis, Festuca* and *Poa* were not included It has been suggested that some species may survive periods of water stress through regulation of osmotic potential by the degradation of stored carbohydrates, particularly fructans, during such periods (Volaire, 1995). *Achillea,* the species that showed greatest drought tolerance in the experiment (in monoculture), is also the only species reported to contain significant amounts of stored fructans in summer.

In mixture, *Achillea* was virtually eliminated from the vegetation following the treatment. As discussed in Chapter 9, frosting had a similar effect. It was noted that *Achillea* tends to perform better in the field in more open swards or bare patches and it is probable that the tall, *Dactylis* -dominated vegetation of the mixture replicates was not conducive to its optimal growth. It may be that, in mixture, shading and below-ground competition reduced the vigour of *Achillea* and made it more vulnerable to drought.

Achillea was shown to be more susceptible to herbivory following the drought treatment. Other species have also been shown to be more palatable to insects during and following drought (G. Masters pers. comm.). It is thought that changes in the carbon: nitrogen ratio in the plant's sap resulting from moisture stress increase the 'quality' of the food source in droughted plants.

10.4.2 CIRSIUM ARVENSE

Cirsium was predicted to respond negatively to the treatment. In both mixture and monoculture, *Cirsium* showed great sensitivity to drought during and in the months after the treatment. In monoculture the shoot biomass was greatly reduced, whereas in mixture the plants disappeared. However, both sets of plants recovered in 1994 and there was no significant difference between the treated plants and the controls. Like *Achillea,* the response of *Cirsium* to drought was similar to its response to frosting. It appeared to show little resistance to the treatment, but great resilience. As with the frosted plants, *Cirsium* appeared to show at least partial recovery from the treatment throughout the release from dormancy of buds on the rhizomes.

The prediction for *Cirsium* was therefore fulfilled.

10.4.3 DACTYLIS GLOMERATA

Dactylis was predicted to show a negative response to the drought in both mixture and in monoculture. Both predictions were fulfilled. In the second season after droughting, however, *Dactylis* had recovered.

A similar experiment, in which cultivars of *Dactylis* from the Mediterranean and Northern Europe were subjected to drought under semi open-sided polyethylene rain shelters was conducted by Volaire (1995). Those cultivars from N.Europe suffered high plant mortality after the summer drought and did not resume growth in the autumn. However, those of Mediterranean origin showed rapid recovery of leaf extension from early September, once the treatment had ceased. The Mediterranean plants, while suffering a decrease in shoot biomass, accumulated strategically significant levels of fructans, while those from N.Europe did not, but instead continuously utilised their reserves resulting in mortality and lack of persistence.

The populations used in the above experiment were of cultivars that had been actively selected to give maximum yield in the climates in which they are grown. No difference in ploidy was reported for the two populations. The Bibury plants, taken from a site in southern England, tended to behave more like the Mediterranean populations in that they showed recovery after the treatment. However, it may be that the drought treatment imposed was not sufficient to result in widespread mortality of the treated plants.

10.4.4 FESTUCA RUBRA

Festuca was predicted to be retarded by drought. In monoculture, significant reduction in shoot biomass occurred in 1993. However in 1994, the mean shoot biomass values (recorded as point-quadrat hits) for the droughted plants was actually greater than the watered plants: 760 to 906 respectively, although the difference was not significant.

In mixture, the mean shoot biomass of the droughted plants was reduced, although not significantly. While flowering performance was reduced, *Festuca* actually appeared to gain some competitive advantage from the treatment, increasing its mean share of the total shoot biomass to nearly 60%, compared with 45% for the watered plants in 1993.

Festuca appeared therefore to exhibit some drought tolerance. Again, as with *Achillea* and *Cirsium*, the results were very similar to those obtained from the frosting treatment. It appears that weakening of *Dactylis* through an external agent, such as drought or frost, benefits *Festuca* to an extent. *Festuca* is well known to be a species that commences growth early in the year. It may be that it is able to escape severe damage from summer drought because of this early growth. It is probable that in the experiment *Festuca* had completed its major growth before the drought treatment was applied, and then survived the treatment by rolling up its narrow leaves.

Festuca therefore appeared to partially fulfil the predictions: being retarded initially but gaining indirect competitive advantage in mixture.

10.4.5 POA PRATENSIS

Poa was predicted to respond negatively to the treatment. The predictions were fulfilled in both mixture and monoculture. Indeed the reduction in the shoot biomass of *Poa* persisted into 1994.

10.4.6 TOTAL VEGETATION SHOOT BIOMASS

As expected, the total vegetation shoot biomass of the mixture bins was significantly reduced in the same season as the drought was applied. This result supports the conclusions from the studies mentioned in the introduction to this chapter, and from the results of the analysis of the Bibury field records, that summer rainfall is a crucial factor in vegetation performance.

10.5 CONCLUSIONS

Of all the treatments imposed, droughting produced the most severe effects on the vegetation. Predictions were at least partially fulfilled for all species. However, the differences between the performance of, for example, *Achillea* and *Festuca*,in mixture and monoculture clearly illustrate the potential effects of weather on the dynamics and diversity of grassland vegetation, and show how weather can act directly on some species while in others the effect is indirect and mediated through competition . This point is addressed further in the final chapter of the thesis.

CHAPTER 11 CONCLUSIONS: THE INFLUENCE OF WEATHER ON THE DYNAMICS AND DIVERSITY OF GRASSLAND PLANT COMMUNITIES

11.1 Introduction

11.2 Individual Species
  11.2.1 Achillea millefolium
  11.2.2 Cirsium arvense
  11.2.3 Dactylis glomerata
  11.2.4 Festuca rubra
  11.2.5 Poa pratensis

11.3 Functional Types
  11.3.1 Forbs
  11.3.2 Grasses
  11.3.3 Forbs and Grasses

11.4 Total Shoot Biomass

11.5 DNA

11.6 Weather and the Dynamics and Diversity of Grassland Vegetation

11.7 Conclusions

11.1 INTRODUCTION

Part 1 of this thesis is concerned with the analysis of the field records collected annually from the Bibury site. It has been shown that, using this data-set, clear plant/weather relationships can be demonstrated for individual species, functional types, and for the vegetation as a whole. This information is highly valuable in its own right. As demonstrated in Chapter 1, there are few long-term studies of comparable breadth, few, if any, with such precise yearly measurements of plant performance, and few of such direct relevance to current research on the possible effects of climate change on indigenous vegetation.

However, as discussed in Chapter 7, this information can be applied strictly only to the Bibury site itself. For example, it could be stated that, at Bibury, *Dactylis glomerata,* is promoted by warm springs. It could not be concluded, on the basis of this evidence alone, that *Dactylis* is generally promoted everywhere by warm springs. The precise mechanism for the promotion of *Dactylis* in the verges at Bibury is also not apparent from analysis of the field records alone. Is it directly promoted as a result of elevated temperatures, or is it indirectly affected, perhaps as a result of the reduced vigour of a competitor?

The experiments described in Part 2 were designed to explore the mechanistic basis of the plant-weather relationships at Bibury and to extend the relevance of the data-set beyond the site itself. By 'verifying' selected plant/weather relationships under controlled conditions, it was hoped firstly to enhance the credibility of the field observations, secondly to demonstrate whether or not the selected relationships might have more general application, and thirdly to disentangle the direct effects of the selected treatments on the plants involved from those mediated through competition. Although only five species were selected for the experiment, it was thought that if the field observations were repeated under controlled conditions for those five species, then it would be reasonable to assume that the other plant/weather relationships detected in the analysis of the field records might also be valid.

In this chapter the success of the experiments described in Part 2 is assessed and an attempt is made, using the results from those experiments, the analysis of the field records, and other published information, to describe the influence of weather on the dynamics and diversity of grassland vegetation.

11.2 INDIVIDUAL SPECIES

The following predictions (taken from table 7.9) were made in Chapter 7 concerning the effects of the different experimental treatments on the selected species in the bins:

	Warming	Drought
Achillea		+
Cirsium	+	-
Dactylis	-/+	-
Festuca	-	-
Poa	-	-

The response of the five species is summarised in this section and their observed responses are compared with the predicted responses.

11.2.1 Achillea millefolium

Achillea was predicted to respond positively to the drought treatment. This it clearly did in monoculture. However, in mixture, *Achillea* was retarded by the treatment and was virtually eliminated from the vegetation. Similar effects were observed following the frosting treatment: promotion in monoculture but weakening in mixture. *Achillea* initially responded positively to the warming treatment in monoculture; however by the end of the warming period, *Achillea* in both mixture and monoculture was retarded by the treatment.

The predicted response was therefore achieved in monoculture. This supports previously published reports of drought tolerance in *Achillea* (e.g. Warwick & Black, 1982). The difference between the performance of *Achillea* in mixture and monoculture can probably be attributed to reduced vigour of the plants in mixture as a result of competition from more robust species. It was demonstrated in Chapter 7 that *Achillea* was the weakest competitor in the control mixture replicates. In the field, the species tends not to grow in dense vigorous swards, but, rather, in more open vegetation. It is likely therefore that, in time, *Achillea* would be eliminated from the synthesised mixtures. The experimental treatments which either promoted vigorous competitors or imposed severe stress on *Achillea* itself hastened that process.

11.2.2 Cirsium arvense

Cirsium was predicted to respond positively to the warming treatment. This it clearly did, in both mixture and monoculture. The initial growth of *Cirsium* was demonstrated to be highly temperature-dependent, with new shoots appearing several weeks earlier in the warmed mixture bins than in the controls. There was also evidence that warmed *Cirsium* plants maintained a height advantage over unwarmed plants for the duration of the warming period. Although there was no difference in shoot biomass as estimated by point-quadrat surveys at the end of the growing season, early shoot emergence and increased height could be expected to confer competitive advantages over other species that do not show a similar immediate response to increased winter and spring temperatures. The observed results again support field observations that shoot growth and emergence are linked directly with mean spring temperatures (Moore, 1975).

Cirsium was also predicted to respond negatively to the drought treatment. Again, this prediction was clearly fulfilled in the same year as the treatment was applied, in both mixture and in monoculture. However, in the following year *Cirsium* appeared to have recovered completely from the treatment and no significant differences were found between control and treated plants. A very similar response was observed following frosting. While *Cirsium* suffered immediate frost damage, the species also demonstrated rapid recovery from the treatment. Indeed, in mixture, it appeared that *Cirsium* was able to gain competitive advantage as a result of weakening of more robust species following the treatment.

11.2.3 Dactylis glomerata

Two predictions were made regarding the response of *Dactylis* to the warming treatment. In the field, *Dactylis* appears to be strongly promoted in the season immediately following a warm spring. However, the species also appears to be retarded following a mild winter (although this is not apparent until one or two years after that mild winter). In the experiments *Dactylis* was clearly and strongly promoted by the warming treatment.

There were also negative effects of the treatment, most notably on flowering and seed-set. It was suggested in Chapter 8 that a reduction in winter vernalisation and subsequent reduction in seed-yield following mild winters may be in some degree responsible for the reduced contribution of *Dactylis* to the total vegetation biomass at Bibury in the second and third years following a mild winter. It has been suggested that a 1° (C) warming might significantly reduce crop yields as a result of failure to initiate or accelerate the flowering process (Parry, 1992). However, the importance of seed regeneration to *Dactylis* in a closed perennial sward is as yet unknown. It is striking that in such swards certain species flower abundantly in some years while in others they are not particularly noticeable. This periodicity in flowering could have serious consequences on the dynamics of a population, although the extent of seed reproduction, or how this type of reproduction is related quantitatively to vegetative reproduction is not clear (Bergh, 1979). The results reported here for *Dactylis* suggest a trade-off between vegetative vigour and flowering.

Dactylis was also predicted to respond negatively to the drought treatment. Again, the prediction was fulfilled, in the same season as the treatment was imposed, in both mixture and monoculture. However, in the following year the plants had recovered.

Dactylis showed immediate and marked sensitivity to the frost treatment, although, by the end of the growing season following the treatment no significant difference was observed between the shoot biomass, as estimated by point-quadrat survey, between the two sets of plants. The immediate damage, and also that observed to the inflorescences, and the subsequent effects on seed-yield, is in accord with previous field observations (Beddow, 1959).

11.2.4 Festuca rubra

Festuca was predicted to respond negatively to the warming treatment. In monoculture, *Festuca* appeared to be promoted by the treatment. However, in mixture, *Festuca* was clearly retarded. In Chapter 8 it was noted that *Festuca* appeared to be retarded indirectly as a result of the promotion of more robust, vigorous species. It was also noted that *Festuca* has a relatively early phenology which, under normal conditions, allows some temporal niche definition in mixed vegetation. Warm winters may however promote more robust species into earlier and more vigorous growth, thereby reducing the competitive fitness of *Festuca.*

Festuca was also predicted to be unusually sensitive to moisture stress. In monoculture, *Festuca* was significantly retarded by the drought treatment. However, in mixture, while exhibiting some reduction in biomass following the treatment, *Festuca* appeared to gain some competitive advantage, significantly increasing its mean share of the total biomass. As discussed in Chapter 10, the promotion of *Festuca* may be a result of a combination of drought avoidance (early growth) and resistance (leaf 'closing' in summer). This implied drought tolerance accords with observations from the Park Grass Experiment. In the drought year of 1976 *Festuca rubra* achieved its peak contribution to the total above-ground biomass in plot 7 (PK plot). The weight percentage of the hay crop from this plot reached 54% for *Festuca* and *Agrostis capillaris* together, a unique value over the 120 year period of the experiment (Bergh, 1979).

Again, a very similar response was observed to the frosting treatment, with *Festuca* appearing to gain some competitive advantage in mixture as a result of its relatively high tolerance of the treatment compared to the other species in the mixture.

The predicted responses for *Festuca* were therefore mostly fulfilled, although the drought treatment may actually have promoted the species in mixture.

11.2.5 Poa pratensis

Poa was predicted to be retarded by both the warming and droughting treatment. Both these predictions were fulfilled. *Poa* responded similarly to *Festuca.* to the warming treatment, being indirectly retarded in mixture, probably as a result of increased competition from more robust species.

In both mixture and monoculture *Poa* was retarded by drought. The reduced performance of *Poa* persisted into the year following the treatment.

The predictions made in Chapter 7 were, therefore, in the main, fulfilled. Where predictions were not fulfilled, logical explanations could be provided.

11.3 FUNCTIONAL TYPES

In Chapter 7 a brief 'profile' of each of the five species included in the experiment was given. No reference was made in those profiles to the classification of each species according to its established strategy *sensu* Grime (1973). Although, in choosing the five species, no consideration was given to their functional type, in this section the results of the experiments described earlier in the thesis will be discussed with reference to those functional types The species are classified according to their functional type in Table 11.1

Table 11.1 Functional Classification of the Five Species Included in the Experiment. Classification is taken from Grime *et al.* (1988).

Species	Classification
Achillea millefolium	CR/CSR
Cirsium arvense	C
Dactylis glomerata	C/CSR
Festuca rubra	CSR
Poa pratensis	CSR

At first glance there appears to be little difference between the selected species in terms of their established strategies. However a more detailed examination reveals more differentiation than is at first apparent.

11.3.1 Forbs

Grime (1979) classifies both *Achillea* and *Cirsium* as competitve-ruderals. Both *Achillea* and *Cirsium* were included in a comparative study by Bostock and Benton (1979) of the reproductive strategies of five perennial members of the Asteracae. The other species included were *Artemisia vulgaris, Taraxacum officinale* and *Tussilago farfara.* The five species were classified on the *r* - *K* continuum. Based on characteristics such as the degree of disturbance and competitiveness of their typical habitats and their 'conservation values' (the amount of living material present in winter), *Achillea* was judged the most *K*-strategic, while *Cirsium* was judged the most *r*-strategic in terms of its vegetative reproductive strategy. Of the two species, *Cirsium* is more closely associated with disturbed productive habitats, while *Achillea* is less tolerant of edaphic disturbance. Some differences exist therefore between these two similarly classified species.

The nature of the response of the two species to the experimental treatments was also different. Both were indirectly retarded by the treatment (warming) that promoted the major competitor in the system, *Dactylis*. Both also responded similarly to the treatments which imposed disturbance on the system (frosting) and stress and disturbance (drought). *Cirsium* responded to defoliation in both instances by producing new shoots from its rhizomes and above-ground stems. It appeared that the rapid response to frosting disturbance actually conferred some competitive advantage in the mixtures. *Achillea*, however, exhibited a more conservative strategy While it too was promoted in monoculture by the frost and drought treatment, it appeared to possess mechanisms that protected and conserved its above-ground biomass, and therefore appeared more 'tolerant' of the imposed treatments. Unlike *Cirsium*, which appeared to gain advantage in mixture following frost-disturbance, *Achillea* seemed seriously weakened following frosting in mixture. The observed responses therefore appear to support the strategic analysis made by Bostock and Benton (1979).

11.3.2 Grasses

Grime (1979) classifies *Festuca* as a stress-tolerant competitor. Grime *et al.* (1979) also state that some populations of *Festuca rubra* tend towards the stress-tolerant strategy. As stated in Chapter 7, this species often forms a non-flowering understory beneath stands of *Arrhenatherum elatius* in roadside vegetation (Grubb, 1982). The evidence from the experiment suggests that *Festuca* was indeed more tolerant than other species in the mixture to the treatments that imposed some stress on the system.

The behaviour of *Dactylis* in the experiment is typical of that expected from a robust competitive species. It was strongly promoted by the warming treatment. This treatment, in effect, increases environmental favourability by reducing external stress and disturbance. The two treatments which imposed external stress and disturbance on the system, frosting and droughting, resulted in significant reductions in the performance of *Dactylis*.

In contrast, *Festuca* was indirectly retarded by the warming treatment. However, following the drought and frost treatment, *Festuca* was, at least temporarily, advantaged. In this instance it is reasonable to assume that the degree of frost and drought tolerance exhibited by *Festuca* allowed that advantage to be gained through the greater sensitivity to stress and disturbance of *Dactylis*.

11.3.3 Forbs and Grasses

The results for all five species strongly support the model described in Chapter 6: competitors being favoured by weather that increases the productivity of a system, while stress-tolerant species and ruderals are advantaged by weather which imposes some form of external stress or disturbance on the system.

11.4 TOTAL SHOOT BIOMASS

The field records from Bibury suggest that, in both vegetation series, shoot biomass is reduced following hot dry summers. In series 7 and 8, shoot biomass also appears to increase following cold winters.

There was no significant difference between the total above-ground biomass of the warmed and unwarmed mixture bins in the experiment. However, the total above-ground biomass of the droughted mixtures was significantly less than that of the watered mixtures. The field observations at Bibury have therefore been supported by the experimental results.

11.5 DNA

The five species were selected for the experiment with no consideration for their nuclear DNA contents. However, by chance, a wide range of nuclear DNA values are encompassed by the chosen species; from 3.1 pg for *Cirsium* to 15.3 for *Achillea.* This range was sufficiently wide for a number of predictions to be tested with regard to species' response to the warming treatment. It was suggested that the shorter cell-cycle associated with a low nuclear DNA content would enable such species to respond more rapidly to increased temperatures early in the growing season. These predictions were fulfilled.

Previous published work has linked nuclear DNA content with plant distribution (e.g. Bennett, 1976: Grime & Mowforth, 1982; Wakamiya et al., 1993) and the timing and rate of spring leaf extension (e.g Grime & Mowforth, 1982, Grime, Shacklock & Band, 1985). The results reported here demonstrate a clear difference in response to increased temperatures early in the growing season between species with low and high nuclear DNA content. Figure 8.34 shows that the 'relative' absolute growth rate (the ratio of the absolute growth rate of warmed plants to controls) is negatively correlated with nuclear DNA content. In other words, species with low nuclear DNA content exhibit an increase in growth rate in response to higher temperatures compared with unwarmed plants. It is particularly interesting that species with high nuclear DNA appear to exhibit *a decrease* in growth rate compared to unwarmed controls. This may indicate high temperature stress in species that are adapted to growth under cooler conditions, or it may indicate competitive disadvantage in such species as a result of increased vigour of promoted low DNA species. The results displayed in Figure 8.34 were taken from plants growing in *mixture*. This suggests that competitive effects are in fact important. If this is the case, the results provide important experimental evidence to support the view that certain species with high nuclear DNA content may be susceptible to competitive suppression following a succession of mild winters (Hodgson & Grime, 1989).

The results support the previous findings of MacGillivray (1993) that species with small nuclear DNA content are more susceptible to damage from severe late frosts than species with large nuclear DNA content (see Section 9.5.6 of this thesis).

11.6 WEATHER AND THE DYNAMICS AND DIVERSITY OF GRASSLAND VEGETATION

Long-term fluctuations in the composition of a plant community may arise from differences in the susceptibility of established plants to factors such as drought, predation or pathogens (Grime, 1979). The direct impact of weather, among many other factors, can be responsible for differences in fitness of populations within plant communities, which may subsequently influence the ability of those organisms to compete with their neighbours for resources (Campbell *et al.*, 1991). The long-term records from the Bibury verges provide an important example of the influence of weather on plant community dynamics.

It was shown in Chapter 7 that *Dactylis* and *Festuca* were the major components of the synthesised plant communities used in the experiment, while *Achillea, Cirsium* and *Poa* were subordinate species. It has been demonstrated that *Dactylis* was clearly the dominant species in the mixtures. The results for *Dactylis* and *Festuca* demonstrate how weather can influence the fitness of dominant components of the vegetation and thereby affect the dynamics and diversity of that vegetation.

Figure 11.1 illustrates the susceptibility of each species to interspecific competition following each treatment. The effect of interspecific competition was calculated for each species, for each treatment, as:

$$CX = (YP-YM) \times 100/YP$$

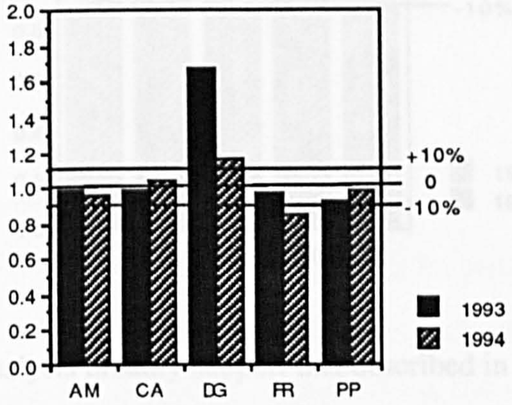
where CX is the percentage reduction in yield potential, YP is the yield in monoculture (the maximum potential yield) and YM is the yield in mixture (Campbell *et al.,* 1991). Yield here is the above-ground biomass as estimated by point -quadrat survey.

This is a different measure of plant performance following a treatment than that employed in the main body of the thesis. Previously, plant performance in treated bins was compared with that in control bins. Here, however, plant performance in treated mixtures is compared directly with plant performance in the comparable treated monocultures to give a measure of the competitive ability of each species in mixture.

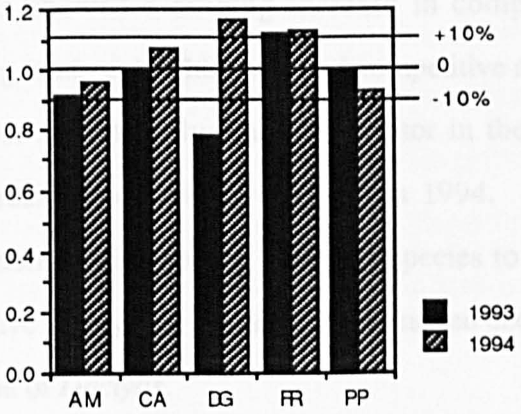
In Figure 11.1, competitive ability is measured as the ratio of the percentage reduction in yield of the species in control bins compared to that in the treated bins: CX(controls)/CX(treated plants). Values of 1.0 or near to 1.0 indicate no difference in competitive ability between the treated plants and the controls. Values of less than 1.0 indicate decreased competitive ability in the treated plants while values greater than 1.0 indicate increased competitive ability in the treated plants. An arbitrary 'significance' level of +/- 10% increase or decrease in competitive ability following treatment is indicated in Figure 11.1. The data on which the figure is based were taken from the shoot biomass tables in Chapters 8, 9 and 10 (October 1993 and August 1994).

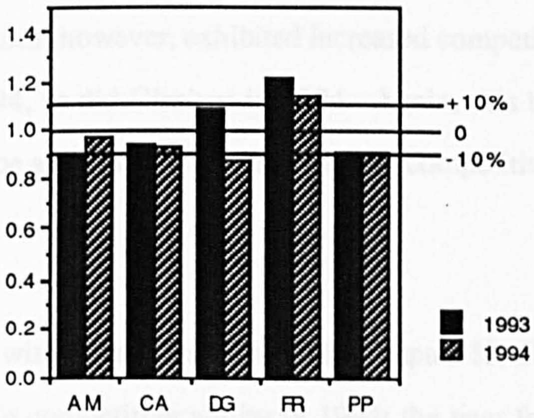
Figure 11.1 The competitive ability of the five species in the experiment following treatment in mixture. Y axis = the ratio of the percentage reduction in yield potential of the treated plants to that of the controls. Horizontal bars indicate increase or decrease in competitive ability.

Warmed



Frosted




Droughted

The results of this analysis broadly support that described in Chapters 8, 9 and 10, but with some notable exceptions.

Warming: *Dactylis* showed a striking increase in competitive ability in 1993 following the warming treatment. This increased competitive ability was maintained in 1994. It is of interest that the only other competitor in the system, *Cirsium*, also showed a slight increase in competitive ability in 1994. All three other species exhibited decreased competitive ability. The one species to show greater than 10% reduction in competitive ability was *Festuca*. As discussed above, this can probably be attributed to promotion of *Dactylis*.

Frost: *Dactylis* showed a striking decrease in competitive ability in 1993 following frosting. This is of interest because, although various measurements made immediately following frosting indicated that *Dactylis* had indeed been weakened, the simple comparison of shoot biomass of the frosted plants with the controls showed no significant difference between the two sets of plants. Here, however, it can be seen that the negative effect of the frost treatment persisted throughout 1993. In 1994, *Dactylis* showed increased competitive ability. This is again a reflection of results reported in Chapter 9, in which *Dactylis* appeared to be stimulated into more vigorous growth in the year after the treatment.

The competitive ability of *Achillea* and *Poa* was also reduced following frosting, as reported earlier. *Festuca,* however, exhibited increased competitive competitive ability in both 1993 and 1994, as did *Cirsium* in 1994. Again, this increase in competitive ability can probably be attributed to the reduction in competitive ability of *Dactylis* in 1993.

Drought: In accord with the results reported in Chapter 10, *Dactylis* showed greater than 10% reduction in competitive ability in 1994; the year following the treatment. *Achillea, Cirsium* and *Poa* also showed reductions in competitive ability. However, *Festuca,* exhibited increased competitive ability in both 1993 and 1994, again probably as a result of the reductions in competitive ability of other species in the mixtures.

It is apparent from these results that weather can directly influence the competitive competitive ability of species in plant communities and that this in turn influences community dynamics and community composition. In particular, external stress and disturbance (here represented by the frost and drought treatments) can reduce the vigour of dominants (*Dactylis*) and thereby indirectly promote subordinate species (such as *Festuca*).

11.7 CONCLUSIONS

In a review of long-term vegetation studies, Bergh (1979) states that, except for some extreme drought periods, the relationship between annual fluctuations in plant performance and weather is obscure. The work described in this thesis has reduced that obscurity for one ecological system.

It has been demonstrated in Part 1 of this thesis that clear plant/weather relationships exist in the Bibury road-verges. Plant performance has been linked with the prevalence of particular weather types or patterns over individual seasons. For the first time, the performance of a terrestrial biological system has been linked to changes in the position of the Gulf Stream in the North Atlantic. Although the precise mechanism linking the ocean current and vegetation dynamics remains unclear, it is now apparent that relationships can be demonstrated between terrestrial, marine and freshwater biological systems and Gulf Stream northerliness.

In Part 2 of the thesis a number of predictions were made, based upon the Bibury field observations, about how five selected species would behave when subjected to 'artificial weather' under controlled experimental conditions. Those predictions were, in the main, fulfilled. Where predictions were not fulfilled, logical explanations could be provided. As a result, precise mechanisms can be suggested to account for the observed field responses of species to weather.

Despite much individual variation in the response of species to different weather variables, a model has been suggested that relates the performance of plant functional types to settled or unsettled seasons. The experimental results verify that model. The experimental results also provide a valuable insight into the potential effects of weather on plant community dynamics and the relative competitive ability of potential vegetation dominants and subordinates. In addition, previous work on the possible relationship between species' nuclear DNA content and frost sensitivity has been supported. Moreover, the potential competitive advantage of species with low nuclear DNA content over those with high nuclear DNA content under unusually warm conditions early in the year has been clearly demonstrated.

REFERENCES

Adams, J. M. & Woodward, F. I. (1992) The past as a key to the future: the use of palaeoenvironmental understanding to predict the effects of Man on the biosphere. *Advances in Ecological Research,* **22**, 257-314.

Aebisher, N. J., Coulson, J. C. & Colebrook, J. M. (1988) Parallel long-term trends across four marine trophic levels and weather. *Nature,* **347**, No 6295, pp 753-755.

Alberch, M. & Corcuera, L. J. (1991) Cold acclimation in plants. Review article No 62. *Phytochemistry* **30,** 3177-3184.

Austen, M. P., Fresco, L. f. M., Nicholls, A. O., Groves, R. H. & Kaye, P. E. (1988) Competition and Relative Yield Estimation and Interpretation at Different Densities and Under Various Nutrient Concentrations using *Silybum marianum* and *Cirsium vulgare*. *Journal of Ecology* **76,** 157-171.

Beddows, A. R. (1959) Biological Flora of the British Isles. *Dactylis glomerata* L. *J.Ecol.* **47**, 223-239.

Bennett, M. D. (1976) DNA amount, latitude and crop plant distribution. *Environmental and Experimental Botany,* **16**, 93-108

Berendse, F., Elberse, W. & Geerts, R. H. M. E. (1992) Competition and Nitrogen Loss from Plants in Grassland Ecosystems. *Ecology* **73,** 46-53.

Bergh, J. P. van den. (1979) Changes in the composition of mixed populations of grassland species. In *The Study of Vegetation.* Ed. M. J. A. Werger. Dr. W. Junk bv Publishers, The Hague.

Bostock, S. J. & Benton, R. A. (1979) The reproductive strategies of five perennial Compositae. *Journal of Ecology,* **67**, 91-107.

Buckland, S. M (1994) *An investigation into the response of limestone grassland to climatic manipulation and species introductions.* PhD thesis, The University of Sheffield, UK.

Burroughs, W, J. (1992) Weather Cycles: Real or Imaginary? Cambridge University Press. Cambridge.

Campbell, B D., Grime, J. P., Mackey, J. M. L. & Jalili, A. (1991) The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. *Functional Ecology,* **5**, 241-253.

Cane, M. A., Eshel, G. and Buckland, R. W. (1994) Forecasting Zimbabwean Maize Yield Using Eastern Equatorial Pacific Sea Surface Temperature. *Nature* **370**, 204-205.

Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1985) *Excursion Flora of the British Isles (3rd Edition).* Cambridge University Press.

Clark, S. J., Tatchell, G. M., Perry, J. N., & Woiwood, I. P. (1992) Comparative Phenologies of Two Migrant Cereal Aphids. *Journal of Applied Ecology,* **92**, 571-580.

CCIRG (1991) *The potential effects of climate change in the United Kingdom. First report of the UK Climate Change Impacts Review Group.* HMSO, London.

Cushing, D. H and Dickson, P. F. (1976) The Biological Response in the Sea to Climatic Changes. *Advances in Marine Biology* **14**, 1-22.

Davies, W. (1938). Vegetation of Grass Verges and Other Excessively Trodden Habitats. *Journal of Ecology* **26**, 38-49.

Dodd, M. E., Silvertown, J., McConway, K., Potts, J. & Crawley, M. (1994a) Stability in the plant communities of the Park Grass Experiment: the relationships between species richness, soil pH and biomass variability. *Philosophical Transactions of the Royal Society, London,* **346**, 185-193.

Dodd, M. E., Silvertown, J., McConway, K., Potts, J. & Crawley, M. (1994b) Application of the British National Vegetation Classification to the communities of the Park Grass Experiment through time. *Folia Geobotanica et Phytotaxonomica, Praha,* **29**, 321-334.

Dodd, M. E., Silvertown, J., McConway, K., Potts, J. & Crawley, M. (1995) Community stability: a 60-year record of trends and outbreaks in the occurrence of species in the Park Grass Experiment. *Journal of Ecology,* **83**, 277-285.

Fitter, A. H., Fitter, R. S. R., Harris, I. T. B. & Williamson, M. H. (1995) Relationships between first flowering date and temperature in the flora of a locality in Central England. *Functional Ecology,* **9**, 55-60.

Freund, J. E. (1988) *Modern Elementary Statistics.* Prentice Hall. New Jersey.

Gamble, J. C.(1994) Long-term Planktonic Time Series as Monitors of Marine Environmental Change. In: Leigh, R.A and Johnston, A.E.(eds) Long-term Experiments in Agricultural and Ecological Sciences. CAB International Oxford.

George, D. G., Hewitt, D. P., Lund, J. W. G. & Smyly, W. J. P. (1990) The relative effects of enrichment and climate change on the long-term dynamics of *Daphnia* in Esthwaite Water, Cumbria. *Freshwater Biology,* **23**, 55-70.

George, D. G. and Taylor, A. H. (1995) UK lake plankton and the Gulf Stream.*Nature* , **378**, 139.

Goldberg, D. E., & Turner, R. M. (1986) Vegetation changes and plant demography in permanent plots in the Sonoran Desert. *Ecology,* **67**, 695-712.

Greig-Smith, P. (1983) *Quantitative Plant Ecology.* Blackwell Scientific Publications. Oxford.

Grime, J. P. (1974) Vegetation classification by reference to strategies. *Nature,* **250,** 26-31.

Grime, J. P. (1979) *Plant Strategies and Vegetation Processes.* John Wiley & Sons. Chichester.

Grime, J. P. (1989) Ecological effects of climate change on plant populations and vegetation composition with particular reference to the British flora. In *Climate Change and Plant Genetic Resource.* (eds M. Jackson, B. V. Ford-Lloyd & M. L. Parry). Belhaven Press, London.

Grime, J. P. (1990) The impact of climate change on British vegetation. In *The Greenhouse Effect: Consequences for Britain.* Ed. R.W. Battarbee & S. T. Patrick. ENSIS Publishing, London.

Grime, J. P. & Mowforth, M. A. (1982) Variation in genome size: an ecological interpretation. *Nature* **299**, 151-153.

Grime, J. P., Hodgson, J. E. & Hunt, R. (1988) *Comparative Plant Ecology.* Unwin Hyman, London.

Grime, J, P., Willis, A, J., Hunt, R. & Dunnett, N, P. (1994) Climate-Vegetation Relationships in the Bibury Road Verge Experiments. In *Long Term Experiments in Agricultural and Ecological Sciences.* Ed. Leigh, R, A. & Johnston, A. E. CAB International, Wallingford.

Grubb, P. J. (1982) Control of Relative Abundance in Roadside *Arrhenatheretum*: Results of a Long-Term Garden Experiment. *Journal of Ecology* **70,** 845-861.

Harberd, D. J. (1961) Observations on Population Structure and Longevity of *Festuca rubra. New Phytologist* **60,** 184-206.

Hays, G.C., Carr, M. R. & Taylor, A. H.. (1993) The Relationship between Gulf Stream Position and Copepod Abundance Derived from the Continuous Plankton Recorder Survey: Separating Biological Signal from Sampling Noise. *Journal of Plankton Research,* **15,** vol 12 1359-1373.

Heide, O. M. (1986) Long Day Control of Flowering in *Poa nemoralis* in Controlled and Natural Environments. *New Phytologist,* **104.** 225-232.

Hendry, G. A. F. (1987) The ecological significance of frunctan in a contemporary flora. *New Phytologist,* **106** (Suppl.), 210-216.

Hillier, S. H., Sutton, F. & Grime, J. P. (1994) A new technique for the experimental manipulation of temperature in plant communities. *Functional Ecology* **8,** 755-758.

Hodgson, J. G. & Grime, J. P. (1989) Effects of the mild winter of 1988/89 on an herbaceous flora in Central England: a test of some predictions. In *The Mild Winter 1988/89* (ed. M. G. R. Cannel). Department of the Environment, HMSO, London.

Hubbard, C. E. (1984) *Grasses. A Guide to Their Structure, Identification, Uses and Distribution in the British Isles.* Penguin, London.

Hulle, M., Coquio, S. & Laperche, V. (1994) Patterns in Flight Phenology of a Migrant Aphid Species. *Journal of Applied Ecology,* **31.** 49-58.

Hunt, R (1990) *Basic Growth Analysis.* Unwin Hyman, London.

Hunt, R., Hope-Simpson, J. F. & Snape, J. B. (1985) Growth of the Dune Wintergreen (*Pyrola rotundifolia* ssp. *maritima*) at Braunton Burrows in relation to weather factors. *International Journal of Biometeorology,* **29**, 323-334.

Hunt, R., Willis, A, J., Ward, L, K., Grime, J, P., Hodgson, J, G., Dunnett, N, P., Sutton, F., Band, S.& Neal, A, M. (1992) *Vegetation and Climate: A Thirty-Five Year Study in Road Verges at Bibury, Gloucestershire, and a Twenty-One Year Study in Chalk Grassland at Aston Rowant, Oxfordshire.* Contract Report to Nuclear Electric.

Johnston, A. E. (1994) The Rothamsted Classical Experiments. In *Long Term Experiments in Agricultural and Ecological Sciences.* Ed. Leigh, R, A. & Johnston, A. E. CAB International, Wallingford.

Jones, P. D., Hulme, H. & Brifta, K. R. (1993) A Comparison of Lamb Circulation Types with an Objective Classification Scheme. *International Journal of Climatolog,.* **13**, 655-663.

Jones, P. D. & Kelly, P. M.(1982) Principal Component Analysis of the Lamb Catalogue of Daily Weather types, Part 1, Annual Frequencies. *Journal of Climatology,* **2**, 147-157.

Kumar, V. & Irvine, D (1971). Germination of Seeds of *Cirsium arvense. Weed Research* **11,** 200-203.

Lamb, H. H. (1964) *The English Climate.* The English Universities Press, London.

Lamb, H. H. (1970) Our changing climate. In *The Flora of a Changing Britain.* Ed. F. Perring. E. W. Classey, Farringdon.

Lamb, H. H. (1972) British Isles Weather types and a Register of the Daily Sequence of Circulation Patterns 1871-1971. *Met.Office.Geophysical Memoirs,* **116.**

Lawes, J. B. & Gilbert, J. H. (1880) Agricultural, botanical and chemical results of experiments on the mixed herbage of permanent meadow, conducted for more than twenty years in succession on the same land. Part II. The botanical results. *Philosophical Transactions of the Royal Society,* **171**, 289-415.

Legendre, P. (1993) Spatial Autocorrelation: Trouble or New Paradigm? Ecology, **74**, 1659-1673.

Levitt, J. (1972) *Responses of Plants to Environmental Stresses.* Academic Press, New York.

Luken, J. O. (1990) Gradual and episodic changes in the structure of *Rhus typhina* clones. *Bulletin of the Torrey Botanical Club* **117**, 221-225.

Maberly, S. C., Reynolds, C. S., George, D. G., Haworth, E. Y. & Lund, J. W. G. (1994) The sensitivity of freshwater planktonic communities to environmental change: monitoring, mechanisms and models. In *Long Term Experiments in Agricultural and Ecological Sciences.* Ed. Leigh, R, A. & Johnston, A. E. CAB International, Wallingford.

MacGillivray, C.W (1993) Extreme climatic events and plant community structure. PhD Thesis. University of Sheffield

Macgillivray, C. W. & Grime, J. P. (1995) Genome size predicts frost resistance in British herbaceous plants: implications for rates of vegetation response to global warming. *Functional Ecology* **9**, 450-460

Mahmoud, A. & Grime, J. P. (1976) An analysis of the competitive ability in three perennial grasses. *New Phytol.,* **77**, 431-435.

Meteorological Office (1956-1992) Monthly Weather Report. HMSO.

Moore, R. J. (1975) The Biology of Canadian Weeds. *Cirsium arvense. Canadian Journal of Plant Science* **55**, 1033-1048.

Musk, L. (1988) *Weather Systems.* Cambridge University Press, Cambridge.

Noble, I. R. (1977) Long-term biomass dynamics in an arid chenopod shrub community at Koonamore, South Australia. *Australian Journal of Botany*, **25**, 639-653.

O'Connor, T. G. & Roux, P. W. (1995) Vegetation changes (1949-71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology,* **32**, 612-626.

Olff, H. & Bakker, J. P. (1991) Long term dynamics of standing crop and species composition after the cessation of fertiliser application to mown grassland. *Journal of Applied Ecology,* **28**, 1040-1052.

Parr, T. W. & Way, J. M. (1988) Management of roadside vegetation: the long-term effects of cutting. *Journal of Applied Ecology,* **25**, 1073-1087.

Parry, M. (1992) The potential effect of climate changes on agriculture and land use. *Advances in Ecological Research,* **22**, 63 - 90.

Peach, W. S., Thompson, P. S. & Coulson, J. C. (1994) Annual and long-term variation in the survival rates of British Lapwings. *Journal of Animal Ecology,* **63**, 60-70.

Pindyck, R. S. & Rubibfield, D. L. (1981) *Econometric Models and Economic Forecasts.* McGraw-Hill Ltd, Tokyo.

Pollard. E. (1988) Temperature, Rainfall and Butterfly Numbers. *Journal of Applied Ecology,* **25**, 819-828.

Rich, T. C. G. & Woodruff, E. R. (1992) Recording bias in botanical surveys. *Watsonia,* **19**, 73-95.

Rind, D., Goldberg, R. & Ruedy, R. (1989) Change in climate variability in the 21st Century. *Climate Change,* **14**, 5-37.

Rodwell, J. S (1992) *British Plant Communities. Volume 3: Grasslands and Montane Communities.* Cambridge University Press, Cambridge.

Rosenzweig, C. (1994) Maize Suffers a Sea-Change. *Nature,* **370**, 175-176.

Silvertown, J. W. (1980) The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. *Journal of Applied Ecology,* **17**, 491-504.

Silvertown, J., Dodd, M. E., McConway, K., Potts, J. & Crawley, M. (1994) Rainfall, biomass variation and community composition in the Park Grass Experiment. *Ecology,* **75**, 2430-2437.

Smith, L. P. (1960) The Relation between weather and Meadow Hay Yields in England. *J. Brit. Grassland Soc.* **15**, 203-208.

Snaydon, R. W. (1991) Replacement or Additive Designs for Competition Studies? *Journal of Applied Ecology* **28**, 930-946.

Snaydon, R. W. (1994) Replacement and Additive Designs Revisited: Comments on the Review Paper by N. R. Sackville Hamilton. *Journal of Applied Ecology.* **31**, 784-786.

Sparks, T. H. & Carey, P. D. (1995) The responses of species to climate over two centuries: an analysis of the Marsham phenological record, 1736-1947. *Journal of Ecology,* **83**, 321-330.

Spiller, D. A. & Schoener, T. W. (1995) Long-term variation in the effect of lizards on spider density is linked to rainfall. *Oecologia,* **103**, 133-139.

Svensson, B. M., Carlsson, B. A., Karlsson, P. S. & Nordell, K. O. (1993) Comparative long-term demography of three species of *Pinguicula. Journal of Ecology,* **81**, 635-645.

Tamm, C. O. (1972) Survival and flowering of perennial herbs. III. The behaviour of *Primula veris* on permanent plots. *Oikos*, **23**, 159-166.

Taylor, A. H. & Stephens, J. A. (1980) Latitudinal Displacements of the Gulf Stream (1966 to 1977) and their Relation to Changes in Temperature and Zooplankton Abundance in the N.E.Atlantic. *Oceanologica Acta,* **3**, 145-149.

Taylor, A. H., Colebrook, J. M., Stephens, J. A. and Baker, N. G. (1992) Latitudinal Displacements of the Gulf Stream and the Abundance of Plankton in the North-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom.* **72**, 919-921.

Taylor, A. H. (1995) North-south Shifts of the Gulf Stream Ocean-atmospheric Interactions in the North Atlantic. *Quarterly Journal of the Royal Meteorological Society . Submitted*

Tilman, D., Dodd, M. E., Silvertown, J., Poulton, P. R., Johnston, A. E. & Crawley, M. J. (1994) The Park Grass Experiment: Insights from the most long-term ecological study. In *Long Term Experiments in Agricultural and Ecological Sciences.* Ed. Leigh, R, A. & Johnston, A. E. CAB International, Wallingford.

Thompson, K. & Baster, K. (1992) Establishment from seed of selected Umbelliferae in unmanaged grassland. *Functional Ecology,* **6**, 346-352.

Thorpe, P. C., Macgillivray, C. W. & Priestman, G. H. (1993) A portable device for the simulation of air frosts at remote field locations. *Functional Ecology* **7**, 503-505.

van den Bergh, J. P. & Elberse, W. Th. (1970) Yields of Monocultures and Mixtures of Two Grass Species Differing in Growth Habit. *Journal of Applied Ecology* **7**, 311-320.

van Cleve, K., Oechel, W. C. & Hom, J. L. (1990) Response of Black Spruce (*Picea mariana*) ecosystems to soil temperature modification in interior Alaska. *Canadian Journal of Forest Research,* **20**, 1530-1535.

van der Meijden, E. (1989) Mechanisms in plant population control. In *Toward a More Exact Ecology.* Ed. P. J. Grubb & J. B. Whittaker. Blackwell Scientific Publications, Oxford.

van der Woude, B. J., Pegtel, D. M. & Bakker, J. P. (1994) Nutrient limitation after long-term nitrogen fertiliser application in cut grasslands. *Journal of Applied Ecology* **31**, 405-412.

Veresoglou, D. S. & Fitter, A. H. (1984) Spatial and Temporal Patterns of Growth and Nutrient Uptake of Five Co-Existing Grasses. *Journal of Ecology* **75**, 259-272.

Volaire, F. (1995) Growth, carbohydrate reserves and drought survival strategies of contrasting *Dactylis glomerata* populations in a Mediterranean environment. *Journal of Applied Ecology*, **32**, 56-66.

Wakamiya, I., Newton, R. J., Johnston J. S. & Price, H. J. (1993) Genome size and environmental factors in the genus *Pinus*. *American Journal of Botany*, **80**, 1235-1241.

Wallen, C., C. (1970) Climates of Northern and Western Europe. Elsevier Publishing Company.

Ward, L (1990) Ecological Impacts: Invertebrates. In *A hot, dry summer (1989) and mild, wet winter (1989/90)* NERC review for the Department of the Environment (ed. M. G. R. Cannell). ITE. Edinburgh.

Warwick, S. I. & Black, L. (1982). The Biology of Canadian Weeds. *Achillea millefolium*. *Canadian Journal of Plant Science* **62**, 163-182.

Watt, A. S. (1971) Factors controlling the floristic composition of some plant communities in Breckland. In *The Scientific Management of Animal and Plant Communities for Conservation*. The 11th Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Wigley, T. M. L., Huckstep, N. J., Ogilvie, A. E. J., Farmer, G., Mortimer, R. and Ingram, M. J. (1985) Historical Climate Impact Assessments. In *Climate Impact Assessment* Eds Kates, R. W., Ausubel, J. H. and Berberian, M. John Wiley & Sons.

Willis, A. J. (1970) The use of chemicals in the management of vegetation: long-term studies of the effects of spray treatments. In *Roadside Verges in Scotland: Their function and management.* Ed J. M. Way. Nature Conservancy Council (Scotland). Edinburgh.

Willis, A. J. (1972) Long-term ecological changes in sward composition following application of Maleic Hydrazide and 2, 4-D. *Proceedings 11th British Weed Control Conference,* 360-367.

Willis, A. J. (1988) The effects of growth retardant and selective herbicide on roadside verges at Bibury, Gloucestershire, over a thirty-year period. *Aspects of Applied Biology,* **16**, 19-26.

Willis, A. J., Folkes, B. F., Hope-Simpson, J. F. & Yemm, E. W. (1959) Braunton Burrows: the dune system and its vegetation. Part 1. *Journal of Ecology,* **47,** 1-24.

Willis, A. J. & Yemm, E. W. (1966) Spraying of roadside verges: long-term effects of 2, 4-D and Maleic Hydrazide. *Proceedings 8th British Weed Control Conference,* 2, 505-510.

Willis, A. J., Dunnett, N. p., Hunt, R. & Grime, J. P. (1995) Does Gulf Stream position affect vegetation dynamics in Western Europe? *Oikos* **73**, 408-410.

Woiwood, I. P. & Harrington, R. (1994) Flying in the Face of Change: The Rothamsted Insect Survey. In *Long Term Experiments in Agricultural and Ecological Sciences.* Ed. Leigh, R, A. & Johnston, A. E. CAB International, Wallingford.

Woodward, F. I. (1992) Predicting plant responses to global environmental change. Tansley Review No 41. *New Phytologist,* **122**, 239-251.

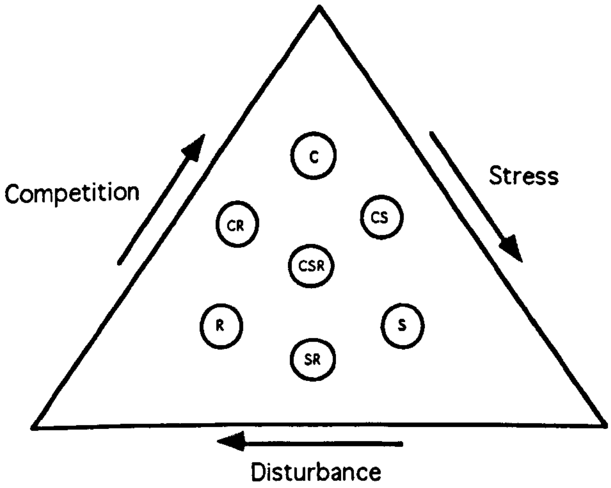
Yemm, E. W. & Willis, A. J. (1962) The effects of Maleic Hydrazide and 2, 4-Dichlorophenoxyacetic acid on roadside vegetation. *Weed Research*, **2**, 24-40.

APPENDIX 1

Established plant strategies (sensu Grime, 1979)

Grime (1979) identifies two factors which limit the accumulation of biomass: 'stress', which constrains the rate and extent of growth, and 'disturbance', which results directly in the destruction of biomass. Stressed habitats are exploited by plants described as 'stress-tolerators' which are generally slow-growing, long-lived evergreen species which are capable of survival for long periods under conditions not conductive to growth. By contrast, in frequently disturbed fertile habitats 'ruderals' prevail. Such plants are rapid growing and short lived. They produce flowers and seeds at an early stage of development. Where there is an abundance of resources and the intensity of disturbance is low (i.e where conditions for plant growth are close to optimal), a third group of species, 'competitors' are found. These large, fast growing species tend to monopolise the available resources leading to the competitive exclusion of most other potential components of the vegetation. In addition to these three primary plant strategies a number of intermediate strategies may be recognised and these are shown positioned on a triangular diagram in Figure 13.1.

Figure 13.1 **Plant Strategies *sensu* Grime (1979).** The three primary strategies (competitor (C), ruderal (R) and stress-tolerator (S)) together with four intermediate strategies (competitive ruderal (CR), sress-tolerant ruderal (SR), stress-tolerant competitor (SC) and C-S-R strategist (CSR) are positioned in a triangular diagram.



This triangular diagram is employed in the thesis to illustrate plant functional type responses to weather at Bibury. Because the are no stress-tolerant ruderals in the vegetation at Bibury, this intermediate strategy has been omitted from the diagrams in the text.

APPENDIX TWO

Summary tables of correlations between Bibury taxa and individual weather variables:

Minimum Temperature

Maximum Temperature

Rainfall (Total)

Rainfall (Days)

Sunshine

Key

P = Positive correlation
N = Negative correlation

Au, Wi, Sp and Su = autumn, winter, spring and summer respectively.

AW and SS = autumn and winter combined, and spring and summer combined respectively.

0 = correlations between plant performance and weather in the 12 months preceding vegetation recording.

1 = correlations between plant performance and weather in the next to previous year before vegetation recrding.

2 = correlations between plant performance two years previous to vegetation recording

MINIMUM TEMPERATURE Series 1-6	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0	AW2	SS2	AW1	SS1	AW0	SS0
litter			N															
Bare Ground															P			
Achillea millefolium																		
Agrostis stolonifera			P				P						P					
Alopecurous pratensis																		
Anisantha sterilis																		
Anthriscus sylvatica																		
Arrhenatherum elatius											P							P
Avenula pubescens																		
Brachypodium pinnatum																		
Bromopsis erecta	P					N				N					N		N	
Centauria nigra																		
Cirsium arvense				N				N	N									
Convolvulus arvensis							P											
Cruciata laevipes																		
Dactylis glomerata		N		N							P		N					P
Elytrigia repens	N																	
Festuca arundinacea								P								P		
Festuca rubra						N				N					N			
Galium aparine												N						
Galium verum										N							N	
Glechoma hederacea		N		N					N				N		N			
Heracleum sphondylium																		
Hypericum perforatum																		
Knautia arvensis																		
Lolium perenne																		
Odontites verna			P															
Phleum bertolonii	N					P												
Plantago lanceolata																		
Poa pratensis																		
Potentilla reptans																		
Ranunculus repens				N							P							
Rumex sp	N	P				P												
Stachys sylvatica										P								
Taraxacum officinale											P							
Tragopogon pratensis																		
Trifolium pratense																		
Trifolium repens																		
Trisetum flavescens																		
Ulmus glabra																		
Urtica dioica																		
Veronica chamaedrys							P											
Vicia sativa																		
Viola hirta																		

MINIMUM TEMPERATURE Series 7-8																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter			P																
Bare Ground															N				
Achillea millefolium																			
Agrostis stolonifera						P													
Alopecurous pratensis																			
Anisantha sterilis																			
Anthriscus sylvatica																			
Arrhenatherum elatius							N												
Avenula pubescens																			
Brachypodium pinnatum																			
Bromopsis erecta			P	P					N						P				
Centauria nigra																			
Cirsium arvense															P				
Convolvulus arvensis		P												P					
Cruciata laevipes		N																	
Dactylis glomerata											P								
Elytrigia repens		P						P						P					
Festuca arundinacea																			
Festuca rubra						P						P				P			P
Galium aparine																			
Galium verum															N				
Glechoma hederacea											P								P
Heracleum sphondylium	N	N				N					P			N		N			
Hypericum perforatum																			
Knautia arvensis																			
Lolium perenne											P								P
Odontites verna																			
Phleum bertolonii																			
Plantago lanceolata			P	P											P				
Poa pratensis																			
Potentilla reptans											P								P
Ranunculus repens			N				P		N						P		P		
Rumex sp						P										P			
Stachys sylvatica										P								P	
Taraxacum officinale			P																
Tragopogon pratensis																			
Trifolium pratense																			
Trifolium repens																			
Trisetum flavescens																			
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys		P												P					
Vicia sativa		P									P			P					P
Viola hirta																			

MAXIMUM TEMPERATURE Series 1-6	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter																			
Bare Ground																			
Achillea millefolium			P				P												
Agrostis stolonifera																			
Alopecurous pratensis	P								N										
Anisantha sterilis																			
Anthriscus sylvatica																			
Arrhenatherum elatius									P		P								
Avenula pubescens																			
Brachypodium pinnatum																			
Bromopsis erecta						N				N									
Centauria nigra																			
Cirsium arvense				N						P									
Convolvulus arvensis							P												
Cruciata laevipes							P												
Dactylis glomerata		N		N				N			P				N				
Elytrigia repens																			
Festuca arundinacea																			
Festuca rubra						N										N			
Galium aparine												N							N
Galium verum																			
Glechoma hederacea		N		N		N								N	N	N			
Heracleum sphondylium																			
Hypericum perforatum																			
Knautia arvensis																			
Lolium perenne																			
Odontites verna							P										P		
Phleum bertolonii								P									P		
Plantago lanceolata									P										
Poa pratensis																			
Potentilla reptans																			
Ranunculus repens				N							P								
Rumex sp																			
Stachys sylvatica																			
Taraxacum officinale							P				P				P	P	P		
Tragopogon pratensis																			
Trifolium pratense																			
Trifolium repens																			
Trisetum flavescens																			
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys							P												
Vicia sativa																			
Viola hirta																			

MAXIMUM TEMPERATURE	Series 7-8																
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0	AW2	SS2	AW1	SS1	AW0	SS0
litter																		
Bare Ground													P					
Achillea millefolium				P														
Agrostis stolonifera																		
Alopecurous pratensis																		
Anisantha sterilis																		
Anthriscus sylvatica				-0.4								P						
Arrhenatherum elatius																		
Avenula pubescens									N		N							N
Brachypodium pinnatum																		
Bromopsis erecta																		
Centauria nigra																		
Cirsium arvense																		
Convolvulus arvensis		P			N		N											
Cruciata laevipes		N										N						
Dactylis glomerata											P							
Elytrigia repens		P																
Festuca arundinacea																		
Festuca rubra						P					P	P			P			P
Galium aparine																		
Galium verum							N											
Glechoma hederacea										P	P						P	P
Heracleum sphondylium											P		N					
Hypericum perforatum																		
Knautia arvensis			P				P							P				
Lolium perenne																		
Odontites verna																		
Phleum bertolonii																		
Plantago lanceolata			P															
Poa pratensis			N															
Potentilla reptans			P								P							P
Ranunculus repens									N									
Rumex sp						P								P	P			
Stachys sylvatica																		
Taraxacum officinale			P															
Tragopogon pratensis																		
Trifolium pratense				P														P
Trifolium repens																		
Trisetum flavescens																		
Ulmus glabra																		
Urtica dioica																		
Veronica chamaedrys	P	P	P										P	P	P			
Vicia sativa		P									P		P					
Viola hirta																		

TOTAL RAINFALL Series 1-6																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter																			
Bare Ground						P													
Achillea millefolium																			
Agrostis stolonifera																			
Alopecurous pratensis														N					
Anisantha sterilis																			
Anthriscus sylvatica																			
Arrhenatherum elatius																			
Avenula pubescens																			
Brachypodium pinnatum																			
Bromopsis erecta																			
Centauria nigra																			
Cirsium arvense											N								
Convolvulus arvensis																			
Cruciata laevipes																			
Dactylis glomerata				P															
Elytrigia repens			N																
Festuca arundinacea			P						P										
Festuca rubra							P												
Galium aparine																			
Galium verum																			
Glechoma hederacea									N										
Heracleum sphondylium																			
Hypericum perforatum		N																	
Knautia arvensis																			
Lolium perenne																			
Odontites verna																			
Phleum bertolonii																			
Plantago lanceolata																			
Poa pratensis	N																		
Potentilla reptans																			
Ranunculus repens																			
Rumex sp																			
Stachys sylvatica																			
Taraxacum officinale																			
Tragopogon pratensis																	N		
Trifolium pratense																			
Trifolium repens																			
Trisetum flavescens	N																		
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys																			
Vicia sativa			P												P				
Viola hirta							P												

TOTAL RAINFALL Series 7-8																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
Litter																			
Bare Ground																			
Achillea millefolium															N				
Agrostis stolonifera			P																
Alopecurous pratensis																			
Anisantha sterilis																			
Anthriscus sylvatica												N							
Arrhenatherum elatius																			
Avenula pubescens																			
Brachypodium pinnatum																			
Bromopsis erecta														N					
Centauria nigra																			
Cirsium arvense								P				N							
Convolvulus arvensis	P		N																
Cruciata laevipes			N																
Dactylis glomerata																			
Elytrigia repens																			
Festuca arundinacea											N								
Festuca rubra	N							N											
Galium aparine																			
Galium verum																			
Glechoma hederacea	N										P								
Heracleum sphondylium						N													
Hypericum perforatum																			
Knautia arvensis																			
Lolium perenne																			
Odontites verna																			
Phleum bertolonii																			
Plantago lanceolata																			
Poa pratensis																			
Potentilla reptans																			
Ranunculus repens																			
Rumex sp																	N		
Stachys sylvatica																			
Taraxacum officinale																			
Tragopogon pratensis																			
Trifolium pratense			N																
Trifolium repens																			
Trisetum flavescens																			
Ulmus glabra																			
Urtica dioica				N															
Veronica chamaedrys																			
Vicia sativa															N				
Viola hirta																			

RAINFALL (DAYS) Series 1-6	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter																			
Bare Ground																			
Achillea millefolium																			
Agrostis stolonifera																			
Alopecurous pratensis																			
Anthriscus sylvatica																			
Arrhenatherum elatius																			
Brachypodium pinnatum																			
Bromopsis erecta											P								P
Anisantha sterilis				N		P									N				
Centauria nigra																			
Cirsium arvense				P	N							P							
Convolvulus arvensis																			
Dactylis glomerata				P											P				
Elytrigia repens																			
Festuca arundinacea								N											
Festuca rubra																	P		
Galium aparine																			
Cruciata laevipes																			
Galium verum																			
Glechoma hederacea		N				N													
Heracleum sphondylium																			
Avenula pubescens																			
Hypericum perforatum		N																	
Knautia arvensis												P							
Lolium perenne																			
Odontites verna																			
Phleum bertolonii																			
Plantago lanceolata																			
Poa pratensis																			
Potentilla reptans																			
Ranunculus repens				P	N										P				
Rumex sp																			
Stachys sylvatica																			
Taraxacum officinale												P							
Tragopogon pratensis																			
Trifolium pratense																			
Trifolium repens								P									P		
Trisetum flavescens															N		P		
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys																			
Vicia sativa			P																
Viola hirta																			

RAINFALL (DAYS) Series 7-8																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter																		N	
Bare Ground						P													
Achillea millefolium				N	P														
Agrostis stolonifera														N					
Alopecurous pratensis																			
Anthriscus sylvatica																			
Arrhenatherum elatius		P																	
Brachypodium pinnatum																			
Bromopsis erecta																			
Anisantha sterilis																			
Centauria nigra			N												N			N	
Cirsium arvense				N								N							
Convolvulus arvensis	P																		
Dactylis glomerata				P								P							
Elytrigia repens																			
Festuca arundinacea																			
Festuca rubra																			
Galium aparine																			
Cruciata laevipes											P								
Galium verum							P												
Glechoma hederacea																			
Heracleum sphondylium						N													
Avenula pubescens											P								
Hypericum perforatum																			
Knautia arvensis		N																	
Lolium perenne																			
Odontites verna																			
Phleum bertolonii																			
Plantago lanceolata																			
Poa pratensis																			
Potentilla reptans																			
Ranunculus repens																			
Rumex sp																	N		
Stachys sylvatica																			
Taraxacum officinale			N																
Tragopogon pratensis		P																	
Trifolium pratense				P															
Trifolium repens					N	P													
Trisetum flavescens																			
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys							N								N				
Vicia sativa			N																
Viola hirta																			

SUNSHINE Series 1-6																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter												P							P
Bare Ground																			
Achillea millefolium																			
Agrostis stolonifera						N													
Alopecurous pratensis		N																	
Anisantha sterilis																			
Anthriscus sylvatica						N													
Arrhenatherum elatius																			
Avenula pubescens																			
Brachypodium pinnatum																			
Bromopsis erecta												N							N
Centauria nigra																			
Cirsium arvense			P						P										
Convolvulus arvensis											P								
Cruciata laevipes																			
Dactylis glomerata				N															
Elytrigia repens			P																
Festuca arundinacea																		N	
Festuca rubra																			
Galium aparine																			
Galium verum																			
Glechoma hederacea																			
Heracleum sphondylium																			
Hypericum perforatum																			
Knautia arvensis																			
Lolium perenne																			
Odontites verna							P							P			P		
Phleum bertolonii							P										P		
Plantago lanceolata																			
Poa pratensis						N								P					
Potentilla reptans																			
Ranunculus repens		P																	
Rumex sp																			
Stachys sylvatica										N									
Taraxacum officinale																			
Tragopogon pratensis																			
Trifolium pratense			P																P
Trifolium repens																			
Trisetum flavescens																			
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys		P																	
Vicia sativa																			
Viola hirta																			

SUNSHINE Series 7-8	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter																			
Bare Ground																			
Achillea millefolium																			
Agrostis stolonifera						N				N									
Alopecurous pratensis																			
Anisantha sterilis																			
Anthriscus sylvatica				N								P							P
Arrhenatherum elatius																			
Avenula pubescens											N								
Brachypodium pinnatum																			
Bromopsis erecta																			
Centauria nigra																			
Cirsium arvense																			
Convolvulus arvensis												P							P
Cruciata laevipes									P		N								N
Dactylis glomerata		P																	
Elytrigia repens		N										P		N					P
Festuca arundinacea																			
Festuca rubra																			
Galium aparine																			
Galium verum																			
Glechoma hederacea														N					
Heracleum sphondylium																			
Hypericum perforatum																			
Knautia arvensis							P												
Lolium perenne		N																	
Odontites verna																			
Phleum bertolonii									P										
Plantago lanceolata						N										N			
Poa pratensis									N	N								N	
Potentilla reptans														P					
Ranunculus repens						N										N		N	
Rumex sp				P			P	P							P		P		
Stachys sylvatica																			
Taraxacum officinale												P							
Tragopogon pratensis																			
Trifolium pratense																			
Trifolium repens																			
Trisetum flavescens																			
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys			P												P				
Vicia sativa			P	P											P				
Viola hirta																			

APPENDIX THREE

Summary tables of correlations between primary functional types and individual weather variables:

Minimum Temperature

Maximum Temperature

Rainfall (Total)

Rainfall (Days)

Sunshine

P = Positive correlation

N = Negative correlation

	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
MAXIMUM TEMPERATURE																			
Series 1-6																			
Total shoot biomass											P								
CR									P		P								
C											P								
S							P												
SC						N				N									
R																			
CSR																			
MAXIMUM TEMPERATURE																			
Series 7-8																			
Total shoot biomass		N										N		N					
CR	N		N											N					
C																			
S			P												P				
SC																			
R																			
CSR																			
MINIMUM TEMPERATURE																			
Series 1-6																			
Total shoot biomass											P								P
CR											P								P
C											P								N
S							P										P		
SC	P					N				N						N		N	
R												N							
CSR																			
MINIMUM TEMPERATURE														P					
Series 7-8																			
Total shoot biomass		N									P			N					
CR			N						P										
C	P				P		N												
S																			
SC									N										
R																			
CSR											P								P

	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
TOTAL RAINFALL																			
Series 1-6																			
Total shoot biomass																			P
CR																			
C				P															
S																			
SC																			P
R																			
CSR																			P
TOTAL RAINFALL																			
Series 7-8																			
Total shoot biomass			P								P	P							P
CR			P																
C																			
S																			
SC						N													
R																			
CSR																			
Rainfall (days)																			
Series 1-6																			
Total shoot biomass												P							P
CR																			
C				P											P				
S																			
SC																			P
R				N													N		
CSR											P								P
Rainfall (days)																			
Series 7-8																			
Total shoot biomass																			P
CR																			
C																			
S															N				
SC							P												
R																			
CSR								P											

SUNSHINE SERIES 1-6	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
TOTAL SHOOT BIOMASS																			
CR							P												
C																			
S														P					
SC												N							N
R																			
CSR																			N
SUNSHINE SERIES 7-8																			
TOTAL SHOOT BIOMASS												N							N
CR																			
C																			
S			P	P											P				
SC						N	N			N						N			
R			P																
CSR										N									

APPENDIX FOUR

Summary tables of correlations between Bibury taxa and weather types

Anticyclonic

Cyclonic

Cyclonic and Westerly

P = Positive correlation

N = Negative correlation

FREQUENCY OF ANTICYCLONIC WEATHER Series 1-6																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter										P									P
Bare Ground			P																P
Achillea millefolium												N							N
Agrostis stolonifera																			
Alopecurous pratensis		P												P					P
Anisantha sterilis				P															
Anthriscus sylvatica																			
Arrhenatherum elatius																			
Avenula pubescens																			
Brachypodium pinnatum																			
Bromopsis erecta											N	N							N
Centauria nigra																			
Cirsium arvense					P														P
Convolvulus arvensis																			
Dactylis glomerata				N											N		N		
Elytrigia repens																			
Festuca arundinacea								P				P					N		N
Festuca rubra																			
Galium aparine																			
Galium cruciata						P									N	P			P
Galium verum																			
Glechoma hederacea															N				N
Heracleum sphondylium																			
Hypericum perforatum																			
Knautia arvensis																			
Lolium perenne																			
Odontites verna																P			P
Phleum bertolonii																	P		P
Plantago lanceolata																			
Poa pratensis						P													P
Potentilla reptans																			
Ranunculus repens					P										N				P
Rumex sp				P											P		P	N	
Stachys sylvatica																			
Taraxacum officinale											N								N
Tragopogon pratensis																			
Trifolium pratense																			
Trifolium repens																			
Trisetum flavescens					N														N
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys				N															
Vicia sativa					P														P
Viola hirta																			

FREQUENCY OF ANTICYCLONIC WEATHER Series 7-8																	
	AU2	**WI2**	**SP2**	**SU2**	**AU1**	**WI1**	**SP1**	**SU1**	**AU0**	**WI0**	**SP0**	**SU0**	**AW2**	**SS2**	**AW1**	**SS1**	**AW0**	**SS0**
litter													**P**				**P**	**P**
Bare Ground			**P**											**P**				**P**
Achillea millefolium																		**N**
Agrostis stolonifera																		
Alopecurous pratensis																		**P**
Anisantha sterilis																		
Anthriscus sylvatica																		
Arrhenatherum elatius																		
Avenula pubescens						**P**				**P**								
Brachypodium pinnatum																		
Bromopsis erecta				**P**											**P**			**N**
Centauria nigra										**P**								
Cirsium arvense		**P**		**P**														**P**
Convolvulus arvensis	**N**		**P**											**P**				
Dactylis glomerata									**N**								**P**	
Elytrigia repens								**P**										**P**
Festuca arundinacea																		**P**
Festuca rubra	**P**																	**P**
Galium aparine		**N**					**P**											
Galium cruciata			**N**				**P**											**P**
Galium verum													**N**		**N**			
Glechoma hederacea																		**N**
Heracleum sphondylium						**P**								**P**	**P**			
Hypericum perforatum												**P**						
Knautia arvensis																		
Lolium perenne					**N**												**N**	
Odontites verna																		**P**
Phleum bertolonii							**P**		**P**									**P**
Plantago lanceolata		**P**				**P**						**N**						
Poa pratensis																		**P**
Potentilla reptans										**P**							**P**	
Ranunculus repens						**P**												**P**
Rumex sp																		
Stachys sylvatica																		
Taraxacum officinale			**P**															**N**
Tragopogon pratensis																		
Trifolium pratense									**P**								**P**	
Trifolium repens																		
Trisetum flavescens																		**N**
Ulmus glabra																		
Urtica dioica																		
Veronica chamaedrys			**P**	**P**										**P**				
Vicia sativa						**P**											**P**	**P**
Viola hirta																		

FREQUENCY OF CYCLONIC WEATHER Series 1-6																				
		AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter																				
Bare Ground																				
Achillea millefolium															N					N
Agrostis stolonifera															N					N
Alopecurous pratensis		N													N					N
Anisantha sterilis					N				N							N				N
Anthriscus sylvatica																				
Arrhenatherum elatius																				
Avenula pubescens																				
Brachypodium pinnatum																				
Bromopsis erecta													P							P
Centauria nigra																				
Cirsium arvense																				
Convolvulus arvensis																				
Cruciata laevipes													P							P
Dactylis glomerata																				
Elytrigia repens																				
Festuca arundinacea										P										P
Festuca rubra					P				P											P
Galium aparine																				
Galium verum							N													N
Glechoma hederacea							N													N
Heracleum sphondylium																				
Hypericum perforatum			N																	
Knautia arvensis					P		N						P						P	P
Lolium perenne																				
Odontites verna												N					N			N
Phleum bertolonii																				
Plantago lanceolata													P							P
Poa pratensis																				
Potentilla reptans																				
Ranunculus repens																				
Rumex sp					N				N							N		N		N
Stachys sylvatica																				
Taraxacum officinale								N												N
Tragopogon pratensis																				
Trifolium pratense																				
Trifolium repens								P										0.356		P
Trisetum flavescens						P			P									P		P
Ulmus glabra												N								N
Urtica dioica									N											N
Veronica chamaedrys													P							P
Vicia sativa					P											P				P
Viola hirta				P				P								P				

FREQUENCY OF CYCLONIC WEATHER Series 7-8																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter			N		P														
Bare Ground		0.361																	
Achillea millefolium			N												N				N
Agrostis stolonifera																			N
Alopecurous pratensis																			N
Anisantha sterilis																			N
Anthriscus sylvatica																			
Arrhenatherum elatius		P		N		P													
Avenula pubescens											P								
Brachypodium pinnatum		N				N													
Bromopsis erecta		-0.39																	P
Centauria nigra			N			N									N				
Cirsium arvense						P						N							
Convolvulus arvensis	P																		
Cruciata laevipes											P								P
Dactylis glomerata				P														N	
Elytrigia repens																			
Festuca arundinacea																			P
Festuca rubra	N																		P
Galium aparine																			
Galium verum														P					N
Glechoma hederacea																			N
Heracleum sphondylium				P		N													
Hypericum perforatum																			
Knautia arvensis																			P
Lolium perenne					P						P								
Cdontites verna																			N
Phleum bertolonii																			
Plantago lanceolata									P										P
Poa pratensis																			
Potentilla reptans										N								N	
Ranunculus repens																			
Rumex sp																			N
Stachys sylvatica																			
Taraxacun officinale																			N
Tragopogon pratensis	N		N												N				
Trifolium pratense											N							N	
Trifolium repens																			P
Trisetum flavescens																			P
Ulmus glabra											N								N
Urtica dioica																			N
Veronica chamaedrys	N		N							N					N				P
Vicia sativa																			P
Viola hirta			P				P												

FREQUENCY OF CYCLONIC & WESTERLY WEATHER Series 1-6																				
		AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter																				
Bare Ground												N								N
Achillea millefolium																				
Agrostis stolonifera																				
Alopecurous pratensis																				
Anisantha sterilis					N				N							N		N		N
Anthriscus sylvatica																				
Arrhenatherum elatius																				
Avenula pubescens																				
Brachypodium pinnatum																				
Bromopsis erecta												P	P							P
Centauria nigra																				
Cirsium arvense						N														N
Convolvulus arvensis																				
Dactylis glomerata				P	P											P				
Elytrigia repens																				
Festuca arundinacea																				
Festuca rubra									P									P		P
Galium aparine																				
Galium cruciata													P		N	P				P
Galium verum									P											P
Glechoma hederacea							N	P												N
Heracleum sphondylium																				
Hypericum perforatum																				
Knautia arvensis													P							P
Lolium perenne																				
Odontites verna																				
Phleum bertolonii																				
Plantago lanceolata													P							P
Poa pratensis																				
Potentilla reptans																				
Ranunculus repens				P		N										P				
Rumex sp					N				N							N		N		N
Stachys sylvatica																				
Taraxacum officinale													P							P
Tragopogon pratensis																				
Trifolium pratense					P															P
Trifolium repens																				
Trisetum flavescens						P			P									P		P
Ulmus glabra																				
Urtica dioica									N											N
Veronica chamaedrys																				
Vicia sativa													P							P
Viola hirta																				

FREQUENCY OF CYCLONIC & WESTERLY WEATHER Series 7-8																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter																			
Bare Ground			N												N				N
Achillea millefolium				N											N				
Agrostis stolonifera																			
Alopecurous pratensis			P																
Anisantha sterilis																			N
Anthriscus sylvatica																			
Arrhenatherum elatius						P													
Avenula pubescens			P																
Brachypodium pinnatum																			
Bromopsis erecta																			P
Centauria nigra											P								
Cirsium arvense																			N
Convolvulus arvensis														P					
Dactylis glomerata				P											P				
Elytrigia repens																			
Festuca arundinacea																			
Festuca rubra																			P
Galium aparine																			P
Galium cruciata																			P
Galium verum																			P
Glechoma hederacea																			N
Heracleum sphondylium						N										N			
Hypericum perforatum																			
Knautia arvensis																			P
Lolium perenne																			
Odontites verna																			
Phleum bertolonii									N										
Plantago lanceolata												P							P
Poa pratensis																			
Potentilla reptans								P											
Ranunculus repens																			
Rumex sp																			N
Stachys sylvatica																			
Taraxacum officinale			N																P
Tragopogon pratensis			N																
Trifolium pratense																			P
Trifolium repens																			
Trisetum flavescens																			P
Ulmus glabra																			
Urtica dioica																			N
Veronica chamaedrys	N	P	N												N				
Vicia sativa																			P
Viola hirta																			

APPENDIX FIVE

Summary tables of correlations between primary functional types and weather types

Anticyclonic

Cyclonic

Cyclonic and Westerly

P = Positive correlation

N = Negative correlation

FREQUENCY OF ANTICYCLONIC WEATHER Series 1-6																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
TOTAL SHOOT BIOMASS																			
CR																			
C															N				N
S														N	N				N
SC												N							[illegible]
R				P															
CSR																			
FREQUENCY OF ANTICYCLONIC WEATHER Series 7-8																			
TOTAL SHOOT BIOMASS																			
CR																			
C																			
S										P									P
SC												N							N
R	P																		
CSR																			
FREQUENCY OF CYCLONIC WEATHER Series 1-6																			
	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
TOTAL SHOOT BIOMASS				P											P				
CR																			
C				P											P				
S												P		N					
SC					P							P							P
R								N											
CSR												P							P
FREQUENCY OF CYCLONIC WEATHER Series 7-8																			
TOTAL SHOOT BIOMASS																			
CR			P																
C			P			P													
S			N			N									N				
SC																			
R											N								
CSR																			

FREQUENCY OF CYCLONIC & WESTERLY																					
WEATHER Series 1-6																					
		AU2	**WI2**	**SP2**	**SU2**	**AU1**	**WI1**	**SP1**	**SU1**	**AU0**	**WI0**	**SP0**	**SU0**		**AW2**	**SS2**	**AW1**	**SS1**	**AW0**	**SS0**
TOTAL SHOOT BIOMASS				**P**									**P**			**P**				**P**
CR				**P**																
C				**P**	**P**								**P**			**P**				
S															**N**					**N**
SC												**P**	**P**							**P**
R					**N**				**N**							**N**		**N**		**N**
CSR													**P**							**P**
FREQUENCY OF CYCLONIC & WESTERLY																					
WEATHER Series 7-8																					
TOTAL SHOOT BIOMASS			**P**									**P**			**P**					**P**
CR																					
C																					
S											**P**									**P**
SC																					
R		**P**																			
CSR																					

APPENDIX SIX

Summary tables of correlations between Bibury taxa and Gulf Stream northerliness.

P = Positive correlation

N = Negative correlation

GULF STREAM NORTHERLINESS SERIES 1-6	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0	AW2	SS2	AW1	SS1	AW0	SS0
litter																		
Bare Ground				N				N				N		N		N		
Achillea millefolium			P									P						P
Agrostis stolonifera																		
Alopecurous pratensis		N	N										N	N				
Anisantha sterilis	N								N	N							N	
Anthriscus sylvatica																		
Arrhenatherum elatius																		
Avenula pubescens																		
Brachypodium pinnatum																		
Bromopsis erecta			P			P												
Centauria nigra																		
Cirsium arvense																		
Convolvulus arvensis																		
Cruciata laevipes					P					P			P					
Dactylis glomerata																		
Elytrigia repens			P											P				
Festuca arundinacea			N		N										N			
Festuca rubra					P													
Galium aparine																		
Galium verum										P					P			
Glechoma hederacea																		
Heracleum sphondylium																		
Hypericum perforatum																		
Knautia arvensis	P	P		P	P							P		P	P		P	P
Lolium perenne																		
Odontites verna																		
Phleum bertolonii								P										
Plantago lanceolata			P				P		P						P		P	
Poa pratensis																		
Potentilla reptans																		
Ranunculus repens																		
Rumex sp	N												N					
Stachys sylvatica																		
Taraxacum officinale			P			P	P					P						P
Tragopogon pratensis																		
Trifolium pratense																		
Trifolium repens																		
Trisetum flavescens																		
Ulmus glabra																		
Urtica dioica					N										N			
Veronica chamaedrys																		
Vicia sativa																		
Viola hirta																		

GULF STREAM NORTHERLINESS SERIES 7-8	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0		AW2	SS2	AW1	SS1	AW0	SS0
litter										P							P		
Bare Ground				N											N				
Achillea millefolium																			
Agrostis stolonifera																			
Alopecurous pratensis																			
Anisantha sterilis																			
Anthriscus sylvatica																			
Arrhenatherum elatius				N	N			N								N	N		
Avenula pubescens																			
Brachypodium pinnatum																			
Bromopsis erecta								N											
Centauria nigra							P			P									
Cirsium arvense		N	N											N	N				
Convolvulus arvensis									N										
Cruciata laevipes																			
Dactylis glomerata					P														
Elytrigia repens																			
Festuca arundinacea																			
Festuca rubra																			
Galium aparine																			
Galium verum											N								
Glechoma hederacea																			
Heracleum sphondylium												P							
Hypericum perforatum																			
Knautia arvensis	P					P					P					P		P	P
Lolium perenne																			
Odontites verna																			
Phleum bertolonii																			
Plantago lanceolata						P													
Poa pratensis										N									
Potentilla reptans										P	P								P
Ranunculus repens																			
Rumex sp						P						P							P
Stachys sylvatica	N			N											N				
Taraxacum officinale																			
Tragopogon pratensis																			
Trifolium pratense																			
Trifolium repens																			
Trisetum flavescens																			
Ulmus glabra																			
Urtica dioica																			
Veronica chamaedrys				N															
Vicia sativa		P						P											
Viola hirta							N												

APPENDIX Seven

Summary tables of correlations between primary functional types and Gulf Stream northerliness.

P = Positive correlation

N = Negative correlation

GULF STREAM NORTHERLINESS SERIES 1-6	AU2	WI2	SP2	SU2	AU1	WI1	SP1	SU1	AU0	WI0	SP0	SU0	AW2	SS2	AW1	SS1	AW0	SS0
Total shoot biomass				P		P								P	P			
CR																		
C																		
S																		
SC			P			P												
R					N			N										
CSR																		
SERIES 7-8																		
Total shoot biomass																		
CR					N		N			N				N				
C																		
S										P	P							
SC																		
R																		
CSR																		