COHABITATION OF SPECIES IN AN ARTIFICIAL, GRASS-LEGUME COMMUNITY ON WHISTLER MOUNTAIN

by

John D. Thompson

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APPROVAL

Name: John D. Thompson

Degree: Master of Science

Title of thesis: Cohabitation of Species in an Artificial, Grass-Legume Community on Whistler Mountain

Examining Committee:

Chairperson: R. Hayter

I. Hutchinson
Senior Supervisor

W.G. Bailey

R.W. Mathewes

R. Turkington
External Examiner
Associate Professor
Department of Botany
University of British Columbia

Date Approved: Sept. 5th 1984

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Cohabitation of Species in an Artificial, Grass-Legume

Community on Whistler Mountain

Author:

(signature)

John D. Thompson

(name)

September 13, 1984

(date)

ABSTRACT

The revegetation of ski-slopes on Whistler Mountain, B.C. was performed in 1980 by Whistler Mountain Ski Corporation, using a grass-legume seed mixture. The manner in which the seeded species cohabit in this artificial, developing community is examined with respect to the differential environmental tolerances and competitive abilities of the seeded species in a spatially heterogeneous environment.

A stratified random sampling procedure, combined with Analysis of Variance and Multiple Range Tests, was employed to examine species cover in relation to the large-scale gradients of altitude and slope angle, and small-scale gradients involving soil properties. Concomitantly, a very fine-scaled approach was performed using contact sampling and association analysis to quantify plant-plant contacts occurring within the sward, and the nature of any species associations.

The overall establishment of seeded species has been very satisfactory. Correlations of the abundance of the four major species, in relation to abiotic and biotic factors, suggest that cohabitation in this community is facilitated by differences in the realized niches of the species.

In the habitat classes favourable to plant growth, the productive species, *Festuca rubra* and *Trifolium hybridum*, preclude the establishment of the slower growing species, *Agrostis tenuis* and *Phleum pratense*. Decreasing productivity of the habitat appears to restrict the more productive species

which, combined with the greater tolerance of the less productive species, facilitates the growth of the latter. The variable growth strategy of _F. rubra_ facilitates its dominance in the community as a whole. The differential rooting habit of _P. pratense_ favours the development of positive associations between these two species, and enables it to maintain its percentage cover on shallow soils. Finally, the similarity in above ground form of _A. tenuis_ and _P. pratense_ encourages these species to be negatively associated in the more productive habitat classes where interference from other species, and between these two species, will be most intense. These effects are mitigated as the environment becomes less favourable for plant growth.

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TABLE OF CONTENTS

Approval ii

Abstract iii

Acknowledgments v

List of Tables ix

List of Figures x

CHAPTER 1 INTRODUCTION 1

1.1: The Underlying Question 1

1.2: Theoretical Background 2

1.3: Framework For Study 8

1.4: Choice Of Study Area 13

1.5: Objectives 17

1.6: Organization 17

CHAPTER 2 THE STUDY AREA 19

2.1: Introduction 19

2.2: Geology and Topography 19

2.3: Climate 21

2.4: Soils 23

2.5: Natural Vegetation 24

2.6: The Study Sites 25

CHAPTER 3 LITERATURE REVIEW 29

3.1: Introduction 29

3.2: Cohabitation: A Question Of Scale 30

3.3: Large Scale Variation 32

3.4: Localised Abiotic Variation 37

3.5: Species Interactions 42

3.6: Choice of Variables 50

CHAPTER 4 METHODS 52

4.1: Introduction 52

4.2: Data Collection 52

4.3: Vegetation Data Analysis 59

CHAPTER 5 RESULTS 67

5.1: Introduction 67

5.2: Overall Vegetation Cover 68

5.3: Large Scale Pattern 70

5.4: Soil Properties 87

5.5: Biotic Influences 103

CHAPTER 6 INTERPRETATION 114

6.1: Framework For Discussion 114

6.2: Large-Scale Pattern 115

6.3: Soil Properties 125

6.4: Timing Of Influence 131

6.5: Biotic Influences 134

6.6: Niche Differences 144

CHAPTER 7 CONCLUSIONS 147

Appendix 1: Altitude/Slope Angle ANOVA Tables 152

Appendix 2: Altitude/Slope Angle Multiple Range Tests 153

Appendix 3: Mulch/Slope Angle Comparison 161

Appendix 4: Altitude/Slope Angle ANOVA For Soil Calcium 164

Appendix 5: Soil Depth/Species Cover Comparison 166

Appendix 6: ANOVA Tables for % Flowering Data 169

Appendix 7: Probability Assumptions For The Association Analysis 172

Bibliography 173

LIST OF TABLES

TABLE PAGE

1 Climatic Data For Alta Lake Meteorological Station, (1951-80) 30 Year Mean Data 22

2 Change In Climate With Increasing Elevation For Cypress Mountain 22

3 Composition of the Seed Mixture 27

4 Comparison of Untransformed and Transformed Species Percentage Cover Data 62

5 Mean Species Cover (+/- SE), Altitude Classes 1-3 69

6 Relationship of Mean Percentage Cover (+/- SE) to Altitude and Slope Angle 72

7 Mean % Cover (+/- SE) in the Mulched Sites 84

8 Soil Analysis Results For Each Site 88

9 Mean Soil Depth (+/- SE) For Each Site 94

10 Mean Soil Depth (+/- SE) For Species Absence and Presence 96

11 Relationship Between Soil Depth and Mean Species Cover (+/- SE) 97

12 Overall Mean % Flowering Of Seeded Species (+/- SE) 104

13 Mean % Flowering of the Four Major Species in Relation to Altitude and Slope Angle 105

14 Count Matrix For Altitude Class 1 107

15 Count Matrix For Altitude Class 2 108

16 Count Matrix For Altitude Class 3 108

17 Count Matrix For The Mulched Data Set 108

18 Appraisal Of Paired Association Data 110

LIST OF FIGURES

FIGURE PAGE

1 Location of Whistler Mountain 20

2 Location of Sampled Ski-Slopes 26

3 Sample Site Location 56

4 Untransformed Variance:Mean Ratio for A. tenuis Sample Data 61

5 Arcsin Transformed Variance:Mean Ratio for A. tenuis Sample Data 63

6 Relationship of % Cover of the 4 Major Species to Altitude and Slope Angle 77

7 Mean Percentage Cover (+/- SE) for A. tenuis Vs. Soil Depth 98

8 Mean Percentage Cover (+/- SE) for F. rubra Vs. Soil Depth 98

9 Mean Percentage Cover (+/- SE) for T. hybridum Vs. Soil Depth 100

10 Mean Percentage Cover (+/- SE) for P. pratense Vs. Soil Depth 100

11 Mean Percentage Cover (+/- SE) for A. alba Vs. Soil Depth 101

12 Mean Percentage Cover (+/- SE) for T. repens Vs. Soil Depth 101

13 Mean Percentage Cover (+/- SE) for P. compressa Vs. Soil Depth 101

14 Mean Percentage Cover (+/- SE) for Bryophytes Vs. Soil Depth 102

15 Mean Percentage Cover (+/- SE) for Bare Soil Vs. Soil Depth 102

16 Significant Species Associations 111

17 Relationship Between Exchangeable Soil Calcium and % Cover of A. tenuis 126

18 Frequency of Exchangeable Soil Calcium Values in Sample Sites 165

CHAPTER 1

INTRODUCTION

1.1: The Underlying Question

The description and interpretation of spatial variation in plant species abundance in a single community is a central concern of biogeography. It is usual to ascribe such variation to changes in the abiotic and biotic environment (Harper, 1977). Often, one species will occur more abundantly than the others in a community, although it is also commonly found that the species growing in a single community can have similar abundance values (Grubb et al., 1982). In this respect it is pertinent to ask "how do the species in a given community cohabit"? This question represents the basis for the present study.

This question is one of a variety of approaches that have been employed to explain how plant communities are structured and the manner in which they develop. Attempts to provide explanations of how species cohabit have focused on one or more of a variety of hypotheses that have been invoked to explain cohabitation patterns. In the following section these hypotheses are briefly discussed to provide a conceptual background to the present study and to enable a relevant framework for study to be developed in section 1.3. Based on this a rationale for selecting the study area is presented in section 1.4 and the objectives of the thesis specified in section 1.5. An appropriate organisation of the study material is then described in section 1.6.

1.2: Theoretical Background

1.2.1: Two Theories Of Diversity

Various hypotheses have been invoked to examine and explain the mechanisms that facilitate species cohabitation in a single community, from which two contrasting theories of community structure and diversity have arisen, based on:

1. non-equilibrium mechanisms that involve a change in species composition (Grubb, 1977; Connell, 1978; Paine and Levin, 1981);
2. the traditional view, that natural communities represent an equilibrium state maintained by spatial variation in the physical environment and competitive exclusion (Whittaker, 1969; MacArthur, 1972; Cody, 1974).

1.2.2: Non-Equilibrium Hypotheses

Firstly, there is the view that communities seldom reach an equilibrium state. Continuously changing environmental conditions and periodic disturbances serve to regulate species composition and to permit large numbers of species to cohabit

(Connell, 1978). High diversity is thus an expression of a continually changing species assemblage, where some populations are invading as others go extinct within the community. According to this theory, a precondition for cohabitation is that factors are present which limit the expression of dominance (Grime, 1979). Two such mechanisms, disturbance and predation, have been invoked to explain diversity in this manner.

Periodic, local disturbances within a plant community have been described as an important mechanism facilitating species cohabitation, community composition reflecting the intensity and frequency with which past disturbances have occurred (Connell, 1978). In accordance with the underlying hypothesis, diversity will be highest when disturbances are intermediate on the scales of frequency and intensity (Eggeling, 1947; Grime, 1973).

Disturbances interrupt and set back the process of competitive elimination, and by causing destruction of the vegetation provide open sites for colonisation. The frequency of such disturbances is often faster than the rates of recovery (Connell, 1978), thus keeping local assemblages in a non-equilibrium state (Platt and Weiss, 1977). As a result, it has been argued that populations seldom reach levels where competition becomes important in determining species abundances (Andrewartha and Birch, 1954). Disturbances are often localised in occurrence, so even where competition may cause local extinction of a species, that species may persist in recently disturbed patches (McAuliffe, 1984). Furthermore, it has been suggested (Loucks, 1970; Grubb, 1977) that species differ in their response to disturbance, the continued occurrence of which thus results in a continually changing species composition, and a high diversity of species.

Predation has also been suggested as an important mechanism facilitating high diversity through its selective effect on plant communities (Harper, 1969), a view that had been strongly propounded by Ehrlich and Birch (1967) who pointed to the profound effects of introduced animals on vegetation patterns.

Predation of the dominant species enhances the ability of the less common species to become established (Grime, 1979). This is a frequency-dependent process and thus helps to maintain diversity (Harper, 1977). This selective effect of predation in creating diversity has been convincingly demonstrated by Paine (1966) for a littoral animal community.

The importance of herbivores as selective feeders on plant populations is well reviewed by Harper (1969; 1977) who cites the classic experiments performed on rabbit exclusion on chalk grasslands in England to describe how the floristic diversity of certain grassland communities can be largely attributed to predation. Furthermore, host-specific herbivores and parasites inflict especially heavy mortality on the offspring in the immediate neighbourhood of the parents, exacerbating the selective effect (Janzen, 1970; Connell, 1971). Finally, predation may further influence diversity through a differential effect on the dispersal of pollen, seeds and fruits (Harper, 1977).

1.2.3: Equilibrium Hypotheses

Several species may cohabit if each is more suited to a different range of environmental conditions (Whittaker, 1969). It has been suggested (Connell, 1980) that two possible mechanisms, spatial variation in the physical environment and differential competitive ability, facilitate this in plant communities.

Firstly, the species may have specific, innate, environmental requirements, so that when they are grown together each establishes best in that part of the site that provides the most suitable environmental conditions (Connell, 1980). This contention is based on a series of empirical and theoretical studies concerned with the examination of species abundances along abiotic gradients (Whittaker and Niering, 1965; Whittaker, 1967; 1969). These led to the general conclusion that while species may have similar habitat tolerances, no two species are exactly the same in this respect. Intuitively, the more specialised the species and the greater the degree of spatial variation, the larger the number of species that can cohabit.

Different species respond in a differential manner to spatial variation in the physical environment (Harper, 1977). Hence, cohabitation may be achieved by a heterogeneous environment determining whether or not there is, at a particular place, a suitable environment for species establishment and growth.

The second hypothesis, which stems from the work of Gause (1934) and de Wit (1960), suggests that, at equilibrium, species dependent on the same resources are unable to coexist indefinitely, i.e. they cannot occupy the same niche, due to the competitive exclusion of one species by another (Hutchinson, 1978). For two or more species to coexist there must be differences between them (Slobodkin, 1961; MacArthur and Levins, 1964; 1967).

However, through differential competitive ability, the component species of a community are able to partition the available resources in a manner that enables their continued cohabitation (Diamond, 1975; Tilman, 1982). At equilibrium, each species is competitively superior in exploiting a particular range of the available resources, and through interference in the growth of other species is able to win over some competitors but lose to others. Each species thus occupies the resource on which it is the most effective competitor (Connell, 1980). This represents niche differentiation (Connell, 1978; van den Bergh and Braakhekke, 1978).

A clear demonstration of this has been provided by Connell (1961) who suggests how the upper limit of occurrence of littoral, sessile animal species is determined by abiotic factors, while the lower limit is primarily controlled by competition. More recently, this view that a reduction of competitive interactions, through niche differentiation, facilitates cohabitation has been emphasised for both animal (Cody, 1974; MacArthur, 1972; Diamond, 1978) and plant communities (Parish and Bazzaz, 1976; van den Bergh and Braakhekke, 1978).

In accordance with this underlying theory, Tilman (1982) demonstrates how diversity will be maximal in moderately resource poor habitats, following the "hump back" model described by Grime (1979). He also offers an alternative to the view that diversity is primarily a function of the nature of past disturbances and their influence on species composition as proposed by Grubb (1977) and Connell (1978). He suggests that disturbance is a process "that influences the relative supply rates of resources for which competition occurs" (p.226), so that it is more important to study these resources, rather than the factors associated with the disturbance itself.

In the context of the present study, it can be asked whether spatial variation in relative abundance is due to habitat partitioning. This may be a function of the differential tolerance ranges of the individual species, or due to a modification of species interactions as the abiotic environment changes, restricting species to a particular range of the environmental gradients present, i.e. their realized niche. This approach is utilised at a variety of scales to examine the question of how similar species in a single community cohabit.

1.3: Framework For Study

Various scales of study provide a framework for describing the manner in which species cohabit in relation to abiotic and biotic factors. These are described in this section to provide a logical framework for the study. To facilitate this, it is suggested that application of the concept of the niche will permit description at each of these scales, whilst permitting any variations in species abundances to be jointly interpreted.

1.3.1: Scale of Study

Most ecological research concerned with the question of how species cohabit in a single community entails describing areas of vegetation at a given point in time and imposing, for the purpose of human study, a framework of scale on the vegetation. Explanations of how species cohabit have been attempted at a variety of such scales, these are considered here at three levels:

1. large-scale, environmental gradients have traditionally been adopted as a basis for study (Whittaker, 1967; Zimmerman and Thom, 1982). The modes of species distribution are scattered along such gradients in accordance with the requirements of the constituent species. Over a particular range of conditions one species may occur more abundantly than the others in a community, this changing as the prevailing environment changes (Whittaker, 1975). In this manner a

variety of species can cohabit by some being preferentially favoured along a specific range of the environmental gradients over which the community occurs. This represents an integral concept in the study of plant geography.

Clear examples of this are provided by Whittaker and Niering (1965) for the distribution of tree species with increasing elevation, and by Pemadasa and Amarasinghe (1982) who attribute the major part of the variation in species abundance for a grassland community to separation along an altitudinal gradient.

The importance of large-scale variation in abiotic conditions has been repeatedly emphasised and extensively reviewed (Whittaker, 1967; 1975). From such studies it is evident that spatial heterogeneity of large-scale abiotic factors enables species to cohabit through the occupation of different sections of the prevailing environmental gradients;

2. small-scale variations in the physical environment have been shown to be important factors influencing community development (Bratton, 1976). Such localised variation in abiotic conditions, along the major, large-scale gradients, produces a mosaic of abiotic factors, and a variety of species may cohabit within the community if they are differentially favoured by specific phases of this mosaic.

   In this approach cohabitation has been principally related to variations in edaphic factors (Snaydon, 1962) and microtopography (Harper and Sagar, 1953). Kershaw (1958; 1959) describes how spatial variation in soil depth enables species to cohabit in a reseeded grassland community. He also emphasised the importance of the combined effects of localised variation in soil depth and variation in rooting strategy as a mechanism facilitating the close cohabitation of the constituent species. This combined effect of small-scale edaphic variation and differences in growth form is being increasingly studied (Berendse 1981; 1982; Fitter, 1982). The literature is also extensively reviewed in Harper (1977). In short, localised abiotic variation, acting along the large-scale gradients can produce a corresponding change in species abundance, thus facilitating cohabitation (Kershaw, 1973);

3. a third, very fine-scale of study adopted here is the "neighbourhood approach" to how individual plants interact. This moves away from the two previously discussed scales by considering the variation in growth forms that species employ, and the consequent interactions that occur at the level of the individual plant.

As Pielou (1974) has demonstrated, the distribution of species along environmental gradients may not be explicable solely in terms of abiotic variation, even if all the relevant gradients could be considered. Cohabitation may be influenced by species interactions both in homogeneous environments (Turkington et al., 1977) and along environmental gradients (Kershaw, 1973; del Moral, 1983). Indeed, the occurrence of such interactions, through the reaction of individual plants to each other, may be an essential element influencing their cohabitation (Harper, 1964b).

Utilising this approach, a biological description of community diversity, as opposed to a geographical description, provided at each of the scales introduced above, can be used to examine the manner in which a species samples its biotic environment. What is relevant here is the adoption of "a plant's-eye-view" to explain variation in species abundance in relation to each other (Harper, 1977). This therefore represents a very fine, third-scale of study at which to examine how species cohabit.

1.3.2: Application of the Niche Concept

In accordance with niche theory (Hutchinson 1958; 1978; MacArthur, 1972), the variables of the abiotic environment represent spatial gradients which can be portrayed as niche axes, and utilised to compare the extent of habitat occupation of individual species in a community. This approach is utilised in the present study to permit joint consideration of how species tolerances and growth requirements, growth form, and interactions between them, facilitate cohabitation along abiotic gradients.

Cohabitation of plant species based on niche differences is difficult to comprehend due to their similar resource requirements (Grubb, 1977) and their sessile nature (Harper, 1977). This has led to fewer studies of plant cohabitation, based on niche differences, when compared with animal populations (Hutchinson, 1978). However, it is being more widely applied to plant communities as it is realised that there appears to be "no reason not to use the concept of the multidimensional niche in plant ecology" (Hutchinson, 1978, p.163).

The concept of the niche is utilised in this study as a descriptive and interpretive tool in order to facilitate a clearer interpretation of the manner in which species cohabit. It is used to describe the individual ways in which species partition their environment in relation to plant-environment and plant-plant interactions, and as an aid to the simultaneous interpretation of any such patterns. It is useful here in that it permits independent description, but joint interpretation, at the three scales of study adopted in this research. In this manner a more precise and confident interpretation can be made from a description of the patterns recorded, whilst avoiding the problems of invoking mechanisms responsible for such patterns (Wiens, 1977; Connell, 1980).

However, it must be emphasised that the niche concept is used here purely as a descriptive and interpretive tool, the theory itself is not being tested. Consequently, a comprehensive analysis of the ecological meaning and relevance of the concept is not presented. Also, the analytical measures developed by Levins (1968) to quantify niche breadth and overlap, in order to assess habitat occupation and possible species interactions, have not been applied to the results of this study. These have not been utilised for two main reasons:

1. the analysis of species data requires an examination of statistical differences in relation to abiotic factors. This would not be provided by niche breadth measures. So, for clarity of presentation, analysis has been restricted to a uniform procedure that detects statistically significant results. These results are then interpreted within the overall framework of the niche concept;
2. the nature of interspecific interactions necessitates their study at a very fine-scale. Hence, this study utilises a sampling and analytical procedure based on plant-plant interactions between individuals that are known to be neighbours in the field. Data for niche overlap are provided by study at a larger scale and are therefore not suited to the neighbourhood approach adopted here.

1.4: Choice Of Study Area

To examine species cohabitation, an artificial, developing grass-legume community, as represented by reseeded ski-slopes on Whistler Mountain, has been chosen for study. The selection of this area for study was prompted by two main considerations, these are described in the following two sections.

1.4.1: Variation In Species Cover

The reseeded slopes occur over a range of environmental conditions that can be portrayed as large-scale abiotic gradients. Along these a patchwork of localised edaphic variation exists.

Concomitant with this variation in abiotic factors, initial observations and consultation with the management staff of Whistler Mountain Ski Corporation indicated that the relative abundance of seeded species was highly variable. Prior to this study, the magnitude and causes of this variation remained unknown. The reseeded ski-slopes therefore represent a suitable location for studying the potential influence of environmental gradients on the relative abundance of species in a single community. The question of how the species cohabit in relation to these gradients can be directly examined due to the uniform manner of the seeding process.

All the species in the seed mixture, by virtue of being sown into the habitat, have the potential to occupy it. Any variations in such habitat occupation can therefore be more directly linked to abiotic or biotic factors than in field studies of natural vegetation. Absence of a species from a particular site in a natural community cannot be used as a basis for invoking processes such as competition, since it may simply be due to low tolerance of the prevailing abiotic conditions and not the response to interference from other species (Connell, 1980), or the lack of dispersal.

Any recorded variation in species abundance in this study will essentially represent niche differences, based on partitioning of the habitat, which can be more validly ascribed to abiotic and biotic factors. In laboratory studies, the "habitat" chosen for experimentation will frequently preclude the possibility of niche differences facilitating cohabitation through habitat partitioning. For this reason field evidence of competitive exclusion is particularly valuable (Begon and Mortimer, 1981). In this respect, this study can employ the concept of the niche as an aid to describing how the species cohabit.

A high density of seeding was employed by Whistler Mountain Ski Corporation to maximise species cover for the purpose of erosion control. Hence, a potentially competitive situation has been created where species interactions may influence their cohabitation. It is possible that the potential cover of many individuals will be suppressed by the competitive success of more vigorous individuals. Similarly, growth of several species may be facilitated through associations based on a more efficient partitioning of the resources. The pattern of such interactions being given direction by the prevailing environment.

Consequently, this artificial community represents an ideal field situation in which to describe species abundances in relation to abiotic factors and potential species interactions. Such a descriptive approach is necessary in an initial study of this nature to establish an empirical framework within which the question of how species cohabit can be addressed. From such results possible interpretations can be made concerning how the species cohabit in terms of niche differences resulting from differential habitat occupation, physiognomy, and interactions with other species.

1.4.2: The Importance Of Revegetation

The importance of revegetation for the prevention of soil erosion on disturbed land is clear (Berglund, 1976). This is of particular relevance to upland areas where a vegetation cover is necessary to prevent soil removal (Watson et al., 1970), and is of special importance in ski-areas where the nature of the terrain exacerbates the problems of soil erosion following removal of the natural vegetation cover (Bayfield, 1974; Beguin and Theurillat, 1981).

It has been recognised that a satisfactory method of revegetating disturbed upland areas, especially ski-slopes, is the seeding of grasses and legumes (Schiechtl, 1980). Monitoring the success of such reseeding, and indeed of all habitat restoration schemes, is of value for future work (Olgeirson, 1974). A study describing the relative abundance of seeded species and total vegetation cover can thus be used to determine the value of the species used in the context of erosion control. The results of such a study are of use for any future revegetation work.

1.5: Objectives

This study utilises a range of reseeded ski-slopes to address the question of how species cohabit in an artificial grass-legume community. The three scales of study, described in section 1.3, are used as a basis to examine this question by pursuing three main objectives:

1. to assess any variation in the relative abundance of the species with respect to large-scale environmental variation;
2. to consider the potential influence of localised environmental variation on species abundance;
3. to examine the extent to which species morphology and plant interactions within the sward influence cohabitation in similar habitats and along environmental gradients.

1.6: Organization

Following this introductory chapter, a description of the general environment of the study area is presented in Chapter 2. This provides the necessary baseline for the selection of environmental gradients along which to examine how the species cohabit.

Chapter 3 comprises a review of previous research on grassland and grass-legume communities relevant to the theme of species cohabitation. This provides a basis for the abiotic variables selected for study and a rationale for considering the potential role of species interactions.

Chapter 4 outlines the sampling procedures and methods of analysis employed to examine cohabitation at the three scales of study. The results are detailed in Chapter 5, and interpreted in respect to these scales of study in Chapter 6. Finally, the major conclusions drawn are presented in Chapter 7.

CHAPTER 2

THE STUDY AREA

2.1: Introduction

The sites chosen for study are located on Whistler Mountain (50 03', 123 00') in the Coast Mountains of southwestern British Columbia (Figure 1). In this chapter the general environmental characteristics of the region are described to provide baseline information on the study sites and their environs. This is followed by a description of the revegetation technique employed in the study sites and the abiotic variation that exists.

2.2: Geology and Topography

Whistler Mountain lies within the Pacific Ranges of the Coast Mountains, which are largely comprised of massive granitic rocks (Camsell, 1917). The geological map of the study area shows these to be mainly quartz diorite of uncertain age (Woodsworth, 1977). The study area was subject to repeated glaciation during the Pleistocene epoch, resulting in a glacially modified, irregularly rounded topography. The summit of Whistler Mountain (2170m) is one such rounded granitic dome. As a result of this glacier activity a variety of slope

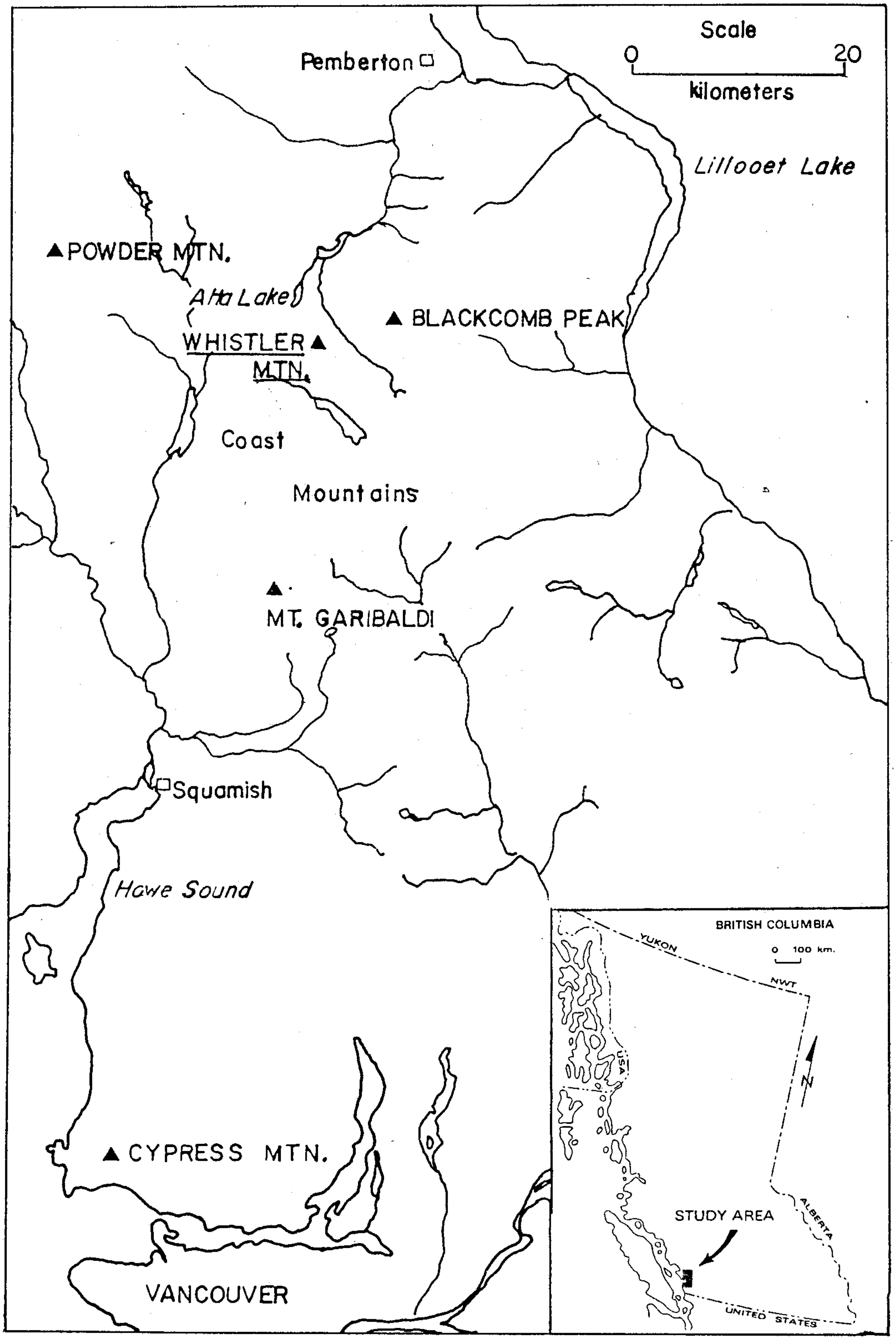


FIGURE I: LOCATION OF WHISTLER MOUNTAIN

gradients exist over the range of elevation encompassed here, combined with a large amount of spatial variation in the amount of substrate overlying the base rock.

2.3: Climate

The maritime influence of the Pacific Ocean maintains a generally mild climate in southwestern British Columbia. From May to September the North Pacific High is located near the coast providing warm temperatures and low precipitation. The Aleutian Low dominates the pressure pattern for much of the rest of the year causing a large number of fall and winter storms to develop and move towards the B.C. coast. The alignment of the Coast Mountains (NW-SE) forces the prevailing westerly winds upwards, producing an orographic effect.

As a result, the study location is characterized by a mild climate, with a wet winter and dry summer precipitation regime. This is detailed in Table 1, for Alta Lake Meteorological Station, situated at an elevation of 668m, at the base of Whistler Mountain.

With increasing elevation a transition takes place from mild, rainy climates to colder, snowy regimes, with summers becoming cooler and shorter (Schaefer, 1978). Such effects are summarised in Table 2 for Cypress Mountain, located 80 km south of Whistler (Figure 1). Although these two mountains have slightly different climatic regimes due to the difference in

Table 1: Climatic Data For Alta Lake Meteorological Station, (1951-80) 30 Year Mean Data.

	Mean Daily Temp. (C)	No. Days Of Frost	Mean Monthly Rainfall (mm)	Mean Monthly Snowfall (mm)
Jan.	-4.4	30	50.5	1845
Feb.	-1.2	26	39.9	1160
Mar.	0.4	28	41.1	862
Apr.	4.4	21	53.6	241
May	9.0	8	45.0	12
Jun.	12.5	0	51.9	T
Jul.	15.3	0	35.7	0
Aug.	14.9	0	48.9	0
Sep.	11.9	2	82.3	0
Oct.	6.5	10	157.8	201
Nov.	0.9	22	115.8	791
Dec.	-2.2	28	84.1	1460
Annual	5.5	175	800.6	6574

LEGEND:
T represents Trace.
(Source:- Environment Canada, 1982).

Table 2: Change In Climate With Increasing Elevation For Cypress Mountain.

Meteorological Station	Elevation (m)	Precip. (mm)	Snowfall (mm)	Mean Annual Temp. (C)
Hollyburn	46	1917	660	10.0
Hollyburn Ridge	951	2439	8110	5.1

(after Schaefer, 1978).

their location, the elevational trend is likely to be very similar. Elevation change thus represents a potentially important, complex of factors requiring consideration in vegetation studies in this area.

2.4: Soils

The study area has been mapped within the ferro-humic podzol landscape of British Columbia (Lord and Valentine, 1978). The generally high moisture level and low temperatures of the soils result in a high organic matter content due to its slow decomposition (Jones and Annas, 1978).

The major soil processes in the study area are the accumulation of complexes of organic matter, iron and aluminium, producing soils with strong podzol horizons and medium-coarse textures (Jones and Annas, 1978). From observation, it is apparent that the mineral soils that are present tend to have been eluviated, grading from light grey to red/yellow/brown soils with increasing depth. This agrees with the general description of the soils present in the Whistler region (Jungen and Lewis, 1978). Although, on the whole, soils appeared to be fairly uniformly leached, and reddish-brown in colour.

Variation in altitude and slope angle may influence the chemical and physical nature of the soils present in the study area. However, because a uniform management technique has been employed it is unlikely that local variation in soil chemistry will exist to an extent which may influence the relative abundance of seeded species. In contrast, given the underlying geology, history of glaciation and the manner in which the slopes were clear cut and bulldozed, spatial variation in soil depth may represent an influence on species abundance and cohabitation.

2.5: Natural Vegetation

The sites selected for study occur in the transition zone between the Coastal Western Hemlock and Mountain Hemlock biogeoclimatic zones of Krajina (1969). Below about 900m, the most humid and productve forest zone, the Coastal Western Hemlock zone, dominates at this latitude. The dominant tree species on these lower slopes of Whistler Mountain is *Tsuga heterophylla* (Raf.) Sarg, Western Hemlock, which grows in association with locally abundant patches of *Pseudotsuga menziesii* (Mirbel) Franco, Douglas Fir, and *Thuja plicata* Donn., Western Red Cedar. Above about 900m these are replaced by *Tsuga mertensiana* (Bong.) Carr, Mountain Hemlock, as the dominant species, with *Abies amabilis* (Dougl.) Forbes, Amabilis Fir, and *Chamaecyparis nootkatensis* (D. Don) Spach., Yellow Cedar, present in lower abundance. These characterize the Subalpine Mountain Hemlock biogeoclimatic zone.

2.6: The Study Sites

2.6.1: Management

On the north-west side of Whistler Mountain ski-runs were clear-cut and bulldozed to smooth the slopes. The location of these areas is shown in Figure 2. The cleared slopes vary in width from about 15m up to about 30m. The following revegetation technique was uniformly applied to these sites.

In the summer of 1980 lime was applied at a rate of 0.225 kg per square meter and worked into the soil by spring tooth cultivator. A grass-legume seed mixture was then applied by machine at a rate of 0.017 kg per square meter. The composition of the mixture is presented in Table 3. NPK fertiliser was applied in the ratio 21:7:14 at a rate of 0.017-0.023 kg per square meter. The slopes were then chain harrowed to provide a two centimetre cover of soil over the seed. Fertiliser has been applied each year during early summer.

In addition, a range of sites were reseeded with cyclone spreaders, and received a straw mulch cover. The location of these areas is also shown in Figure 2.

2.6.2: Environmental Variation

The ski-slopes that received the treatment described above have varying site characteristics. Preliminary investigation revealed spatial variation in two large-scale abiotic gradients,

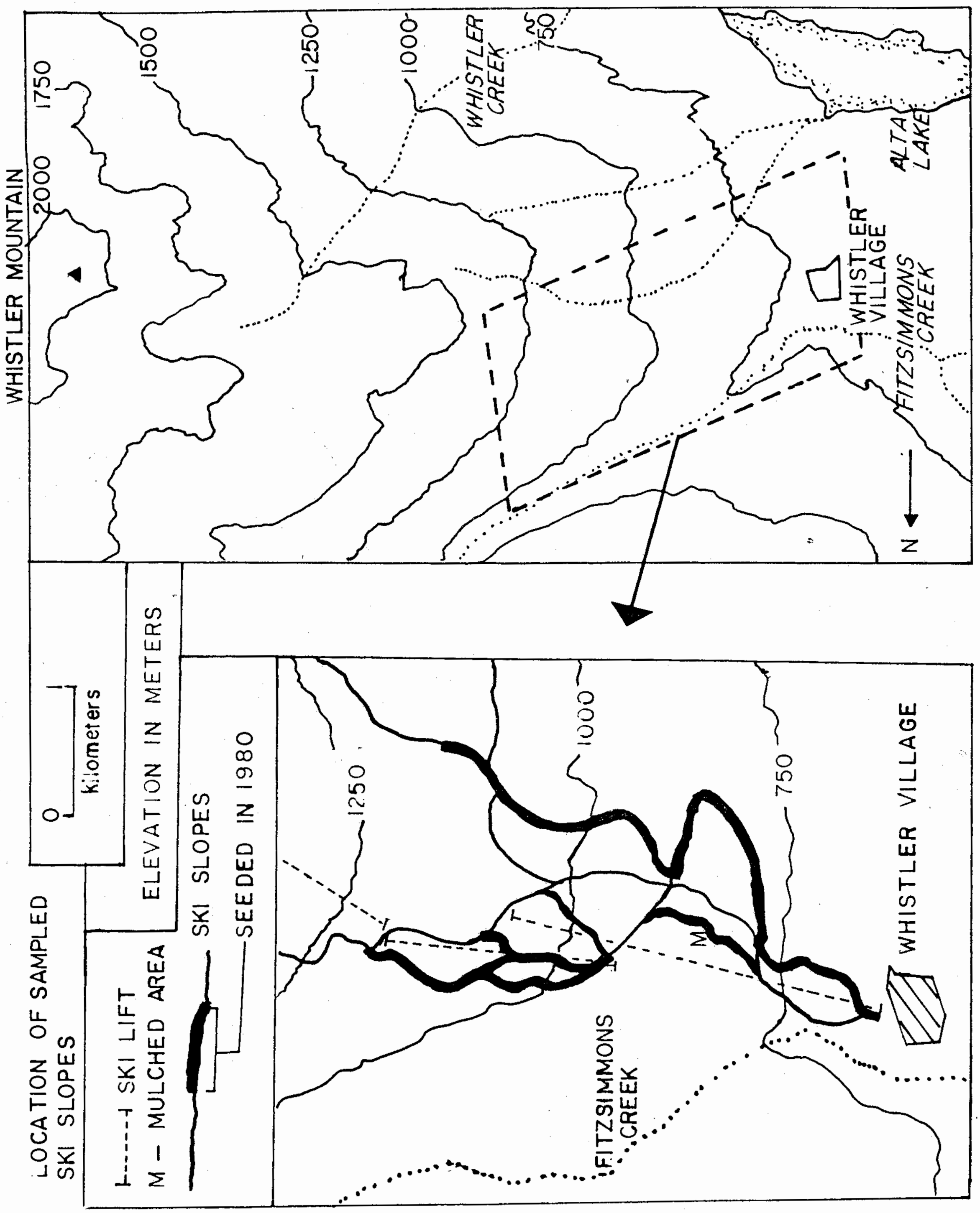


FIGURE 2: LOCATION OF SAMPLED SKI-SLOPES

Table 3: Composition of the Seed Mixture.

Species	% by weight	No. seeds per kg (millions)
Agrostis alba L. (Red Top)	15	11.02
Agrostis tenuis (Sibth). (Colonial Bentgrass)	20	18.74
Festuca rubra L. (Creeping Red Fescue)	25	1.36
Phleum pratense L. (Timothy)	15	2.87
Poa compressa L. (Canada Bluegrass)	10	5.51
Trifolium hybridum L. (Alsike Clover)	10	1.55
Trifolium repens L. (White Clover)	5	1.77

The clover seed was inoculated with Rhizobium bacteria. Data for the number of seeds per kg refers to the number of seeds per kg of pure seed and is presented to give a representation of relative seed size.
This follows Murray (1979) for the grass species and Cooper (1977) for the legumes.
Throughout this thesis nomenclature follows Hitchcock et al. (1969).

namely altitude and slope angle. Altitude ranges from 675m at the base of the mountain to 1150m, the maximum elevation of sites seeded as described. Angle of slope varies considerably, grading from flat areas to slopes with gradients of approximately 30 degrees.

With respect to localised abiotic variation, the uniform management technique employed makes variation in properties such as soil chemistry to be unlikely. However, the presence of rock outcrops, ridges, hollows and loose stones indicated soil depth to be highly variable over the study area. Finally, all the seeded slopes are on the north side of the mountain. For this reason the variation in aspect which exists is not thought to cause climatic variation significant enough to influence the relative abundance of the seeded species.

CHAPTER 3

LITERATURE REVIEW

3.1: Introduction

In designing a vegetation field study it is necessary to consider previous studies to present a theoretical background to the research. Hence, this review provides a discussion of how previous research has approached the question of how species cohabit, with particular reference to grassland and grass-legume communities. This provides:

1. a rationale for adopting the three scales of study at which to examine species cohabitation;
2. the necessary foundation for the selection, method of sampling and analysis of abiotic variables;
3. a basis for the methodology adopted to examine the possible influence of biotic factors on species abundance.

To achieve these aims the chapter is divided into sections which illustrate the importance of studying cohabitation at a variety of scales (3.2); large-scale abiotic variables (3.3); localised abiotic variation(3.4); and a combination of species interactions and growth form, both across and within habitat classes (3.5).

3.2: Cohabitation: A Question Of Scale

In any plant community there are several scales at which species cohabitation may be studied. Traditionally, a large-scale geographic approach has been utilised and species patterns have been interpreted principally in terms of environmental gradients (Whittaker, 1967; Zimmerman and Thom, 1982). This is based on the notion that a variety of species may cohabit if each is preferentially favoured in a specific phase of the habitat gradient.

However, it has become increasingly evident that localised variations in environmental factors operating along these large-scale gradients can produce a corresponding variation in the vegetation (Kershaw, 1973). These localised variations can be used as an additional aid to examine cohabitation patterns. Pemadasa and Amarasinghe (1982) focused on large-scale environmental variation to elucidate overall phytosociological diversity in montane grasslands , whilst Amarasinghe and Pemadasa (1982) examined the small-scale distribution of the four major species. In this manner they attempted to obtain a "fuller understanding of the phytosociological relationships in the behaviour of the species"(p.17).

At both scales the habitat variables form environmental gradients representing niche axes. Each species is distributed along these on the basis of its own habitat preferences and relationships with other species. This introduces a third scale at which to examine species cohabitation, that of species interactions.

The response of a species population to a gradient may affect other species and, consequently, their habitat relationships (Whittaker et al., 1973). Until recently there has been little consideration of how species interactions influence their cohabitation along environmental gradients and within habitat classes. However, species abundances can be markedly influenced by their interrelationships in contrasting (del Moral, 1983) and homogeneous (Turkington et al., 1977) environments. In this respect, the manner in which a plant grows will have important consequences in differing abiotic conditions (Kershaw, 1973), and also with respect to associated species (Turkington and Harper, 1979b). Species morphology may thus represent an important influence on cohabitation patterns.

The concept of the niche, although having a highly abstract framework, allows for the close examination of the distribution of species and how they grow and interact in a community (Solbrig and Solbrig, 1979). Clearly, the scales of study are not totally independent, joint consideration is necessary if valid interpretations are to be made. Utilisation of environmental gradients as niche axes and the description of growth and interactions along these axes is suggested to promote a more precise interpretation in this study of how the plant species cohabit in an artificial, developing, grass-legume community.

3.3: Large Scale Variation

3.3.1: Introduction

> "Perhaps the commonest differentiation between plant species is in response to the lateral variation in conditions in a habitat" (Harper, 1977, p.714).

There are considerable site differences which can influence plant growth in montane environments (Berg, 1974). According to Brooke et al. (1969) the major abiotic influences on the montane vegetation in southwestern British Columbia are the length of the growing season, topographic position, drainage, and edaphic characteristics. The influence of these variables is considered in this thesis under the headings of altitude, slope angle, and soil properties. Altitude and slope angle are considered in this section, whilst discussion on edaphic factors is reserved to section 3.4.

3.3.2: Altitude

Altitude has a major effect on the distribution of plants in montane environments (Whittaker, 1967). In British Columbia the influence of altitude on the major tree species and associated vegetation has been extensively studied and its importance emphasized (Krajina, 1965; 1969). Similar studies elsewhere have described close correlations between altitude and vegetation patterns. In a series of studies in the southern U.S.A., Whittaker and Niering (1964; 1965) have clearly demonstrated the importance of elevation as a gradient influencing species abundance. Similarly, a large part of the variation in occurence of the major species in montane grasslands in Sri Lanka has been correlated with altitude (Pemadasa and Amarasinghe, 1982).

However, in itself, altitude is a variable of only indirect relevance to plant growth. Along a gradient of increasing elevation many factors change concomitantly. Brooke et al. (1969) describe elevation as a stronger climatic control than latitude on the pattern of vegetation in B.C. This may be due to a combination of climatic factors such as an increase in the amount and persistence of snow, lower mean temperatures, increasing potential solar radiation, accentuation of the effects of slope and exposure, more frequent crossing of the freeze-thaw boundary, and variation in the amount of rainfall. Altitude thus represents a complex climatic gradient, influencing plant establishment and growth primarily by a shortening of the growing season.

Geyger (1977) has stressed the significance of elevation in some central European grasslands, documenting a four week delay in growth for every 500m gain in altitude. A similar trend is apparent in the present study area. Here the start of the growing season can be delayed by up to two months over the range of altitude encompassed, a fact witnessed during fieldwork in

1983. This can have a marked effect on the relative abundance of species in natural and artificial communities.

According to Whittaker (1967) it is reasonable to assume a decrease in the productivity of a habitat with increasing elevation, due to the shorter growing season and increased climatic severity. Such low productivity has been shown to have an important effect on vegetation patterns due to a reduction in competitive ability (discussed in section 3.4), and also because of the need for species to be able to tolerate the increased environmental severity (Belsky and del Moral, 1982). Indeed it has been noted that "stress tolerance" is more important than competitive ability in such low productivity habitats (del Moral, 1983).

As in natural communities, the climatic requirements for development, flowering, growth and survival differ between species in artificial communities (Hughes, 1965). Bayfield (1980) examined the establishment of a grass seed mixture on ski-slopes on Cairngorm, Scotland. A satisfactory sward was established at all altitudes up to 1100m, although not all the species did equally well. Declines in grass productivity with altitude have been noted by Morris and Thomas (1972). However, in their study in northern England, variations may be partly attributed to variations in soil type. In Scotland, Hunter and Grant (1971) demonstrated similar declines as solely attributable to climate. Climate also appears to be one of the major factors governing the usefulness of clovers in herbage production (Chestnutt and Lowe, 1970).

Evidently, the possible influence of climatic factors, as expressed along a gradient of increasing elevation, on the relative abundance of seeded species in this study warrants consideration.

3.3.3: Slope Angle

The amount of soil moisture available for uptake by plant roots is influenced by aspect and angle of slope (Yeaton and Cody, 1979). Aspect is not thought to vary in a manner significant enough to influence the abundance of the seeded species. In contrast, a wide variety of slope gradients exist in the study area which may infuence species abundances.

The importance of slope to the types and numbers of plants that occupy a site has long been recognised (Dix, 1958). Run-off is correlated with slope angle in a manner which causes it to decrease with decreasing slope angle. A gradient of increasing moisture content is thereby created after a period of rainfall, whereby soil moisture availability increases with decreasing slope angle (Jackson, 1967). Slope angle can thus be used as an index of moisture availability (Whittaker, 1967).

Soil moisture availability is an important factor that can affect the establishment of species in seed mixtures (Dix, 1958). This arises from the fact that desiccation is an acute hazard facing seedling populations (Harper, 1977). In itself, soil moisture is a complex factor that can influence plant distribution, in terms of amount, depth and duration. It can have differential effects when in very low or very high quantities. Low moisture levels limit growth by desiccation, high levels can limit growth by reducing the oxygen available to the roots (Gauch, 1982).

Desiccation and waterlogging can influence species abundances by restricting the establishment of seedlings and the growth of mature plants (Spedding and Diekmahns, 1972). Evidence of this is supplied by Finn et al. (1961), who describe how some species of grass are more tolerant of spring flooding than others. A particularly clear example of how species may partition their environment along a gradient of soil moisture is provided by Werner and Platt (1976). They ascribe the close cohabitation of six species of Solidago to separation along this gradient. Similarly, variations in the abundance of species in sub-alpine meadow complexes have been partly attributed to topography through its influence on water availability (Belsky and del Moral, 1982).

The differential effects of soil erosion and sedimentation, due to slope angle variation, can limit plant growth (Gauch, 1982). On steeper slopes the snowpack exerts a strong horizontal force which has a shearing effect on soils (Brooke et al., 1969). This can be strong enough to push loose stones down inclines (Mathews and Mackay, 1963). Variation in slope can thus influence species abundance through this effect on soil stability (Belsky and del Moral, 1982). A factor which invites consideration in this respect is the possible influence of mulching on the vegetation. This has been shown to be an important technique for minimizing soil loss and moisture stress on sloping ground (Dyrness, 1975).

Evidently, the complex of climatic factors represented by an altitudinal gradient and variation in slope through its effect on moisture and stability have the potential to influence the relative abundance of plant species. Their influence on how the species in the community under study cohabit thus warrants consideration.

3.4: Localised Abiotic Variation

3.4.1: Introduction

Although the relative abundance of herbaceous plant species may change along the major gradients of altitude and slope, small-scale gradients are of equal importance (Bratton, 1976). Extensive reviews of the literature (Greig-Smith, 1964; Kershaw, 1973; Whittaker, 1967) attest to the importance of localised variation in edaphic factors to the relative abundance of species in a community. This has been emphasized for populations in upland areas (Bliss, 1969). In the context of the present study edaphic variation can be considered under two headings, soil chemistry and soil depth.

3.4.2: Soil Chemistry

It is a common fact that the abundance of certain plant species can be closely correlated with variation in the chemical properties of the soil. For example, complex patterns of natural vegetation and soil chemistry have been revealed by Hall (1971) on downland in England. Similarly, Snaydon (1962) has described how, on hill pasture, T. repens is closely related to variation in soil chemical factors.

The response of artificial communities to variations in soil chemistry has also been extensively studied , due to the importance of productivity and yield in these systems. The classic Park Grass experiments at Rothamstead, England, provide detailed evidence of how particular grass and legume species may be influenced by soil chemistry (Lawes Agricultural Trust, 1966). Similar evidence for the differential tolerance of individual species for combinations of soil chemical factors is presented throughout the literature (Bradshaw et al., 1964; Crossley and Bradshaw, 1968; Thurston, 1969). Such evidence is usefully reviewed elsewhere (van den Bergh, 1968; Spedding and Diekmahns, 1972), where it is emphasized that fertilization can have an important effect on species abundances. In the case of disturbed alpine areas, fertiliser applications are essential for the establishment of a plant cover (Brown et al., 1976).

However, it has also been shown that differential species response to fertilizers depends more upon site characteristics, and tends to influence vigour rather than relative abundance

(Hull et al., 1962). The results of del Moral (1983) for a subalpine meadow community, suggest that where major nutrients show little differentiation and are fairly uniform, it is unlikely that nutrient differences that do occur will be the cause of any recorded vegetation patterns. Similarly, spatial variation in the relative abundance of species in grass-legume communities are often not the result of differences in soil chemistry (Turkington et al., 1977; Turkington and Harper, 1979a).

Uniform application of fertiliser and lime indicates that adequate nutrients are available throughout the study area, and that variation in pH will be minimal. Combined with this, the wide tolerance of the agricultural-type grasses, seeded in this study area, to nutrient and pH variation (Spedding and Diekmahns, 1972), and the similarity of legumes in this respect (Ignatieff and Page, 1958; Smetham, 1977), make it unlikely that variation in soil chemistry will be an important factor influencing species cohabitation.

Furthermore, the difficulties imposed by their non-independent variation, their analysis in large numbers of replicates, and describing the relevant variables in a field study, confounds their interpretation. Future discussion will therefore centre on clear-cut differences, which may be related to variation in altitude and slope angle.

3.4.3: Soil Depth

An important axis of niche space is the depth of soil and its relationship to rooting depth (Berendse, 1981). Variation in rooting depth has been suggested as a possible mechanism facilitating the cohabitation of a variety of grass species (Milthorpe, 1961). This is particularly relevant where spatial variation in soil depth occurs (Kershaw, 1958; 1959).

The importance of spatial variation in soil depth as an influence on the cohabitation of grasses and grass and legume species is well documented. Hall (1971) explains how the overall pattern of species in downland vegetation is governed by localised variations in soil depth. Fitter (1982) describes a situation whereby diversity of a grassland community is greater on shallow soils than on deeper soils, due to the restriction of growth of the dominant species.

The species specificity of seedling establishment in relation to such small-scale abiotic variation has been emphasized by Harper and Sagar(1953). They explain how the distribution of three species in the genus Ranunculus is primarily related to microtopography and its effect on soil depth and water table relations. Kershaw (1958; 1959) describes the pattern of the major species in a reseeded, upland grassland community, and stressed the importance of spatial variation in soil depth as an influence on species cohabitation. He notes the manner in which Agrostis tenuis initially occupies the shallow soils, spreading from these centres to give a final uniform cover. Meanwhile, the other species are restricted to the deeper soils. This indicates that species with large mean rooting depths cannot form a fully developed root system on shallow soils, causing failure of the plant (Kershaw, 1958). Species with a shallow root system were able to coexist with those with a deeper root system by partitioning of the soil environment, this being achieved through the spatial occupation of areas of different soil depth and vertical segregation in deeper soils (Kershaw, 1959).

The studies of Salisbury (1952) indicate that some of the floristic diversity of English chalk grassland may be produced by diversification in rooting depth of the constituent species. More recently, Platt and Weiss (1977) have documented how the structure and development of root systems of fugitive prairie plants reflect, in part, differential patterns of resource utilisation.

Variation in rooting depth is an innate characteristic of the species seeded in the present community, and as such it may influence species cohabitation in a manner unrelated to any possible interference effects from other species. However, such vertical separation in rooting systems can lessen or eliminate potential interference between species (Whittaker, 1969). In grassland communities differential rooting depths, combined with spatial variation in soil depth, have become recognised as an important mechanisms facilitating their cohabitation (Parish and Bazzaz, 1976; Berendse, 1982; Fitter, 1982; Veresoglou and

Fitter, 1984). It is therefore necessary to consider how growth form and species interrelationships can influence cohabitation along and within the abiotic gradients described.

3.5: Species Interactions

3.5.1: Introduction

The degree of establishment is influenced by many factors, including the nature of the associated species (Milthorpe, 1961), with interactions between plants comprising an important factor influencing the relative abundance of species in swards planted at high densities (Trenbath, 1976).

The community under study here is an artificially reseeded plant assemblage in which the species are not genetically specialized with respect to each other. During the establishment of such mixtures a dynamic plant community develops in response to species interactions controlled by variations in abiotic factors (Turkington and Cavers, 1979) and those due solely to the attributes of the species themselves (Turkington et al., 1977). Extensive reviews presented elsewhere (Donald, 1963; Harper, 1961; 1964a; 1977; Schoener, 1983) attest to the importance of species interactions as influences on species cohabitation.

The objective here is to consider pertinent examples in the literature which provide a framework for studying species cohabitation at a very localised scale. This illustrates how species interactions may be important in determining how species cohabit within homogeneous environments, and how such interactions may be modified as the prevailing environment changes, thus altering the manner in which the species cohabit.

3.5.2: Scale of Study

> "...the essential qualities which determine the ecology of a species may only be detected by studying the reaction of its individuals to their neighbours..." (Harper, 1964b, p.149).

The variety of such reactions is considered in this thesis under the blanket term of "interference" (following Harper, 1961), since it is impossible in a field study such as this to state definitively that any associations are due to particular processes such as "competition". Where the term competition is used it refers to the tendency of adjacent plants to use the same limited resource (Grime, 1979).

Since the presence of an individual can alter the environment of its neighbours, it is necessary to take a "plant's-eye-view" of how species sample their biotic environment (Harper, 1977). Such a neighbourhood approach is critical for plants, where spatial relationships between individuals may be important features of how the species cohabit. This represents the third scale at which the question of how species cohabit is addressed in this research.

3.5.3: Interactions Along Abiotic Gradients

Under different conditions of the environment the outcome of species interactions may be different (Kershaw, 1973). Each species in a community is distributed along a complex range of habitat gradients on the basis of its own requirements and its relationship with other species (Whittaker et al., 1973). Species response curves are thus further influenced by their interactions with one another along these gradients (Cormack, 1979). However, until very recently there has been little consideration of how species interactions are related to variations in the abiotic environment.

In the theoretical framework developed by Grime (1979) interactions are limited by productivity, as determined by abiotic gradients. Interference can operate over the entire range of such gradients, but will vary in intensity and rate. This point is emphasized by del Moral (1983), who documents how habitat heterogeneity produces a productivity gradient which controls species interference in a mosaic of vegetation types. Although he concluded that differential success was largely attributable to interspecific competition (at least in productive habitats), variation in abiotic factors governed how the species interact with each other. Similarly, Fitter (1982) suggests that where the rooting of dominant grass species is restricted, their competitiveness is reduced, enabling less competitive species to establish larger cover values.

The underlying theory here is that plant species which are potential competitors for a limited resource may be able to cohabit as a result of differences in their realized niches, even though their fundamental niches may show considerable overlap (Begon and Mortimer, 1981). In this respect, it is important to recognise that abiotic variation can have a differential effect on the competitive ability of different species in a single community. This can modify how the species interact and thus influence their distribution along abiotic gradients.

A classic demonstration of this in plant communities is that of Tansley (1917). He determined how the distribution of two grassland herbs can be explained by direct relation to abiotic variation and the extent to which interference from neighbouring plants modified this reaction. This has been equally well demonstrated by Harper and Chancellor (1959) who document a modification of species response to abiotic variation that may be due to changing species interactions as the physical environment alters. More recently, Sharitz and McCormick (1973) have documented a strict zonation of annual plants in relation to soil depth on granite outcrops. Their results suggest that this zonation is not simply a reflection of the tolerance range of the individual species, since their fundamental niches cover the whole range of abiotic conditions under study. Apparently, the species are restricted to a small fraction of the environment, their realized niche, through the effect of interspecific competition, the result of which changes with variation in physical conditions.

A variety of removal experiments have, essentially, demonstrated this fact that differential response to the abiotic environment may be determined by the tolerance of individual species and the differential effect of the physical environment on their competitive abilities. Putwain et al. (1968) report how <u>Rumex</u> <u>acetosella</u> only becomes the dominant species in the presence of grasses and dicotyledons in conditions of low fertility. Subsequent removal experiments showed how the realized niche of <u>Rumex</u> was able to expand in the absence of the grasses and other herbs (Putwain and Harper, 1970). Fowler (1981) revealed a pattern of "diffuse competition" among the herbaceous species in a North Carolina grassland. This influenced the high degree of spatial heterogeneity in their relative abundance under different conditions (Fowler and Antonovics, 1981). However, further experimental studies (Fowler, 1982) did not follow Grime's (1979) hypothesis that competitive interactions increase in more favourable environments. Instead, species interactions changed in a highly individualistic manner in relation to environmental variation. The importance of such idiosyncratic effects has also been emphasized by Wiens (1977). Nevertheless, in the context of the present study, all these examples emphasise a single point. Resource/habitat partitioning between the species in a single community can occur with respect to spatial variation in abiotic factors, and is modified by interspecific competition, which changes as the physical environment alters, influencing the manner in which the species cohabit.

Clearly, the physical factors of the environment can have a major effect on species interrelationships. Consideration of the possible joint effects of the abiotic and biotic environment is therefore necessary. The abiotic gradients in this study represent a useful vantage point from which to examine possible species interactions in different habitat classes. This may provide further evidence of how the species cohabit.

3.5.4: Interactions Due To The Biotic Environment

Interactions between neighbouring plant species are continuous, and where abiotic conditions are relatively constant, represent the principal factors directing community composition (Turkington and Cavers, 1979). The importance of species associations for cohabitation in artificial communities has long been recognised (Roberts and Olson, 1942; Aberg et al., 1943). Such work has indicated that the close cohabitation of grasses and legumes is facilitated by differential exploitation of the soil environment. It has also become evident that grasses and legumes differ in their aggressiveness towards each other (Chestnut and Lowe, 1970; Turkington and Harper, 1979c). In certain cases legumes have been unable to compete successfully with vigorously growing grasses, resulting in their elimination from the sward (Dyrness, 1975). This is usually due to poor competitive ability for nutrients (Haynes, 1980).

However, Turkington et al. (1977) provide evidence that the relative abundance of species in a grass-legume community is dictated not simply by spatial exclusion or differential soil exploitation. They describe a complex series of associations between the various species. The species themselves are the prime determinants of each other's distribution, in terms of "ecological combining ability". Similarly, Aarssen et al. (1979) and Turkington and Harper (1979a; 1979b) have stressed the importance of biotic factors to community development in grass-legume swards.

In this study I examine only the possible influence of growth, morphology and spatial interference on the pattern of relative abundance. Associations due to some form of ecological combining ability cannot be considered since the community was sampled in only its fourth growing season. The detection of such associations necessitates the study of relatively permanent pastures. However, the development of initial temporary associations has been shown to be a rapid process in developing grass-legume swards (Turkington and Cavers, 1979). Their influence on cohabitation is therefore considered in this study.

Wherever plants grow in close proximity, differences in physiognomy represent an important means by which they cohabit (Grime, 1977). Concomitant with variations in root habit (section 3.4.3) above ground variations in morphology plus variations in seed and seedling characteristics may also influence relative establishment and cohabitation. Turkington and Harper (1979a) describe how the very different growth forms of Trifolium repens and Lolium perenne may permit them to dominate a semi-natural grassland community. Similarly, Turkington and Cavers (1979) describe how legumes with a similar tussock growth form exhibit negative associations due to the intense interference effects restricting cohabitation.

During establishment the rate of emergence and seedling growth can influence species composition of a sward (Spedding and Diekmahns, 1972). Differences in seedling growth under similar and dissimilar conditions have been recorded (Blaser et al., 1956), whilst Chippendale (1949) has shown that emergence rate varies between forage species, even under optimum conditions. Where productivity is limited, low yielding and less productive species tend to be more successful than productive species (Spedding and Diekmahns, 1972).

The importance of seed size has long been recognised as an influence on the relative establishment of grassland species (Milton, 1935; Hunt, 1964). A close relationship exists between seed weight and seedling vigour (Herriott, 1958), and the influence of initial embryo size is readily apparent when small-seeded grass species are sown with larger seeded species (Chippendale, 1932; Milthorpe, 1961). Even under optimal conditions, in mixed-species populations the young plants from small seeds are at a disadvantage in terms of seedling vigour and relative establishment (Black, 1958; Harper and Clatworthy, 1963). Although variations in abiotic factors will influence this, the seed characteristics themselves play an important role in seedling establishment under such conditions (Harper et al., 1970). For example a reduction in water availability is a more acute problem for small seeds than large ones (Harper and Benton, 1966). Such factors become increasingly important when seeds have a high density in the soil (Harper, 1977).

Evidently, the influence of growth form may be critical in determining how species in grassland and grass-legume communities cohabit. This can occur with respect to differential habitat occupation and species interactions along abiotic gradients and within habitat classes. It must be recognised, however, that the pattern of such interactions may be diffuse and unpredictable under field conditions.

3.6: Choice of Variables

Clearly, the factors discussed in this chapter do not represent all the possible influences on species cohabitation in grassland and grass-legume communities. Localised, periodic disturbances (Grime, 1973; Grubb, 1977; Connell, 1978) and predation (Harper, 1969; 1977), have been described as important mechanisms facilitating cohabitation through their effect on species composition and the maintenance of a nonequilibrium state. However, their relevance in the context of the present study is limited. Hence the manner in which they are suggested to influence species cohabitation is not discussed in detail here.

Similarly, seasonality of growth is a further dimension along which to examine cohabitation. Its relevance in grass-legume communities has been emphasized, due to different seasonal cycles of leaf production amongst the constituent species (Harper, 1977; Turkington and Harper, 1979b), and because of the seasonality of association formation (Aarssen et al., 1979). Similar, asynchronous growth has been recorded for flowering time in grassland communities (Wells,1972), and its effect on plant competition emphasized (Scarisbrick and Ivins, 1970). However, the climatic conditions and the relatively short growing season prevalent in the study area make it unlikely that temporal variation in flowering and growth can have a noticeable effect on species cohabitation. Also, the importance of flowering time is not thought to be relevant in a young community of predominantly wind pollinated plants.

In short, the abiotic gradients discussed in this chapter can influence species cohabitation by permitting the species to partition their habitat in respect to their differential tolerance ranges. It is also evident that species response to these gradients is modified by interactions between the species, which restricts them to certain ranges of the abiotic gradients, i.e. their realized niche, where they are more effective competitors. In turn, these interactions are modified as the physical environment alters.

CHAPTER 4

METHODS

4.1: Introduction

In this chapter the design of the field survey, the sampling techniques, and the analytical procedures employed at each scale of study are presented, in conjunction with a rationale for their selection and use in this research.

4.2: Data Collection

4.2.1: Purpose

The objectives of the sampling procedure were:

1. to record the variation in abiotic factors for the seeded areas and to quantify the relative abundance of seeded species in relation to this variation;
2. to quantitatively describe any patterns of possible species interactions.

For these purposes a stratified, random sampling procedure was adopted as a basis for study. In this section the design of this procedure is outlined, followed by a description of the sampling techniques employed within this framework.

4.2.2: Survey Design

A preliminary survey of the reseeded slopes was undertaken in May 1983 to record the variation in major abiotic factors over the seeded areas. Aspect, using a compass, and angle of slope, with an Abney level, were mapped for all the slopes receiving the treatment described in section 2.1. Preliminary observations were also made on edaphic characteristics.

With respect to aspect, the ski-slopes seeded in 1980, as described in section 2.2, have compass bearings of between 300 degrees west and 45 degrees east. Although this variation represents approximately 30% of the total azimuth, it is all in a predominantly northern direction. For this reason, the variation in potential solar radiation received is not thought to vary in a manner which will influence the relative abundance of seeded species, in samples at similar elevations.

In contrast, the variation in slope angle which exists may represent an important influence on species abundances, through its effect on the moisture regime of a site. Gradients were recorded ranging from flat areas to angles of up to 30 degrees.

The range of altitude encompassed, determined by reference to topographic maps of the mountain, is from 675m at the base of the mountain to 1150m.

Based on these observations, a stratified random sampling procedure was adopted to record the vegetation cover on the slopes. This was designed as follows.

Altitude was stratified into three classes, 675-850m, 850-1000m, and 1000-1150m, to provide a primary, elevational gradient along which to examine species relative abundance. The seeded areas were categorised into topographic units based on angle of slope. Field observations suggested that variation in species abundances diminished with increasing slope angle. Topographic units were therefore allocated to slope classes with the range of slope angle in any one class being twice that in a preceeding class. Five slope angle classes were constructed in this manner, namely, less than 2, 3-4, 5-8, 9-16, and greater than 16 degrees of slope. Following this procedure the maximum amount of variation in species abundance could be recorded along this gradient in a manageable fashion. These represent slope classes one to five respectively.

All topographic units were assigned to cells in an altitude/slope matrix. Any units which bore evidence of post-seeding disturbance (e.g. vehicle tracks) were discarded from the sample set. Within each cell the aim was to have three replicate units, however in cases where the topographic units occupied large areas, two replicate units per cell was thought satisfactory. Initially, the largest topographic units (hereafter referred to as sites) were allocated to cells in the matrix. The required replication was then obtained by filling the cells with smaller sites. The number of samples taken in each site was determined by its area, as described in section 4.2.3. Hence, two large sites could give as much replication, in terms of sample numbers, as three smaller sites. In such instances the selection of a third site for sampling was deemed unnecessary. In addition, a range of mulched sites was sampled. The location of all the sites is shown in Figure 3.

4.2.3: Sampling Procedure

Each site was randomly sampled, using random number tables, with a point frame, to determine overall and individual species percentage cover. In this method a linear frame of ten pins is placed at the sample location and the species contacted by each pin recorded. Each pin may contact more than one species, hence percentage cover values can exceed 100%. This sampling method was chosen for the following reasons:

1. clipping techniques could not be employed due to the need to maintain the vegetation cover on the slopes;
2. density measurements are impractical in such grassland communities, percentage cover providing a more practical and objective method due to the large degree of neighbouring plant overlap in the sward (Greig-Smith, 1964);
3. where density measurements are impractical, cover gives a more accurate assessment of pattern than frequency, and is not dependent on quadrat size (Kershaw, 1973);
4. the data collected are suitable for standard ecological analytical techniques and for comparison with previous studies of this nature.

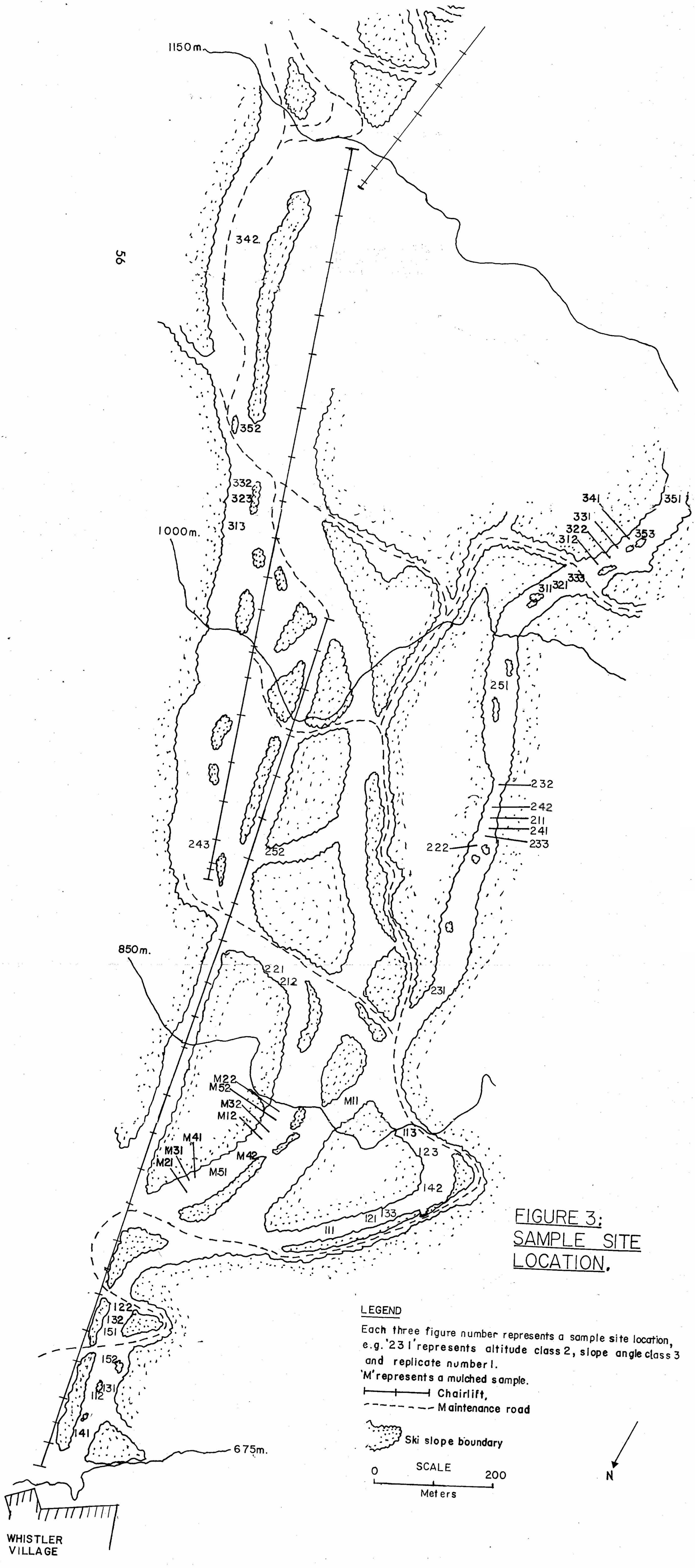


FIGURE 3: SAMPLE SITE LOCATION.

The number of samples was determined by the need to increase sample size with increasing area in a manageable fashion. The formula adopted equated the number of samples to half the square root of the area of the site.

As can be observed in Table 6 (Chapter 5) the number of samples tends to decrease with decreasing slope angle. This is due to the smaller size of sites with low slope areas.

A measure of percentage flowering was obtained for each species by recording whether or not each shoot contacted was flowering. This information was collected in order to give an insight into any variations in vigour and strategy of growth between the species and between the habitat classes.

Concomitant with the percentage cover survey, the first and tenth pins (to increase replication) on the frame were utilised as sampling points in a "contact sampling" procedure. This quantifies plant to plant contacts within the sward, as described by Yarranton (1966), and has been adapted (Turkington et al., 1977) and modified (de Jong et al., 1983) for use with grass-legume communities.

Data were collected using the recommended strategy of de Jong et al. (1983). The species first touched by the pin (species i) represents the sampling point, and is recorded along with the next different species (species j) which it contacts, nearest to the pin. To overcome the problem of determining what represents an individual plant each shoot was recorded as an individual. When species i did not touch another individual 'no contact' was recorded. If species i and j were the same, species j was reselected until j was a new species. If the only contacts that species i made were with shoots of the same species, this was recorded as 'no contact'. This subset of information was not used in the recommended analytical procedure (de Jong et al., 1983) which is only suitable for the detection of interspecific associations. However, it was retained to give an estimate of the degree of "clumping". This sampling method avoids the possibility of erroneously recording and analysing data where the same plant has been recorded twice, by removing the problem of distinguishing between individuals of the same species.

In placing the point frame, care was taken not to disturb the vegetation and the long axis placed in the fall line (purely for consistency). Sampling was carried out in July and August 1983 and proceeded from low to high elevation sites in order to sample the vegetation at as similar stage in the growing season as possible. For each sample soil depth was recorded (after the vegetation had been sampled) at each end of the frame by use of a calibrated screw-type soil auger. If the depth exceeded 35cm "greater than 35cm" was recorded. The two measures were combined to give a mean soil depth for each sample.

For each site one composite soil sample was collected for chemical analysis. This comprised ten cores taken at random (using random number tables) within the site, from the top ten centimetres of soil, using a soil auger. These were bagged and transported to the laboratory for analysis. A LaMotte

Combination Soil Testing Outfit, model STH-14, was used to determine nitrate nitrogen, nitrite nitrogen, ammonia nitrogen, available phosphrous, available potassium, exchangeable calcium, magnesium, manganese, and ferric iron. The pH of each soil sample in distilled water was also determined using a pH meter.

4.3: Vegetation Data Analysis

4.3.1: Percentage Cover

The significance of any correlation between the relative abundance of species and the altitude/slope matrix was assessed using a two-way analysis of variance technique (ANOVA). In the field survey the number of replicates falling into the cells of the cross-classification of altitude and slope were unequal. A fixed-effects, non-orthogonal ANOVA design was thus employed for analysis. This technique was performed using the computer package programs described in The BMDP Manual (Dixon, 1983). This procedure was also used for the percentage flowering data.

The ANOVA tests whether treatments have a significant effect, but gives no information, if the null hypothesis is rejected, on which of the treatments are significantly different. Further analysis is required to specify this.

For this purpose a modified form of Duncan's (1955) Multiple Range Test, suitable for determining the statistical difference between sample means based on unequal numbers of replicates was utilised. This procedure, described by Kramer

(1956), indicates where the significant effects of abiotic factors, the overall significance of which has been shown by ANOVA, occurs. The combined use of these two procedures enables significant differences between treatment means to be identified. This permits a more detailed interpretation of the results.

4.3.2: Data Transformation

The random nature of the sampling procedure ensures that there is error independence in the data, which is required for use of the ANOVA technique. However, estimates of percentage cover from samples of plant populations tend not to be normally distributed about their mean value, nor with a variance independent of the mean (Fisher and Yates, 1948). The values for skewness and homogeneity of variance (Table 4) combined with a plot of the variance:mean ratio for Agrostis tenuis (Figure 4) illustrate this general trend.

Two transformations of the data were tried, arcsin and log(x +1). Both of these have been recommended for use on percentage cover data (Goodall, 1952; Green, 1979 respectively). Their effects on skewness (which is zero for a true normal distribution) and variance are shown in Table 4 and Figure 5.

Clearly, the arcsin transformation has a greater beneficial effect in reducing skewness for those species to be analysed using the ANOVA procedure. The skewness values are not reduced to zero, and consequently do not represent a true normal

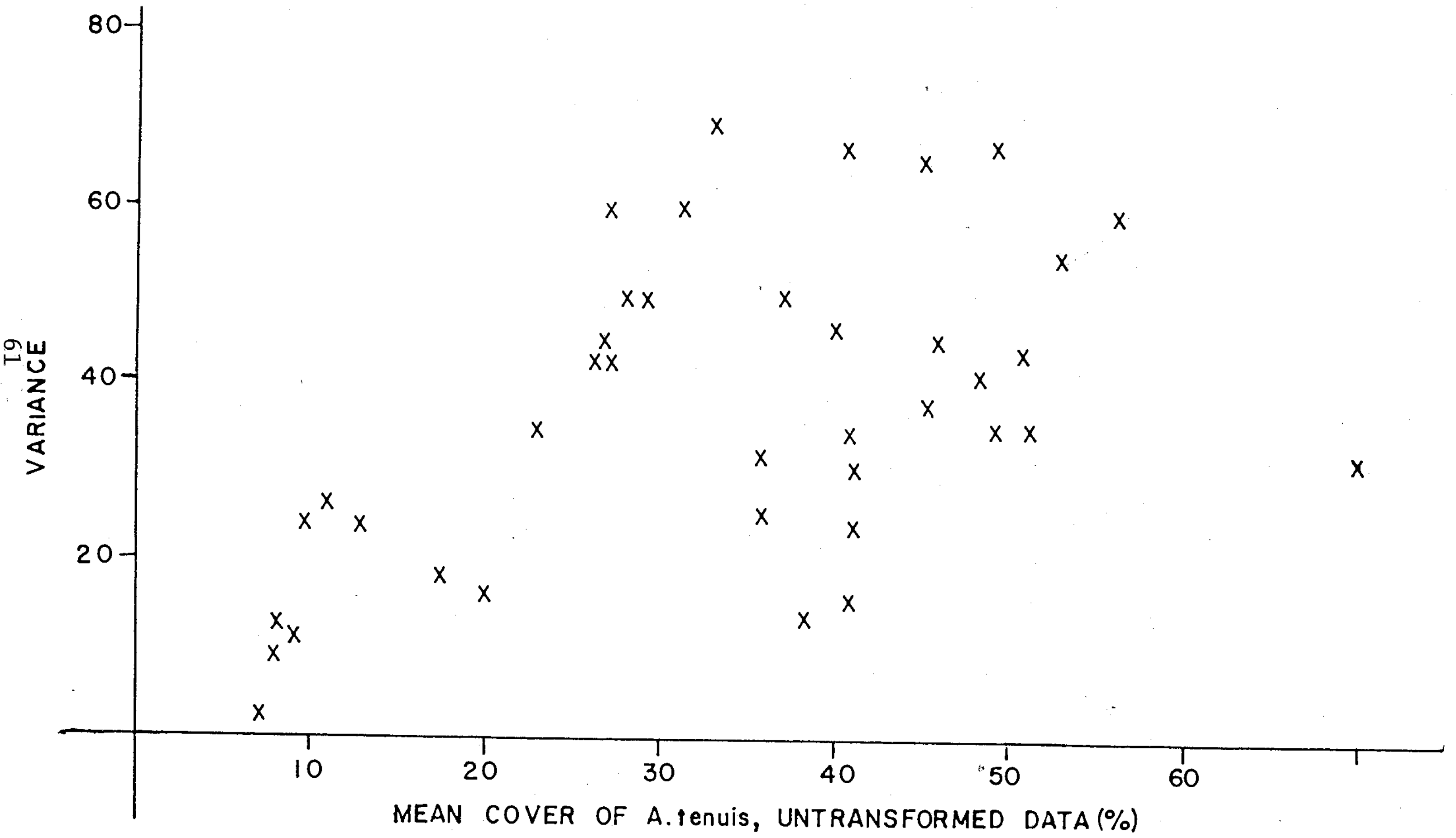


FIGURE 4: UNTRANSFORMED VARIANCE:MEAN RATIO FOR <u>A. tenuis</u>
SAMPLE DATA.

Table 4: Comparison of Untransformed and Transformed Species Percentage Cover Data.

	Skewness			Probability of Variance Homogeneity	
	Untransf. data	Log(x+1) transf.	Arcsin transf.	Untransf. data	Arcsin data
Agrostis alba	2.61	1.00	1.25	-	-
Agrostis tenuis(*)	0.35	-0.57	-0.21	0.025	0.160
Festuca rubra(*)	0.11	-0.87	-0.25	0.171	0.005
Phleum pratense(*)	0.91	-0.09	0.15	0.000	0.247
Poa compressa	3.86	2.48	2.34	-	-
Trifolium hybridum(*)	1.12	0.46	0.68	-	-
Trifolium repens	2.82	1.77	1.70	-	-

LEGEND:

(*) Species data examined by ANOVA.

- No significance value presented due to the presence of zero variance values.

The arcsin transformation is represented by the square root of (original value/100), after Fisher and Yates (1948).

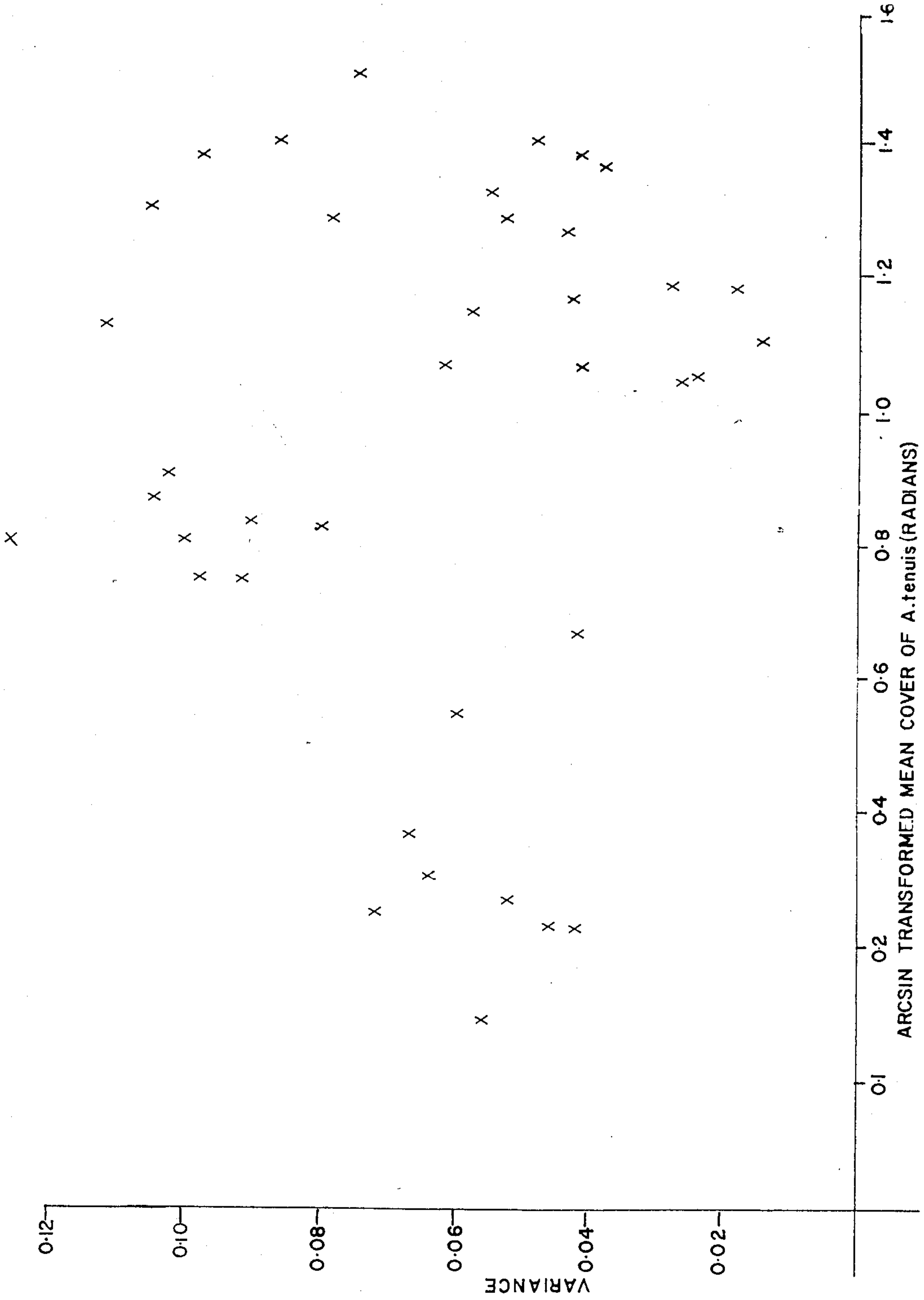


FIGURE 5 : ARCSIN TRANSFORMED VARIANCE:MEAN RATIO FOR A. tenuis SAMPLE DATA.

distribution. However, it is generally assumed that sampled and transformed population data follows an approximate normal distribution, as this population appears to do, and that the ANOVA procedure is robust to such small degrees of non-normality (Ito, 1980; Underwood, 1981).

The removal of any dependence of the variance on the mean sample values by the arcsin transformation is shown clearly in Figure 5. Its influence on variance heterogeneity is generally beneficial, although _F. rubra_ does show an opposite trend. However, the ANOVA technique is considered to be extremely robust against heterogeneity of variance (Ito, 1980), and only gross violations of this assumption invalidate its use (Underwood, 1981). Furthermore, this author outlines the usefulness of the arcsin transformation to ensure that treatment effects are additive, especially when interaction effects are of concern.

The previous discussion indicates that only gross violations of the assumptions governing the use of the ANOVA procedure can influence the outcome of the analysis. The use of the ANOVA procedure, concomitant with an arcsin transformation of the data, is therefore thought to be fully justified, in terms of satisfying the underlying assumptions. Furthermore, the applicability of ANOVA techniques and arcsin transformation to percentage cover data collected using a point cover frame is well established (Goodall, 1952; Greig-Smith, 1964; Kershaw, 1973).

4.3.3: Contact Sampling Data

The contact sampling data were tabulated for each altitude class and for the mulched data set in the form of individual count matrices. Following de Jong et al. (1983) the principal diagonal was zero throughout and the distinction between species i and species j retained by keeping the matrix unfolded, i.e. in its original rectangular form.

Each count matrix was analysed using a computer package program supplied by R. Turkington in the Botany Department at the University of British Columbia. The theoretical basis of this program is given in de Jong et al. (1983).

In using this procedure it is necessary to select an appropriate model for testing the data. The probability of each species occuring as species i and j for each matrix (presented in Appendix 7) and the fact that the species subject to statistical analysis all have an erect form of growth allowed for the proportionality assumption, that for each species the probability of occurrence as species i equals the probability of occurrence as species j, to be made.

The hypothesis tested was that of random association among the species. In the appraisal of paired association significance values it was therefore assumed that all associations, other than those under test, are non-random. In consequence, the two degree of freedom test, as used by de Jong et al. (1983), was adopted as a basis for significance testing. In the analysis an iterative calculation is performed in which a chi-square statistic is used to indicate significant non-random, associations. This is calculated for each species pair, concomitant with two indices of association that indicate whether any non-random associations are positive or negative.

However, it must be realised that this method of sampling and analysis has been developed for large numbers of samples in uniform abiotic environments. As will become evident, the habitat classes used to construct the count matrices do not represent uniform abiotic environments and species cohabitation will likely be influenced by this. Also, the sample sizes are relatively small, in comparison with other studies that have used this procedure, due to an overall time constraint. These considerations clearly influence the validity of the use and interpretation of this method. However, conventional practice necessitates that the expected number of counts in each cell should be at least five. Examination of the results was therefore restricted to the major species in the community. Furthermore, the restrictive nature of the two degree of freedom test and the cautionary nature in which the method is used, and the results discussed, are thought to make its use valid here.

CHAPTER 5

RESULTS

5.1: Introduction

The results of the vegetation survey and the soil sampling procedure are presented in this chapter in accordance with the basic theme of examining how the species in an artificial, developing, grass-legume community cohabit. This enables the types of differences that occur between the species to be outlined in relation to:

1. spatial variation in large-scale abiotic factors (section 5.3);
2. localised edaphic variation (section 5.4);
3. morphology and interactions within the sward (section 5.5).

As a baseline for describing the variation in relative abundance that exists, and because the community has been seeded for the primary purpose of erosion control, the overall vegetation cover is first described in section 5.2.

5.2: Overall Vegetation Cover

The establishment of a vegetation cover in the study area has been relatively successful. The mean occurrence of bare ground is only 5%, resulting in a mean total vegetative cover of 95%. Similarly, 90% of the vegetated area consists of seeded species. The mean cover values for seeded and non-seeded species are presented in Table 5. Non-seeded species, with the exception of bryophytes, have been grouped together because of their low individual cover values.

Clearly, Festuca rubra is the dominant species in this artificial, developing community. Three other species, Agrostis tenuis, Phleum pratense and Trifolium hybridum, combine with F. rubra to make up the major part of the vegetation cover. These species have mean cover values greater than their percentage occurrence in the seed mixture. The remaining species have mean cover values lower than their percentage occurrence in the seed mix. This is especially so for Poa compressa.

Bryophytes account for the major part of non-seeded species cover. The predominant, non-seeded, vascular species are Dactylis glomerata, Phalaris arundinacea, Equisetum spp. and Epilobium angustifolium.

Table 5: Mean Species Cover (+/- SE),
Altitude Classes 1-3.

Species	Mean Cover (%) +/- SE
Agrostis alba	8.4 +/- 0.6
Agrostis tenuis	32.6 +/- 1.1
Festuca rubra	41.0 +/- 1.2
Phleum pratense	23.1 +/- 1.0
Poa compressa	2.0 +/- 0.2
Trifolium hybridum	19.7 +/- 1.1
Trifolium repens	3.8 +/- 0.4
Total Seeded Species	90.1 +/- 0.7
Bryophytes	9.1 +/- 0.7
Non-seeded Vascular Species	4.9 +/- 0.4
Bare	5.3 +/- 0.5

LEGEND:
SE represents the standard error of the mean.

Total Seeded Species represents the total cover of seeded species as a group, not the sum of the individual species cover values.

5.3: Large Scale Pattern

5.3.1: Introduction

The percentage cover data has been categorised according to sample sites and is presented as a species/sample site matrix in Table 6. There are clear variations in the relative abundance of species with respect to each other and sample sites. Various trends are apparent with respect to slope and altitude.

The subsequent analysis of species data is restricted to the four major species: Agrostis tenuis, Festuca rubra, Phleum pratense and Trifolium hybridum. The three other seeded species, and non-seeded species, have mean cover values of less than 10%. The occurrence of such minor species is usually more a matter of chance than an indication of ecological conditions (Gauch, 1982). As a result they tend to be scattered at random along environmental gradients (Whittaker et al., 1973). Statistical analysis of cover data for these species is therefore thought to be invalid, and they are considered solely in a descriptive manner.

In response to the observation of possible trends in the species data the percentage cover values for the four major species were grouped into an altitude/slope angle cell matrix. A 2-way ANOVA was computed on these data to test the hypothesis that species cover values are not significantly correlated with altitude and slope angle. The ANOVA Tables are presented in Appendix 1. Any significant differences were then examined using

Legend For Table 6.

Altitude Class	1	2	3
Range(m)	675-850	850-1000	1000-1150

Slope Angle Class	1	2	3	4	5
Range (degrees)	0-2	3-4	5-8	9-16	+16

Table 6: Relationship of Mean Percentage Cover (+/- SE) to Altitude and Slope Angle.

Cell No.	Alt. Class	Slope Angle Class	Rep. No.	No. of Samples	Agrostis alba	Agrostis tenuis
1	1	1	1	10	5.0+/- 1.7	8.0+/- 2.9
2	1	1	2	9	7.8+/- 6.6	17.7+/- 4.6
3	1	1	3	9	5.6+/- 2.4	26.7+/- 6.9
4	1	2	1	17	0.0+/- 0.0	8.9+/- 2.8
5	1	2	2	7	8.5+/- 2.6	31.4+/- 9.4
6	1	2	3	10	2.0+/- 1.3	26.0+/- 6.5
7	1	3	1	14	40.7+/- 8.6	11.4+/- 4.4
8	1	3	2	10	19.0+/- 6.2	10.0+/- 4.9
9	1	3	3	10	3.0+/- 2.1	20.0+/- 4.2
10	1	4	1	30	19.6+/- 3.6	12.7+/- 2.9
11	1	4	2	15	2.0+/- 1.4	33.3+/- 6.9
13	1	5	1	23	7.4+/- 2.9	9.6+/- 2.2
14	1	5	2	8	8.8+/- 0.5	28.7+/- 7.9
16	2	1	1	9	12.2+/- 4.9	37.8+/- 4.0
17	2	1	2	9	2.2+/- 1.5	34.4+/- 5.0
19	2	2	1	9	2.2+/- 2.2	36.7+/- 7.4
20	2	2	2	8	21.3+/- 2.3	41.2+/- 6.7
22	2	3	1	14	1.4+/- 1.0	36.4+/- 4.1
23	2	3	2	8	12.5+/- 4.1	36.3+/- 6.2
24	2	3	3	8	6.3+/- 4.2	27.5+/- 7.5
25	2	4	1	10	4.0+/- 2.2	53.0+/- 7.3
26	2	4	2	14	5.7+/- 2.0	41.4+/- 4.3
27	2	4	3	14	0.7+/- 0.7	7.1+/- 3.0
28	2	5	1	25	10.0+/- 2.1	45.2+/- 3.9
29	2	5	2	10	0.0+/- 0.0	41.0+/- 8.2
31	3	1	1	9	7.7+/- 3.2	41.1+/- 4.2
32	3	1	2	14	5.0+/- 2.0	46.4+/- 5.7
33	3	1	3	8	1.3+/- 1.2	45.0+/- 8.9
34	3	2	1	9	7.8+/- 1.5	56.7+/- 8.1
35	3	2	2	9	5.6+/- 2.4	41.1+/- 5.9
36	3	2	3	12	3.3+/- 2.3	49.2+/- 7.5
37	3	3	1	9	10.0+/- 3.3	27.8+/- 8.1
38	3	3	2	10	1.0+/- 1.0	51.0+/- 6.0
39	3	3	3	12	10.8+/- 3.6	70.0+/- 5.2
40	3	4	1	9	6.7+/- 2.9	40.0+/- 7.3
41	3	4	2	25	10.4+/- 2.0	49.2+/- 3.9
43	3	5	1	20	6.0+/- 2.0	28.5+/- 5.0
44	3	5	2	6	11.7+/- 3.1	51.7+/- 8.7
45	3	5	3	9	13.3+/- 4.1	48.9+/- 6.8

Table 6 (cont.)

Cell No.	Festuca rubra	Phleum pratense	Poa compressa
1	50.0+/- 8.9	9.0+/- 3.5	5.0+/- 5.0
2	68.8+/- 8.4	18.8+/- 5.9	6.7+/- 3.3
3	54.5+/- 7.1	20.0+/- 4.1	3.3+/- 2.4
4	62.3+/- 5.5	3.5+/- 1.5	2.3+/- 1.8
5	45.7+/- 5.3	14.2+/- 4.3	4.2+/- 8.9
6	43.0+/- 8.7	30.0+/- 7.9	1.0+/- 1.0
7	35.7+/- 9.6	28.5+/- 7.1	1.4+/- 0.9
8	44.0+/- 6.7	19.0+/- 4.3	1.0+/- 1.0
9	45.0+/- 7.3	16.0+/- 5.4	1.0+/- 1.0
10	23.3+/- 4.2	12.3+/- 4.1	1.0+/- 0.6
11	22.0+/- 6.4	26.7+/- 6.2	1.3+/- 1.3
13	60.9+/- 5.6	25.2+/- 4.6	0.0+/- 0.0
14	57.5+/- 6.2	31.2+/-11.0	7.5+/- 4.1
16	25.6+/- 6.3	15.6+/- 5.0	1.1+/- 1.1
17	55.6+/-10.3	12.2+/- 5.2	1.1+/- 1.1
19	52.2+/- 9.5	10.0+/- 3.3	0.0+/- 0.0
20	32.5+/- 7.0	3.8+/- 1.8	0.0+/- 0.0
22	20.0+/- 4.3	10.0+/- 3.5	0.0+/- 0.0
23	50.0+/- 5.3	33.8+/- 7.3	2.5+/- 1.7
24	58.7+/- 6.4	7.5+/- 3.1	1.3+/- 1.2
25	52.0+/- 5.3	8.0+/- 4.4	1.0+/- 1.0
26	39.3+/- 3.7	18.6+/- 4.2	0.7+/- 0.7
27	57.1+/- 8.8	30.0+/- 5.6	6.4+/- 2.5
28	40.4+/- 5.3	22.8+/- 3.7	0.4+/- 0.4
29	52.0+/- 5.1	61.0+/- 5.2	0.0+/- 0.0
31	12.2+/- 3.2	25.6+/- 8.2	1.1+/- 1.1
32	19.3+/- 6.3	46.4+/- 5.7	2.9+/- 2.2
33	17.5+/- 8.0	43.8+/- 4.6	0.0+/- 0.0
34	44.4+/- 5.8	20.0+/- 6.0	1.1+/- 1.1
35	27.8+/- 5.9	27.8+/- 5.2	2.2+/- 1.5
36	31.7+/- 6.1	20.8+/- 5.4	2.5+/- 1.3
37	35.6+/- 7.8	50.0+/- 6.5	5.6+/- 1.8
38	43.0+/- 8.0	31.0+/-10.2	2.0+/- 1.3
39	28.3+/- 4.7	20.0+/- 4.2	0.0+/- 0.0
40	60.0+/- 7.6	36.7+/- 7.1	3.3+/- 1.7
41	30.4+/- 4.8	20.4+/- 3.7	4.0+/- 1.3
43	43.0+/- 5.2	30.0+/- 4.5	2.5+/- 1.0
44	55.0+/- 8.5	26.7+/- 9.9	1.6+/- 1.6
45	43.3+/- 6.2	37.8+/- 7.9	1.1+/- 1.1

Table 6 (cont.)

Cell No.	Trifolium hybridum	Trifolium repens	Total Seeded Species
1	55.0+/- 7.5	7.0+/- 3.4	89.0+/- 7.0
2	16.6+/- 5.3	5.6+/- 3.4	98.9+/- 0.1
3	40.0+/- 8.2	11.1+/- 5.6	96.7+/- 1.7
4	34.2+/- 5.1	2.9+/- 1.7	86.5+/- 3.4
5	0.0+/- 0.0	0.0+/- 0.0	85.7+/- 4.8
6	44.0+/- 7.5	10.0+/- 2.6	98.0+/- 1.3
7	19.2+/- 7.1	1.4+/- 1.0	99.2+/- 0.7
8	3.0+/- 2.1	2.0+/- 2.0	82.0+/- 4.1
9	26.0+/- 8.2	16.0+/- 5.4	91.0+/- 4.8
10	5.3+/- 2.8	0.6+/- 0.4	66.7+/- 5.2
11	28.0+/- 6.4	7.3+/- 3.3	85.3+/- 3.9
13	0.9+/- 0.8	0.0+/- 0.0	89.1+/- 2.9
14	22.5+/- 8.6	6.3+/- 5.0	100 +/- 0.0
16	5.6+/- 3.4	1.1+/- 1.1	82.2+/- 4.3
17	60.0+/-10.0	7.8+/- 2.8	94.4+/- 4.4
19	52.2+/-10.4	8.8+/- 3.5	92.2+/- 5.7
20	41.2+/- 8.7	11.2+/- 4.0	98.8+/- 1.2
22	53.5+/- 5.4	2.1+/- 1.5	92.8+/- 3.0
23	15.0+/- 7.1	1.3+/- 1.2	100 +/- 0.0
24	40.0+/-10.7	1.3+/- 1.2	96.3+/- 2.6
25	16.0+/- 7.0	5.0+/- 3.1	91.0+/- 1.6
26	8.6+/- 3.6	3.6+/- 2.0	94.3+/- 1.8
27	33.5+/- 6.1	7.1+/- 2.6	95.7+/- 2.0
28	4.4+/- 1.8	4.0+/- 2.4	88.4+/- 8.5
29	59.0+/- 4.6	4.0+/- 2.2	97.0+/- 2.1
31	13.3+/- 5.8	1.1+/- 1.1	81.1+/- 4.5
32	7.1+/- 5.1	0.7+/- 0.7	87.8+/- 4.1
33	7.5+/- 7.5	0.0+/- 0.0	80.0+/- 5.6
34	13.3+/- 5.0	3.3+/- 2.3	96.7+/- 1.7
35	17.8+/- 4.6	3.3+/- 2.3	91.1+/- 5.4
36	37.5+/-10.2	7.5+/- 3.0	91.7+/- 5.9
37	12.2+/- 4.0	3.3+/- 1.7	98.9+/- 1.1
38	30.0+/- 8.8	3.0+/- 1.5	93.0+/- 4.7
39	6.7+/- 3.6	4.2+/- 1.5	95.8+/- 2.6
40	4.4+/- 2.4	2.2+/- 2.2	98.9+/- 1.1
41	2.0+/- 1.0	0.4+/- 0.4	92.0+/- 2.8
43	9.5+/- 3.2	0.5+/- 0.2	89.5+/- 2.5
44	3.3+/- 3.3	0.0+/- 0.0	98.3+/- 1.7
45	3.3+/- 2.4	0.1+/- 0.1	92.2+/- 3.2

Table 6 (cont.)

Cell No.	Bryophytes	Non-seeded Vascular Species	Bare Soil
1	26.0+/- 7.7	10.2+/- 5.4	2.0+/- 2.0
2	7.8+/- 6.6	0.0+/- 0.0	0.0+/- 0.0
3	4.4+/- 2.9	5.6+/- 3.8	2.2+/- 1.5
4	3.5+/- 1.9	31.0+/- 8.2	0.6+/- 0.6
5	11.4+/- 4.6	0.0+/- 0.0	4.3+/- 2.9
6	5.0+/- 3.1	12.0+/- 2.9	3.0+/- 3.0
7	0.0+/- 0.0	0.0+/- 0.0	0.0+/- 0.0
8	11.0+/- 6.9	0.0+/- 0.0	12.0+/- 2.0
9	3.0+/- 1.5	11.0+/- 7.3	4.0+/- 4.0
10	4.7+/- 1.8	11.9+/- 5.4	19.3+/- 3.8
11	24.0+/- 7.9	15.3+/- 4.4	4.0+/- 1.9
13	14.3+/- 2.0	0.0+/- 0.0	6.0+/- 1.6
14	0.0+/- 0.0	2.4+/- 1.4	0.0+/- 0.0
16	10.0+/- 5.8	0.0+/- 0.0	15.6+/- 5.0
17	5.6+/- 5.6	3.0+/- 1.6	3.3+/- 3.3
19	15.6+/- 6.5	1.0+/- 1.0	4.4+/- 4.4
20	11.3+/- 5.2	0.0+/- 0.0	0.0+/- 0.0
22	14.3+/- 3.6	5.0+/- 3.1	7.8+/- 3.5
23	11.3+/- 4.0	0.0+/- 0.0	0.0+/- 0.0
24	1.3+/- 1.2	4.0+/- 2.0	1.3+/- 1.2
25	15.0+/- 5.8	0.0+/- 0.0	4.0+/- 2.7
26	14.3+/- 4.8	0.0+/- 0.0	3.6+/- 1.3
27	7.8+/- 1.9	0.0+/- 0.0	2.1+/- 1.6
28	15.2+/- 3.4	0.0+/- 0.0	5.2+/- 2.4
29	1.0+/- 1.0	6.0+/- 4.0	0.0+/- 0.0
31	21.1+/- 5.4	0.0+/- 0.0	6.7+/- 2.3
32	4.3+/- 2.5	0.0+/- 0.0	11.4+/- 4.0
33	30.3+/-12.2	0.0+/- 0.0	12.5+/- 5.6
34	5.6+/- 5.5	11.1+/- 2.6	1.1+/- 1.1
35	0.0+/- 0.0	0.0+/- 0.0	7.8+/- 4.3
36	15.8+/- 6.2	0.0+/- 0.0	1.7+/- 1.7
37	4.4+/- 4.4	1.0+/- 1.0	1.1+/- 1.1
38	1.1+/- 0.4	0.0+/- 0.0	4.0+/- 3.1
39	5.8+/- 3.1	0.0+/- 0.0	3.3+/- 2.6
40	1.1+/- 1.1	0.0+/- 0.0	1.1+/- 0.0
41	4.4+/- 2.6	0.0+/- 0.0	6.4+/- 2.1
43	6.0+/- 2.8	0.5+/- 0.5	6.5+/- 1.8
44	0.0+/- 0.0	0.0+/- 0.0	1.6+/- 1.6
45	0.0+/- 0.0	5.6+/- 2.1	3.3+/- 2.4

the modified range test procedure of Kramer (1956). These calculations and results are presented in Appendix 2. The variation in abundance of the four major species is now considered.

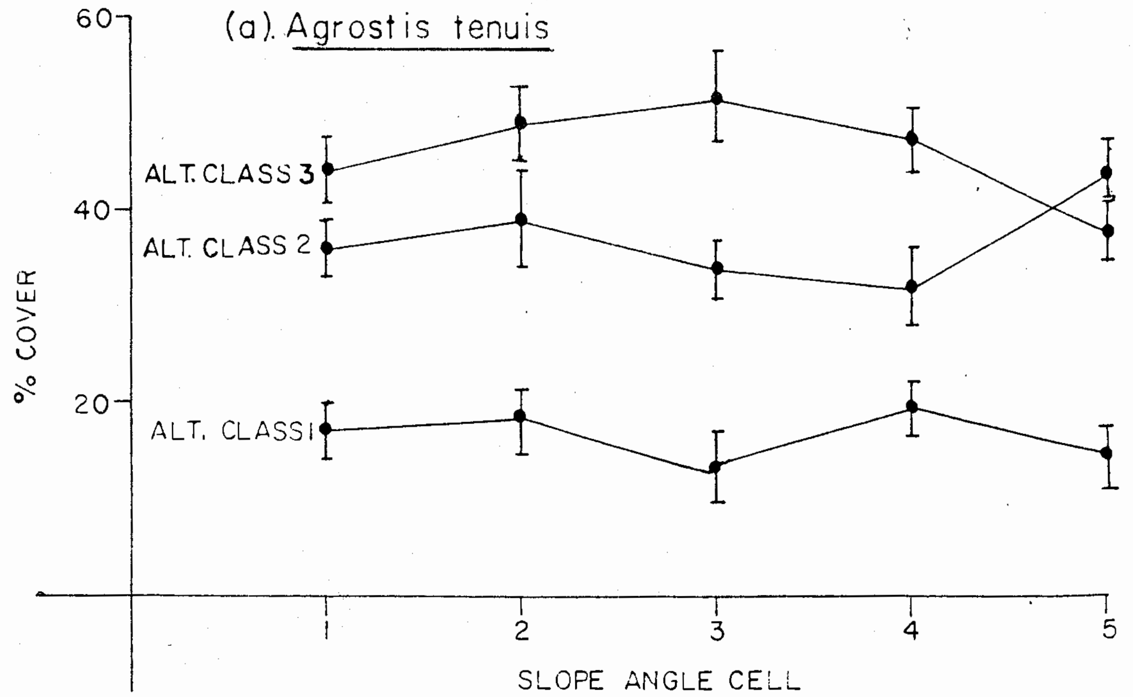
5.3.2: Agrostis tenuis

As shown in Figure 6a the percentage cover of *A. tenuis* tends to increase with increasing altitude. This relationship is significant ($p<0.001$), with all three mean values for each class being significantly different from each other ($p<0.05$).

5.3.3: Festuca rubra

A significant interaction effect ($p<0.001$) was detected for the relationship between altitude and slope angle and the percent cover values of *F. rubra*. Figure 6b indicates a decrease in cover with increasing altitude. From the range tests it was found that the mean for the highest altitude samples is significantly less ($p<0.01$) than that for the lower altitude classes. The latter two are not statistically different.

The cover values plotted in Figure 6b suggest that the influence of slope angle on this interaction effect is the result of certain cells in the matrix having markedly lower values, rather than the result of any general trend. The significance of slope angle within each altitude class was tested by 1-way ANOVA. Significant differences were detected in


(a). *Agrostis tenuis*

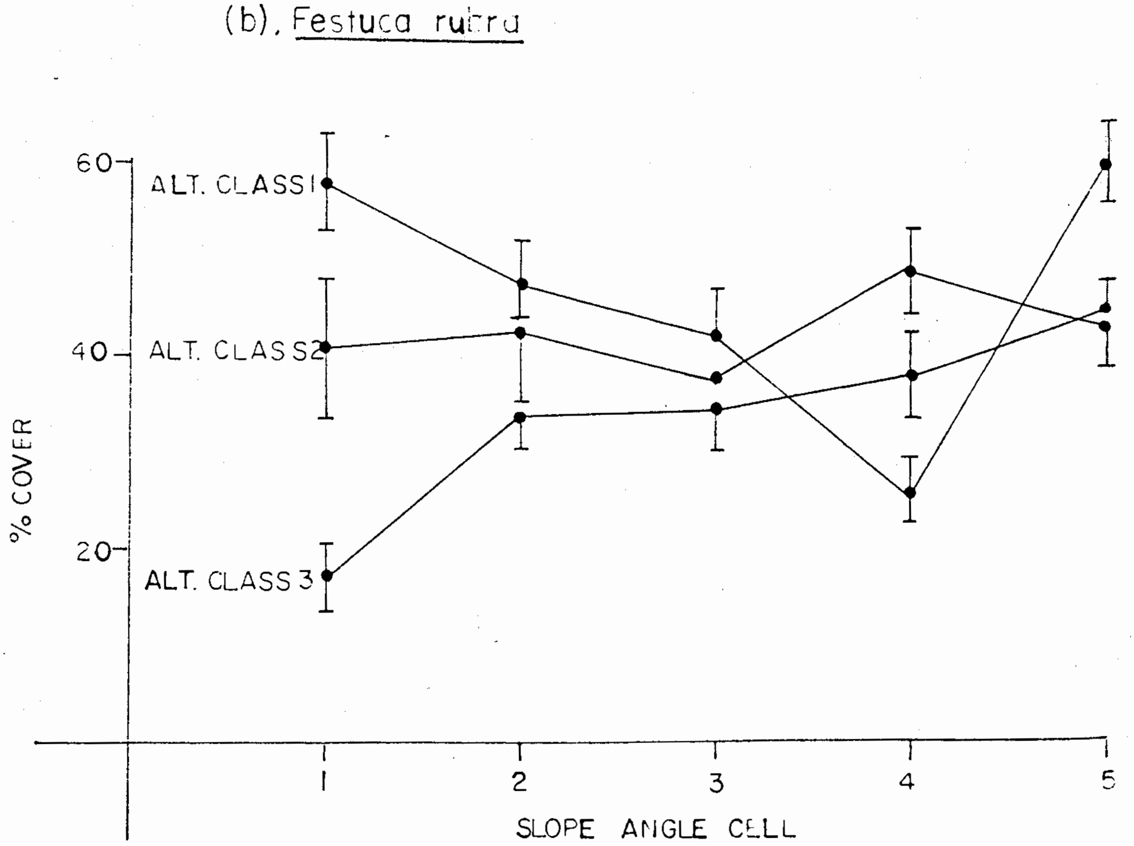
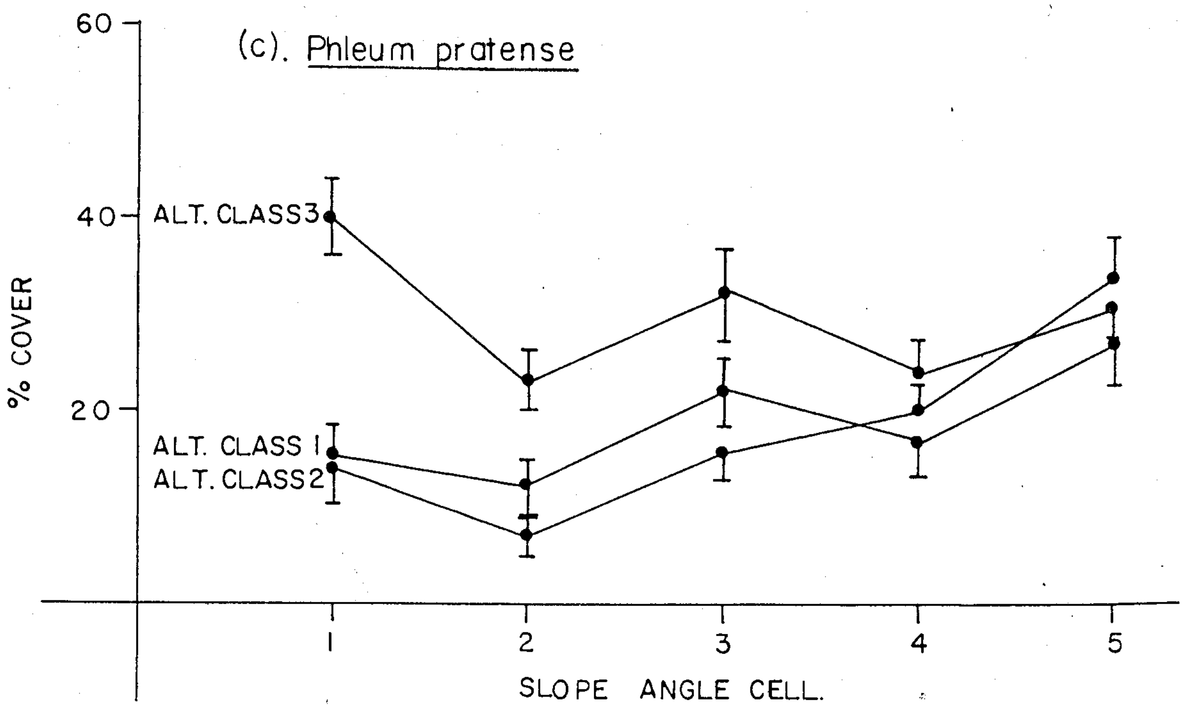
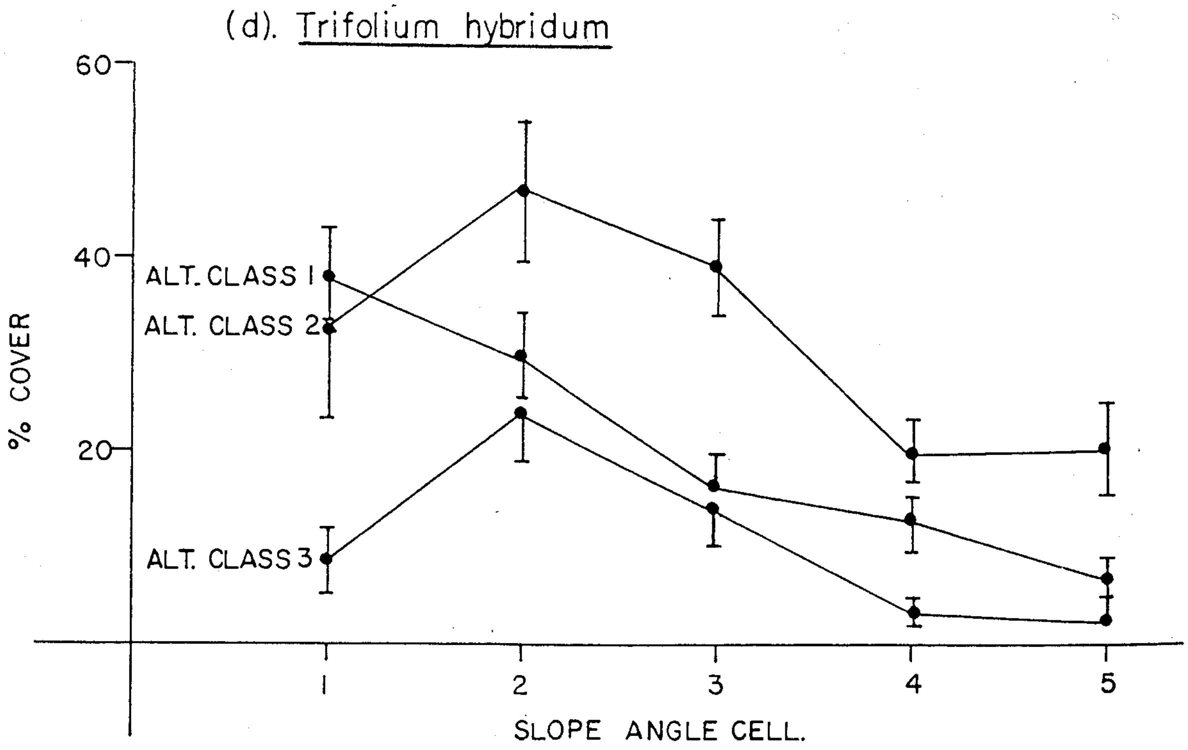

(b). *Festuca rubra*

FIGURE 6: RELATIONSHIP OF % COVER OF THE 4 MAJOR SPECIES TO ALTITUDE AND SLOPE ANGLE.



(c). *Phleum pratense*



(d). *Trifolium hybridum*

FIGURE 6: (Cont.)

the lowest and highest altitude classes (p<0.001), but not in class 2.

For the lowest altitude class the range test gave the following result:

```
slope angle class    4 3 2 1 5
                         -----
                       ---
```

Where two slope angle classes are underscored by the same line their mean cover values are not significantly different (p<0.01). Mean cover values increase from left to right. In this case the abundance of <u>F. rubra</u> is significantly less in slope angle class 4 (p<0.01), which corresponds to a slope angle of 8-16 degrees, than in the other classes. The latter show very little statistical difference.

The range tests for the highest altitude class indicated that the mean for slope angle classes is significantly lower in the flat sites compared with all the other slope angle means (p<0.01). The latter show no statistical differences amongst themselves:

```
slope angle class    1 2 3 4 5
                       -------
```

5.3.4: <u>Phleum</u> <u>pratense</u>

As depicted in Figure 6c cover values for this species tend to increase with increasing elevation and slope angle. A significant interaction effect of altitude and slope angle was detected (p<0.05). As indicated by the range tests this species has statistically similar values in the two lowest altitude classes, both of which are significantly different from the mean value for the highest altitude class ($p<0.01$).

The relationship with slope angle is more variable. Significant differences occur in the two lower altitude classes ($p<0.05$ and $p<0.001$ respectively), but not in the highest altitude class. In the lowest class the following relationship was established:

```
slope angle class   2 4 1 3 5
                    -------
                          ---
```

So, this species shows significantly greater cover values on the steepest slopes. It is noticeable that its % cover is less in class 4 than either 1 or 3. This class also gave anomalous results for *F. rubra*. In the middle altitude class a similar, albeit more gradual, relationship exists:

```
slope angle class   2 1 3 4 5
                      -----
                    -----
```

Clearly, the steepest slopes , i.e. those with angles greater than 16 degrees, exhibit a significantly greater cover value than all the shallower gradients ($p<0.05$). The latter display a gradual statistical increase with increasing slope angle.

5.3.5: *Trifolium hybridum*

Altitude and slope angle also have a significant interaction relationship with this species ($p<0.01$). As shown by

Figure 6d its distribution is almost a "mirror image" of that recorded for P. pratense. The mean values for each altitude class are all significantly different from each other ($p<0.01$), cover tending to decrease with increasing altitude. What is worthy of note here is the marked decrease in the highest altitude class.

Variation in slope angle exhibits a significant relationship ($p<0.001$) with cover values within all three altitude classes, and displays an interesting trend. Within the lowest altitude class the following relationship exists:

```
slope angle class   5 4 3 2 1
                    -----
                          ---
```

T. hybridum is therefore more abundant on the gentler, drier slopes. In class 2 a slightly different relationship exists:

```
slope angle class   4 5 1 3 2
                    -----
                        -----
```

Here, T. hybridum exhibits a statistical preference for the intermediate sites on the gradient, being restricted in the very wet and very dry sites. A similar, although slightly less marked, relationship exists in the highest altitude class:

```
slope angle class   4 5 1 3 2
                          ---
                      -----
                    -----
```

The optimum habitat thus appears to shift to slightly better drained sites with increasing altitude. All significance values for this species are at the $p<0.05$ level.

5.3.6: Other Seeded Species

The relative abundance of the three other seeded species in each site is shown in Table 6. Clearly, *Poa compressa* exhibits the lowest percentage cover values throughout the study area. Its cover values are consistently less than its proportion in the seed mixture. *Agrostis alba* displays a much larger degree of variation in cover values. But, despite its 15% proportion of the seed mixture it maintains low cover values in the developing community. Although *Trifolium repens* was seeded at a lower rate (5%) than these two species, its cover values are consistently greater than those for *P. compressa* and compare favourably with *A. alba* in the lower two elevation classes. In the highest altitude class sites, however, *A. alba* shows consistently greater cover values than *T. repens*.

5.3.7: Non-seeded Species

Bryophytes show no consistent trends in percentage cover values with respect to the large scale environmental gradients. However, a fairly large degree of variation does exist between sites, in some of which colonisation has been relatively successful (see Table 6).

In contrast, non-seeded vascular species exhibit a reduction in overall cover values and variation in species composition with increasing altitude. On the lowest elevation slopes this group is composed predominantly of *Dactylis glomerata*, *Phalaris arundinacea* and *Equisetum spp<font normal>.,* the latter two occurring mostly on slopes with low gradients. In the higher elevation sites Epilobium angustifolium becomes the major component of this group of species. Other local and ruderal species were recorded during the course of the vegetation survey, but only to a very limited extent.

5.3.8: Mulched Sites

The mean cover values of each species in the mulched sites, together with their overall means in this data set are presented in Table 7. A 2-way ANOVA was performed using this matrix and that for the altitude class 1 species/sample site matrix to test the hypothesis that the four dominant species are not significantly influenced by mulching over the range of slopes encompassed in the study area. The relevant ANOVA Tables and range tests are given in Appendix 3.

A. tenuis showed a significant difference ($p<0.05$) with respect to slope angle. This appears to be due to decreasing cover with increasing slope in the mulched samples. However, in the mulched data this species exhibits a high degree of variation between replicates, especially on the shallow slopes and flat areas. Consequently, no further statistical analysis for this species was undertaken, although a possible interpretation of these observations is provided in section 6.2.5.

F. rubra displayed a significant interaction effect ($p<0.001$). This appears to be mainly due to slope angle, but is

Table 7: Mean % Cover (+/- SE) In The Mulched Sites.

Slope Angle Class	Rep. No.	No. of Samples	Agrostis alba	Agrostis tenuis	Festuca rubra
1	1	12	20.8+/- 5.8	10.8+/- 4.3	64.2+/- 0.4
1	2	6	3.3+/- 2.1	42.0+/-10.5	30.0+/-10.3
2	1	6	10.0+/- 6.3	8.3+/- 4.7	38.3+/-12.2
2	2	9	1.1+/- 1.1	48.9+/-11.0	30.0+/- 9.1
3	1	12	8.3+/- 4.4	10.0+/- 4.8	40.8+/- 5.7
3	2	6	0.0+/- 0.0	31.7+/- 1.2	50.0+/- 6.8
4	1	11	0.9+/- 0.9	35.5+/- 5.6	40.0+/- 5.7
4	2	12	0.8+/- 0.8	18.3+/- 5.3	30.6+/- 6.5
5	1	24	15.0+/- 3.1	16.7+/- 3.6	32.9+/- 5.0
5	2	6	1.7+/- 1.7	11.7+/- 1.0	40.0+/-13.2
Overall Mean		104	7.9+/- 1.7	21.7+/- 2.3	39.1+/- 2.4

Slope Angle Class	Rep. No.	No. of Samples	Phleum pratense	Poa compressa
1	1	12	10.8+/- 3.6	0.8+/- 0.8
1	2	6	20.0+/- 8.1	1.7+/- 1.7
2	1	6	16.7+/- 4.2	0.0+/- 0.0
2	2	9	15.6+/- 3.4	0.0+/- 0.0
3	1	12	28.3+/- 6.0	5.8+/- 2.6
3	2	6	26.7+/- 4.2	0.0+/- 0.0
4	1	11	16.4+/- 4.5	0.0+/- 0.0
4	2	12	21.7+/- 5.3	10.0+/- 2.5
5	1	24	25.8+/- 2.8	1.2+/- 0.7
5	2	6	40.0+/- 1.0	0.0+/- 0.0
Overall Mean		104	22.0+/- 1.7	2.3+/- 0.6

LEGEND:

Slope Angle Class	1	2	3	4	5
Range (degrees)	0-2	3-4	5-8	9-16	+16

Table 7 (cont.)

Slope Angle Class	Rep. No.	No. of Samples	Trifolium hybridum	Trifolium repens	Total Seeded Species
1	1	12	3.3+/- 2.2	0.8+/- 0.8	94.2+/- 1.5
1	2	6	28.3+/-10.8	0.0+/- 0.0	90.0+/- 6.3
2	1	6	50.0+/- 1.2	3.3+/- 2.1	91.7+/- 1.7
2	2	9	14.4+/- 7.8	2.2+/- 1.5	87.8+/- 4.9
3	1	12	30.8+/- 8.4	9.2+/- 3.4	93.3+/- 2.8
3	2	6	35.0+/- 8.9	6.7+/- 2.1	96.7+/- 2.1
4	1	11	47.3+/- 4.7	9.1+/- 3.4	98.2+/- 1.2
4	2	12	7.5+/- 3.5	0.8+/- 0.8	70.8+/- 6.7
5	1	24	12.1+/- 4.0	2.1+/- 1.7	83.3+/- 2.8
5	2	6	10.0+/- 3.7	3.3+/- 2.1	88.3+/- 4.7
Overall Mean		104	21.0+/- 2.4	3.7+/- 0.8	88.2+/- 1.4

Slope Angle Class	Rep. No.	No. of Samples	Bryophytes	Bare Soil
1	1	12	2.5+/- 1.3	5.0+/- 1.5
1	2	6	8.3+/- 4.0	6.7+/- 3.3
2	1	6	30.0+/-13.4	3.3+/- 2.1
2	2	9	7.8+/- 5.5	8.9+/- 2.0
3	1	12	9.2+/- 3.8	3.3+/- 2.6
3	2	6	1.7+/- 1.7	3.3+/- 2.1
4	1	11	8.2+/- 4.0	1.8+/- 1.2
4	2	12	30.0+/- 8.2	20.0+/- 6.0
5	1	24	22.1+/- 5.1	9.5+/- 1.6
5	2	6	0.0+/- 0.0	13.3+/- 4.2
Overall Mean		104	13.8+/- 2.1	8.0+/- 1.1

highly variable, as can be seen with reference to Appendix 3.

P. pratense again shows a significant relationship with slope angle ($p<0.001$). As already described it shows an increase in cover with increasing slope angle in the lowest altitude class. A similar trend is shown in the mulched data set:

```
slope angle class   1 2 4 3 5
                    -----
                      -------
```

The mean cover in the flat sites is significantly lower ($p<0.05$) than the range encompassed by the other slopes. Once again this species occurs most abundantly on the steepest slopes.

T. hybridum also exhibits a significant interaction effect ($p<0.001$). The variation that occurs with respect to slope angle in the muched data set follows a similar pattern to that described previously for this species:

```
slope angle class   1 5 4 2 3
                    ---
                      -----
                        -----
```

The very wet and the very dry sites tending to have significantly lower mean cover values than the intermediate sites on this gradient ($p<0.05$). Although this trend is less marked than in the higher altitude classes.

5.4: Soil Properties

5.4.1: Soil Chemistry

The results of the soil chemical analyses are presented in Table 8. These analyses were performed to test for any variation in soil chemical factors attributable to variation in altitude or slope angle and to examine the possible influence of soil chemistry on species abundance.

Exchangeable potassium and calcium, nitrate nitrogen and pH do exhibit variability between sites. However, only calcium displays a consistent and significant ($p<0.01$) trend in comparison with altitude and slope. This trend is a significant decrease with increasing altitude. The highest altitude class has a significantly lower mean value than the lowest altitude class. Although neither of these differ significantly from the intermediate altitude class, their values follow the general trend. The relevant cell means, ANOVA Tables and range tests are presented in Appendix 4, along with a histogram of calcium values to validate normality assumptions. The possible influence of this trend on species relative abundance is discussed in section 6.3.1. No such trends exist for nitrates, potassium or pH (see Table 8), and visual comparison with species abundance data (Table 6) does not suggest any consistent relationships. The inconsistent nature of the variation in this data is suggested to be due to the manner in which the slopes were prepared for seeding.

Table 8: Soil Analysis Results For Each Site.

ALTITUDE CLASS 1

Slope Class	Rep. No.	Potash (kg/ha)	Nitrate Nitrogen (kg/ha)	Nitrite Nitrogen	Ammonia Nitrogen	Ferric Iron
1	1	446	33	n	n	s
1	2	290	11	n	n	s
1	3	390	33	n	s	m
2	1	290	33	n	n	s
2	2	335	33	n	n	s
2	3	335	11	n	s	s
3	1	390	33	n	n	s
3	2	290	11	n	n	s
3	3	290	33	n	n	s
4	1	390	56	n	n	s
4	2	335	45	n	n	m
5	1	335	45	n	n	s
5	2	290	11	n	s	s

ALTITUDE CLASS 2

Slope Class	Rep. No.	Potash (kg/ha)	Nitrate Nitrogen (kg/ha)	Nitrite Nitrogen	Ammonia Nitrogen	Ferric Iron
1	1	245	22	n	s	s
1	2	390	33	n	n	s
2	1	390	22	n	n	s
2	2	290	22	n	n	h
3	1	290	33	n	n	m
3	2	446	22	n	n	m
3	3	335	11	n	n	h
4	1	335	67	n	n	s
4	2	233	22	n	n	s
4	3	245	22	n	n	s
5	1	335	22	n	n	s
5	2	357	33	n	n	s

LEGEND:

Altitude Class	1	2	3
Range (m)	675-850	850-1000	1000-1150

Slope Angle Class	1	2	3	4	5
Range (degrees)	0-2	3-4	5-8	9-16	+16

n, nil;
s, small; i.e may be deficient in the soil;
m, medium; i.e. adequate amounts available for normal plant growth;
h, high; i.e. more than adequate amounts available for normal plant growth.
pH values represent the pH of each soil sample

in distilled water.

Some variables are presented numerically, others categorically. This is simply a result of the manner in which the soil testing kit presents the results.

Table 8 (cont.)

Slope Angle	Rep. No.	Potash (kg/ha)	Nitrate Nitrogen (kg/ha)	Nitrite Nitrogen	Ammonia Nitrogen	Ferric Iron
ALTITUDE CLASS 3						
1	1	290	11	n	n	h
1	2	335	11	n	s	h
1	3	245	33	n	s	m
2	1	245	11	n	n	h
2	2	335	11	n	n	h
2	3	290	45	n	n	s
3	1	446	22	n	s	s
3	2	245	22	n	n	m
3	3	390	22	n	n	s
4	1	245	22	n	n	m
4	2	335	22	n	s	m
5	1	223	22	n	s	m
5	2	390	22	n	n	m
5	3	290	45	n	n	s
MULCHED SAMPLES						
1	1	290	33	n	n	s
1	2	290	22	n	n	m
2	1	390	56	n	s	s
2	2	335	11	n	n	m
3	1	335	67	n	n	s
3	2	223	22	n	n	s
4	1	335	67	n	n	s
4	2	290	112	n	n	s
5	1	335	22	n	n	s
5	2	290	33	n	n	s

Table 8 (cont.)

Slope Class	Rep. No.	Mn	P	Ca (ppm)	Mg	pH
ALTITUDE CLASS 1						
1	1	s	h	2100	m	6.3
1	2	s	h	1000	s	5.6
1	3	s	h	1400	s	5.7
2	1	s	h	2800	s	5.7
2	2	s	h	1400	m	6.5
2	3	s	h	1000	m	5.3
3	1	s	h	1000	s	6.0
3	2	s	h	2100	s	6.1
3	3	s	m	1400	s	5.4
4	1	s	h	1000	m	5.3
4	2	s	h	700	s	5.1
5	1	s	h	700	m	6.2
5	2	s	m	1400	m	5.6
ALTITUDE CLASS 2						
1	1	s	m	1000	s	5.5
1	2	s	h	1400	s	5.9
2	1	s	h	1200	s	5.5
2	2	s	h	700	s	5.1
3	1	s	h	1200	s	5.3
3	2	s	h	1000	s	4.7
3	3	s	h	700	s	5.3
4	1	n	h	350	s	5.3
4	2	s	h	150	s	4.8
4	3	s	m	2100	s	6.0
5	1	s	h	1000	s	5.4
5	2	s	h	1000	s	5.2

Table 8 (cont.)

Slope Class	Rep. No.	Mn	P	Ca (ppm)	Mg	pH
ALTITUDE CLASS 3						
1	1	s	h	350	s	5.0
1	2	s	h	350	s	5.8
1	3	s	h	1000	s	6.1
2	1	s	m	150	s	5.4
2	2	s	m	700	s	5.7
2	3	s	h	700	s	4.3
3	1	n	m	2100	m	5.7
3	2	s	h	350	s	4.1
3	3	n	h	150	s	5.6
4	1	s	m	350	s	5.2
4	2	s	m	150	s	4.9
5	1	s	h	150	s	5.6
5	2	s	h	150	s	5.2
5	3	n	h	350	s	5.3
MULCHED SAMPLES						
1	1	s	h	1000	s	5.3
1	2	s	s	1000	s	5.1
2	1	s	h	1000	m	5.4
2	2	s	h	350	s	5.1
3	1	s	h	1000	m	6.0
3	2	s	h	2100	s	6.2
4	1	s	h	700	s	5.9
4	2	s	h	1400	s	5.4
5	1	s	h	700	s	5.8
5	2	s	h	1400	s	5.4

The scale of exchangeable phosphorus and ferric iron ratings are non-ordinal and were therefore not examined for statistical variation in the ANOVA framework. Table 8 clearly shows little variation and no consistent trends in phosphorus values. Ferric iron, however, does show noteworthy variation in occasional samples. The possible influence of this on species abundance is discussed in Chapter 6. Nitrite nitrogen, ammonia nitrogen, manganese and magnesium values show very little or no variability between samples.

5.4.2: Soil Depth

Mean soil depth values for each site are presented in Table 9. There is a large amount of variation between sites. This does not appear to be related to altitude, although a possible slight trend appears to exist in relation to slope angle. However, as discussed in Chapters 3, 4 and 6, soil depth is thought to be more important as a localised environmental variable. Due to the large variation it displays both within and between sites, its importance is discussed as a localised variable rather than by invoking gross correlations with slope angle.

Following Kershaw (1958) the mean soil depth in which each species is present and absent was computed from the initial sample data. The results are presented in Table 10. There are no marked differences, although some of the variation merits comment and further investigation. Of the seeded species, T. hybridum and F. rubra appear to be more common on deeper soils.

Table 9: Mean Soil Depth (+/- SE) For Each Site.

Alt. Class	Slope Class	Replicate Number		
		1	2	3
1	1	24.8 +/- 3.5	10.2 +/- 1.2	14.1 +/- 2.6
1	2	32.5 +/- 1.3	8.6 +/- 1.3	13.2 +/- 1.9
1	3	28.6 +/- 2.6	13.5 +/- 1.7	16.6 +/- 2.7
1	4	16.3 +/- 1.4	14.5 +/- 3.7	-
1	5	10.0 +/- 1.2	25.5 +/- 2.6	-
2	1	27.8 +/- 2.5	29.7 +/- 1.6	-
2	2	24.4 +/- 2.4	28.5 +/- 3.1	-
2	3	14.8 +/- 2.1	17.0 +/- 2.8	26.6 +/- 2.3
2	4	17.3 +/- 2.9	23.2 +/- 2.6	27.1 +/- 1.7
2	5	16.1 +/- 1.4	28.5 +/- 1.2	-
3	1	27.6 +/- 2.8	13.3 +/- 1.3	29.3 +/- 0.9
3	2	23.9 +/- 2.3	11.1 +/- 1.6	22.3 +/- 3.2
3	3	8.9 +/- 0.7	15.4 +/- 2.9	22.2 +/- 2.9
3	4	13.7 +/- 2.3	17.2 +/- 1.5	-
3	5	11.6 +/- 1.0	15.7 +/- 1.2	9.8 +/- 0.7
M	1	25.8 +/- 4.0	13.0 +/- 3.0	-
M	2	10.7 +/- 1.6	13.6 +/- 2.4	-
M	3	11.4 +/- 1.8	12.5 +/- 3.3	-
M	4	12.0 +/- 1.3	4.9 +/- 0.9	-
M	5	16.9 +/- 1.7	12.8 +/- 3.2	-

LEGEND:

Altitude Class	1	2	3
Range(m)	675-850	850-1000	1000-1150

Slope Angle Class	1	2	3	4	5
Range (degrees)	0-2	3-4	5-8	9-16	+16

The mulched data set are represented by the letter M.

Bryophytes have a mean soil depth for absence noticeably greater than that for presence, which suggests a tendancy for this group of plants to grow more abundantly on the shallower soils. No other clear trends appear to exist in this data.

Seven categories of soil depth were established, numbered from 1-7 with increasing soil depth, and the mean percentage cover of each species in each category calculated (Table 11, Figures 7-15). Soil depth does have an influence on species cover values, because, intuitively, percentage cover will be restricted on shallow soils where space will limit growth. What is interesting here is the subtle differences in individual species response.

The four major species were examined by 1-way ANOVA and multiple range tests (see Appendix 5). The results for the remaining species have not been subject to statistical analyses, but are presented and discussed in similar fashion.

A. tenuis is significantly related to variation in soil depth ($p<0.01$), and displays the following trend along the gradient:

```
soil depth category   1 4 7 6 2 3 5
                      -------
                        ---------
                            -------
```

It is restricted in low soil depths ($p<0.05$), having larger cover values in the intermediate categories (Figure 7).

Mean cover values for *F. rubra* are significantly correlated ($p<0.05$) with soil depth. Category 1 has a significantly lower value than all the other categories, which despite statistical

Table 10: Mean Soil Depth (+/- SE) For Species Absence and Presence.

Species	Frequency (No. Samples)	Mean Soil Depth (cm)	+/- SE
ABSENCE.			
A.alba	271	19.5	0.61
A. tenuis	78	18.6	1.16
F. rubra	55	16.2	1.45
P. pratense	120	19.4	0.93
P. compressa	400	19.0	0.49
T. hybridum	226	16.1	0.62
T. repens	362	18.5	0.53
Bryophytes	304	19.4	0.53
PRESENCE.			
A. alba	200	17.9	0.66
A. tenuis	393	18.8	0.49
F.rubra	416	19.2	0.47
P. pratense	351	18.6	0.51
P. compressa	71	17.6	1.12
T. hybridum	245	21.3	0.61
T. repens	109	19.2	0.84
Bryophytes	167	17.5	0.83

Table 11: Relationship Between Soil Depth and Mean Species Cover (+/- SE).

	Soil Depth Category (cm)						
	0-5	6-10	11-15	16-20	21-25	26-34	+35
Number of Samples	27	99	83	76	71	53	62
Species							
Agrostis alba	3.7 +/- 1.2	8.5 +/- 1.2	9.2 +/- 1.3	10.7 +/- 1.6	5.5 +/- 1.5	5.1 +/- 1.3	12.4 +/- 2.7
Agrostis tenuis	21.5 +/- 4.2	33.3 +/- 2.2	35.6 +/- 2.7	29.2 +/- 2.8	39.7 +/- 3.0	31.5 +/- 3.4	28.9 +/- 2.9
Festuca rubra	25.6 +/- 5.1	38.6 +/- 2.7	40.1 +/- 2.6	44.6 +/- 3.0	45.5 +/- 3.0	40.4 +/- 3.8	42.4 +/- 3.4
Phleum pratense	22.9 +/- 4.5	23.7 +/- 2.1	18.7 +/- 2.1	23.2 +/- 2.6	27.2 +/- 2.7	28.7 ;/- 3.2	18.6 +/- 2.5
Poa compressa	1.8 +/- 0.8	1.7 +/- 0.4	2.1 +/- 0.5	2.1 +/- 0.7	2.4 +/- 0.8	1.9 +/- 1.1	1.6 +/- 0.6
Trifolium hybridum	5.6 +/- 1.8	11.3 +/- 2.1	15.0 +/- 2.4	18.4 +/- 2.7	28.9 +/- 3.5	33.2 +/- 4.0	25.0 +/- 3.3
Trifolium repens	1.5 +/- 0.7	3.1 +/- 0.8	4.1 +/- 1.1	4.8 +/- 1.0	4.9 +/- 1.2	4.3 +/- 1.1	2.7 +/- 0.8
Bryophytes	30.0 +/- 5.5	8.1 +/- 1.3	7.7 +/- 1.5	5.1 +/- 1.2	6.9 +/- 1.6	1.3 +/- 2.8	7.4 +/- 1.7
Bare Soil	13.9 +/- 2.8	8.0 +/- 1.4	6.9 +/- 1.3	3.3 +/- 0.8	2.5 +/- 0.9	2.1 +/- 0.9	3.1 +/- 1.0

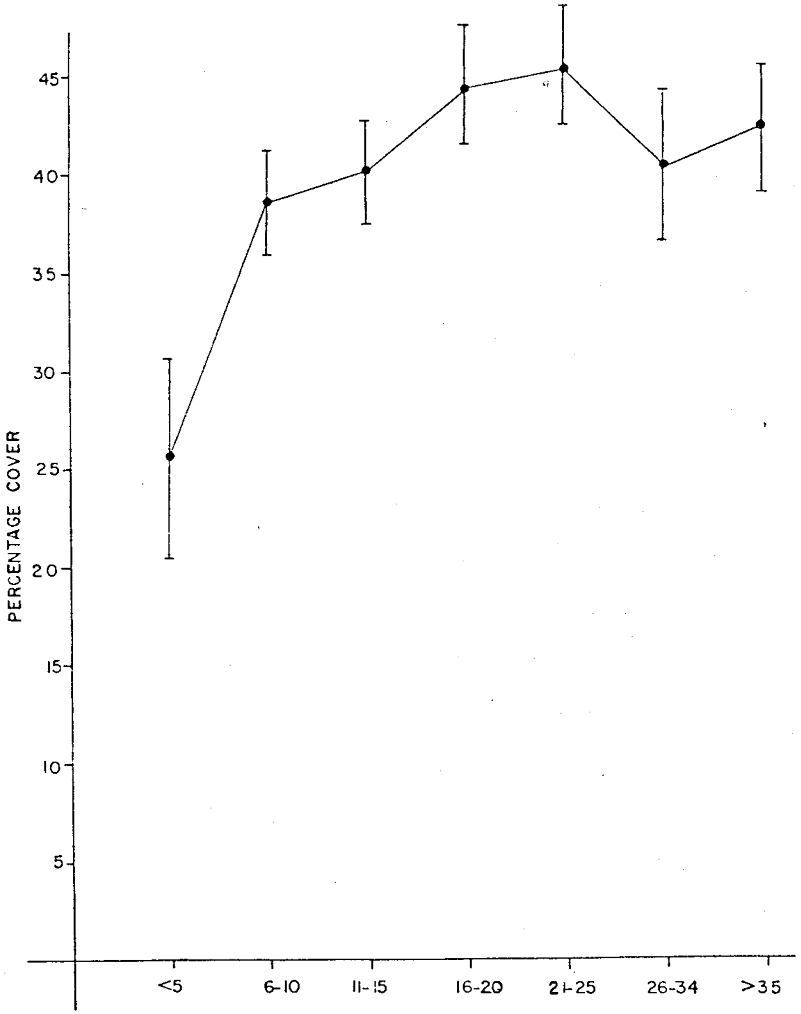


FIGURE 8 : MEAN PERCENTAGE COVER (± SE) FOR F. rubra Vs SOIL DEPTH.

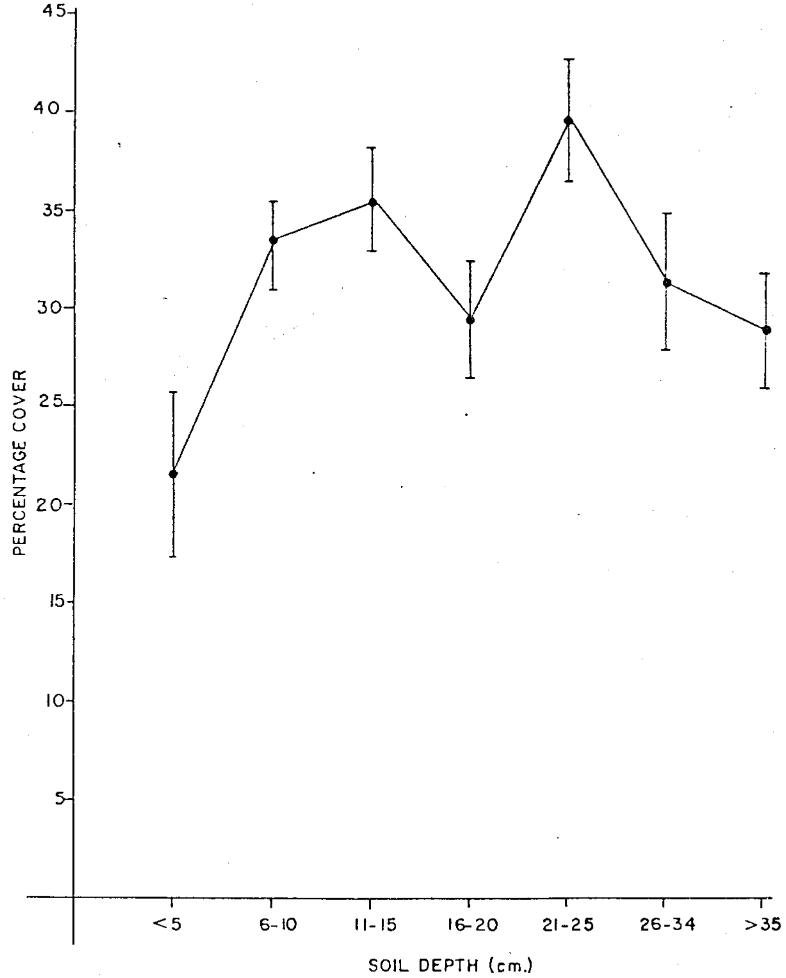


FIGURE 7 : MEAN PERCENTAGE COVER (±SE) FOR A. tenuis Vs. SOIL DEPTH.

similarity show a general increase with increasing soil depth (Figure 8).

T. hybridum is also significantly correlated with soil depth ($p<0.001$). It displays an increase in cover with increasing soil depth, as shown by Figure 9. This trend is significant ($p<0.05$) as follows:

```
soil depth category     1 2 3 4 7 5 6
                        -----
                          -----
                              ---
                                -----
```

In contrast, *P. pratense* is not significantly influenced by variation in soil depth, and appears to grow equally well on the very shallow soils (Figure 10). Its percentage cover decreases markedly in the deepest class, in similar fashion to the other major species, with the exception of *F. rubra*.

A. alba does show variation in cover between the categories of soil depth, however this appears to lack any trend, other than its slight restriction on very shallow soils and its increased abundance on the deepest soils, as shown in Figure 11. *T. repens* and *P. compressa* show no variation (Figures 12 & 13), other than a slight tendancy to establish larger cover values on the intermediate soil depths.

Bryophytes are markedly more common on the shallow soils than on all the deeper soil categories, which show little variability (Figure 14). A similar trend is evidenced for the existence of bare soil (Figure 15).

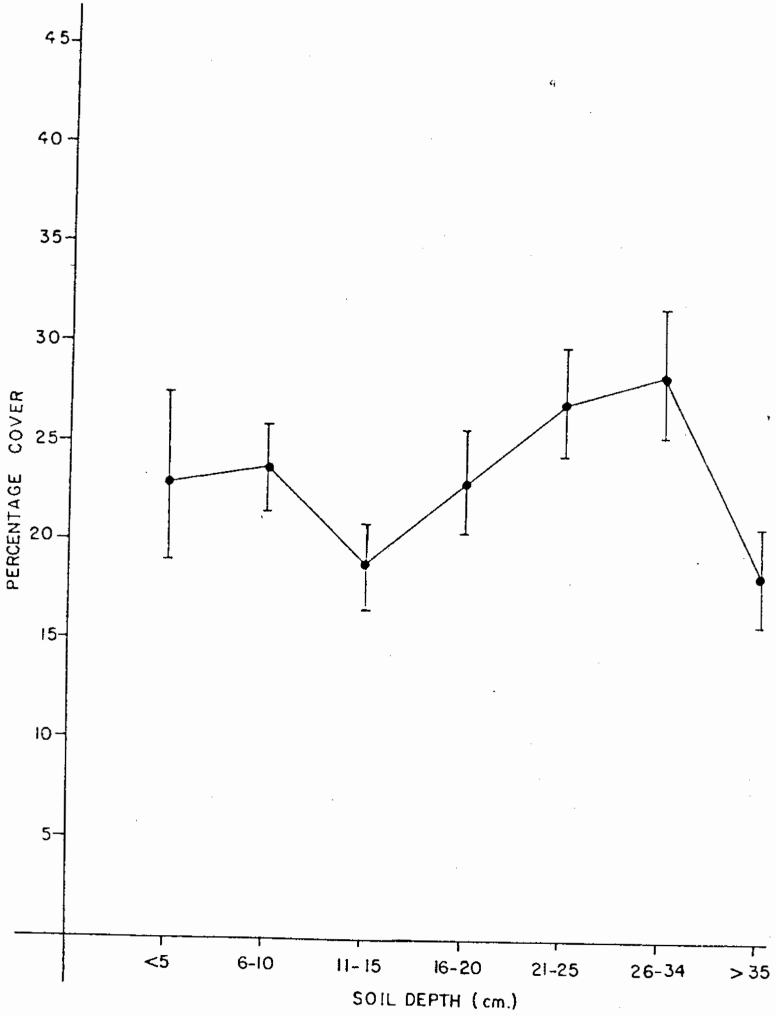


FIGURE 10: MEAN PERCENTAGE COVER (± SE) FOR <u>P. pratense</u> Vs SOIL DEPTH.

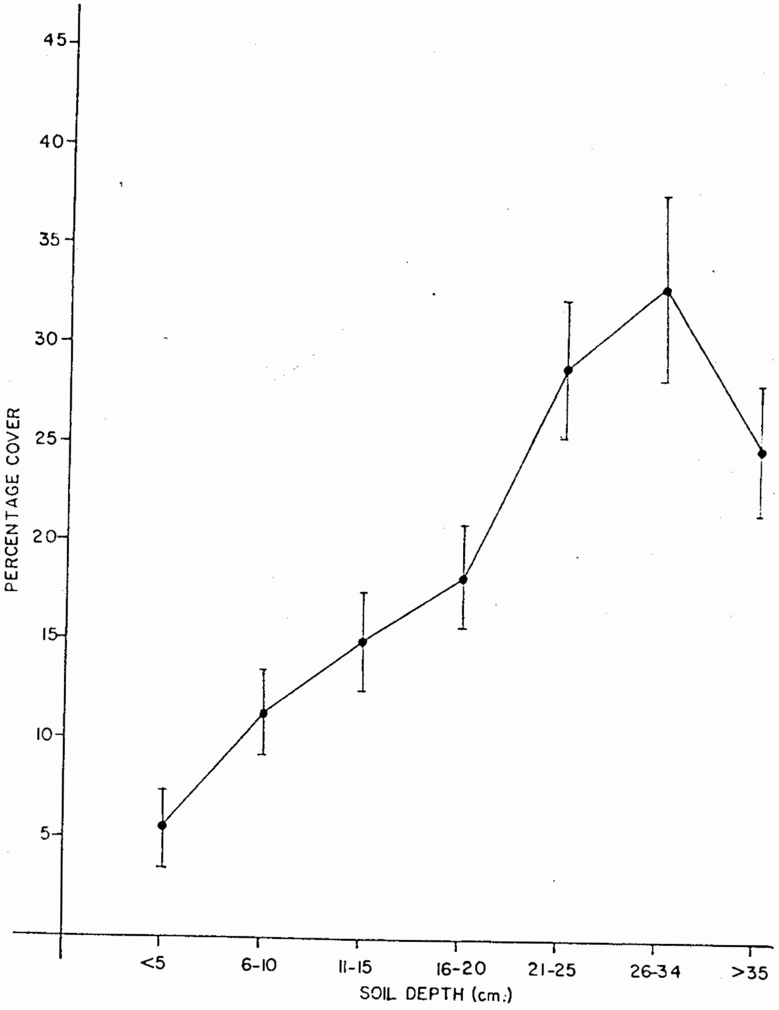


FIGURE 9: MEAN PERCENTAGE COVER (±SE) FOR <u>T. hybridum</u> Vs. SOIL DEPTH.

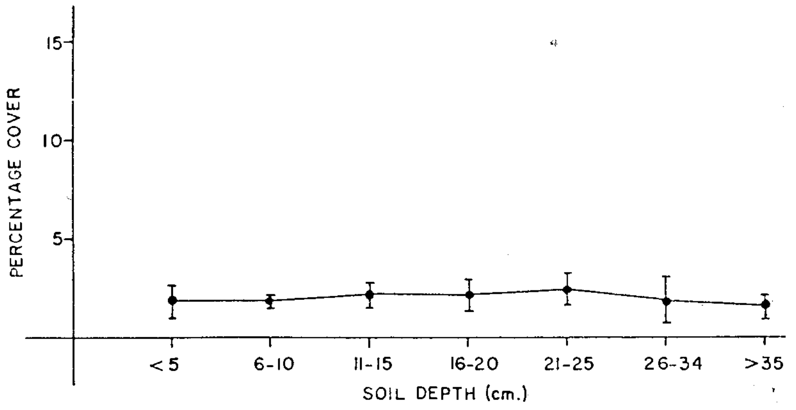


FIGURE 13: MEAN PERCENTAGE COVER (±SE) FOR *P. compressa* Vs. SOIL DEPTH.

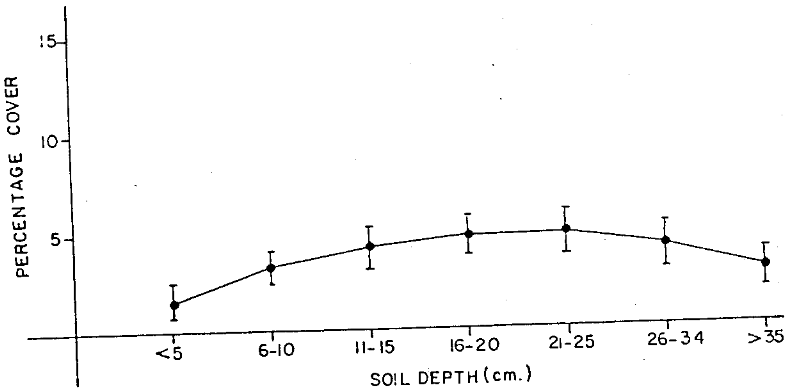


FIGURE 12: MEAN PERCENTAGE COVER (±SE) FOR *T. repens* Vs SOIL DEPTH.

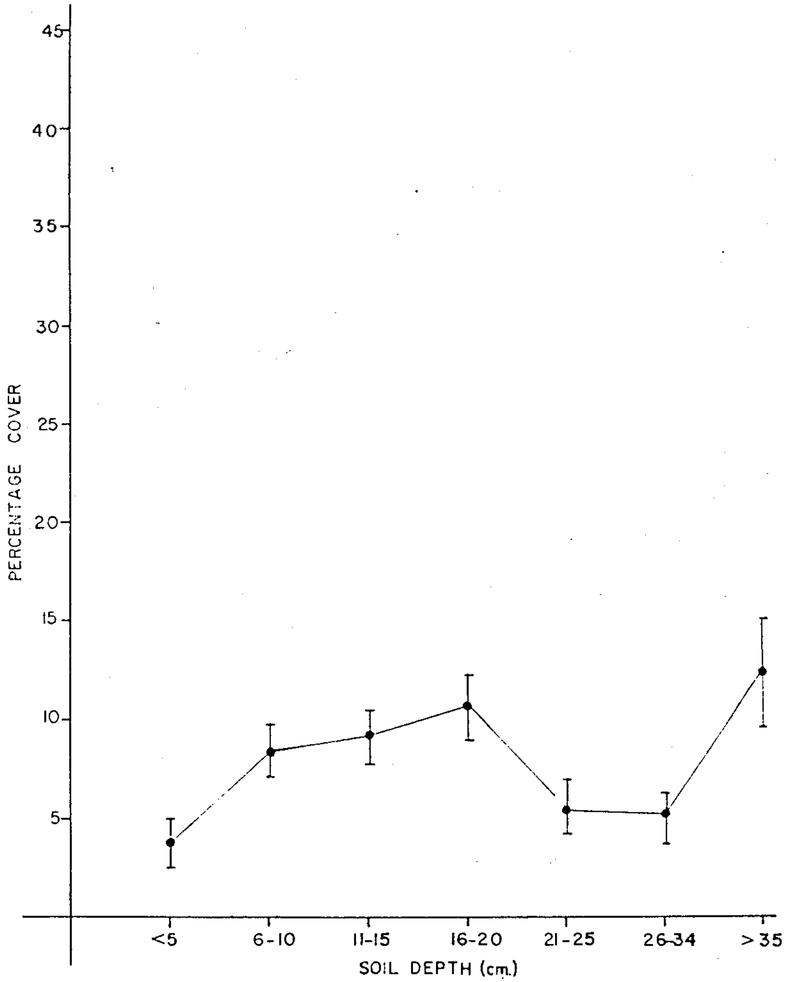


FIGURE 11: MEAN PERCENTAGE COVER (± SE) FOR *A. alba* Vs. SOIL DEPTH.

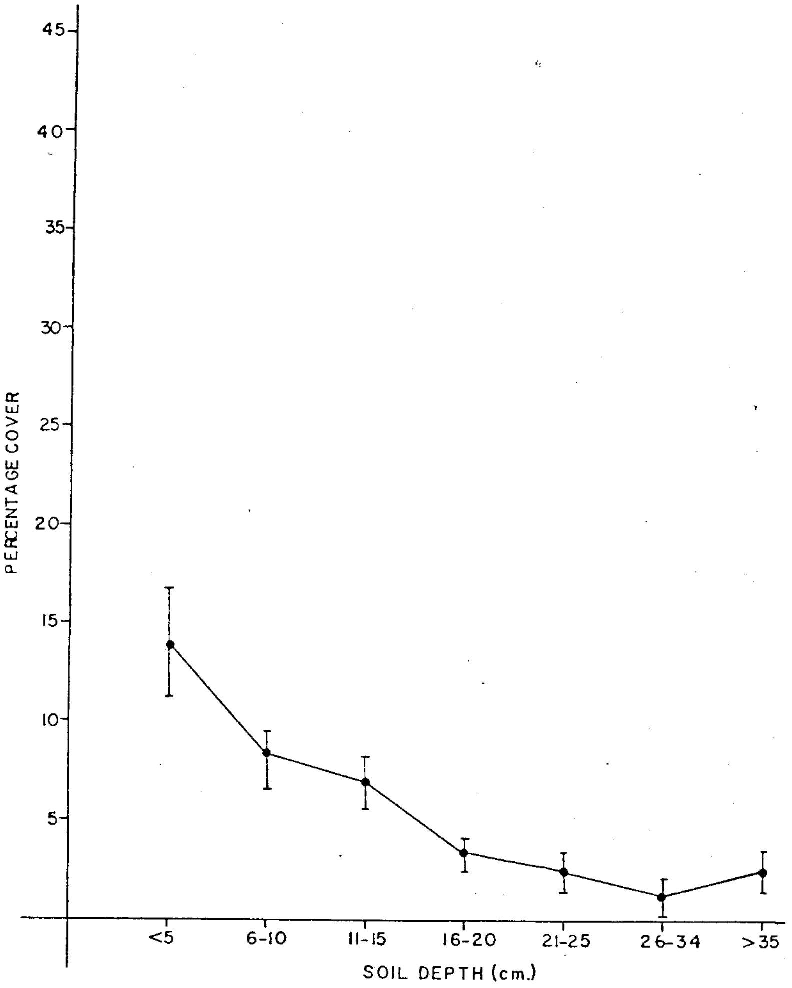


FIGURE 15 : MEAN PERCENTAGE COVER (±SE) FOR BARE SOIL Vs. SOIL DEPTH.

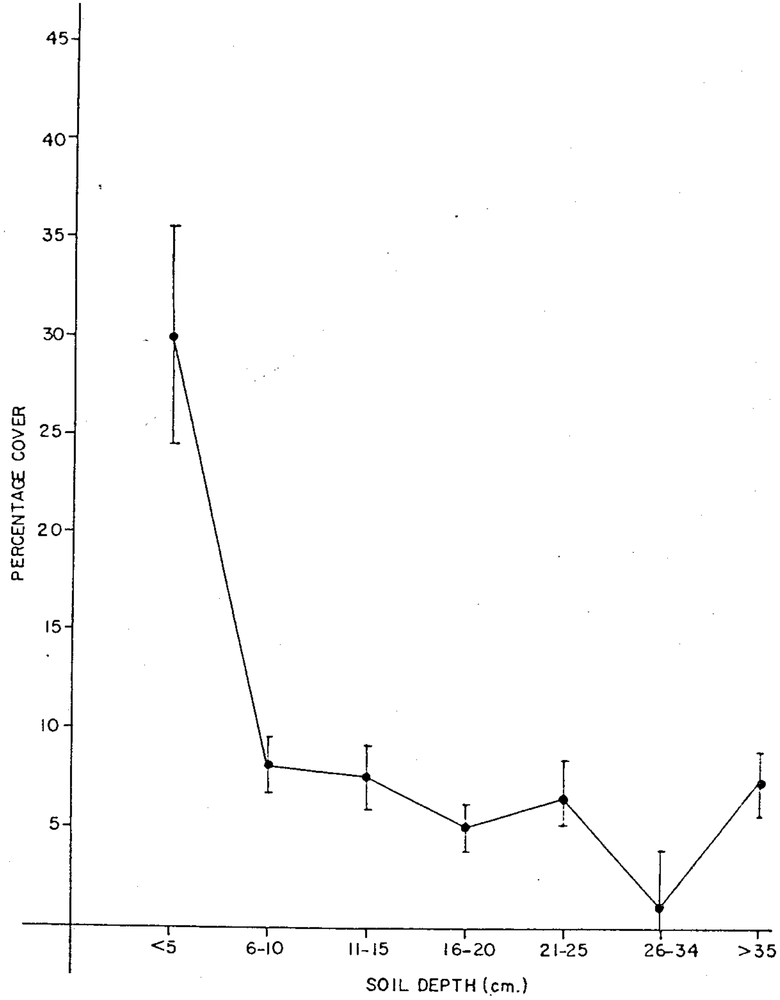


FIGURE 14: MEAN PERCENTAGE COVER (±SE) FOR BRYOPHYTES Vs SOIL DEPTH.

5.5: Biotic Influences

5.5.1: Percentage Flowering

The percentage occurrence of shoots recorded as flowering for each species in the study area as a whole is given in Table 12. Individual site values are tabulated in Appendix 6. *A. tenuis* clearly shows the greatest degree of flowering. *T. hybridum* and *P. pratense* show lower flowering, but still much larger than *F. rubra* which exhibits a marked propensity towards vegetative rather than reproductive growth. The latter has distinctly lower percentage flowering values than the other three major species in the community.

Of the less common species, the grasses have relatively large percentage flowering values, whilst *T. repens* has a much lower value.

The relationship between percentage flowering of the four major species and the altitude/slope angle matrix is shown in Table 13. A 2-way ANOVA was performed to test the hypothesis that there is no relationship between these variables. The relevant ANOVA Tables are given in Appendix 6.

The percentage flowering of *A. tenuis* is significantly correlated with altitude ($p<0.01$), increasing with altitude in a similar fashion to its cover values (Table 13). A similar significant trend ($p<0.01$) is revealed for *P. pratense*. This suggests an increase in vigour of these two species with increasing altitude. Variation in percentage flowering of *F.*

Table 12: Overall Mean % Flowering Of Seeded Species (+/- SE).

Species	% Flowering	+/-	SE
Agrostis alba	44.3	+/-	3.1
Agrostis tenuis	53.9	+/-	1.9
Festuca rubra	8.8	+/-	1.1
Phleum pratense	31.1	+/-	2.0
Poa compressa	40.9	+/-	5.7
Trifolium hybridum	40.4	+/-	2.4
Trifolium repens	16.4	+/-	3.1

Table 13: Mean % Flowering (+/- SE) of the Four Major Species in Relation to Altitude and Slope Angle.

Slope Angle Class	Altitude Class 1	Altitude Class 2	Altitude Class 3
Agrostis tenuis			
1	40.8 +/- 9.7	49.7 +/- 6.2	83.5 +/- 4.9
2	39.3 +/- 8.2	37.8 +/- 6.3	80.9 +/- 4.9
3	38.4 +/- 9.3	45.7 +/- 5.6	74.3 +/- 4.9
4	30.6 +/- 6.9	36.7 +/- 5.1	66.6 +/- 5.4
5	17.0 +/- 6.4	59.6 +/- 5.6	72.1 +/- 5.7
Festuca rubra			
1	9.9 +/- 4.2	5.1 +/- 2.8	5.6 +/- 5.6
2	12.5 +/- 2.5	4.8 +/- 2.7	12.1 +/- 5.3
3	12.4 +/- 4.3	3.2 +/- 1.6	6.3 +/- 3.8
4	16.5 +/- 5.5	6.3 +/- 2.3	4.7 +/- 1.8
5	13.2 +/- 4.1	3.1 +/- 1.8	10.7 +/- 3.1
Phleum pratense			
1	20.6 +/- 7.1	25.1 +/- 9.2	63.3 +/- 6.4
2	32.8 +/- 8.9	0.0 +/- 0.0	42.6 +/- 8.1
3	13.9 +/- 4.3	14.7 +/- 6.1	35.2 +/- 8.1
4	26.5 +/- 5.3	17.8 +/- 5.0	41.1 +/- 8.1
5	13.2 +/- 4.1	3.1 +/- 1.8	10.7 +/- 3.1
Trifolium hybridum			
1	12.7 +/- 2.8	21.7 +/- 5.8	85.6 +/- 9.0
2	24.5 +/- 5.1	18.8 +/- 4.1	76.9 +/- 7.6
3	14.3 +/- 4.9	39.5 +/- 5.3	47.9 +/-10.6
4	12.7 +/- 4.7	48.3 +/- 8.3	100.0 +/- 100
5	28.1 +/-12.9	75.7 +/- 7.4	55.2 +/-11.8

LEGEND:

Altitude Class	1	2	3
Range(m)	675-850	850-1000	1000-1150

Slope Angle Class	1	2	3	4	5
Range (degrees)	0-2	3-4	5-8	9-16	+16

rubra is also significantly related to variation in altitude although this appears to be due to a marked decrease in altitude class 2. No general trend appears to exist however. T. hybridum exhibits an interaction effect ($p<0.001$) but the low sample size for some of the data cells and the high variability of the data for this species render interpretation meaningless (see Appendix 6).

5.5.2: Interspecific Contacts

The count matrices for the contact sample data are presented in Tables 14-17, one table being constructed for each altitude class and the mulched data set respectively.

Significant associations detected are presented in Table 18. Combined with these, a number of apparent trends exist in the data. The significant trends in association are portrayed in Figure 16. The following conclusions can be drawn:

1. the only significant associations in the lowest altitude class involve species with very low abundance values. In this respect these associations are statistically invalid and are thus ignored throughout the analysis. What is noteworthy is the low number of contacts A. tenuis makes as species i with F. rubra as species j, in comparison with those made by the other major species. P. pratense and T. hybridum make twice as many contacts with F. rubra, although they do not make twice as many overall contacts in this matrix. Also, A. tenuis and P. pratense make a

Table 14: Count Matrix For Altitude Class 1.

Species	1	2	3	4	5	6	7	Total	
1	-	6	6	3	1	2	1	19	(11)
2	7	-	10	5	0	8	5	35	(24)
3	9	14	-	27	2	23	3	78	(30)
4	12	4	21	-	0	6	2	30	(15)
5	2	1	1	1	-	1	1	7	(0)
6	1	10	23	9	0	-	1	44	(4)
7	1	1	2	1	0	1	-	6	(0)
Total	32	36	63	46	3	41	13	234	

Legend For Tables 14-17.

Species 1 = Agrostis alba.
Species 2 = Agrostis tenuis.
Species 3 = Festuca rubra.
Species 4 = Phleum pratense.
Species 5 = Poa compressa.
Species 6 = Trifolium hybridum.
Species 7 = Trifolium repens.

Values in parentheses represent intraspecific contacts, not used in the statistical analyses.

Altitude Class	1	2	3
Range (m)	675-850	850-1000	1000-1150

Table 15: Count Matrix For Altitude Class 2.

Species	1	2	3	4	5	6	7	Total	
1	-	6	1	0	0	1	0	8	(0)
2	6	-	38	10	0	15	0	69	(9)
3	3	23	-	21	3	12	6	68	(6)
4	1	8	24	-	1	9	2	45	(0)
5	0	0	1	1	-	0	0	2	(0)
6	3	22	22	17	0	-	0	64	(1)
7	0	1	3	0	0	0	-	4	(0)
Total	13	60	89	49	4	37	8	260	

Table 16: Count Matrix For Altitude Class 3.

Species	1	2	3	4	5	6	7	Total	
1	-	13	1	3	1	1	0	19	(0)
2	6	-	41	75	3	15	0	140	(17)
3	0	10	-	14	1	2	1	28	(0)
4	2	44	25	-	0	9	2	82	(0)
5	0	0	0	1	-	0	0	1	(0)
6	1	18	3	7	0	-	0	29	(0)
7	0	1	0	0	0	0	-	1	(0)
Total	9	86	70	100	5	27	3	300	

Table 17: Count Matrix For The Mulched Data Set.

Species	1	2	3	4	5	6	7	Total	
1	-	1	9	5	0	1	0	16	(0)
2	3	-	17	10	1	5	1	37	(10)
3	5	15	-	25	1	6	3	55	(9)
4	6	2	16	-	1	9	1	35	(5)
5	0	0	0	0	-	0	0	0	(0)
6	1	3	18	9	1	-	4	36	(1)
7	0	1	2	1	0	0	-	4	(0)
Total	15	22	62	50	4	21	9	183	

Legend for Table 18.

Species 1 = Agrostis alba.
Species 2 = Agrostis tenuis.
Species 3 = Festuca rubra.
Species 4 = Phleum pratense.
Species 5 = Poa compressa.
Species 6 = Trifolium hybridum.
Species 7 = Trifolium repens.

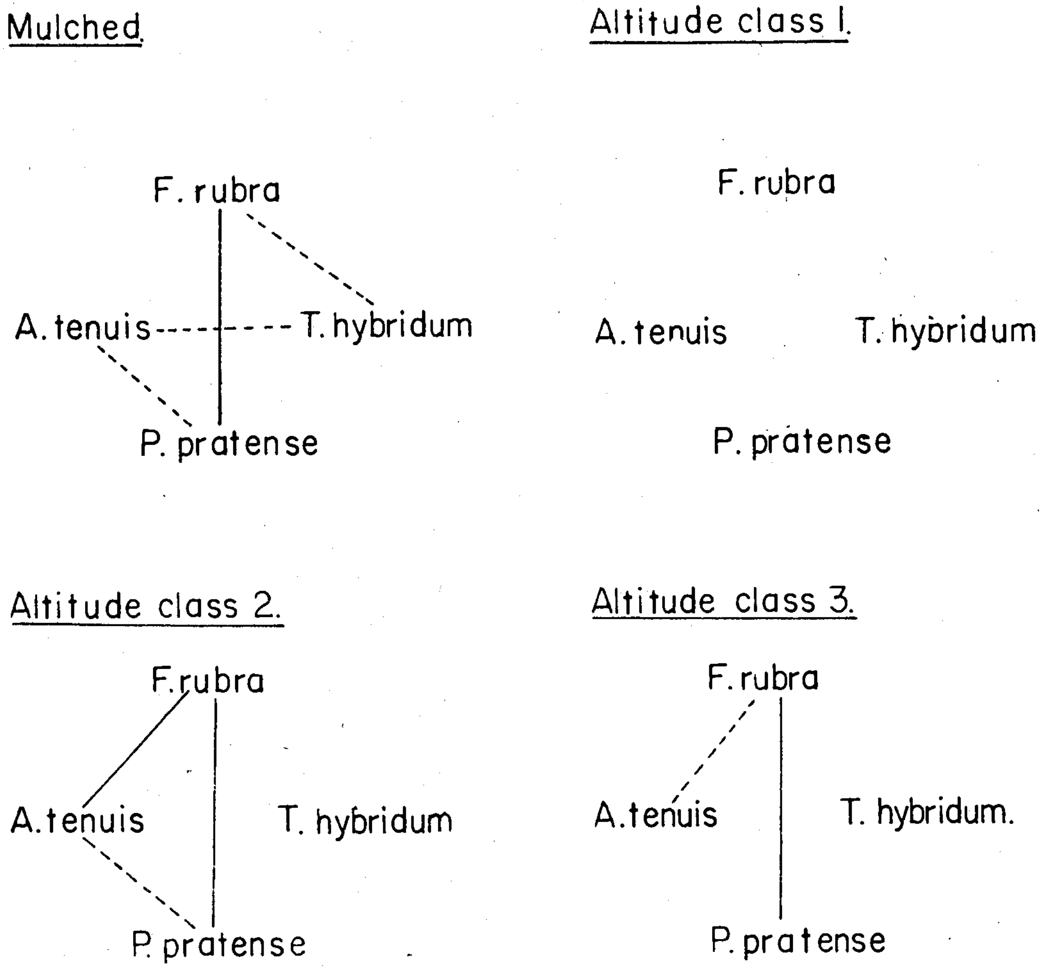
An * represents a statistically significant ($p<<0.05$) species association.

I1 and I2 are two indices calculated to assess whether the non-random associations are positive or negative.
I1 varies between -1 (absolute negative association) and +infinity (absolute positive association).
I2 is symmetrical about zero.

Altitude Class	1	2	3
Range (m)	675-850	850-1000	1000-1150

Table 18: Appraisal of Paired Association Data.

Species Association	Chi-Squared Probability	I1	I2
MULCHED SAMPLES			
2-3	0.621	0.04	0.08
2-4	0.041*	-0.21	-1.07
2-6	0.026*	-0.43	-1.20
3-4	0.048*	0.15	0.23
3-6	0.011*	-0.04	-0.36
4-6	0.976	0.03	0.06
ALTITUDE CLASS 1			
2-3	0.360	-0.14	-0.30
2-4	0.151	-0.34	-0.85
2-6	0.806	0.08	0.14
3-4	0.571	0.06	0.11
3-6	0.400	0.07	0.14
4-6	0.308	-0.19	-0.47
ALTITUDE CLASS 2			
2-3	0.015*	0.09	0.11
2-4	0.042*	-0.28	-0.68
2-6	0.191	-0.09	-0.23
3-4	0.016*	0.21	0.39
3-6	0.191	0.74	0.84
4-6	0.342	-0.05	-0.21
ALTITUDE CLASS 3			
2-3	0.015*	0.02	-0.37
2-4	0.190	-0.02	-0.09
2-6	0.085	-0.01	0.06
3-4	0.000*	0.38	0.57
3-6	0.844	-0.14	-0.33
4-6	0.682	-0.13	-0.28


Mulched

Altitude class I.

Altitude class 2.

Altitude class 3.

SIGNIFICANT ASSOCIATIONS
($p < 0.05$) DETECTED BY X^2

------- Negative
——— Positive

The associations between the 4 major species are presented here in relation to the 4 habitat classes for which count matrices were constructed. Significant associations represent non-random pairwise associations.

Figure 16: Significant Species Associations

proportionately low number of contacts with each other. Neither of these trends is statistically significant but are both thought worthy of comment;

2. in altitude class 2 similar trends become statistically significant ($p<0.05$). *A. tenuis* and *P. pratense* both have significant positive associations with *F. rubra* and display a significant negative association with each other. *F. rubra* and *T. hybridum* make proportionately few contacts and are almost significantly negatively associated ($p<0.051$);
3. in the highest altitude class *A. tenuis* exhibits a negative association with *F. rubra*. Noticeably, *F. rubra* (as species i) makes proportionately fewer contacts with *A. tenuis* (as species j) than with *P. pratense* (as species j). Yet *A. tenuis* (as species i) appears to contact *F. rubra* (as species j) in a manner consistent with other species and altitude classes. *P. pratense* and *F. rubra* again show a significant positive association. Finally, *A. tenuis* and *P. pratense* do not show a negative association, in contrast to the trends observed in the other matrices.
4. In the mulched data set similar trends to those described above are apparent. *A. tenuis* and *P. pratense* again show a significant negative association. Such negative associations were also detected between *F. rubra* and *T. hybridum* and between *A. tenuis* and *T. hybridum*. Finally, a positive association was once more detected between *F. rubra* and *P. pratense*.

5.5.3: Tussocking

During the contact sampling procedure occasions arose where a species would only make contact with shoots of the same species or would make no contacts at all. These two situations were combined to give an estimate of the clumping behaviour of the different species. These data have not been statistically analysed, but are presented in Tables 14-17 in parentheses in each row of the matrix. Two clear results are apparent:

1. A. tenuis shows the greatest tendency towards a tussock form, as illustrated by its large number of isolated occurences;
2. F. rubra shows a greater propensity to clump with decreasing elevation and in the mulched sites.

CHAPTER 6

INTERPRETATION

6.1: Framework For Discussion

Niche theory (MacArthur, 1972; Whittaker et al., 1973; Hutchinson, 1978) would predict that the plants of a community such as this will partition the habitat among them:

1. according to their own specific environmental preferences and growth forms;
2. in response to interactions with other species.

The results of this study are discussed within this framework in order to describe species response at the three scales of study. However, a descriptive research project based on field sampling cannot definitively show whether any detected relationships are the direct cause of patterns in species cohabitation. Consequently, speculative, not definitive, interpretations are provided.

The establishment of seeded species has, on the whole, been very satisfactory. The mean total cover shows little variation between sites (Table 6). This indicates the suitability of this type of restoration and management regime for disturbed, montane, recreation areas in this region, at least for altitudes between 675m and 1150m. A comparable result has been documented for ski-areas in Scotland by Bayfield (1980). The establishment of grass and grass-legume swards on ski-slopes in mainland Europe has also led Schiechtl (1980) to note their suitability for such restoration programs.

The results presented in this study demonstrate a great deal of variation in the relative abundance of the seeded species. This is discussed under the headings of Large-Scale pattern, Soil Properties, Timing of Influence and Biotic Influences to permit possible interpretation of how the species cohabit in relation to abiotic and biotic factors. Finally, under the heading of Niche Differences, these factors are considered jointly, as axes in niche space, to facilitate interpretation of how the species cohabit.

6.2: Large-Scale Pattern

"Site characteristics affect the species composition in developing, artificial grass/legume communities" (Turkington and Cavers, 1979, p.2710). The results presented in this study indicate that niche differences may be recognised in gross correlations of the habitat occupation of the four dominant species along the gradients of altitude and slope angle.

6.2.1: *F. rubra*

The dominance of *F. rubra* in the community is not unexpected. It comprises 25% of the seed mixture and would thus be expected to form a major component of the developing community. Its mean cover is 40.1% and in some sites has established values of up to 70% (see Table 6), much larger values than its initial proportion of the seed mixture. These high values may be because F. rubra, once established, is capable of substantial vegetative propagation (Harberd, 1961), spreading to form dense swards which have a large number of small tillers (Troughton, 1961). F. rubra has been successfully established under similar conditions in Scotland (Bayfield, 1980), and in general performs particularly well on reseeded hill soils in Britain (Spedding and Diekmahns, 1972). It is a vigorously growing species tolerant of a wide variety of habitats (Hitchock, 1971).

Hunt (1964) has demonstrated the superior productiveness and persistence of F. rubra with respect to other species. This may further account for the high cover values recorded for this species. However its percentage cover decreases significantly with increasing elevation. It is reasonable to equate increase in altitude with a decrease in environmental productivity (Whittaker, 1967). It has also been demonstrated that under conditions of decreasing productivity the more productive species suffer a greater relative reduction in vigour (Bradshaw et al., 1964; Spedding and Diekmahns, 1972; Grime, 1979). It is therefore suggested that the decrease in cover of F. rubra with increasing altitude is at least partly due to decreasing productivity of the habitat.

Its relationship with slope angle does not show a general trend and the statistical differences are thought to be due to factors other than just differences in moisture availability. Within the lowest altitude class _F. rubra_ has significantly lower cover values in slope angle class 4 than in the other classes. This may be due to a disturbance factor. Class 4 includes site 1.4.1 which has the lowest mean total cover of seeded species and the greatest percentage of bare soil in the study (see Table 6). It is also the only site in which _Tussilago farfara_ occurs, a species that is recognised as an opportunistic coloniser of disturbed ground (Harper, 1977). This site is located adjacent to the village centre (Figure 3), and consequently receives more human use than other sites. Thus, the possibility of human disturbance, combined with a low mean soil depth may help explain the low cover values recorded.

Within the highest altitude class _F. rubra_ is significantly restricted in the flat sites in comparison with the other slope angle classes. The sites in this class are very prone to waterlogging, due to the combined effects of altitude (causing increased rainfall and snow retention) and a flat gradient. As a result of the development of heavy snowpacks and increased precipitation the soils can become saturated for long periods of the growing season. Furthermore, the soils have the potential to become waterlogged more frequently during periods of summer rainfall, a trend which is accentuated by the accumulation of runoff and lower drainage capabilities associated with these areas. The sites comprising this class also have high levels of ferric iron in the soil (Table 8), which can be taken up in toxic amounts by plants in waterlogged situations (Jones and Etherington, 1971). *F. rubra* is regarded as a species sensitive to flooding, its growth being retarded in waterlogged situations, and to high levels of ferric iron (Davies and Singh, 1983). A combination of excess moisture and high levels of ferric iron may thus have limited the establishment and growth of *F. rubra* in these sites.

Further evidence for this effect of excess water and high levels of ferric iron is provided by the mulched data set. Here the lowest values for *F. rubra* cover occur in the low slope angle sites with greater than average ferric iron concentrations (compare Tables 7 & 8).

6.2.2: *T. hybridum*

Legume species have been shown to be restricted in situations where climate, through its influence on the length of the growing season and the mean temperature and rainfall experienced during the growing season, limits productivity (Chestnut and Lowe, 1970). In this study area *T. hybridum* appears to follow this trend, having significantly lower cover values with increasing altitude and slope angle. The shorter growing season and increased climatic severity associated with increasing altitude thus appear to restrict the relative abundance of *T. hybridum*.

This species exhibits an interesting trend with respect to slope angle. With increasing altitude its highest abundance values shift from the flat slopes to the more freely draining, gentle slopes. This may be due to the flat sites becoming too wet with increasing altitude (with the further restriction on the growing season). There is also the possible influence of ferric iron in the flat areas of the highest altitude class. In all three altitude classes this species displays significantly lower cover values on the steeper slopes. A similar pattern is shown along the slope gradient in the mulched data set (Table 7), where lower cover values are recorded for the two extremes of the gradient.

Success in relation to water availability depends on the efficiency and completeness with which a species exploits the soil-water environment (Haynes, 1980). Clovers tend to have less ramified roots than grasses (Evans, 1977) and so the volume of soil they explore is less. Hence they are more negatively affected by very dry conditions (Johns, 1972). This may be a reason for the reduction in cover values on steeper slopes.

6.2.3: Differential Habitat Occupation

That the modes of species distribution curves are individually scattered along environmental gradients is well documented (Whittaker, 1975; Gauch, 1982). Common species may show separation along these gradients which reflects their different environmental requirements and/or reduces the potential interference between them (Whittaker et al., 1973). *A. tenuis* and *P. pratense* display mirror image distribution patterns in relation to altitude and slope angle when compared with *F. rubra* and *T. hybridum* (Figure 6). This differential habitat occupation of the major species causes total cover values to remain consistently high whilst the relative abundance of the individual species varies markedly. Such variation in habitat occupation facilitates the cohabitation of the species in the community as a whole, and may be due to dissimilar environmental preferences and/or the result of interactions between the species. The possible influence of these two factors on the relative abundance of the four major species is discussed in the following two sections.

6.2.4: *A. tenuis*

The value of *A. tenuis* for upland revegetation programs has long been recognised (Davies, 1940). It is commonly regarded as having a low productivity (Davies, 1960; Cowling and Lockyer, 1965). It is therefore slow to establish after reseeding, but can eventually form a dense sward that dominates large areas of permanent grassland (Welsh Plant Breeding Station, 1962, cited in Spedding and Diekmahns, 1972). Furthermore, it grows well on poor soils (Hubbard, 1968).

This combination of ecological properties is invoked to help explain the increase in cover of this species with increasing altitude in this study. Since it is slow to establish and low in productivity it may be restricted in the productive, low altitude sites where the more productive species, F. rubra and T. hybridum, can rapidly establish, thus pre-empting the available space. However, as the cover of these species is restricted with increasing altitude, A. tenuis can establish larger cover values due to an increase in available space. The underlying notion here is that highly productive species, which are generally held to be those with a greater competitive ability (van den Bergh, 1969), are less competitive with low-yielding species under sub-optimal environmental conditions (van den Bergh, 1968). Thus, as Grime (1979) emphasises, the most obvious effect of increasing environmental severity is to restrict species of high competitive ability, enabling the less productive species to become established. It is suggested here that this mechanism facilitates the cohabitation of A. tenuis with the more productive species along a gradient of decreasing habitat productivity, as determined by increasing elevation. Furthermore, the restriction of F. rubra in areas of the mulched slopes with high ferric iron concentrations is paralleled by an increase in the cover of A. tenuis (Tables 7 & 8).

6.2.5: P. pratense

Phleum pratense is regarded as a "non-aggressive" grass, being one of the slowest cultivated grasses to establish and come into full production (Spedding and Diekmahns, 1972). This species has very small seedlings which grow slowly (Chippendale, 1949), enabling faster growing seedlings in the developing community to pre-empt the available reources in the productive, low altitude sites. So, applying the same reasoning as in section 6.2.4, this species is also restricted to establishing large cover values in the high altitude sites where the more productive species are limited.

P. pratense grows best on moist, heavy soils (Hubbard, 1968), yet in the lower two altitude classes it displays significantly larger cover values on the steeper, drier slopes. This can be tentatively explained by the significant restriction of T. hybridum on the steeper slopes providing more available space for its growth, combined with P. pratense's low moisture requirement for establishment (Chippendale, 1949).

In the highest elevation sites it expands its range to include the lower slope classes. This may be due to the restriction of the more productive species from this altitude class as a whole, the additional restriction of these species due to waterlogging and toxic levels of ferric iron, and its tolerance of short periods of spring flooding (Finn et al., 1961).

6.2.6: Other Seeded Species

The low abundance values of the three remaining seeded species render interpretation of any cover variation difficult. However, two comments can be made with respect to their relative abundances in the community.

T. repens. shows a decrease in cover values with increasing altitude. It is feasible that this is due to increasing climatic severity and a shortened growing season, similar to the effect on T. hybridum and in agreement with the results reported by Chestnutt and Lowe (1970).

Poa compressa displays consistently low cover values despite occupying 10% of the seed mixture. Since it has been cultivated for pastures on poor soil in British Columbia (Hubbard, 1969) and in the U.S.A. (Hitchcock, 1971), it is relevant to ask why its abundance in this community is so low. Possible explanations lie in the fact that it has poor seedling vigour relative to other grass species (Berg, 1974), and has been found to germinate very slowly (Stuckey, 1941). In a crowded, developing community these factors may limit its establishment, due to a limit on available space.

Aarssen et al (1979) describe it as a "clumped species", and where it has become established in the study area it was observed to have such a well-defined tussock form. So, it may be restricted to situations where it can fully develop this natural tussock form.

6.2.7: Non-seeded Species

The extent of invasion of sown swards by self-sown species will vary from site to site but can be extensive at low elevations, decreasing in rapidity and extent with increasing altitude (Bayfield, 1976).

Bryophyte colonisation has been successful, with an overall cover of 9.1%, although not as extensive as reported for ski-slopes in Scotland by Bayfield (1980). Although their mean cover values for each site do show considerable variation, this does not appear to be related to the altitude and slope gradients. Discussion of this variation is reserved to section 6.3.2.

The invasion of sites by non-seeded vascular plants is much lower, with an overall mean cover value of 4.9%. In contrast to the bryophytes, this group appears to be limited by altitude. This may be due to a combination of increasing climatic severity, shorter growing seasons, the presence of fewer species and increasing distance from seed sources. These factors will also be those most likely to be responsible for the variation in species composition with altitude. Bayfield (1980) has reported a similar trend.

Slope angle does not appear to influence their cover values as a group. However, as with altitude, it does appear to influence the species composition of this group. In the lowest elevation class the flatter, moister sites contain Equisetum spp. and Phalaris arundinacea as the major species in this group. In contrast, the steeper, drier slopes have Dactylis glomerata as the dominant species in this group of plants.

6.3: Soil Properties

6.3.1: Soil Chemistry

The results of the soil chemical analyses indicate that soil chemistry has no consistent influence on species relative abundance, apart from the possible influence of ferric iron already discussed, and the variation in exchangeable calcium levels. Surprisingly, this variation in calcium concentration shows no correlation with soil pH. This may be due to the fact that pH is influenced by many factors, e.g. fertility and soil structure, so that its relationship with variables such as calcium becomes obscure under field conditions. It is emphasised elsewhere (van den Bergh, 1969) that for these reasons any relationship between pH and vegetation pattern is extremely difficult to detect under field conditions.

The overall decrease in calcium with increasing elevation suggests a possible influence on species cohabitation. However, comparison of mean site values for species cover and exchangeable calcium values revealed only one clear trend. This is an increase in cover of *A. tenuis* as calcium levels decrease. This relationship is shown in Figure 17, which also indicates a high degree of variability in this trend that is thought to render any statistical analyses invalid. Nevertheless the following comments can be made.

It is possible that the low cover values of this species on the low elevation slopes is the result of high calcium levels in

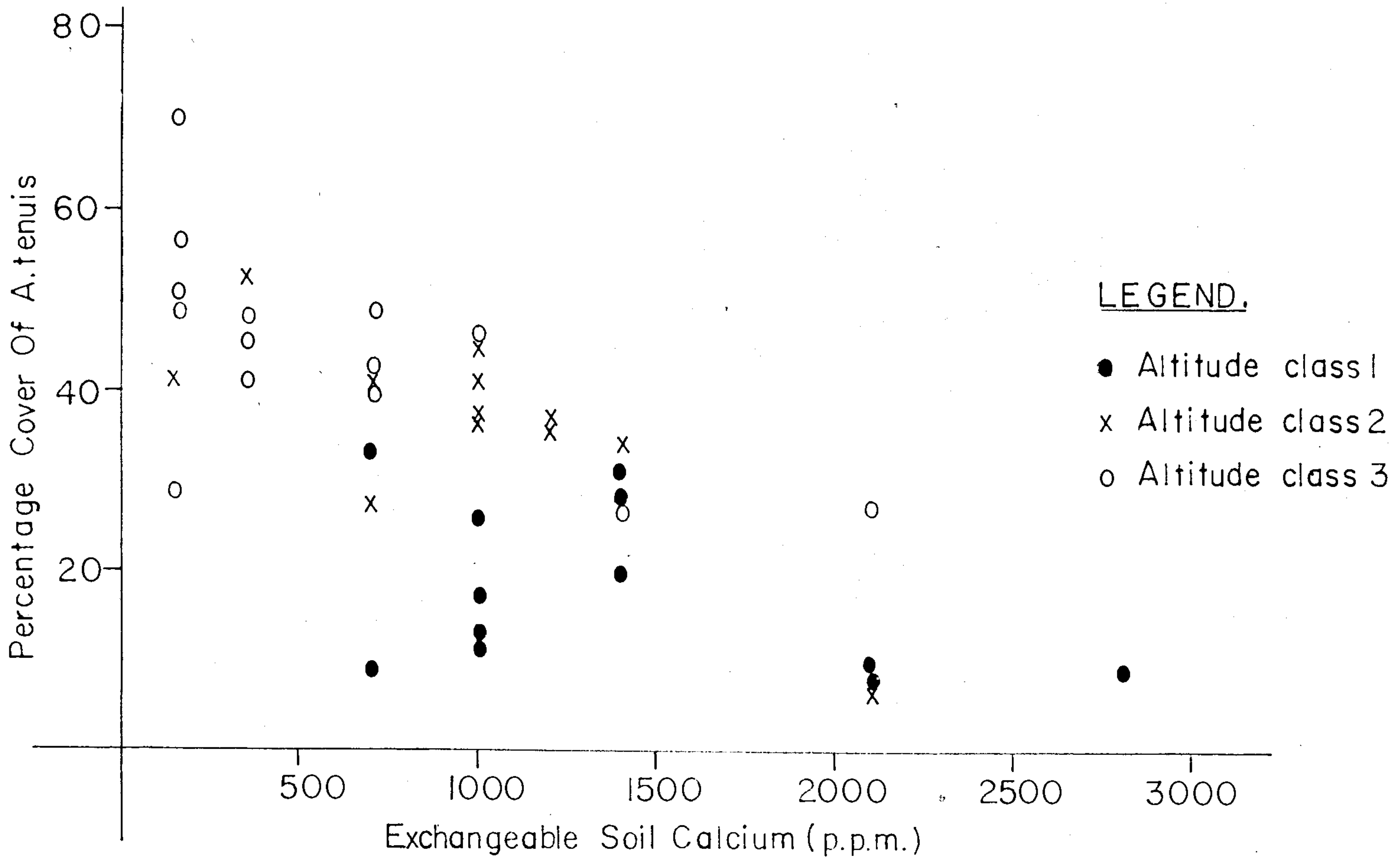


FIGURE 17. RELATIONSHIP BETWEEN EXCHANGEABLE SOIL CALCIUM AND % COVER OF <u>A. tenuis</u>.

the soil, rather than the result of restriction by more productive species. Furthermore, the decrease in soil calcium with increasing altitude enables it to establish larger cover values. This would agree with Thurston (1969), who describes A. tenuis as a species tolerant of acidic soils that contain low levels of exchangeable calcium. Under such conditions it tends to have a higher yield than associated species. So the variation in relative abundance of A. tenuis could be the result of restriction of other species due to increasing climatic severity and low calcium levels, or a preference for soils with low calcium levels.

The high degree of variation apparent in Figure 17 suggests that the abundance of this species is more likely to be due to the restriction of the other species. This inference is further substantiated by a more detailed consideration of Figure 17. At each calcium level there is still a tendancy for the low elevation areas to have lower cover values than the higher altitude slopes. This is particularly evident at the level of 1000ppm, suggesting that although soil calcium does influence the abundance of A. tenuis other factors, related to changes in altitude, are involved. The lack of any correlation between the other major species and soil calcium lends further weight to this inference. It is of course possible that these other factors are totally responsible for the variation in abundance and the apparent correlation with calcium levels is simply due to an independent decrease with increasing altitude. However, it is suggested here that the most feasible explanation will involve both soil calcium levels and the factors already discussed. Increasing climatic severity and low levels of soil calcium combine to restrict the more productive species with increasing altitude. This, in conjunction with the low productivity and tolerance of low calcium levels permits the establishment of large cover values of A. tenuis.

The confounding of variables, so often characteristic of spatial relationships (Green, 1979) is particularly apparent here. The difficulty of attaching any ecological significance to variation in soil chemical properties is further exemplified by the data for the mulched site 4,2. This site has the largest nitrate concentration in this study (Table 8). Yet it has a relatively low mean total cover of seeded species of 71% (Table 7). It also has a low mean soil depth (Table 9) and a relatively large proportion of bare soil (Table 7). Hence, it is possible that the high nitrate concentration is in fact due to the low levels of vegetation cover and consequent lack of nutrient removal from the soil.

Clearly, the influence of soil chemistry on the cohabitation of the species in this community can only be defined by controlled experimentation. Furthermore, any variation in soil chemistry will tend not to be related to variation in altitude and slope angle because of the manner in which the slopes were cleared and reseeded. Given this, and the lack of consistent trends when compared with species abundance, it is suggested that chemical properties play a minor role in determining how the species in this community cohabit.

6.3.2: Soil Depth

The close cohabitation of grass and legume species can be a result of differential exploitation of the soil environment (Roberts and Olson, 1942; Aberg et al., 1943; Kershaw, 1959). In this respect the relationship between soil depth and root growth form represents an important niche axis along which species may partition their habitat (Berendse, 1982; Fitter, 1982).

The fact that *P. pratense* is not restricted by shallow soil depth in a manner consistent with the other major species suggests that the occupation of areas of shallow soil is an important means whereby this species can maintain its abundance in the community, and thus cohabit with the other species. This is further substantiated by the fact that the mean soil depth on which it is present is less than that for which it is absent (Table 10). It has also been documented elsewhere that *P. pratense* predominantly roots at a shallow depth in the soil (Garwood, 1967).

The restriction of the cover of the other major species on shallow soils is not surprising. What is notable, however, is the decrease in cover of *A. tenuis*, *P. pratense* and *T. hybridum* in the deepest soil depth category. In contrast, *F. rubra* maintains a high percentage cover in this category (Figure 8). Its vigorous nature and propensity for vegetative spread possibly allow it to maintain a degree of competitive dominance in this category at the expense of the other major species.

T. hybridum cover is closely correlated with soil depth, having the narrowest range on this gradient (Figure 9). This marked preference for deeper soils is further substantiated by it having the largest difference between mean soil depth for presence and absence of all the seeded species (Table 10). One possible explanation for this preference is the fact that it usually has a well developed tap root system (Spedding and Diekmahns, 1972), the development of which is limited in shallow soils. A similar differential response of species with contrasting rooting habits to spatial variation in soil depth has been described by Kershaw (1958; 1959).

The importance of bryophytes as pioneers of bare ground is well known (Leach, 1931; Marsh and Koemer, 1972). Their establishment in areas such as this can be influenced by substrate type and the growth of other plant species (Bayfield, 1976, 1980). Their markedly greater cover values on shallow soils (Figure 14) may be attributable to the restriction of seeded species in such sites. On deeper soils bryophytes are likely to be limited by lack of space and shading caused by the development of a crowded seedling community.

Evidently, the relationship between soil depth and rooting habit may play an important role in determining how the species in this community cohabit. Differentiation in root distribution between coexisting species has been documented by Parish and

Bazzaz (1976), through extensive research by Berendse (1979, 1981, & 1982), and by Veresoglou and Fitter (1984). The differential occupation of the soil depth gradient by the species in this community and their known differences in rooting habit combine to lend further weight to the view of these authors that spatial variation in soil depth and innate differences in rooting habit are important influences upon cohabitation.

6.4: Timing Of Influence

The variation that occurs between sample sites make it an interesting feature of these field data that although the environmental gradients appear to influence the species in a differential manner they do not do so as an "all or nothing" effect (sensu Harper, 1977). What appears to be the case is that the probability of a given seedling becoming established is altered. This then influences the percentage cover that the species will attain. However, the mature plants may also be differentially influenced by their abiotic environment. So, at what stage in the life cycle are percentage cover values affected? Are variations in habitat occupation due to differential seed and seedling establishment or the result of differential tolerances of the mature plants?

The seedling stage is a particularly hazardous stage in the life cycle of most species (Harper, 1967). Since seedlings have low assimilate reserves, a poorly established root system and have to make the transition from autotrophic to heterotrophic nutrition, they can more easily succumb to environmental stress. This is further exacerbated in this developing community by the high density of seeds sown, permitting a large degree of species interaction. However, the physiology of a mature plant may differ from that of the seedling (Chippendale, 1949). This author has shown that _P. pratense_ has a low moisture requirement for germination, but does require moist conditions later in its growth.

Furthermore, the relative numbers of individuals reaching maturity will not simply be a function of seedling establishment and mature plant tolerance, nor of the proportion of each species in the seed mixture. Seed size serves to further complicate the analysis of spatial pattern (Kershaw, 1973).

In mixed populations the young plants from small seeds are at a disadvantage compared to those species with larger seeds (Black, 1958; Harper and Clatworthy, 1963). This is particularly important when the seedlings experience density stress (Harper et al., 1970). Table 3 shows the number of seeds contained in 1kg for each species, an indication of their relative seed size. _F. rubra_ and _T. hybridum_ have distinctly larger seeds than the other two major species in the community. This will enhance their competitive dominance over the latter species, since they can start growth with a greater embryonic capital and thus establish larger cover values in the lower altitude sites. This strengthens the interpretation of their differential habitat occupation in low and high altitude sites presented in section 6.2 based on the productivity and rate of establishment of the species.

It has also been reported that the problem of desiccation is reduced for small seeds, due to their large soil contact/surface area ratio (Harper and Benton, 1966). In this respect the small seeds of P. pratense may represent a possible means by which this species is able to increase its percentage cover values on the steeper slopes where the cover of the other species, in particular T. hybridum, is limited. The fact that A. tenuis does not exhibit a similar trend suggests that this response is due to a combination of seed size, low moisture requirement for germination, and restriction of other species either due to desiccation or shallow soils.

Such considerations, combined with the fact that species do not show an "all or nothing" effect, indicate that the balance between species composition will depend on differential habitat occupation at the seed, seedling and mature plant stages of their life cycles. Obviously, effects on one stage will not be independent of those on other stages in the life cycle. Similarly, the influence of environmental gradients are not entirely independent. Their use here as niche axes, however, has served to facilitate the communication and interpretation of how the variation in relative abundance may be attributable to ecologically significant variables.

6.5: Biotic Influences

6.5.1: Interspecific Associations

> "In any interpretation of a descriptive vegetation study based on the biology of the constituent species the manner in which individuals cope with their immediate environment of neighbours should be emphasised" (Aarssen et al, 1979, p.2695).

In an artificial, developing, grass-legume community, Turkington and Cavers (1979) have described the importance of neighbouring species interactions as influences on community development. The results presented in this thesis illustrate that even in a community where the relative abundance of species can be correlated with spatial variation in the abiotic environment, relationships between the species themselves may also be important factors influencing their cohabitation. It is crucial to realise here that complex relationships can exist between grasses and legumes in such communities (Turkington et al., 1977).

As Silvertown (1983) has emphasised, negative associations between species may be due to species interaction or the result of niche differences totally unrelated to any possible species interaction. Likewise, positive association may be due to some form of combining ability or simply the result of similar environmental requirements. In natural and semi-natural communities interpretation of field data in terms of species interactions is therefore questionable. However, in an artificial community such as this where the species have been seeded in a uniform, high density manner, patterns of species association can be compared over different habitats and valid interpretations made concerning possible species interactions.

Species that tend to form clumps tend to be negatively associated (Turkington and Cavers, 1979). The fact that *A. tenuis* and *P. pratense* tend to make fewer contacts with each other than with *F. rubra* is interesting in this respect, especially given the vigorous nature of the latter species. *A. tenuis* exhibits the greatest propensity for isolated occurrences, its percentage flowering values are high, and it is well known as a tussock-forming species (Hubbard, 1968; Turkington and Harper, 1979b). *P. pratense* is also a tufted species (Evans, 1927; Hubbard, 1968; Hubbard, 1969). In contrast, *F. rubra* displays a preference towards vegetative rather than reproductive growth (Table 12) and exhibits a more "loosely-clumped", rhizomatous growth form (Hubbard, 1968). As previously mentioned it is capable of vigorous growth and can thus form dense swards (Harberd, 1961). Hence, in this community it can employ two strategies:

1. vigorous growth where it becomes established in the productive, low altitude sites, enabling it to dominate large areas of the sward, facilitating its high cover values;
2. a tendancy to spread vegetatively between established

tussocks of the other species. In this manner it can "fill in" the gaps in the sward and thereby maintain high cover values. This possible strategy may account for its increased cohabitation with the tussock forming species.

A similar situation has been described by Turkington and Cavers (1979) for legume species. They showed how two clumped species were unable to cohabit with each other but could cohabit freely with species showing stoloniferous growth. The tussock growth form of _A. tenuis_ and _P. pratense_ restricts their vegetative spread in areas where _F. rubra_ establishes large cover values, since they cannot employ the second strategy. Their morphological construction, resulting from the repeated production of tillers on the main stem and on successive orders of tillers, also makes them susceptible to degradation. In a relatively short period in a crowded community the soil volume available for root exploitation is completely exhausted. As a clump becomes dense and the tussock accumulates undecayed remains, rooting of tillers becomes limited. This may increase the possibility that the plant will succumb to competition from vigorously growing neighbours (Spedding and Diekmahns, 1972). A similar situation has been described for tussock forming range grasses by Canfield (1957) who documents how an increase in death risk occurs as the plants grow larger.

This interpretation is further substantiated by the fact that _F. rubra_ displays more significant positive associations with _P. pratense_ than with _A. tenuis_. The differential rooting habits of these species described earlier may enable such closer cohabitation with P. pratense, through a reduction in underground interference.

Where abiotic conditions restrict the productivity of a community, species interactions are not thought to be important influences on their relative abundance (Muller, 1952). This reduction of species interactions in less productive environments has been subject to extensive theoretical consideration (see Grime, 1979). In contrast to the other altitude classes, there is no evidence for a negative association between A. tenuis and P. pratense in the highest elevation class. The reduction in cover values of the other major species may allow them to cohabit more freely, due to an increase in available space and a reduction in competitive stress. At low altitude F. rubra and T. hybridum tend to pre-empt a large part of the available space. As suggested this may restrict the establishment of larger cover values by A. tenuis and P. pratense. In addition it may cause these two species to compete with each other for the remaining space, this exacerbating the restrictive effect. According to the predictions of Grime (1979) interference between these two species will be reduced in the highest elevation class, due to a decrease in habitat productivity, hence they would not be expected to display a negative association.

The lack of other species with which to form more positive associations, will also tend to raise the number of expectable contacts these two species will make. Consequently they display significantly larger cover values and increased values for percentage flowering.

This interpretation is strengthened by the fact that *F. rubra* exhibits a decrease in clumping in the higher altitude areas which may simply be due to its decrease in cover or, because this decrease appears to be proportionately greater than that for its cover values, it may be the result of a decrease in vigour. Consequently, this species will tend to put more reliance on the second of the two strategies suggested above to describe its growth in the community. Since it tends, therefore, to "fill in" rather than "dominate" the sward its interference in the growth of other species will be less.

However, a negative association is detected between *A. tenuis* and *F. rubra* in this altitude class. This appears to be the result of the very low number of contacts made by *F. rubra* on *A. tenuis* (Table 17). This agrees with the above suggestion that *F. rubra* is more dependent on the second of its two growth strategies in the higher altitude sites. It is further suggested that *F. rubra* tends to make more contacts with *P. pratense*, by virtue of their differential rooting depths, enabling closer cohabitation at a very localised scale. The more similar rooting habits of *A. tenuis* and *F. rubra* not facilitating such close cohabitation.

6.5.2: Legume Behaviour

Any associations detected for T. repens are ignored due to the very low abundance values recorded for this species. However, the associations detected for T. hybridum , its growth habit and behaviour in the sward, and the possible reasons for it attaining much larger cover values than T. repens, merit further discussion.

Differential exploitation of the soil environment can be invoked to explain the negative associations T. hybridum displays with A. tenuis and F. rubra but not with P. pratense in the mulched habitat class. It is important to recognise here the differential effect of the scale adopted to examine the vegetation. Utilising a "plant's-eye-view" P. pratense and T. hybridum grow most abundantly on different ranges of the slope angle gradient in this community, and so will not be expected to make as many contacts within each altitude class. They also appear to separate out along a gradient of spatial variation in soil depth. However, no negative association is detected between these two species. Although they occupy different areas on the large- and small-scale abiotic gradients they appear to cohabit closely at the very localised scale of study adopted here. Once more, differences in rooting habit provide a possible explanation. The fact that these two species have marked differences in rooting strategy may enable them to cohabit much more closely. In addition, they have been shown, elsewhere, to combine well (Robinson, 1949), and Davies (1960) describes P.

pratense as an excellent companion crop with legumes. However, their differential, large-scale habitat occupation will prevent the establishment of any positive association. The similarity in rooting depth of *T. hybridum* and the other major species, in an environment highly favourable to plant growth (low altitude and mulched) may prevent such close cohabitation at the very localised scale. This emphasises the importance of studying the vegetation at a variety of scales in order to detect the possible influences on species cohabitation.

T. hybridum was seeded at a proportion by weight of 10% in the seed mixture. Yet it frequently attains cover values much larger than this. In contrast, *T. repens* rarely attains cover values larger than its original proportion of the seed mixture of 5% (see Table 6). There are several possible explanations, which, in combination, may account for their differential success. Intuitively, the very fact that *T. hybridum* was seeded at twice the proportion will be crucial for it attaining larger cover values. But this alone cannot completely account for its proportionately larger cover values in the developing community.

T. repens exhibits a preference for deep soils with well balanced water relationships (Gittins, 1969). *T. hybridum*, on the other hand, is a more tolerant species which can withstand wet soils (Stapledon, 1923; Robinson, 1949). It is therefore feasible that its larger cover values are due to a wider environmental tolerance.

The primary root in T. repens is a tap root, but its activity soon diminishes and it usually dies within 18 months (Tesar and Ahlgren, 1950). The adventitous roots which then dominate the rooting activity of this species are confined to the top 15cm of soil, (Spedding and Diekmahns, 1972), where interference with the ramified roots of grasses will be greater. In comparison, the well developed tap root system of T. hybridum, although limiting its development in shallow soils, may enable more efficient utilisation of the soil environment with the seeded grasses, especially those such as P. pratense, which root predominantly at shallow depths.

Legumes have essentially two forms of growth, creeping and erect. The creeping habit is exemplified by T. repens (Erith, 1924). Its short stem (25-75mm) bears alternately arranged leaves, in the axils of which buds develop to form stolons. Due to the short internodes on the stem these tend to radiate horizontally (Spedding and Diekmahns, 1972). In contrast, T. hybridum provides an example of the erect habit, and so in the first year of growth it can have its meristematic apex well above ground level, this facilitating its establishment in a crowded seedling community. Furthermore, it is regarded as an aggressive legume species in terms of its ability to compete with companion crops (Blaser et al, 1956). It has been further emphasised elsewhere that the legumes that exhibit the more erect form of growth habit should be better able to compete favourably with the grass component of the sward (Rhodes and

Stern, 1978), and that "shading is detrimental to their growth" (Spedding and Diekmahns, 1972). Personal observation of the growth of these species in the study area and the data for percentage flowering (Table 12) indicate that these two legumes do adopt such growth habits in this community. This, therefore, represents a possible means by which the differential establishment of these two species has occured.

In an artificial, grass-legume community Turkington and Cavers (1979) describe how T. pratense assumes dominance among the legumes, exerting strong "competitive pressures" on T. repens. The similar growth form of T. hybridum (Stapledon, 1923; Robinson, 1949) may enable it to do likewise in this community. Growth form, both above and below ground, combined with a larger seeding input and a wider range of environmental tolerance therefore appear to represent potential means whereby T. hybridum, to a far greater extent than T. repens, can cohabit with the grasses in this developing community.

6.5.3: Limitations

Sometimes assumptions cannot be fully satisfied and recommended procedures must be modified in order for a complete statistical examination of a set of biological data to be made. The onus in such a case is then on the writer to proceed with caution in interpretation and to make it clear where such limitations occur and their possible influence on the outcome of the analysis.

The results and interpretations of possible biotic influences are presented in a cautionary manner here because it must be realised that:

1. there are differences in the distribution of the species with respect to abiotic gradients;
2. each count matrix has a low sample size when compared with other studies;
3. it has been assumed that, for each species, the probability of occurrence as species i is the same as that for occurrence as species j in the contact sampling procedure. Reference to Appendix 7 indicates variation in this respect, especially for _F. rubra_;
4. there are important pitfalls in inferring processes of species interaction from short term descriptive studies such as this (Wiens, 1977; Connell, 1980). Cohabitation has been described and interpreted in relation to suggested, ecologically important abiotic variables. However, biotic interpretation has necessarily been limited to a discussion of possible influences. These have not been consistent, possibly due to the "youthful stage" of the community (cf. Aarssen et al., 1979), the unpredictability of interactions in multi-species mixtures (Fowler, 1982), and the fact that they are the result of what Wiens (1977) describes as an "intermittent process".

Nevertheless, complex relationships do appear to exist in artificial, developing, grass-legume communities (Turkington and

Cavers, 1979). Their possible occurrence therefore warrants consideration in a study such as this, which has attempted to describe the manner in which species cohabit in a given community. Such considerations have been limited to possible influences, since the recognition of causal, definitive effects require experimental investigation. But it is thought that the methodology and results have been validly used as a necessary aid to outline the possible influence of species interactions on community development and the manner in which the species cohabit.

6.6: Niche Differences

The abiotic gradients and possible biotic influences can be conceived as forming, in combination, a multidimensional space, in which each species has its own distinctive position representing its niche in the community. The axes of such niche space warrant joint consideration if the manner in which the species cohabit is to be explained in a clear and valid fashion. Such joint consideration is the objective of this section.

From the results presented here, inferences can be made concerning the manner in which niche differences facilitate cohabitation of the species. Correlation of species abundance with abiotic variation suggests habitat partitioning along the gradients of the physical environment studied here. Furthermore, it is suggested that niche differences are maintained by species interactions, the species tending to disperse their populations along the various niche axes so that interference between them is reduced by habitat differences. Each species therefore establishes larger cover values in those parts of the environment where it is a more effective competitor. This being controlled by the tolerance ranges and growth requirements of the individual species.

The less productive grass species, A. tenuis and P. pratense, appear to be restricted from part of their fundamental niche, the low-elevation, high-productivity habitats, by the combined effect of direct interference from the more productive species, whose vigorous growth pre-empts the available space, and competition between each other for the remaining space in the community. The increase in cover of the less productive species with increasing altitude is thought to be due to their greater degree of tolerance of the increasing environmental severity and the consequent restriction of the more productive species, rather than a preference of the former species for these habitats. As a result, "competitive release" appears to occur, facilitating cohabitation along the abiotic gradients. In this manner the realized niches of the species are separated by a combination of differential tolerance, growth and competitive ability, the latter being modified by changes in the physical environment.

F. rubra and T. hybridum have fundamental niches "included" within those of the less productive grasses. However, due to their competitive dominance in the productive habitats they can occupy part of the fundamental niche of the less productive species, tending to restrict them from establishing large cover values. Hence, the realized niches of A. tenuis and P. pratense are much smaller than their fundamental niches, which cover the entire range of abiotic variation encompassed. In contrast, the realized and fundamental niches of the more productive species, over this range of abiotic variation, are essentially the same.

The parallel with the removal type experiments described in Chapter 3, in which potential competitors for a limited resource can cohabit by virtue of niche differences, is quite striking. However, this is only a plausible explanation based on observational field data. An alternative is that the species may cohabit simply as a result of differential tolerance ranges, and not in any way the result of species interactions. The problems of disentangling such alternatives are well known (Harper, 1977). Nevertheless, the results of the association analysis and the fact that A. tenuis and P. pratense were seeded in the low altitude habitats, where they have an equal tolerance of the prevailing physical environment, suggests that their distribution is limited by interference from the more vigorous species. Although the proposed interpretation can only invoke the occurrence of interference in the past to help explain the present pattern of differences in the realized niches of the species, it is thought to be the most feasible.

CHAPTER 7

CONCLUSIONS

The results of this study have demonstrated the importance of studying a plant community at a variety of scales if potential influences on how the species cohabit are to be correctly identified. In this respect three conclusions can be drawn:

1. large-scale abiotic variation may influence cohabitation patterns through its relationship with species-specific requirements for growth;
2. localised edaphic factors represent possible mechanisms for cohabitation through their relationship with species growth preferences and growth habit;
3. a combination of species interactions and variations in growth form at the scale of the individual plant can facilitate close cohabitation in similar habitat classes and along environmental gradients.

Correlations of the abundance of the four major species in the community along the gradients of altitude and slope angle suggest that cohabitation is facilitated by differential habitat occupation. This is in accordance with the tolerance ranges of the individual species and in a manner which reduces the potential interactions between the species, which are modified as the physical environment changes. It is suggested that increasing severity of the complex of factors represented by these gradients somehow restricts the more productive species, F. rubra and T hybridum. This in turn facilitates the growth of A. tenuis and P. pratense.

Consideration of niche theory indicates that such patterns may be due to specific environmental preferences or partly the result of changing species interactions along the abiotic gradients. Competitive dominance of the vigorous and productive species appears to preclude the establishment of the slower establishing species in the classes favourable to plant growth. These effects being mitigated with incresing severity of the habitat.

Variation in soil chemistry appears to have a limited influence on species relative abundance. High levels of ferric iron in poorly drained areas in the highest elevation class appear to restrict the percentage cover of F. rubra. Soil calcium concentration tends to decrease with increasing altitude, further contributing to a reduction in the productivity of the habitat. The tolerance of A. tenuis to low levels of calcium may further facilitate its cohabitation with the more vigorous species along the elevational gradient.

In contrast, soil depth is significantly correlated with variations in species relative abundance. The percentage cover of all the major species is restricted on shallow soils, excepting that of P. pratense which grows equally well on shallow soils. This has an apparent relation with rooting strategy and appears to influence cohabitation patterns of the species. In addition, bryophytes show a marked preference for areas of shallow soils.

Within the altitude classes, localised habitat partitioning and complementarity of growth form may further reduce the potential competition between certain species. The variable growth strategy of F. rubra and the different rooting habit of P. pratense appear to favour the development of positive associations by these species. The similarity in above-ground form of P. pratense with A. tenuis possibly influences the tendancy for these species to be negatively associated in situations where interference is likely to be great. Such effects again being reduced as the environment becomes less favourable to overall plant growth. In this manner, the nature of species interactions may change in direction and intensity as the abiotic environment alters.

The results are not merely of academic importance. The seeding of bare ground on Whistler Mountain with a grass-legume seed mix and the management technique employed has demonstrated the suitability of this method of restoration for similar, disturbed, montane areas in the region. Overall differences in the relative abundance of the seeded species, combined with the variation recorded at each of the three scales of study, suggests potentially useful species and species combinations. The results also indicate those species which could possibly be witheld from future seeding programs. Although sowing the mixture as a whole over the range of sites has been shown to enable species to partition their environment and hence efficiently exploit the abiotic gradients with respect to individual preferences and interactions with neighbouring species. This resulting in the high total cover values recorded for the sites as a whole.

The patterns of cohabitation described appear to demonstrate niche differences among the species in an artificial, developing, grass-legume community. The principal conclusion that can be drawn here is that the cohabitation of species in this community is facilitated primarily through differences in their realized niches. In short, separation of the four major species along the large- and small-scale abiotic gradients is suggested to represent habitat partitioning influenced by the tolerance range and physiognomy of each species. It is further suggested that the species tend to disperse their populations along these gradients such that interference between them is reduced by habitat differences. These interference effects are in turn modified by changes in the physical environment. Within the habitat classes, niche differences, in terms of physiognomy, are thought to facilitate the cohabitation of species at a very localised scale, again because of a reduction in interference.

Clearly, the discussion of the results of this study has been greatly facilitated by use of the concept of the niche. It has enabled independent description of the factors influencing the relative abundance of the species, whilst permitting their simultaneous interpretation. This has allowed a more clear and confident explanation of how the species cohabit to be made.

Finally, it is suggested that the results of this thesis, and the manner in which they have been interpreted, are applicable to future revegetation programs of a similar nature, and may help throw light on how natural and semi-natural communities develop and their constituent species cohabit.

APPENDIX 1: ALTITUDE/SLOPE ANGLE ANOVA TABLES

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Agrostis tenuis					
Mean	14.56	1	141.56	1783.26	0.000
Slope	0.14	4	0.03	0.44	0.779
Altitude	13.50	2	6.75	85.03	0.000
A-S Int.	1.15	8	0.14	1.81	0.073
Error	36.20	456	0.07		
Festuca rubra					
Mean	196.08	1	196.08	1964.69	0.000
Slope	1.92	4	0.48	4.82	0.001
Altitude	2.18	2	1.09	10.94	0.000
A-S Int.	6.91	8	0.86	8.65	0.000
Error	45.56	456	0.10		
Phleum pratense					
Mean	78.12	1	78.12	894.36	0.000
Slope	2.50	4	0.62	7.15	0.000
Altitude	3.26	2	1.63	18.64	0.000
A-S Int.	1.56	8	0.20	2.63	0.024
Error	39.83	456	0.09		
Trifolium hybridum					
Mean	59.03	1	59.03	529.36	0.000
Slope	8.56	4	2.12	19.20	0.000
Altitude	5.92	2	2.96	26.56	0.000
A-S Int.	2.53	8	0.32	2.84	0.004
Error	50.84	456	0.11		

A-S Int. represents the altitude/slope angle interaction effect.

APPENDIX 2: ALTITUDE/SLOPE ANGLE MULTIPLE RANGE TESTS

Where the 2-way ANOVA revealed overall significant differences the multiple range test was employed to examine where these differences occur. In applying such a test it is important to use a systematic procedure. Beginning with the largest mean value in the range under study, the difference between it and the smallest mean are compared with the appropriate critical range. If a significant difference is recorded the largest mean is then compared with the second smallest mean value in the range. This is continued until no significant difference is found in the comparison. The second largest mean is then contrasted with the other mean values in the same manner.

In Chapter 5 significant differences in each range are expressed by underscoring those classes whose means do not differ statistically. Throughout the appendices each species is considered independently, using transformed data. The abbreviation NS means that there is no significant difference between the mean values in the range under test, S signifies the standard deviation, and n refers to the number of quadrats in each class. The exact formulae used and procedure followed are described by Kramer (1956). Finally, the actual values of each altitude and slope angle class are those given in Chapter 4.

Agrostis tenuis

Altitude Class	1	2	3
Mean Cover	0.339	0.621	0.727
n	172	138	161

s=0.329

Range	Calc. F	Probability
3-1	5.00	<0.01
3-2	1.29	<0.01
2-1	3.48	<0.01

Festuca rubra

(a) Altitude Range Test

Altitude Class	1	2	3
Mean Cover	0.703	0.700	0.577
n	172	138	161

s=0.346

Range	Cacl. F	Probability
1-3	1.62	<0.01
1-2	0.04	NS
2-3	1.50	<0.01

(b) Slope Angle ANOVA Within Altitude Classes

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Altitude Class 1					
Means	5.94	4	1.48	14.50	0.000
Error	17.14	167	0.10		
Altitude Class 2					
Means	0.37	4	0.09	0.86	0.488
Error	14.22	133	0.11		
Altitude Class 3					
Means	2.89	4	0.72	7.98	0.000
Error	14.15	156	0.09		

(c) Slope Angle Range Tests

ALTITUDE CLASS 1

Slope Angle Class	Mean	n
4	0.421	28
3	0.661	34
2	0.812	34
1	0.856	45
5	0.903	31

s=0.319

Range	Calc. F	Probability
5-4	2.61	<0.01
5-3	1.37	<0.01
5-2	0.52	NS
1-4	2.55	<0.01
1-3	1.21	<0.05
2-3	0.88	NS
3-4	1.33	<0.01

ALTITUDE CLASS 3

Slope Angle Class	Mean	n
1	0.319	31
2	0.588	30
3	0.602	31
4	0.634	34
5	0.719	35

s=0.322

Range	Calc. F	Probability
5-1	2.29	<0.01
5-2	0.74	NS
4-1	1.27	<0.01
3-1	1.57	<0.01
2-1	1.48	<0.01

Phleum pratense

(a) Altitude Range Test

Altitude Class	1	2	3
Mean	0.359	0.387	0.538
n	172	138	161

s=0.315

Range	Calc. F	Probability
3-1	2.30	<0.01
3-2	1.84	<0.01
2-1	0.35	NS

(b) Slope Angle ANOVA Within Altitude Classes

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Altitude Class 1					
Means	0.98	4	0.24	2.54	0.042
Error	16.11	167	0.09		
Altitude Class 2					
Means	2.24	4	0.56	6.84	0.000
Error	10.88	133	0.08		

Altitude Class 3 - Not Significant.

(c) Slope Angle Range Tests

ALTITUDE CLASS 1

Slope Angle Class	Mean	n
2	0.277	28
4	0.299	34
1	0.347	34
3	0.415	45
5	0.483	31

s=0.316

Range	Calc. F	Probability
5-2	1.12	<0.05
5-4	1.05	<0.05
5-1	0.77	NS
3-2	0.81	NS

ALTITUDE CLASS 2

Slope Angle Class	Mean	n
2	0.185	17
1	0.305	18
3	0.319	30
4	0.394	38
5	0.578	35

s=0.319

Range	Calc. F	Probabilty
5-2	1.88	<0.01
5-1	1.32	<0.01
5-3	1.43	<0.01
5-4	1.11	<0.05
4-2	1.01	<0.05
4-1	0.44	NS
3-2	0.62	NS

Trifolium hybridum

(a) Altitude Range Test

Altitude Class	1	2	3
Mean	0.341	0.477	0.218
n	172	138	161

s=0.377

Range	Calc. F	Probability
2-3	3.15	<0.01
2-1	1.68	<0.01
1-3	1.58	<0.01

(b) Slope Angle ANOVA Within Altitude Classes

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Altitude Class 1					
Means	5.03	4	1.25	11.8	0.000
Error	18.77	167	0.11		
Altitude Class 2					
Means	3.49	4	0.87	5.89	0.000
Error	19.65	133	0.15		
Altitude Class 3					
Means	2.53	4	0.64	7.96	0.000
Error	12.42	156	0.08		

(c) Slope Angle Range Test

ALTITUDE CLASS 1

Slope Angle Class	Mean	n
1	0.606	28
2	0.512	34
3	0.306	34
4	0.219	45
5	0.131	31

s=0.373

Range	Calc. F	Probability
1-5	2.58	<0.01
1-4	2.25	<0.01
1-3	1.66	<0.01
1-2	0.52	NS
2-5	2.16	<0.01
2-4	1.82	<0.01
2-3	1.20	<0.05
3-5	0.99	NS

ALTITUDE CLASS 2

Slope Angle Class	Mean	n
2	0.752	17
3	0.637	30
1	0.513	18
4	0.351	35
5	0.325	38

s=0.411

Range	Calc. F	Probability
2-5	2.07	<0.01
2-4	1.87	<0.01
2-1	0.99	NS
3-5	1.77	NS
3-4	1.65	<0.05
1-5	0.91	NS

ALTITUDE CLASS 3

Slope Angle Class	Mean	n
2	0.433	31
3	0.299	30
1	0.166	31
5	0.149	34
4	0.075	35

s=0.306

Range	Calc. F	Probability
2-4	2.05	<0.05
2-5	1.62	<0.05
2-1	1.52	<0.05
2-3	0.70	NS
3-4	1.27	<0.05
3-5	0.85	NS
1-4	0.52	NS

APPENDIX 3: MULCH/SLOPE ANGLE COMPARISON

(a) ANOVA Tables

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Agrostis tenuis					
Mean	34.17	1	34.17	358.19	0.000
Mulch	0.28	1	0.29	3.02	0.083
Slope	0.94	4	0.24	2.47	0.045
M-S Int.	0.30	4	0.07	0.79	0.533
Error	25.37	266	0.09		
Festuca rubra					
Mean	118.57	1	118.57	1208.50	0.000
Mulch	0.37	1	0.37	3.80	0.052
Slope	2.98	4	0.75	7.61	0.000
M-S Int.	2.39	4	0.59	6.10	0.000
Error	26.10	266	0.10		
Phleum pratense					
Mean	38.82	1	38.82	478.95	0.000
Mulch	0.24	1	0.24	3.00	0.084
Slope	1.57	4	0.39	4.84	0.001
M-S Int.	0.21	4	0.05	0.76	0.628
Error	21.56	266	0.08		
Trifolium hybridum					
Mean	33.51	1	33.51	289.92	0.000
Mulch	0.04	1	0.04	0.37	0.549
Slope	2.96	4	0.74	6.40	0.000
M-S Int.	3.12	4	0.78	6.85	0.000
Error	30.75	266	0.12		

M-S Int. represents the mulch/slope angle interaction effect.

(b) Slope Angle Range Tests

(i) ANOVA Tables

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Phleum pratense					
Means	0.85	4	0.22	3.86	0.006
Error	5.45	99	0.66		
Trifolium hybridum					
Means	1.78	4	0.45	3.68	0.008
Error	11.97	99	0.12		

(ii) Range Tests

Phleum pratense

Slope Angle Class		
1	0.295	18
2	0.378	15
4	0.409	23
3	0.516	18
5	0.538	30

s=0.247

Range	Calc. F	Probability
1-5	1.15	<0.05
1-3	0.94	<0.05
1-4	0.51	NS
2-5	0.72	NS

Trifolium hybridum

Slope Angle Class	Mean	n
1	0.218	30
5	0.231	18
4	0.453	23
2	0.467	15
3	0.534	18

s=0.365

Range	Calc. F	Probability
1-3	1.50	<0.05
1-2	1.11	<0.05
1-4	1.19	<0.05
1-5	0.06	NS
5-3	1.31	<0.05
5-2	0.98	NS
4-3	0.40	NS

APPENDIX 4: ALTITUDE/SLOPE ANGLE ANOVA FOR SOIL CALCIUM

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Altitude	4735186	2	267593	6.74	0.004
Slope	1327445	4	331861	0.94	0.455
A-S Int.	839885	8	104985	0.30	0.959
Error	8781666	25	351266		

A-S Int. represents the altitude/slope angle interaction effect.

Altitude Class	1	2	3
Mean Soil Calcium (ppm)	1385	983	500
n	13	12	14

s=654

RANGE	CALC. F	PROBABILITY
3-1	3250	<0.01
3-2	1736	NS
2-1	1420	NS

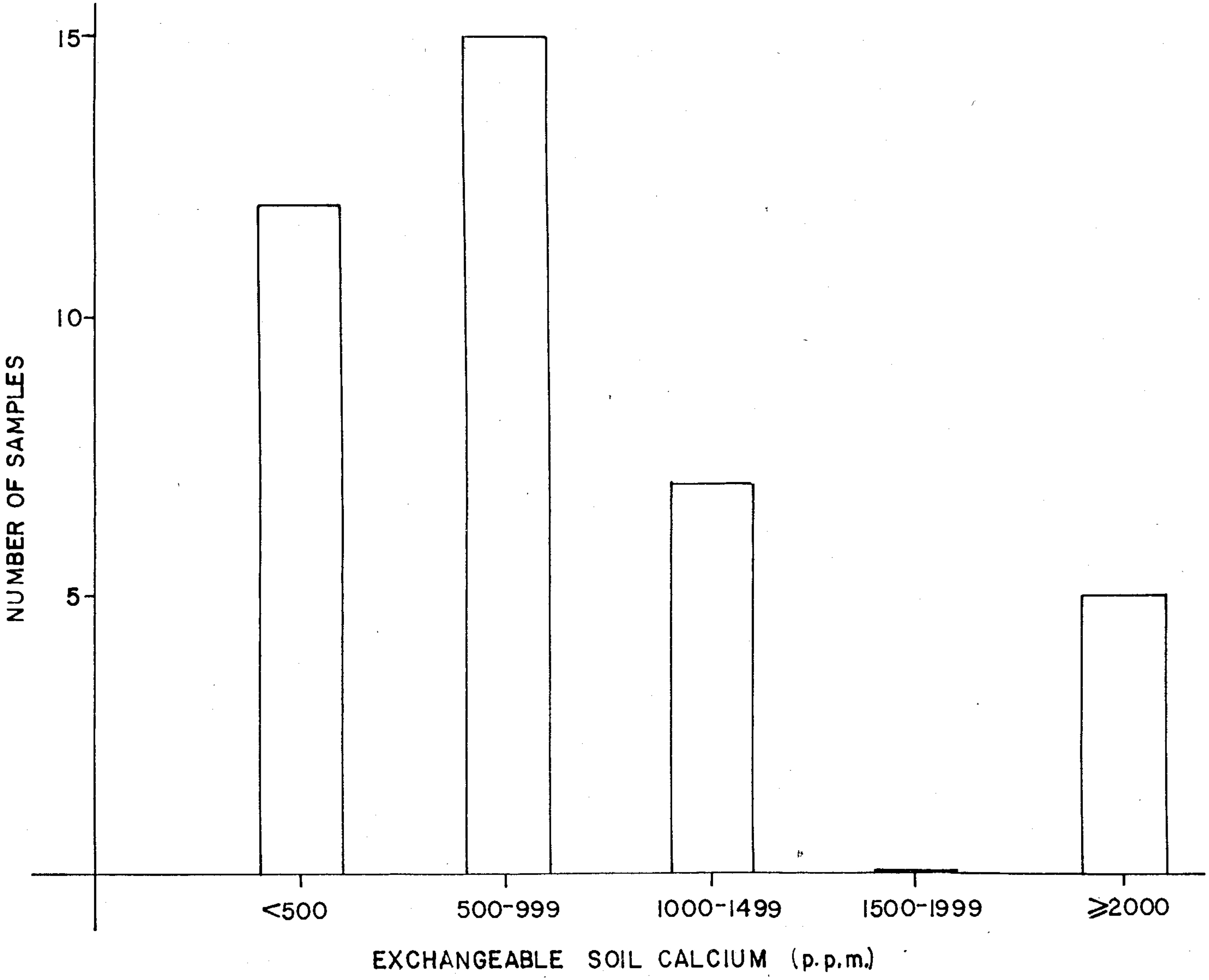


FIGURE 18:
FREQUENCY OF EXCHANGEABLE SOIL CALCIUM VALUES IN SAMPLE SITES.

APPENDIX 5: SOIL DEPTH/SPECIES COVER COMPARISON

(a) ANOVA Tables

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Agrostis tenuis					
Soil Depth	1.89	6	0.316	3.00	0.007
Error	48.98	464	0.106		
Total	50.88	470			
Festuca rubra					
Soil Depth	1.89	6	0.316	2.69	0.014
Error	54.46	464	0.117		
Total	46.78	470			
Phleum pratense					
Soil Depth	1.24	6	0.207	2.11	0.051
Error	45.54	464	0.098		
Total	46.78	470			
Trifolium hybridum					
Soil Depth	7.02	6	1.170	9.07	0.000
Error	59.86	464	0.129		
Total	66.88	470			

(b) Range Tests

Soil Depth (cm)	<5	6-10	11-15	16-20	21-25	26-34	>35
Class No.	1	2	3	4	5	6	7

Agrostis tenuis

Soil Depth Class	Mean	n
1	0.393	27
4	0.498	76
7	0.515	62
6	0.531	53
2	0.510	99
3	0.609	83
5	0.642	71

s=0.326

Range	Calc. F	Probability
1-5	1.56	<0.01
1-3	1.38	<0.01
1-2	1.15	<0.01
1-6	0.82	NS
4-5	1.23	<0.05
4-3	0.99	NS
7-5	1.03	<0.05
6-5	0.86	NS

Festuca rubra

Soil Depth Class	Mean	n
1	0.426	27
2	0.634	99
6	0.653	53
3	0.661	83
7	0.689	62
4	0.706	76
5	0.709	71

s=0.346

Range	Calc. F	Probability
5-1	1.77	<0.01
5-2	0.68	NS
4-1	1.76	<0.01
7-1	1.61	<0.01
3-1	1.50	<0.01
6-1	1.36	<0.01
2-1	1.35	<0.01

Trifolium hybridum

Soil Depth Class	Mean	n
1	0.131	27
2	0.204	99
3	0.279	83
4	0.322	76
7	0.433	62
5	0.467	71
6	0.534	53

s=0.377

Range	Calc. F	Probability
1-6	2.41	<0.01
1-5	2.10	<0.01
1-7	1.85	<0.01
1-4	1.21	<0.05
1-3	0.94	NS
2-6	2.74	<0.01
2-5	2.39	<0.01
2-7	2.00	<0.01
2-4	1.09	NS
3-6	2.05	<0.01
3-5	1.65	<0.01
3-7	1.30	<0.05
3-4	0.38	NS
4-6	1.61	<0.01
4-5	1.24	<0.05
4-7	0.92	NS
7-6	0.76	NS

APPENDIX 6: ANOVA TABLES FOR % FLOWERING DATA

SOURCE	SUM OF SQUARES	DEGREES OF FREEDOM	MEAN SQUARE	F	PROBABILITY
Agrostis tenuis					
Altitude	27.37	2	13.62	56.87	0.000
Slope	1.25	4	0.38	1.59	0.176
A-S Int.	3.67	8	0.42	1.76	0.084
Error	90.14	378	0.24		
Festuca rubra					
Altitude	1.76	2	0.68	6.70	0.001
Slope	0.09	4	0.05	0.51	0.730
A-S Int.	0.52	8	0.04	0.43	0.900
Error	41.96	401	0.10		
Phleum pratense					
Altitude	13.25	2	6.63	24.39	0.000
Slope	1.87	4	0.47	1.72	0.140
A-S Int.	3.39	8	0.42	1.56	0.140
Error	91.61	337	0.27		
Trifolium hybridum					
Altitude	21.62	2	10.83	54.98	0.000
Slope	2.12	4	0.67	3.44	0.009
A-S Int.	9.89	8	1.13	5.77	0.000
Error	45.11	231	0.19		

A-S Int. represents the altitude/slope angle interaction effect.

Number of Recorded Shoots Flowering (f), and Percentage Flowering (%) in Each Sample.

Sample	Agrostis alba		Agrostis tenuis		Festuca rubra		Phleum pratense	
	f,	%	f,	%	f,	%	f,	%
1,1,1	5,	0	6,	0	9,	7	5,	10
1,1,2	2,	92	7,	71	9,	13	8,	25
1,1,3	4,	75	7,	45	9,	10	8,	23
1,2,1	0,	0	9,	42	17,	13	5,	20
1,2,2	5,	20	6,	42	7,	11	5,	27
1,2,3	2,	50	8,	35	9,	14	9,	43
1,3,1	12,	45	8,	29	11,	1	10,	23
1,3,2	7,	29	5,	43	10,	17	8,	4
1,3,3	2,	0	9,	43	9,	21	7,	13
1,4,1	20,	21	19,	24	23,	20	10,	28
1,4,2	2,	75	11,	20	10,	10	11,	25
1,5,1	8,	23	13,	14	23,	18	17,	10
1,5,2	4,	0	7,	22	8,	0	8,	22
2,1,1	5,	57	9,	41	8,	3	6,	15
2,1,2	2,	0	9,	58	8,	8	6,	35
2,2,1	1,	100	9,	31	8,	3	5,	0
2,2,2	8,	52	8,	45	7,	7	3,	0
2,3,1	2,	100	14,	29	11,	5	7,	4
2,3,2	5,	23	8,	64	8,	2	8,	7
2,3,3	2,	16	7,	58	8,	2	4,	50
2,4,1	3,	33	9,	39	10,	1	3,	25
2,4,2	6,	33	14,	25	14,	5	11,	17
2,4,3	1,	100	5,	63	12,	12	14,	17
2,5,1	15,	45	25,	54	22,	3	21,	10
3,1,1	5,	40	9,	91	7,	14	6,	45
3,1,2	5,	100	14,	81	7,	0	14,	72
3,1,3	1,	0	8,	77	4,	0	8,	62
3,2,1	7,	29	9,	67	9,	17	7,	21
3,2,2	4,	100	9,	95	8,	17	9,	38
3,2,3	2,	100	11,	79	10,	4	10,	62
3,3,1	6,	25	6,	63	8,	4	9,	24
3,3,2	1,	100	10,	80	9,	3	7,	79
3,3,3	8,	10	12,	74	11,	11	10,	14
3,4,1	4,	75	9,	72	9,	10	9,	53
3,4,2	15,	73	24,	64	21,	3	22,	36
3,5,1	8,	52	16,	67	18,	13	18,	43
3,5,2	5,	50	6,	61	6,	3	5,	36
3,5,3	6,	92	9,	88	9,	11	8,	80

Sample	Poa compressa f, %	Trifolium hybridum f, %	Trifolium repens f, %
1,1,1	1, 20	9, 14	4, 0
1,1,2	4, 50	6, 10	3, 58
1,1,3	2, 0	8, 14	4, 43
1,2,1	2,100	15, 18	3, 0
1,2,2	2, 50	0, 0	0, 0
1,2,3	1, 0	10, 33	7, 39
1,3,1	2, 0	7, 18	2, 0
1,3,2	1,100	2, 0	1, 0
1,3,3	1, 0	9, 15	8, 38
1,4,1	3, 33	4, 11	2, 0
1,4,2	1, 50	11, 13	5, 32
1,5,1	0, 0	1, 0	0, 0
1,5,2	3, 44	7, 32	2, 0
2,1,1	1, 0	3, 11	1, 0
2,1,2	1,100	8, 26	5, 22
2,2,1	0, 0	9, 15	5, 15
2,2,2	0, 0	8, 23	5, 0
2,3,1	0, 0	14, 32	2, 0
2,3,2	2, 50	5, 37	1, 0
2,3,3	1,100	7, 36	1, 0
2,4,1	1,100	4, 10	3, 0
2,4,2	1, 0	5, 17	3, 0
2,4,3	6, 25	12, 74	6, 39
2,5,1	1, 0	6, 61	3, 30
2,5,2	0, 0	10, 84	3, 58
3,1,1	1, 50	5, 77	1, 0
3,1,2	2, 50	3,100	1, 0
3,1,3	0, 0	1, 83	0, 0
3,2,1	1,100	5, 32	2, 0
3,2,2	2, 50	7,100	2, 0
3,2,3	3, 33	9, 84	5, 45
3,3,1	5, 0	7, 29	3, 0
3,3,2	2, 50	6, 90	3, 0
3,3,3	0, 0	4, 19	5, 0
3,4,1	3,100	3,100	1, 0
3,4,2	8, 44	4,100	1, 0
3,5,1	5, 40	8, 38	5, 0
3,5,2	1, 0	1,100	0, 0
3,5,3	1, 0	2,100	1, 0

APPENDIX 7: PROBABILITY ASSUMPTIONS FOR THE ASSOCIATION ANALYSIS

	Marginal Totals		P(k)=Q(k)	P(k)not=Q(k)	
	i	j	P(k)	P(k)	Q(k)
ALTITUDE CLASS 1					
Agrostis tenuis	35	36	0.143	0.149	0.138
Festuca rubra	78	63	0.337	0.333	0.344
Phleum pratense	45	46	0.189	0.192	0.186
Trifolium hybridum	44	41	0.176	0.188	0.164
ALTITUDE CLASS 2					
Agrostis tenuis	69	60	0.254	0.265	0.237
Festuca rubra	68	89	0.314	0.262	0.382
Phleum pratense	45	49	0.172	0.173	0.170
Trifolium hybridum	64	37	0.194	0.246	0.138
ALTITUDE CLASS 3					
Agrostis tenuis	140	86	0.452	0.467	0.421
Festuca rubra	28	70	0.136	0.093	0.170
Phleum pratense	82	100	0.284	0.273	0.305
Trifolium hybridum	29	27	0.077	0.967	0.065
MULCHED CLASS					
Agrostis tenuis	37	22	0.157	0.202	0.109
Festuca rubra	55	62	0.348	0.301	0.414
Phleum pratense	35	50	0.227	0.191	0.254
Trifolium hybridum	36	21	0.151	0.197	0.103

n.b. Only the 4 major species are included here, hence the probability data do not sum to 1.0.

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