The pioneer plant community: Studies on roadside verges, glacier forelands and other disturbed habitats in Southern Norway.

Robbins, Jane Alison

Robbins, Jane Alison (2007) *The pioneer plant community: Studies on roadside verges, glacier forelands and other disturbed habitats in Southern Norway..* thesis, Swansea University.
http://cronfa.swan.ac.uk/Record/cronfa43095

THE PIONEER PLANT COMMUNITY: STUDIES ON ROADSIDE VERGES, GLACIER FORELANDS AND OTHER DISTURBED HABITATS IN SOUTHERN NORWAY

JANE ALISON ROBBINS

Submitted to the University of Wales in fulfilment of the requirements for the Degree of Doctor of Philosophy

Swansea University

2007

Fortundalen, Breheimen

In a vast and marginal world
The very fine edge of things
The warp of space
And the weft of time

(From a poem by Robert Cook)

DECLARATION

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed ....

Date ....4/7/07...

STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s).

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed ....

Date ....4/7/07...

STATEMENT 2

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed ....

Date ....4/7/07...

ABSTRACT

The nature and variability of pioneer vegetation on roadside verges, glacier forelands and other disturbed habitats within the Jotunheimen-Jostedalsbreen region of Norway are assessed. Patterns of species distribution are analyzed in relation to altitude, continentality and mean weighted Ellenberg indicator values for light, moisture, pH and nitrogen.

Non-metric multidimensional scaling, cluster analysis and multi-response permutation procedure demonstrate that pioneer vegetation is a non-random assortment of species that can be classified into three communities and six sub-communities within a continuum. Altitude is a dominant influence on pioneer colonization at the regional scale, independently accounting for 17% of the total variance explained. Continentality, although strongly correlated with altitude, has an additional independent effect of 8%. Substrate pH, nutrient availability and disturbance factors are also important environmental influences. Habitat-related effects are evident in the colonization of low altitude glacier forelands by a *Festuca ovina-Poa alpina* community restricted to high altitudes on roadsides, and in the restriction of the *Deschampsia cespitosa-Plantago major* community to roadside sites. A third community (*D. flexuosa-Salix glauca*) is present on less disturbed pioneer sites.

Analysis of the relative heterogeneity of successional stages (measured by mean Sørensen dissimilarity) shows that, on the glacier forelands, succession generally proceeds from a single pioneer community (65% dissimilarity) to a more heterogeneous climax stage (76% dissimilarity) indicating successional divergence in a harsh environment dominated by abiotic influences. As altitude increases, a longer time span is required for divergence to develop. The roadside vegetation develops from a more variable pioneer stage (81% dissimilarity) consisting of a number of communities to a less variable climax stage (77% dissimilarity) with stronger biotic controls. The degree of convergence decreases with altitude. Within the highest altitudinal zone (above 1600 m) successional trajectories are parallel. Roadside sites at the lowest altitudes (<400 m) show evidence of divergence due to the influence of human activity.

ACKNOWLEDGEMENTS

I would like to thank:

John Matthews for his invaluable guidance and boundless enthusiasm;

Robert Cook, Alexander Fuller, John Matthews, Geraint Owen and Paul Richards for fieldwork assistance;

The University of Wales for financial support;

Anna Ratcliffe for producing the maps;

Robert Cook for his constant encouragement and support.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

1 INTRODUCTION

This thesis focuses on vascular plant species in the pioneer stage of primary succession in the Jotunheim and Jostedalsbreen regions of southern Norway. The nature and variability of pioneer colonizers on roadside verges, glacier forelands and a number of additional disturbed habitats are examined, and the question of whether pioneers within these habitats form repeatable communities or random assemblages of species is addressed.

The spatial distribution of pioneer vegetation is investigated, particularly in relation to altitudinal and continental gradients, and Ellenberg's indicator values are used to assess additional environmental influences on pioneer colonization. Primary successional trajectories are also analyzed by comparing the variability of pioneer vegetation with that of later stages of succession. Emphasis is placed on identifying evidence of the influence of altitude on patterns of convergence or divergence.

Understanding the pioneer phase of vegetation establishment is a vital component of successional theory and has practical application to the fields of land reclamation and habitat restoration. The chosen study area provides an opportunity to examine pioneer vegetation in a range of frequently disturbed habitats across an altitudinal gradient of 40 to 1860 m a.s.l. and an east-west range of approximately 100 km.

1.1 Vegetation succession

Vegetation succession is a process whereby, following initial colonization by pioneer plants, changes in species composition and abundance occur through time. Succession occurs in all ecosystems and its study is fundamental to our understanding of the ecological, biological and geographical processes that occur either in response to the creation of new land surfaces (primary succession) or the disturbance of existing communities (secondary succession). Research into successive stages of colonization and the pathways along which ecosystems develop is vital to understanding the processes that have resulted in our current ecosystems and to predicting future responses to environmental change. This is particularly important in light of the effects of global climate change which are likely to result in a higher frequency and magnitude of ecosystem disturbances (Walker and del Moral 2003). Human activity also has an impact on vegetation succession through the creation of artificial surfaces for potential colonization and through land management practices, which are concerned with encouraging, modifying or preventing successional processes. Whatever the cause of a disturbance, it results in an opportunity for the establishment or re-establishment of successional processes, and in each case, it is the pioneer species that initiate this. It is therefore important to understand this initial phase of succession and the factors that affect it.

The pioneer vegetation recorded in this study constitutes the initial stage of primary rather than secondary succession. Primary succession can be defined as "the establishment and subsequent development of the first assemblage of species on a previously unvegetated surface" (Miles and Walton 1993, p vii), which occurs on a variety of sites, including land uncovered during glacial retreats, sand dunes, lava flows, river bars, and artificially constructed features such as roads and industrial sites. The main feature distinguishing primary from secondary succession is the initial absence of organic matter, soil and propagules. In practice, however, a sharp distinction between primary and secondary succession is arbitrary, as there is a continuum between the colonization of barren ground and the colonization of disturbed patches. The primary successional habitats included within this study are generally characterized by substrates with low resource levels and lack any organic matter or a seed bank.

The first stage of both primary and secondary succession is the arrival and establishment of the initial colonizers, a pioneer plant being defined as "a plant that colonizes a disturbed area, thereby initiating succession" (Walker and del Moral 2003, p 349). Studies focusing specifically on the pioneer stage are much fewer than those involving the processes and patterns of change in subsequent successional stages. However, relevant previous research includes studies of pioneer seed dispersal, the requirements for pioneer seedling establishment, the floristic composition of the pioneer stage of colonization in a number of different habitats, and the age structure of pioneer populations. The term "climax" vegetation is used in this thesis to describe relatively stable communities which, although not necessarily in complete equilibrium with the environment, are no longer showing significant successional change (Pardoe 1996)

1.2 Plant communities

Throughout this thesis, evidence is sought for the existence of patterns in the distribution of pioneer species. Distinct groups of species may occur repeatedly and constitute pioneer plant "communities". Alternatively, species composition and abundance may vary independently along gradients of species turnover; or colonization may appear to be random. The extent to which species are assembled into a number of recognizable, recurring communities or follow either individualistic or random patterns of distribution is an important aspect of variability in vegetation and has not previously been examined at the pioneer stage of succession. The community-continuum debate of vegetation science is therefore central to this thesis and is summarized in Chapter 2 (Section 2.6).

As the identification of evidence for the existence of pioneer plant communities is a fundamental aim of this thesis, it is important to clarify further the use of the term "community". There is little consensus in the literature regarding the definition of this term, especially over the extent to which it implies species interaction or integration. As a result, its use in describing vegetation is often inconsistent. For example, Poore (1964, p 213) suggests that: "the idea of integration should be an essential part of any definition of the community and that any unorganized grouping of plants or animals should be excluded; the term 'assemblage' could perhaps be used for such". A looser definition is "all individuals of any species living in the same area or all individuals of any species which interact with each other" (Gillman 1996, p 109). Duffey (2004) makes a plea for the continuation of the traditional definition of the community i.e. denoting implicit interaction between organisms. Perhaps a solution lies in Austin's (2005) recent definition of a community as having four components: a consistent floristic composition, uniform physiognomy, occurring in a particular environment and occurring at several locations. While there is no explicit reference to species interaction in this definition, Austin considers that consistent composition and physiognomy are a result of interactions to be implicit. Within the context of this thesis, Austin's definition is considered appropriate. Although the pioneer stage of succession may not be greatly influenced by species interactions, some form of interaction is probable in all but the most sparsely colonized terrain.

1.3 Study location

A considerable body of research has been carried out into many aspects of primary succession on glacier forelands in the Jotunheim and Jostedalsbreen regions of south-central Norway (see Matthews (1992) for a comprehensive review). The patterns of successional change within this habitat are therefore relatively well understood and provide an invaluable framework within which to place the current research on the pioneer stage. Furthermore, knowledge of primary succession on glacier forelands constitutes an important point of reference for studies of other pioneer habitats, such as roadside verges, within the same study area. The latter habitat presents, moreover, an opportunity to study a series of sites along an altitudinal and regional gradient which is much more comprehensive than that obtainable from glacier foreland sites alone.

The temperature gradient related to altitude, with its associated increases in precipitation, snowfall, frost action and wind velocity at higher altitudes, results in characteristic zones and belts of climax vegetation within the study area. Similarly, a west-east continentality gradient of precipitation and temperature variation also occurs, from wetter oceanic localities in the west with less extreme seasonal climatic variation, to drier continental localities in the east, with more marked seasonal fluctuations in temperature. The response of pioneer vegetation to these factors has not been previously investigated.

The two main habitats investigated, roadsides and glacier forelands, provide contrasting conditions for pioneer colonization on disturbed ground, the former consisting of gravels which tend to be well-drained and the latter consisting of a wide range of substrate textures, from silts to boulders, with a continuous input of moisture from glacial meltwater during the growing season. The roadside sites are, of course, artificial constructions and are subject to direct human influence, whereas the glacier forelands provide a natural contrast, the majority of sites being rarely visited by people or animals. A small data set of additional pioneer habitats, representing a wide range of conditions from low altitude river outwash plains to high altitude frost-patterned ground, provide a measure of pioneer variability across habitat types for comparison with data from the two main habitats.

1.4 Aims, objectives and expected key outcomes

The overall aim of this thesis is to investigate the nature of pioneer vegetation on disturbed sites in the Jotunheim and Jostedalsbreen regions of southern Norway. The focus is on describing and explaining the variability of pioneer communities and discussing the ecological implications of this variability, especially for the theory of succession. There are five specific objectives:

1. To describe the pioneer vascular plant species of roadside verges, glacier forelands and additional pioneer habitats
2. To ascertain the extent of variability of initial plant colonizers within these habitats
3. To relate these findings to altitudinal gradients and regional influences
4. To assess environmental influences on pioneer vegetation using Ellenberg's indicator values;
5. To investigate the influence of altitude on successional trajectories

These are expected to lead to the following key outcomes.

- The main focus of this study is the pioneer stage itself, which is expected to yield new data on the degree of variability and habitat-specificity displayed by pioneer vegetation.

- The study is likely to contribute to knowledge and understanding of geographical variations in pioneer vegetation and in successional trajectories at a regional scale.

- The study is also likely, particularly through the application of Ellenberg indicator values, to provide further explanation of environmental influences at the habitat scale.

- Finally, the study demands a comprehensive, multivariate, analytical approach to investigating pioneer and early successional communities, which is likely to be of use elsewhere.

1.5 Thesis outline

Chapter 1 has introduced the aims, objectives and conceptual framework of the thesis. Chapter 2 provides a review of the literature, summarizing the findings of previous research and placing the study within the context of existing knowledge and theory. This includes a review of research into factors influencing pioneer colonization, models of primary succession and relevant studies relating to successional trends. Ways in which this thesis aims to extend existing knowledge are also listed. Chapter 3 gives a detailed description of the study area and study sites and describes the research strategy and methods used for data collection and data analysis. Justification is also given for the choice of specific multivariate techniques of ordination and classification.

The four results chapters of the thesis (Chapters 4 to 7) are constructed around a number of specific questions related to and expanding on the research objectives: Chapter 4 describes the roadside pioneer vegetation and presents results relating to the variability in species composition and abundance of the roadside pioneer sites. The extent to which the pioneer roadside vegetation can be classified into a number of predictable communities is the focus, and indicator species are identified for each proposed community. Chapter 5 follows a similar structure, first in relation to the glacier foreland pioneer sites.

Second, it presents results from the 'additional pioneer habitats'. Third, it includes a combined analysis of all pioneer sites. These results are used to assess the extent to which pioneer species and/or communities are restricted to specific habitats. Chapter 6 relates pioneer variability and pioneer community distribution to altitudinal and continental gradients. Mean Ellenberg indicator values are presented in this chapter to provide an additional assessment of environmental influences on pioneer colonization. In Chapter 7, variability within the pioneer stage of succession is compared with that of later stages of succession to address the question of whether successional patterns are primarily convergent or divergent. These patterns are then explored in relation to a number of altitudinal zones. Ellenberg indicator values are again used, in this case providing a potential contribution to understanding successional processes.

Chapter 8 presents an integrated discussion of the results, their implications for successional theory and their relationship to previous research. This includes a discussion of the strengths and limitations of the methodology. Chapter 9 summarizes the key findings of the thesis, and makes a number of suggestions for extending the work.

2 LITERATURE REVIEW

2.1 Introduction

The purpose of this review is to place the project within the context of existing ecological and biogeographical theory and to examine its relationship to previous research. Studies that have contributed to our understanding of the pioneer stage of primary succession provide the focus for this review, together with research that has addressed the question of subsequent successional trajectories. This is followed by a summary of relevant conceptual models and debates. Finally, ways in which this study attempts to test or develop the conclusions of prior research are outlined.

By far the most intensively studied primary successional habitats with direct relevance to this thesis are glacier forelands and, for this reason, these are considered first within each section. The literature on pioneer vegetation of roadside verges is contrastingly sparse and, in some cases, no directly relevant research was identified. A number of other pioneer habitats have been studied in considerable depth; the extensive body of work published following the 1980 eruption of Mount St Helens, Washington, is extremely relevant to this thesis and is therefore referred to frequently.

2.2 The nature and variability of pioneer community

The nature of the pioneer community refers to the general characteristics of the initial vegetation, including species richness, most frequent taxa and life-history characteristics such as dispersal methods and the capacity for vegetative reproduction. Variability is most often considered in terms of the predictability or stochasticity of the pioneer vegetation and has been addressed using a variety of methods including classification and ordination techniques and dissimilarity coefficients as a measurement of heterogeneity.

2.2.1 Nature

A large number of studies of primary vegetation succession have recognized the role of specific pioneer taxa in initiating succession and the existence of a 'pioneer stage' or 'pioneer community'. Many have also characterized the pioneer stage as typically having low species richness, sparse plant cover and few life-forms compared with later stages (see Matthews (1992) and Walker and del Moral (2003) for comprehensive reviews). Succession following initial colonization most often progresses from the relatively simple structure of the pioneer phase to an increase in the number of hemicryptophytes and woody chamaephytes, eventually resulting in the multi-layered vegetation structure of later successional stages.

The general nature of pioneer species in primary successional habitats (including glacial moraines, river bars, volcanic substrates and sand dunes) has been reviewed by Chapin (1993) who found that early pioneers tend to have small wind-dispersed seeds, lack dormancy requirements, have a high germination success rate, a high potential for photosynthesis and nutrient uptake and a high relative growth rate compared to later successional species. Species that are capable of symbiotic nitrogen fixation can play an important role in primary succession but their ability to disperse to early pioneer sites is hindered by large seed size. Early pioneers in primary succession, unlike those in secondary succession, tend to be perennial species. Matthews' review (1992) confirms that pioneer species on glacier forelands tend to have a lower seed mass than later colonizing species but a higher relative growth rate.

The conclusions of studies that have investigated mycorrhizal associations in pioneer vegetation have not been consistent. Analysis of community assembly along proglacial chronosequences in north-west Svalbard (Hodkinson et al. 2003) showed that the earliest colonizers were often species with ectomycorrhizal associations. However, Cazares et al. (2005) working at Lyman glacier foreland, Washington, found that non-mycorrhizal species predominated during early succession. Similarly, Jones and Henry (2003) noted that most of the early successional species on Twin Glacier foreland, Canada, were not observed to have mycorrhizal associations.

2.2.2 Variability

2.2.2.1 Glacier forelands

Variability within the pioneer stage on glacier forelands has been addressed both qualitatively and quantitatively. Matthews (1992, p 172) cites references to the "pattern of poorly-defined, loosely-organized assemblages in the early stages of succession" e.g. Friedel's (1938) use of the terms 'pre-communities' and 'half-communities' and Solomina's (1989) 'simple groupings, with progression towards defined communities in later stages. Matthews also quotes Spence (1989) who describes pioneer succession in front of glaciers on Mount Kenya as appearing to be 'haphazard' and Persson (1964) who considers pioneer species in front of Skaftafellsjokull, Iceland, to 'appear in a more or less occasional mixture'. Elven (1978b) found haphazard pioneer assemblages followed by increasingly distinct vegetation types with increasing numbers of interspecific associations from 90 years onwards.

However, a number of studies of primary succession on glacier forelands in southern Norway have described consistent groups of species within the pioneer stage. Matthews (1978a) recognized a core group of pioneer species on Storbreen glacier foreland, Jotunheim, and a number of species which were considered to be indicators of recent deglaciation. Whittaker's (1987) analysis of vegetation data from Storbreen confirmed the distribution of these typical pioneer species and a subsequent (1993) paper included population-level studies of six of the core pioneer species. A similar group of early pioneer species was identified in northern Sweden by Stork (1963) and in front of Hardangerjokulen, southern Norway, by Elven (1978a). Investigation of pioneer species on patterned ground on three glacier forelands in Jotunheimen consistently found three of Matthews' core pioneers (Haugland and Beatty 2005). In the Italian Alps, Caccianiga et al. (2001) identified similarities between pioneer communities on three glacier forelands, and Caccianiga and

Andreis (2004) identified a pioneer community divided into three sub-associations on recent and/or disturbed moraines in front of eight glacier forelands. Two of Matthews' core pioneer species were also studied by Erschbamer and Retter (2004) as key pioneers on a glacier foreland in the central Austrian Alps.

2.2.2.2 Roadsides

Studies of roadside vegetation have tended to focus on the impacts of road construction and use on plant communities (e.g. Truscott et al. 2005), on the vegetation of relatively undisturbed roadside verges (e.g. Ullmann et al. 1995, Hovd and Skogen 2005), and on the colonization of disturbed roadsides by non-native invasive species (e.g. Johnston and Johnston 2004, Arevalo et al. 2005). Few studies have focussed on pioneer plant communities on disturbed roadsides or on factors influencing primary succession on roadside verges. An exception to this is a study by Rentch et al. (2005) of roadside plant communities in the mountains of West Virginia which showed that pioneer assemblages tend to vary between roads rather than according to methods of road construction or type of landform.

2.2.2.3 Other pioneer habitats

Walker and del Moral's (2003) survey of research into primary succession in a variety of habitats suggests that strong stochastic influences result in a highly variable pioneer stage which can include novel and disharmonious assemblages of species. They conclude that, because few pioneer species are adapted for long-distance dispersal, chance events tend to determine which species reach isolated areas and the initial stage of primary succession is therefore considered to be unpredictable. This supports Van der Valk's (1992) conclusion that initial vegetation in a variety of primary successional sites is highly variable and site-specific, depending on dispersal from adjacent areas, local conditions and annual climate fluctuations.

Studies of early primary succession on mudflows and pumice surfaces on Mount St. Helens (del Moral et al. 2005) suggest that establishment order is variable and pioneers consist of a probabilistic rather than deterministic assembly of species, similar sites having different pioneer species composition due to varying degrees of isolation and the influence of stochasticity and life-history traits. Early succession is considered to consist of an accumulation of individuals, with interactions only later resulting in species replacements (del Moral and Jones 2002).

There is therefore a general consensus on the unpredictability of pioneer plant assemblages with the exception of a number of studies of glacier foreland pioneer zones, which have shown more consistent species colonization. However, the nature of the pioneer species appears to be more consistent, with a tendency for pioneers to be perennials with small wind-dispersed seeds and high relative growth rates.

2.3 Factors influencing pioneer colonization

The processes involved in pioneer colonization and in later successional change are not analyzed directly in this thesis. However, these processes have important implications for the nature and variability of the pioneer stage and relevant research into these factors is therefore summarized. The main focus for research into processes operating at the pioneer stage of succession has been on factors influencing seed availability and seedling establishment. Although species interactions may occur in early succession, they are thought to have most influence on species that follow the initial pioneers. The question of species interactions during the pioneer stage was assessed on Storbreen glacier foreland, Norway, by Whittaker (1993), who found that vegetation cover was sparse up to 30 years post-deglaciation and most established plants after 10 years of succession did not exhibit any signs of interaction above or below ground. Frenot et al. (1998) also found that pioneers on glacier forelands in the Kerguelen Islands had very superficial root systems, which were rarely found to be in contact with those of other individuals. Research which is most relevant to the pioneer stage therefore includes studies of seed dispersal, germination requirements and the characteristics of ‘safe sites’ (Harper et al. 1961) for seedlings. The effects of altitude and continentality on general plant distribution are also reviewed.

2.3.1 Dispersal

The pioneer stage of primary colonization is controlled largely by the availability of seeds at a specific site and of conditions suitable for the germination, growth and establishment of seedlings (safe-sites). Seed availability is influenced by seed numbers, dispersal mechanisms and proximity of donors as well as the timing of a disturbance in relation to seed dispersal. Landscape factors such as the degree of isolation of a primary successional site and the existence of barriers to dispersal such as mountains and large bodies of water can also play a prominent role in filtering possible colonizers.

2.3.1.1 Glacier forelands

Ryvarden's (1971) study of seed dispersal at Hardangerjökelen glacier foreland, Norway, found that 90% of all seeds trapped on the foreland were species typical of the pioneer stage. Surprisingly, seeds that travelled less than 5 m were dominated by those adapted for wind-dispersal, while those without obvious dispersal adaptations dominated the group that had travelled more than 5 m from the nearest possible source. Traps immediately in front of the glacier collected seeds from only 2 to 7 species and the number of seeds decreased with proximity to the glacier. A further study by Ryvarden (1975) of winter-dispersed seeds blown across snow-covered ground concluded that pioneer colonization in front of the glacier was not a result of selective dispersal. However, the most common pioneer species did yield the highest number of trapped diaspores. Stocklin and Bäumler (1996) also found that early pioneer plants in front of the Morteratsch glacier in the Swiss Alps produced a large number of small seeds adapted for wind dispersal but that a dispersal distance of more than 10 m was unusual.

Seed arrival at pioneer sites in Glacier Bay, Alaska, (Chapin III et al. 1994) was found to be limited by dispersal distance in early-successional communities. Availability of propagules and species life history traits are considered to explain the patterns of primary succession at Glacier Bay, and the example is given of the low density of spruce and alder in the pioneer stage, which was not found to be the result of either their inability to germinate, or of poor seedling growth and survival.

2.3.1.2 Roadsides

Because pioneer roadside vegetation is in close proximity to established vegetation, there are parallels with studies of expansion from refugia. Fuller (1999, in Walker and del Moral 2003) found that species in adjacent vegetation may expand vegetatively into disturbed sites although their seeds may not be capable of establishing and that mature vegetation is also more likely to attract animal vectors. A study of plant succession on roads created from the drainage of polders in The Netherlands (Nip-van der Voort et al. 1979) showed that the order of species colonization was strongly influenced by dispersal mechanisms. Water-dispersed species which were already *in situ* colonized first, followed by wind-dispersed species and then those introduced by animals and human activities, finally followed by autochorous species. The initial composition of the verges was therefore a result of dispersal mechanisms.

2.3.1.3 Other pioneer habitats

Initial colonization by random long-distance dispersal into suitable microsites was considered to be the cause of a highly variable pioneer vegetation on Mount St. Helens (del Moral and Jones 2002) and the contents of seed traps also exhibited a high level of species variability with the exception of those placed adjacent to established vegetation. However, the effects of established vegetation on pioneer colonization were found to be limited and the authors conclude that dispersal factors are often the sole determinant of early successional species composition. Correlations between environmental factors and species composition 13 years after the 1980 eruption were found to be very weak, the most important influences being landscape effects and dispersal limitations (del Moral et al. 2005). del Moral and Bliss (1993) found that once a pioneer species has established, recruitment is more likely to be from that individual than from long-distance dispersal. The study confirmed that species with good dispersal mechanisms are often poor stress tolerators and *vice versa*, resulting in colonization rates being strongly influenced by the overall level of stress in a particular habitat.

A study by Boussuyt et al. (2003) of primary succession on sand dunes found wind-dispersed species to be the initial colonizers, with competitive and ruderal species eventually being replaced by stress-tolerators. The number of pioneer species was not found to be dependent on the degree of isolation of the site but this did affect the characteristics of the colonizing of the species. Leyer (2006) cites dispersal mechanisms and the degree of connectivity with the main river channel to be the predominant influences on pioneer species composition on floodplains in Germany.

2.3.2 Establishment

Walker and del Moral's (2003) review of primary succession found that successful germination, growth and establishment is influenced by factors such as substrate texture, shelter, moisture and nutrient availability, according to the requirements of individual species, and that the importance of safe-sites is primarily related to the degree of environmental stress, as competition and seed predation are not usually important early in succession. Chapin's (1993) review also found that favourable microsites are essential for pioneer seedling survival, especially for the growth of root systems. The substrates of pioneer zones tend to have an initially low organic content and nitrogen availability, low water-holding capacity and low cation exchange capacity, but nitrogen accumulates rapidly if pH, mineral toxicity and climatic factors do not inhibit it and if colonizers are able to arrive. The absence of mycorrhizae is also considered a possible limit to primary colonization and this may be an effect of the relatively high substrate pH, which inhibits ectomycorrhizal associations and slows the growth of woody species. Chapin cites dispersal limitations, low soil fertility and poor water holding capacity as the main obstacles to initial colonizers, with evidence of trade-offs between traits that promote dispersal and those that promote seedling establishment. After initial colonization, subsequent changes are considered to reflect competitive balance and patterns of life-cycle traits such as longevity and growth rate.

2.3.2.1 Glacier forelands

On glacier forelands, initial site conditions, particularly substrate type and texture and levels of moisture and disturbance, have a major effect on the ability of pioneers to colonize due to the consequent availability of microsites for establishment (Matthews 1992). Ecesis (establishment and persistence) is considered more important than migration in accounting for species composition and abundance in the pioneer stage and several studies showed that successful seedlings become the focus for further colonization, with aggregation of plants around an isolated pioneer. Stocklin and Baumler (1996) found that the main determinant of germination success was the moisture content of the soil, with requirements varying between species and only a small number of species able to tolerate the cold wet conditions adjacent to the glacier. The availability of safe sites became increasingly important for pioneers on older and drier terrain and the species that persisted from the pioneer stage through to later successional stages tended to have the capacity for clonal growth.

On Lyman glacier foreland, USA, Jumpponen et al. (1999) and Jones and del Moral (2005a) confirmed the predominant influence of abiotic factors on initial colonizers, concluding that successful colonization only occurred on sites with characteristic physical attributes (concave surfaces, proximity to large rocks and coarse substrate) and that early life-cycle stages (dispersal and germination) were more important than later stages (establishment and reproduction) in determining the distribution and abundance of the pioneer species studied. The characteristics of safe sites were consistent with conditions that would trap seeds and either provide greater moisture levels or protect against water loss. The importance of microsites (in the form of shelter provided by existing vegetation or by stones > 2 cm^2) for the emergence of pioneer seedlings on slightly older ground (25 year old moraine) was verified at Rotmoosferner glacier foreland, Austria, by Schlag and Erschbamer (2000).

A study of vegetation succession on patterned ground within the pioneer zone of three glacier forelands in Jotunheimen, Norway (Haugland and Beatty 2005) found that microsites rather than landscape scale patterns had a major influence on pioneer persistence. Frost action was thought to delay succession as the disturbed centres of sorted circles providing sites for continued pioneer colonization. Furthermore, lack of frost action on the surrounding terrain was also considered to enhance soil acidity, suggesting that the decline in pioneers is due to a fall in substrate pH as well as decreasing moisture. This supports Matthews' (1992) view that the rapid fall in pH with increasing terrain age on glacier forelands is a possible cause of the decline in pioneer species with time. Initial colonizers are assumed to require uncontested resources and their decline on older terrain is possibly due to lower moisture and/or nutrient levels or changes in nutrient availability as a result of lower soil pH (Matthews and Whittaker 1987). Whittaker in his 1993 study of plant populations on Storbreen glacier foreland concluded that a decrease in pH due to leaching of minerals from glacial till, a lowering of moisture levels and a decline in the availability of safe sites restricted pioneer species on older ground, while a limited supply of propagules influenced colonization on the youngest ground.

2.3.2.2 Other pioneer habitats

The importance of microsites, with most seedlings establishing in association with small rocks, undulating areas or edge habitats was confirmed for pioneers on Mount St Helens (del Moral and Bliss 1993). Facilitation is also considered to be an important factor in controlling early primary succession, with nurse plant effects recorded. However, established plants were also observed to inhibit or not affect other potential colonists. Of particular interest is the study by del Moral and Eckert (2005) which found that refugia, instead of dispersing directly into surrounding barren ground, formed oases for the establishment and further dispersal of pioneer species. Studies of early primary succession on mudflows and pumice surfaces on Mount St. Helens (del Moral et al. 2005) suggest that chance and landscape factors are as important as site characteristics in determining species colonization. However, the existence of safe sites and nutrient inputs were needed before most species colonized.

Walker et al. (2006), in New Zealand found species characteristics to be poor indicators of colonization success compared with microsite preferences of individual species. Ecke and Rydin (2000), studying coastal primary succession in Sweden, found that species present at different stages of succession showed little variation in CSR strategies. Early succession was characterized by species able to tolerate and recover from disturbance ('disturbance-tolerators') rather than ruderals or stress tolerators.

2.3.3 Altitude

The general effects of altitude on plant colonization are well-documented, although the specific effects of altitude on pioneer species colonization do not appear to have been studied. Burrows (1990) outlines the major factors affecting vegetation which are correlated with increasing altitude in the temperate zone: decreasing air pressure (affecting atmospheric density and moisture properties); increasing ultraviolet light intensity; increasing frequency and severity of storms; increasing frequency and velocity of winds; increasing cloud cover; declining air temperature (at a rate of approximately 0.6°C for every 100 m ascended but with diurnal and seasonal variation and according to aspect); increasing precipitation (but drought can occur and substrates are often well-drained); increasing snowfall frequency and length of snow cover (snow insulates the ground in winter but shortens the growing season; abundant water is present in the thaw period); increasing frost action causing most disturbance on bare, snow-free sites; increasing erosive action including fluvial and mass-movement processes on slopes; decreasing microbial activity and nutrient cycling; decreasing soil nitrogen but often with high cation levels.

Alpine plants require adaptive mechanisms to enable survival and functioning in an environment of short summers and long winters (Bliss 1971). It is generally agreed that the effects of altitude constitute a complex of variables and include a decrease in species diversity with elevation (Austrheim 2002, Bruun et al. 2006). The latter paper describes two opposing forces acting on species composition with increasing altitude: a declining species pool and decreasing intensity of competition. Research has also shown that at high elevations, where abiotic stress is severe, interactions between plants are mainly positive e.g. nutrient accumulation, providing shade and protection from disturbance and herbivores (Callaway et al. 2002). The changing altitudinal distributions of alpine flora in relation to increasing global temperatures are a current cause for concern and have been documented by Grabherr et al. (1994) in the Austrian and Swiss Alps and by Klanderud and Birks (2003) in the Jotunheim region of Norway. Studies such as that by Heer and Körner (2002) have shown that pioneer plants at high elevations, especially grasses, may respond to the addition of nutrients by increasing biomass.

Dluglosch and del Moral (1999) examined floristic heterogeneity along an elevation gradient and found similar species composition but lower heterogeneity at lower elevations where the vegetation was more mature. They concluded that chance events were more likely at higher elevations where fewer successful colonizations occur relative to the available area. Del Moral and Ellis (2004) found that early successional vegetation on lahars showed decreasing within-plot similarity with elevation and with distance from a propagule source.

2.3.4 Continentality

Within the study area, there is also a gradient of continentality, from the western oceanic climate, with relatively high precipitation, to the eastern continental climate, with lower precipitation and greater seasonal extremes of temperature. Austrheim et al. (2005) investigated variation in the abundance and life-history traits of herbs between alpine habitats in oceanic and sub-continental regions of southern Norway and concluded that the major differences were due to the underlying geology, with lower soil pH at the oceanic site influencing species richness, while the importance of life-history traits in explaining local abundance and regional distribution of species was also stronger at the acidic site.

2.4 Successional trajectories

The trends in vegetation composition that occur during succession involve a number of patterns, which can vary according to the effects of environmental influences such as altitude. These trends include the rate of succession, the number of stages between pioneer and climax vegetation, the extent of any increase in species richness and changes in the relative variability of each stage. This thesis focuses on the latter trend as a logical extension of the consideration of variability in the pioneer stage and its comparison with later stages.

Following initial colonization by pioneers, a number of successional trajectories are possible, including convergent, divergent, parallel, network, retrogressive and deflected pathways. Succession is, therefore, not expected to lead to a deterministic end-point as proposed by Clements but is more loosely defined as a process of change over time which is not necessarily linear and rarely results in equilibrium (Walker and del Moral 2003). The term directionality is now used to describe species turnover rather than a process leading to a deterministic climax vegetation. The following is a descriptive summary of the main types of trajectory.

In successional convergence, vegetation that is initially highly variable becomes more homogeneous with time and is eventually dominated by species found in the surrounding mature vegetation. This has parallels with Clements' theory of a predictable climax vegetation in that initially heterogeneous vegetation succeeds to a single endpoint. Convergence of species composition requires low stochasticity and processes dominated by biological (competitive) interactions and is thought to be less frequent in primary succession than is generally believed (Walker and del Moral 2003). There are therefore two aspects to convergence: a decline in heterogeneity and a process of change that culminates in a single vegetation type. Floristic convergence is considered to be common where there are barriers to dispersal that limit the number of species able to colonize (Rydin and Borgegard 1988) and in species-poor, stressful environments which reduce the importance of chance (Hatton and West 1987). However, according to Walker and del Moral's (2003) survey, overall evidence suggests that floristic convergence is most likely where there are few limitations to dispersal and initial conditions are fairly homogeneous, allowing rapid vegetation development.

In divergent succession, pioneer vegetation may be either homo- or heterogeneous, but becomes increasingly variable with time. This may be due to environmental heterogeneity, disturbance, priority effects, minor differences in initial conditions (chaos) or random effects (stochasticity). Divergent seres are thought to be common when stochastic processes or habitat variation allow local dominance of species, which is then accentuated by species interactions. In alpine tundra, for example, dominant species exert less control on microclimate and light than their counterparts in forests and this effect is enhanced by vegetative proliferation of many alpine species leading to greater variability of the mature vegetation (Burrows 1990). There therefore appears to be a tendency for divergent pathways to be associated with relatively severe environments and for convergence to be associated withy relatively strong biotic controls (Matthews 1992).

Parallel succession occurs when variation in initial conditions results in the development of more than one successional pathway, which maintains the effects of the original differences. Species turnover, therefore, does not lead to variation in the degree of similarity between each successional pathway. Parallel succession tends to occur when seres are isolated or on sites with a number of sharply contrasting environments and may persist but is more likely to eventually diverge or converge or form a network (Walker and del Moral 2003). Networks occur when a number of pathways lead to the same endpoint and deflection is the result of disturbance changing a successional pathway by influencing particular species (Walker and del Moral 2003). Retrogression may also occur in seres subject to repeated disturbances and, on longer time scales, as soil fertility declines, due to extensive weathering and leaching of minerals.

Questions regarding the variability of successional patterns and trajectories have been addressed in a number of research contexts. Of particular relevance to this thesis are those that have investigated the effects of altitude on the relative variability or heterogeneity of successive stages of plant colonization and the implications of these findings for models of succession. However, no studies of successional trajectories in roadside vegetation have been identified.

2.4.1 Glacier forelands

Evidence from Norwegian glacier forelands is generally consistent with the concept of divergent pathways in the early stages of succession and in relatively severe environments (Matthews 1992). Faegri described convergent successional pathways in the sub-alpine zone of southern Norway in front of four glaciers, convergence occurring in the later tree-dominated stages (Faegri 1933, in Matthews 1992). Convergence was also identified by Birks (1980) in front of Klutlan Glacier, Canada, in association with tall shrubs and trees, while divergence followed by convergence was identified in New Zealand (Archer 1973, Wardle 1980, in Matthews 1992). Vetaas (1994) analysed data from five dated terminal moraines on Bødalen glacier foreland in southern Norway and found that floristic differences between the groups decreased with time, suggesting successional convergence.

Elven (1978b, in Matthews 1992) found strongly divergent pathways on forelands of Flatisen and Osterdalsisen glaciers, Norway. At Flatisen, the pioneer community diverges to a variety of sub-alpine communities, with drainage and snow conditions considered to be the most important controls. Further evidence for divergent pathways of primary succession comes from Matthews (1979b, 1999), who found that the limited array of species on alpine glacial moraines resulted in relatively homogeneous pioneer communities, with greater floristic variation and more distinct communities occurring at later stages. Recurrent disturbance in stressful habitats is cited by Matthews and Whittaker (1987) as a cause of divergence, with multiple mature communities developing despite similar initial conditions. On Storbreen glacier foreland, lower and higher elevation sites were found to diverge from a similar pioneer stage; there was a general decline in vegetation heterogeneity on sites up to 50 years post-deglaciation, followed by an increase in heterogeneity after 200 years. Retrogression due to continued disturbance was also common after 50 years. Matthews (1992) summarized the results of individual studies as follows: in the sub-alpine zone, strong biotic controls leads to convergence; in the alpine zone, succession is slower and strongly divergent; in the high-alpine zone, concepts of convergence and divergence may have little meaning, due to high levels of abiotic control and low levels of autogenesis.

Jones and del Moral (2005b) found that at small scales (1 m^2 plots), vegetation on Coleman glacier foreland, Washington, became less heterogeneous during early succession, followed by increasing heterogeneity on mature sites, due to breaks in the canopy, whereas at larger scales (100 m^2 plots) heterogeneity was at its lowest earlier in succession. Both scales showed a more homogeneous pioneer than climax vegetation, suggesting successional divergence. Parallel successional pathways with little convergence or divergence were identified by Schubiger-Bossard (1988, in Matthews 1992) at Rhonegletscher foreland, Switzerland, where patchy environmental conditions influenced initial colonists and each patch developed independently with persistent differences. Habitat heterogeneity then imposed constraints that prevented convergence or divergence. Raffl et al. (2006) studied successional patterns on Rotmoosferner glacier foreland in the Austrian Alps and found two alternative successional pathways attributed to differing environmental factors. Evidence of multiple successional pathways was also identified by Fastie (1995) at Glacier Bay, Alaska, which he attributed to landscape factors and life history traits affecting the order of arrival of species.

2.4.2 Other pioneer habitats

Vegetation on mudflows and pumice plains on Mount St. Helens (del Moral et al. 2005) since the 1980 eruption has not yet had sufficient time for development to enable assessment of whether succession in these habitats is following a convergent or divergent trajectory. However, as plant succession was found to be slower at higher elevations, due to a shorter growing season, an elevational gradient has been used to study the trajectory *in lieu* of a chronosequence. Species assemblages were found to be more influenced by chance effects at higher elevations and consequently more heterogeneous. Over the first 10 years of monitoring, the vegetation became less variable, as cover increased, followed by increasing heterogeneity with cover ranging from 10-100%. As the authors point out, however, reduction in homogeneity does not necessarily result in convergence, as later shifts in dominance may reverse this trend. The formation of several hundred "potholes" on the eastern Pumice Plain of Mount St. Helens has provided sites with similar environmental conditions in which to study changes in percentage similarity in pioneer species composition with time. Over the first six years, the study showed that, although cover increased, species composition did not change markedly and each site developed its own successional trajectory due to priority effects. Del Moral (1998) also found that the stochastic nature of initial species composition on lahars could persist.

Lepš et al. (2000) studied succession at 930 m a.s.l. in the Krusne Hory Mountains, Czech Republic, on a site where areas of topsoil had been removed, and identified divergence from a single community of stress-tolerant ruderals to either grass-dominated or shrub-dominated communities dependent mainly on soil properties. Successional divergence was also identified by Bossuyt et al. (2003) on wet dune slacks along the Belgian and French coasts, attributed to stochastic variation in species accumulation, due to dispersal limitations. The authors also concluded that the size and degree of isolation of each site influenced the rate and direction of succession, reinforcing divergent trajectories, but that community composition in the early stages of succession did not differ greatly according to the degree of isolation. A study of primary succession in the Hawaiian rainforest (Aplet and Vitousek 1994) found that community composition was affected by the harsher conditions at higher altitudes and that succession followed distinctly different pathways at each altitude.

From the majority of these studies, a pattern emerges of generally divergent trajectories in harsh environments but with some evidence of convergence in environments where dominance by trees occurs. Retrogressive and parallel patterns of succession have also been identified.

2.5 Models of primary succession

Surveys of the main models of primary plant succession are covered by Matthews (1992) and Walker and del Moral (2003). They will not therefore be described comprehensively here, but models that are specifically relevant to the pioneer stage of succession are outlined briefly.

Autogenic models include Grime's three strategies of adaptation to competition, stress and disturbance (Grime 2001), and Noble and Slatyer's three vital attributes, which include method of arrival and ability to persist, ability to establish and mature and life-cycle attributes (including time needed to reach reproductive maturity and duration of the population and propagules pool) (Noble and Slatyer 1980). Walker and Chapin (1987) proposed a model which assesses the relative importance of a number of processes including facilitation, longevity, presence of mycorrhizae, stochastic events and seed arrival which are all potentially relevant to the pioneer stage of primary succession. Tilman's resource-ratio model (1985) assumes that succession is driven by vegetation responses to changing resource levels and that different resources limit different species.

The two models of Egler (1954), relay floristics (RF) and initial floristic composition (IFC), both have implications for the pioneer stage. In the RF model, groups of species successively appear and disappear, each assemblage providing suitable conditions for the next, whereas in the IFC model all species are able to colonize from the start of succession but predominate at different stages due to differences in life-cycles. Egler considered initial conditions to have a lasting effect on community composition and held the view that early and climax stages of succession were both determined by chance.

The influence of random events is also incorporated into more recent mathematical models, including the carousel model (van der Maarel and Sykes 1993), which represents the arrival of seeds and their establishment in safe-sites as a series of chance events. Species with the highest relative abundance in the seed rain and lowest seedling mortality are expected to succeed.

Invasion models (van Hulst 1992) are designed to predict the successional influences of the pioneer stage of succession. Van Hulst's model assumes that colonization is independent of previous inhabitants and is therefore highly relevant to primary succession. Limits to the number of possible pioneer species (dispersal limitations) and to the availability of colonization sites (safe-site limitations) are thought to introduce a level of predictability in which species with the highest relative abundance in the seed rain and lowest seedling mortality will succeed. In Peet's (1992) competitive-sorting model, population interactions result in succession from an initially random collection of pioneer species to a predictable community of the most successful competitors.

Svoboda and Henry (1987) sought to address the lack of attention given to the role of environmental factors in primary succession with a model incorporating the relative importance of biological driving forces and environmental resistance. Matthews' (1992) geoecological model includes environmental driving forces which facilitate succession. In this model, physical, chemical and biological processes are coupled and have changing levels of relative influence according to environmental severity. Assembly rules which describe filters to community membership imposed on a regional species pool also combine environmental and biological factors (Keddy 1992), while Weiher and Keddy (1995) propose a model of community assembly along an axis of decreasing environmental severity and increasing competitive adversity. In fact, Gleason (1926) proposed that pioneer vegetation is controlled by immigration factors plus a variable environment, stating that adjacent vegetation has the best opportunity for migration but that the formation of pioneer communities is the result of chance.

The pioneer stage of succession is therefore considered to be subject to a combination of biological and environmental influences, which affect the ability to reach a site, become established and complete a life-cycle. Different levels of predictability versus stochasticity are apparent, according to individual models. The possible role of environmental facilitation is largely ignored by most models.

2.6 Community-continuum hypotheses

2.6.1 The community-continuum debate

The debate regarding community and continuum theories of vegetation is summarized here as it is relevant to both the temporal (successional) and spatial (altitudinal and regional) distribution and dynamics of pioneer species.

The fundamental division in successional theory remains that between the contrasting approaches of Clements (1916, 1936) and Gleason (1917, 1927), the former proposing a deterministic, directional model, in which recognizable seres lead to a predictable climax community according to regional climatic conditions, and the latter focussing on the unpredictable nature of the successional process, which is dependent on the properties of the individual species present rather than being an emergent property of the ecosystem as a whole. Clements' theory predicts the formation of increasingly stable communities as succession proceeds due to increasing interactions between dominant species, resulting in a vegetation community that he likened to an integrated 'super-organism'. The pioneer stage, according to Clements, has a deterministic composition but with lower community integration than later stages, due to the comparatively weak influence of species interactions. According to Gleason, the species composition of the pioneer stage is a result of chance immigration (a "fortuitous juxtaposition of individuals").

Based on these two theories, the debate developed beyond successional processes into wider ecological questions regarding the spatial distribution of vegetation, centring on whether plants form communities of repeatable groups of species or are distributed individualistically. Gleason's ideas were developed by Whittaker (1951, 1967), Curtis and McIntosh (1951), Curtis (1955) and McIntosh (1958, 1967), who regarded vegetation as varying continuously (in terms of composition and abundance) along environmental gradients but without necessarily denying the existence of communities. For example, Whittaker in his 1967 paper on gradient analysis of vegetation cites Brown and Curtis's view (1952) that communities are "colours" which we recognize within a vegetational "spectrum". The question of whether vegetation continuously intergrades or forms distinct stands was therefore also introduced.

Community and continuum concepts have increasingly been considered as complementary (Goodall 1963, McIntosh 1967) and the development of complex methods of quantitative data analysis in the later part of the 20th century has enabled a more objective appraisal of the two major concepts. It is now widely accepted that the community and continuum concepts of vegetation are not mutually exclusive. Models have been proposed which explain community structure along a spatial gradient; for example the hierarchical continuum concept of Collins et al. (1993), which combines the individualistic distribution of species with the core-satellite species hypothesis (Hanski 1982), within a hierarchical assemblage structure (Kolasa 1989).

Austin (2005, p 81) summarizes the current view: "Whether vegetation is discontinuous or continuous depends on the perspective of the viewer. Viewed from a landscape perspective it is often discontinuous. In environmental space it is usually thought to be continuous". He stresses that the causes of variation in vegetation remain unresolved. He also reminds us that no comprehensive tests of either hypothesis have been published, that these concepts are entirely descriptive with no causative or mechanistic basis and that the properties of the community or continuum have not been specified with enough precision for them to be distinguished statistically.

Of particular relevance to this thesis is the assertion that supporters of the community concept restricted their data to stable stands of climax vegetation. Indeed, Daubenmire (1966) considered disturbed vegetation to form "bridging" between "distinct stable types", and suggested that evidence of a continuum is only found when disturbed or seral stands of vegetation are included. Responses to Daubenmire's 1966 paper, however, put forward the view that disturbed areas cannot be excluded in a meaningful study of vegetation (e.g. Cottam 1966). This point is particularly important in arctic-alpine vegetation, where substrate stability may be considered unusual. The issue of whether disturbed areas should be included when sampling vegetation to test the continuum-community "spectrum" continued to be debated, with critics of the continuum concept claiming that it is an "artifact" of including heterogeneous vegetation. Research to date has not addressed these patterns of vegetation change within the context of pioneer vegetation and it is therefore useful to use this debate as the basis for multiple working hypotheses on the nature of pioneer vegetation.

A distinction also needs to be made between the concepts of concrete and abstract vegetation communities, the term 'nodum' being suggested by Poore (1964) to describe abstract ecological units. Whittaker (1967) refers to Poore's noda as reference points along a largely continuous pattern of variation in vegetation and considers communities to be abstract concepts extracted from a continuum of variation along environmental gradients. He cites the niche concept and its implication of avoidance of competition as contradicting the idea that species would evolve towards natural clusters with similar distributions. Gleason (1939) also made a distinction between the abstract association and the concrete community, his individualistic concept being applied to the former. According to Austin (2005), both continuum and community theories are abstract constructs; the continuum concept referring to continuous variation in abstract environmental space and the community-unit or association referring to an abstract unit based on 'concrete' geographical space.

2.6.2 Studies of the community-continuum hypotheses of variation in vegetation

Little research has directly attempted to resolve the community-continuum debate. Shipley and Keddy (1987) tested hypotheses regarding the distribution of species' boundaries along a gradient of water depth and found that neither the individualistic hypothesis nor the community-unit hypothesis was supported. They conclude that consideration of multiple working hypotheses regarding community structure is necessary, rather than addressing a simple dichotomy. The distribution of vascular plants within climax vegetation along an altitudinal gradient of 300 to 2810 m a.s.l. on Mount Hermon, Israel, was analysed by Auerbach and Shmida (1993) for evidence of discrete communities. They found discontinuities but no evidence of discrete communities, with aggregation of species elevational boundaries only occurring at the treeline (1200 m a.s.l.). Kessler (2000) used Shipley and Keddy's (1987) method of looking for zones of high floristic turnover to define community boundaries and assess whether cryptogams are distributed in discrete communities along altitudinal gradients in the Andean rain forests. Discontinuities in community composition were found to correspond to sharp ecological boundaries, such as changes in geological substrate and a steep humidity gradient. Well-defined zones were also more apparent in species-poor communities. It is interesting to note the findings of Beals (1969) in Ethiopia, where more discontinuous variation in vegetation with altitude was found along steep gradients, gentle gradients being associated with more of a continuum of variation.

2.7 Summary and conclusions

The preceding review indicates that there is evidence to support both random and predictable pioneer species composition in the early stages of primary succession. Pioneer colonization has been shown to be influenced by a number of factors, including dispersal mechanisms and distance from sources of propagules, the availability of safe-sites for germination and seedling growth, species life history traits, facilitation, the presence of symbiotic mycorrhizae, together with abiotic factors such as substrate pH and moisture levels. However, the extent to which each of these factors influences pioneer vegetation appears to be highly variable and most authors agree that there is also a strong element of stochasticity. Successional trajectories are also variable, but evidence is most consistent with divergence in relatively severe environments and convergence in less severe environments where biotic control has more effect. Parallel trajectories tend to occur where local environmental variation increases the likelihood that the influence of priority effects will continue throughout succession.

This review has highlighted the lack of knowledge about the pioneer community in general and the variability in species composition of pioneer vegetation in particular. This provides the focus for the present thesis, which also attempts to address the following specific shortcomings of previous work:

1. Few studies have focussed principally on the pioneer stage of primary succession.

2. Variability within the pioneer stage of colonization has rarely been measured quantitatively.

3. The existence of predictable species assemblages or communities within the pioneer stage of succession has not been assessed.

4. The extent to which pioneer species are habitat-specific within a particular region has not been investigated.

5. The effects of altitude and continentality on pioneer vegetation have not been investigated.

6. The study of frequently disturbed roadsides as a pioneer habitat providing a continuous elevational gradient has been neglected as a source of information on variability in primary succession.

7. Successional trajectories in relation to altitude have not previously been investigated with a large data set or one that covers a continuous altitudinal gradient.

3 SITE DESCRIPTIONS AND METHODOLOGY

"The most important decision an ecologist makes is where to stop the car." Anon

This chapter includes a general description of the sites chosen for data collection and the methodology used in both data collection and analysis.

3.1 The study area

Fieldwork was carried out as part of the annual Jotunheim Research Expedition to south-central Norway during July and August of 2004 and 2005. The study area includes the Jotunheim and Jostedalsbreen regions of Norway between latitudes of 61° and 62°N and longitudes of 6 and 9°E. This area lies approximately 100 to 200 km from the west coast and includes an altitudinal range from sea level to 2469 m.

The Jotunheim region includes the highest mountain range in northern Europe (Galdhøppigan reaches 2469 m) and lies mainly above the birch tree-line (at approximately 1000 - 1200 m), although a number of valleys extend below the alpine zone. The mean annual air temperature is -3.1°C with a July mean of 5.7°C and a January mean of -10.7°C, and the mean annual precipitation is 860 mm at an altitude of 1413 m (Sognefjell meteorological station) (Aune 1993, Førland 1993). However, the area is situated at the transitional junction between the maritime west and the more continental east, and individual study sites therefore reflect this climatic divide. There are approximately 300 glaciers and small ice caps within the Jotunheim area and the lower limit of discontinuous permafrost is about 1490 m (Isaksen 2002). According to Loffler and Finch (2005), the transition from low to mid-alpine vegetation zones occurs at around 1350 m. An area of 1151 km^2 is protected under national park status and the main land uses are outdoor recreation and summer grazing of sheep, goats, cattle and domestic reindeer. The underlying geology is fairly uniform, consisting of pyroxene granulite gneiss with small areas of mylonite and peridotite.

The Jostedalsbreen region includes the largest ice-cap in mainland Europe, which gives rise to approximately fifty outlet glaciers. The altitudinal range of this region is from sea-level to 1957 m, with the tree-line descending to approximately 840-880 m. Much of the study area lies below the tree-line within the birch and pine woodland. Data from the Bjørkhaug i Jostedalen meteorological station (324 m) gives a mean annual air-temperature of 3.7° C, a July mean of 13.4° C, a January mean of -4.9° C and a mean annual precipitation of 1380 mm (Aune 1993, Førland 1993). Outdoor recreational pursuits and agriculture (grazing and arable) are the main land uses and a number of major hydro-electric power plants are also situated in the area. Approximately 1310 km^2 of the Jostedalsbreen region has National Park status. The underlying geology is predominantly an acidic granitic gneiss.

South-central Norway includes a strong continentality gradient between the western coast and the Scandes mountains. The Jostedalsbreen region is influenced by an oceanic climate, with higher precipitation and a lower treeline, while the Jotunheim region has a more continental climate with lower mean precipitation, greater seasonal extremes of temperature and a higher treeline. The underlying geology also contributes to the general west-east gradient of vegetation variation and influences soil pH, the bedrock in the Jostedalsbreen region being more acidic.

Changes in land use have been documented in central Norway, with a reduction in summer grazing over the period 1960 to 1993 (Olsson et al. 2000) and a reduction in fuel wood harvesting. Cattle grazing has become much more restricted to enclosed areas, while the number of sheep grazing above the tree-line has increased significantly since 1949. Below the tree-line, there has been a considerable transition from heathland and grassland to woodland in the areas studied. The number of working summer farms in Norway has decreased from 44,000 in 1907 to 2,855 in 1997, while tourism is becoming an increasingly important activity for farm owners and others. There has also been a loss of semi-natural hay meadows and increasing transfer of land to arable production. Olsson et al. (2004) also document the decline in agriculture in sub-alpine areas of Jotunheimen, where forest succession is resulting in loss of semi-natural grasslands and heathlands.

The climax vegetation of the study area as a whole is traditionally divided into four sub-zones (Moen 1987), the altitudinal ranges of which vary according to local conditions:

1. Below the tree-line, birch (*Betula pendula* ssp. *tortuosa*) and pine (*Pinus sylvestris*) are accompanied by warmth-demanding tree species, such as elm (*Ulmus* spp.) and alder (*Alnus* spp.) However, much of the natural vegetation is replaced by agricultural crops and grazing meadows.
2. The low-alpine zone is dominated by bilberry heath (*Vaccinium myrtillus*) and willow scrub (*Salix* spp), combined with snow-bed communities (e.*g. Veronica alpina, Sibbaldia procumbens, Leontodon autumnalis, Rhodiola rosea*).
3. In the mid-alpine zone, shrub communities are replaced by grassy heaths (e.g. *Carex bigelowii, Festuca ovina, Juncus trifidus*), the only common shrub being *Salix herbacea.*
4. The high-alpine zone is characterized by scattered vegetation with no continuous cover; typical vascular species include *Luzula* spp*, Ranunculus glacialis* and *Salix herbacea*.

3.1.1 Roadsides

The study area contains a number of single-track roads which are largely free from snow from June to September and which are used predominantly by tourists for access to accommodation and long-distance walking trails and also for engineering access to hydro-electric power plants (Figure 3-1). Most roads are un-metalled. In all cases, the roadside verges consist of a loose, well-drained, gravel substrate, which is disturbed annually when the roads are cleared of snow (Figures 3-2 and 3-3). The verges also tend to be more frequently disturbed where the roads have been widened to create passing-places for vehicles. On these areas, the gravel is periodically replaced. Eleven roads (Figure 3-4 and Table 3-1) were sampled across the study area to provide a comprehensive altitudinal (40 to 1860 m) and regional (31 to 116 km east from the most westerly glacier foreland) range of pioneer roadside vegetation. In effect, almost all un-metalled roads were sampled. A number of roads were partially metalled but this did not extend to the verge.

Table 3-1. Roads sampled. (Distance east is measured from the most westerly glacier foreland.)

Code	Name	Altitudinal Range (m a.s.l.)	Mean distance east (km)	Approximate length (km)	No. of sites per road
A	Nystølen	40-540	31.25	5.2	26
B	Vetlestølsdalen	340-1040	37.85	7.4	36
C	Sprongdalen	840-1200	43.7	3.9	19
D	Fortundalen	80-1260	62.05	22.7	60
E	Helgedalen	820-1300	63	5.7	25
F	Storevatnet	1240-1440	69.35	5.6	11
G	Leirdalen	900-1400	83.2	14.4	26
H	Mytingi	600-880	89.1	2.7	15
I	Juvvasshytta	1200-1860	92.4	9.5	34
J	Visdalen	780-1100	94.75	9.2	16
K	Veodalen	780-1400	115.55	30.4	32

Figure 3-1. Single-track road Fortundalen (1200 m).

Figure 3-2. Roadside verge Leirdalen (1400 m).

Figure 3-3. Roadside verge Leirdalen (1000 m).

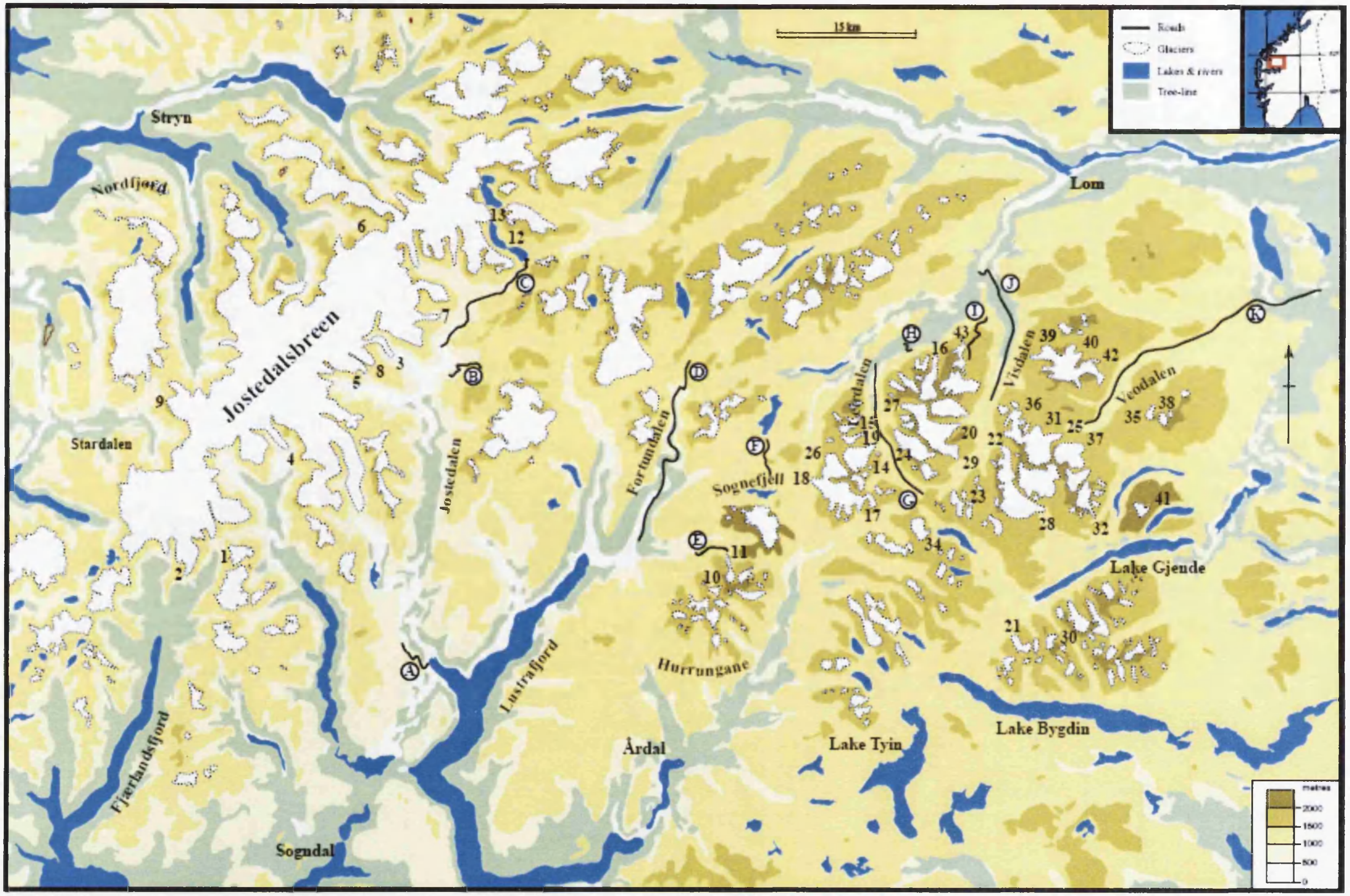


Figure 3-4. Map of study area showing roads and glacier forelands. [Roads are indicated by upper case letters (see Table 3-1) and glacier forelands by numbers (see Table 3-2)]

As a number of the roads used in the study had been constructed within the last twenty years for access to hydro-electric power plants, it was necessary to ensure that the vegetation recorded was not the result of artificial seeding of verges by the utility company (Norsk Hydropower). Detailed information was therefore obtained of the seed mixtures which would have been used for such purposes and it was found that the species bore no relationship to those recorded in this project (Anon 2005).

3.1.2 Glacier forelands

Species data were already available for 42 glacier forelands in both the Jostedalsbreen and Jotunheim regions (J A Matthews, unpublished). The data were supplemented by collection of species from Gjuvbreen glacier foreland to extend the altitudinal range of the data set to 1860 m, to match that of the roadside data set. The sites range in altitude from 80 m to 1860 m and have an east-west range of over 100 km (Figure 3-4 and Table 3-2). Distance east for all sites is measured from a point 5km west of Haugabreen foreland.

The lower altitude forelands (below 1100 m) are all in the Jostedalsbreen region to the west of the study area, while the higher altitude forelands are, with two exceptions (Vivakulen and Austerdalsnutin), in the Jotunheim region. A number of the glacier forelands in this data set have been studied intensively (see Matthews (1992) for a comprehensive summary) but analysis of the pioneer zone and successional trajectories of such a large number of forelands has not previously been conducted.

As this study focuses on the pioneer stage of vegetation succession, all forelands, where recording of pioneer vegetation was possible, were included in the initial stages of the analysis (n = 42). West Grotbreen foreland was excluded as pioneer vegetation was not present. For analysis of successional patterns, only forelands with species data on four stages of succession were included (n = 39). (Species data were not available on the 1930s stage at Austabotbreen, West Nautgardsbreen and Gråsubreen forelands and these three sites were therefore excluded.)

Table 3-2. Glacier forelands sampled. (Distance east is measured from the most westerly glacier foreland.)

Code	Name	Altitude (m a.s.l.)	Distance east (km)
1	Suphellabreen	80	10
2	Bøyabreen	100	5.7
3	Nigardsbreen	400	29.6
4	Austerdalsbreen	420	19
5	Bergsetbreen	580	24.5
6	Bødalsbreen	700	24.9
7	Fåbergstølsbreen	780	35.2
8	Tuftebreen	880	27.3
9	Haugabreen	900	4.7
10	Ringsbreen	1100	60.5
11	Styggedalsbreen	1280	65.3
12	Vivakulen	1280	39.9
13	Austdalsnutin	1300	40.1
14	Storbreen	1380	80.7
15	Hurrbreen	1380	80.2
16	Storgjuvbreen	1380	88
17	Sandelvbreen	1400	40.6
18	Bøverbreen	1420	74.4
19	Veslbreen	1420	80.4
20	Tverrabreen	1440	90.1
21	Slettmarksbreen	1460	95.7
22	Hellstugubreen	1480	95.3
23	Visbreen	1500	89.6
24	S Illabreen	1520	84.7
25	Veobreen	1530	100.9
26	Leirbreen	1540	76.3
27	N Illabreen	1580	85.1
28	Memurbreen	1580	98.7
29	Bukkeholsbreen	1600	90.1
30	Svartdalsbreen	1600	100
31	Styggebreen	1600	92.2
32	Tjukningsbreen	1600	104.2
33	Austabotbreen	1620	59.8
34	Høgvalgbreen	1620	86.9
35	W Nautgardsbreen	1660	110.6
36	W Veobreen	1700	98.2
37	N Veobreen	1700	98.7
38	E Nautgardsbreen	1730	111.7
39	W Grotbreen	1770	99.1
40	E Grotbreen	1780	103.3
41	Besshobreen	1780	109.9
42	Gråsubreen	1800	104.2
43	Gjuvbreen	1860	90.5

Glacier forelands, particularly within the pioneer zone adjacent to the glacier (Figures 3-5 and 3-6), are subject to direct and indirect disturbance due to the proximity of the glacier and are subject to strong winds, low air temperatures and continuous meltwater inflow during the summer. The newly deglaciated substrates are in the process of adjusting to the removal of glacier ice and consist predominantly of unconsolidated, water-saturated sediments (Matthews 1999).

Figure 3-5. Pioneer zone, Storbreen glacier foreland.

Figure 3-6. Pioneer plants, Storbreen glacier foreland.

3.1.3 Additional pioneer habitats

Species data from a number of additional types of pioneer habitat were also collected across the two study regions (Figure 3-7 and Table 3-3). Vegetation was recorded at 34 sites including river gravels (4 sites), river outwash plains (3 sites), river levées (4 sites), debris flows and debris flow levées (9 sites), gravel tips and pits (6 sites), patterned ground (4 sites) and avalanche tracks (4 sites). The sites range in altitude from 240 to 1860 m and have an east-west range of 76 km.

Table 3-3. Additional pioneer habitats sampled. (Distance east is measured from the most westerly glacier foreland.)

Code	Name	Altitude (m a.s.l.)	Distance east (km)
RB1	River Bar Leirdalen	900	81.3
S1	Grandane Fabergstols	500	38.3
S2	Sandur Erdalen	600	29.4
RL1	River Levee Fabergstols	490	36.8
RL2	River Levee Fabergstols	330	36.3
RL3	River Levee Jostedalen	600	37.9
RL4	River Levee Jostedalen	540	38.6
RO1	River Outwash Fabergstols	490	37
RO2	River Outwash Storbreen Foreland	1150	81.7
RO3	River Outwash Leirdalen	1080	81.5
RO4	River Outwash Nigardsbreen	280	33.5
DF1	Debris Flow Leirdalen	980	81.5
DF2	Debris Flow Leirdalen	1450	85.5
DF3	Debris Flow Leirdalen	1260	83.3
DF4	Debris Flow Fabergstolsbreen	620	35.6
DF5	Debris Flow Fabergstolsbreen	620	35.7
DF6	Debris Flow Fabergstolsbreen	620	35.8
DFL1	Debris Flow Levee Leirdalen	980	81.5
DFL2	Debris Flow Levee Leirdalen	1460	85.5
DFL3	Debris Flow Levee Leirdalen	1260	83.4
GT1	Gravel Tip Leirdalen	920	81.5
GT2	Gravel Tip Leirdalen	1320	83.7
GT3	Gravel Tip Leirdalen	980	81.6
GT4	Gravel Tip Sprangdalen	1060	44.1
GP1	Gravel Pit Nigardsbreen	280	33.4
GP2	Gravel Pit Jostedalen	600	37.9
PG1	Patterned Ground Styggedalsbreen	1280	65.2
PG2	Patterned Ground Juvasshytte	1750	92
PG3	Patterned Ground Juvasshytte	1860	91.4
PG4	Patterned Ground Juvasshytte	1800	91.5
AT1	Avalanche Track Jostedalen	520	38
AT2	Avalanche Track Jostedalen	520	37.6
AT3	Avalanche Track Austerdalen	240	15.6
AT4	Avalanche Track Leirdalen	1460	85

Figure 3-7. Map of study area showing additional pioneer sites. (See Table 3-3 for key to sites.)

River gravels (bars) and outwash plains (sandar) (Figure 3-8) are directly affected by the discharge of glacial meltwater streams which transport and deposit eroded material and sediment from higher to lower elevations. Shifting active channels continually disturb the colonizing vegetation. Flooding of land adjacent to rivers also occurs annually with spring snow-melt and after high rainfall and leads to the creation of natural and/or man-made river levées (Figure 3-9). The four river levées sampled were all constructed in response to the 1979 Jostedal flood. Riverside gravel deposits are also removed for road maintenance and are stored as roadside gravel tips. Two types of disturbance therefore result: artificial gravel pits and tips, both of which provide opportunities for pioneer colonization.

Patterned ground (Figure 3-10) occurs as a result of cryoturbation in which particles of different sizes are sorted by differential frost heave (Matthews 1999). This creates either sorted circles, due to larger particles being moved to the margins and fine particles to the centre, or stone stripes due to the differential downslope movement of particles of different size on sloping terrain. Both types of disturbance create areas for pioneer plant colonization. In addition, mass-movement processes, such as debris-flows (Figure 3-11) and avalanche tracks (Figure 3-12), damage or remove existing vegetation and create opportunities for pioneer establishment.

Figure 3-8. River outwash Leirdalen (900 m).

Figure 3-9. River levée, Jostedalen (600 m).

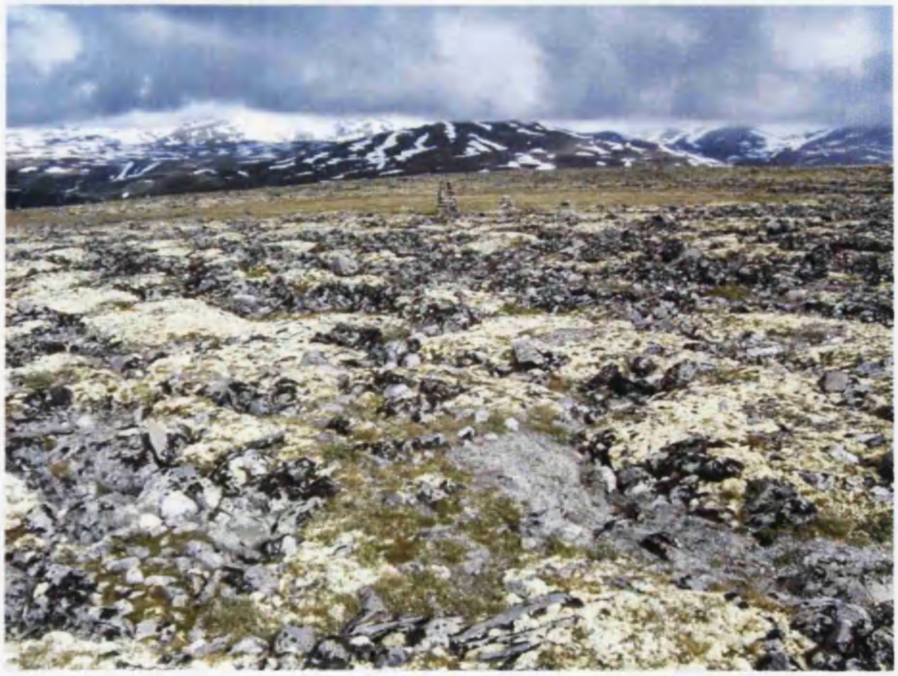


Figure 3-10. Patterned ground, Juvasshytte (1800 m).

Figure 3-11. Debris flows, Leirdalen (1460 m).

Figure 3-12. Avalanche track, Austerdalen (200 m).

3.2 Data collection

3.2.1 Chronosequence approach

The traditional method of investigating successional change through time is to use the chronosequence approach (substituting space for time) in data collection. A problem with this method lies in the underlying assumption that environmental factors other than time are unimportant and limitations are inevitably inherent in a method that makes generalized assumptions about the ecological history of a site. However, extensive research into primary plant succession, particularly on glacier forelands, has been conducted using this approach and the relative simplicity of ecosystems found on roadsides and recently-deglaciated terrain, together with the sampling methods used, make site-specific conditions less of a confounding factor. For a comprehensive survey of this approach see Matthews (1992) and Walker and del Moral (2003). A recent assessment of the validity of the chronosequence approach (Foster and Tilman 2000) found that data collected using this method accurately predicted changes in species abundance over the period of the study.

For the roadside and glacier foreland sites, a chronosequence approach was used to differentiate sites of pioneer and mature status respectively. Roadside vegetation was recorded at two successional stages, the pioneer stage on unconsolidated gravel adjacent to the road and the climax stage within the adjacent established vegetation. On the glacier forelands, four stages of succession were recorded at increasing distances from the glacier snout: pioneer vegetation on the most recently deglaciated ground (up to ten years since deglaciation); vegetation associated with the 1930 moraine (approximately 70 years since deglaciation); vegetation associated with the 1750 moraine (approximately 250 years since deglaciation); and climax vegetation on ground outside the foreland, which has been deglaciated for approximately 10,000 years. Terrain age on the glacier forelands was estimated from dated glacial moraines using a combination of methods including historical evidence and lichenometry (Bickerton and Matthews 1992, 1993, Matthews 2005). At forelands not dated by these methods, analogue '1930' and '1750' moraines were generally recognizable on morphological grounds. Only the pioneer stage of succession was recorded for the additional pioneer habitats data set.

3.2.2 Site selection

Individual sites along each road were selected according to substrate and altitude. Selection on the basis of substrate required an un-compacted and un-surfaced area of loose gravel at the edge of the road. These sites generally showed evidence of recent colonization by plants characterized by sparse vegetation and low plant cover. However, there is a danger of using a circular argument if, in employing this definition, the vegetation is judged to be in the pioneer stage solely based on these criteria. Therefore, in choosing suitable sites the condition of the substrate took priority over the perceived stage of colonization and there were occasions when the recorded vegetation included species such as dwarf shrubs which are more usually associated with later stages of succession. Sites were sampled approximately 20 m a.s.l. apart using maps and an altimeter. Recording of sites at 20 m altitudinal intervals was considered sufficient to provide good coverage of the altitudinal range of the roads within the time allowed. The altimeter was calibrated twice each day at sites of known altitudes to correct for changes in air pressure.

In each case, the first quadrat (0.04 m^2) was placed in a position which would include the individual plant nearest the middle of the road, and subsequent contiguous quadrats were placed parallel with the edge of the road. The number of quadrats per site was determined by the species number (see below). At each site, species were also recorded on adjacent established vegetation. In this case, the first quadrat was placed within a representative patch of vegetation and subsequent quadrats were placed parallel to the road. In most cases, extreme gradients were avoided and, as roadside edges are generally fairly well drained, the driest side of the road was selected for recording of established vegetation, avoiding boggy areas.

On the glacier forelands, contiguous (1 m^2) quadrats were recorded at increasing distances from the glacier snout within each successional zone (see below). In each case, the starting point was the individual plant within that zone which was closest to the glacier snout. Where possible, the transects were placed on ground with an even, stable surface and avoiding stream courses to ensure similar moisture regimes.

Sites that provide examples of early plant colonization at additional types of pioneer habitat were recorded by placing the first quadrat at a point where plants were establishing close to the source of disturbance (i.e. in newly available areas for plant colonization on the selected landform). For example, river gravel vegetation was recorded along a series of quadrats parallel to the course of the river to include the area closest to the river. In the case of avalanche tracks and debris flows, the freshest substrate was identified.

3.2.3 Vegetation recording

Vegetation was recorded using relative shoot frequency as a measure of species abundance. The advantages of using relative frequency as a measure of abundance are: (1) it is a rapid method of assessment allowing a large number sites to be recorded within the time available for fieldwork; (2) it is a relatively objective method, as only the presence of a species is recorded, rather than an assessment of its size or how many individuals are present; and (3) it avoids the necessity of delineating individual plants, where growth form makes this difficult. Its disadvantages are twofold: (1) it is not possible to make direct comparisons between data sets if quadrats differ in size; and (2) it provides less information than if counts of individual plants are made (Kent and Coker 1992, Bullock 1996).

On the roadside sites, the relative frequency of species in the pioneer and established stages of succession was recorded using 0.04 m^2 quadrats. This size of quadrat was the most appropriate for the size and shape of the pioneer sites encountered. Recording continued until 100 occurrences of species had been reached at each site, providing a measure of the relative frequency of each species at that site (Figure 3-13). Sites on additional types of pioneer habitat were also sampled using 0.04 m^2 quadrats, so that direct comparison with the roadside sites is possible.

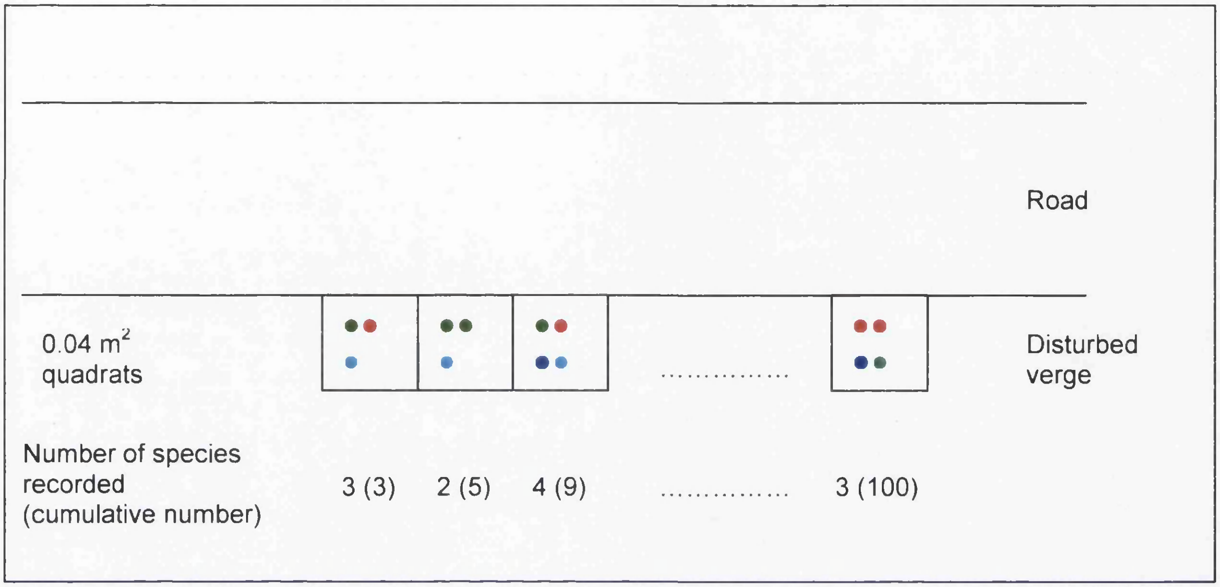


Figure 3-13. Diagrammatic representation of data collection method for roadside verges. (Colours indicate different species.)

For the glacier foreland sites, the data are in the form of the occurrence of species abundance in a series of 1 m^2 quadrats (2 m x 0.5 m). This also produces a measure of relative frequency although, as stated above, the use of different quadrat sizes means that the two data sets are not directly comparable. The different quadrat sizes used for roadsides and other pioneer habitats (0.04 m^2) and glacier forelands (1 m^2) must therefore be taken into account when the data sets are compared.

3.2.4 Testing the compatibility of different quadrat sizes

As the data collection method uses relative species abundance rather than absolute numbers, and the analytical methods focus on placing the species in rank order of importance, the results may not be so greatly affected by quadrat size. In order to directly assess the differences between results obtained using the two quadrat sizes, a comparison was made of data from 1 m^2 and 0.04 m^2 quadrats for relative pioneer species abundances on Storbreen glacier foreland and relative climax species abundances adjacent to Fåbergstølsbreen glacier foreland. Within the Storbreen glacier foreland pioneer zone, the same 11 species were recorded using both size quadrats but the 0.04 m^2 quadrat recorded an additional two species at low relative frequencies (Figure 3-14). If only the five most frequent species are considered, four of these attain this rank when both quadrat sizes are used. For the Fåbergstølsbreen climax vegetation (Figure 3-15), the same 12 species were recorded using both size quadrats and there were only minor differences in the relative frequency of species for both methods, for example greater relative frequencies of *Vaccinium uliginosum* and *Melampyrum sylvaticum* using the larger quadrat size.

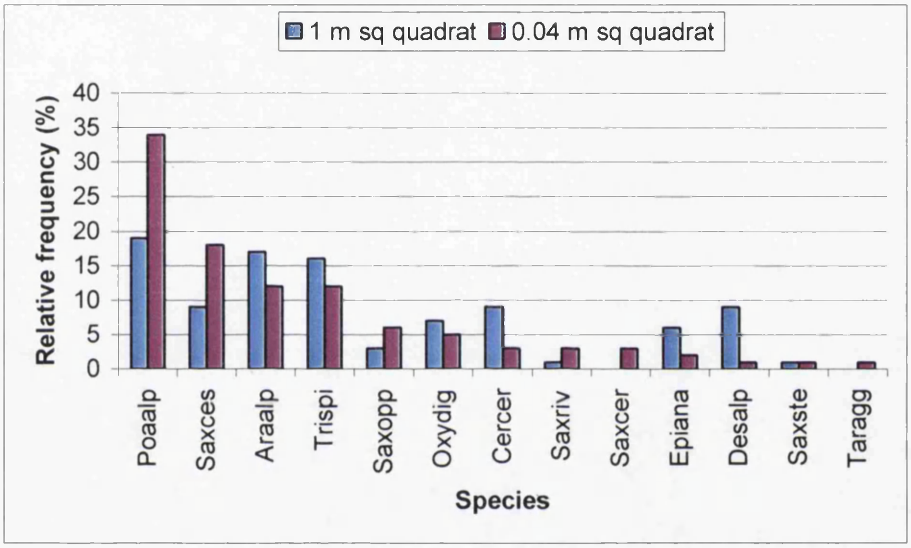


Figure 3-14. Relative frequency of pioneer vegetation on Storbreen glacier foreland using two quadrat sizes.

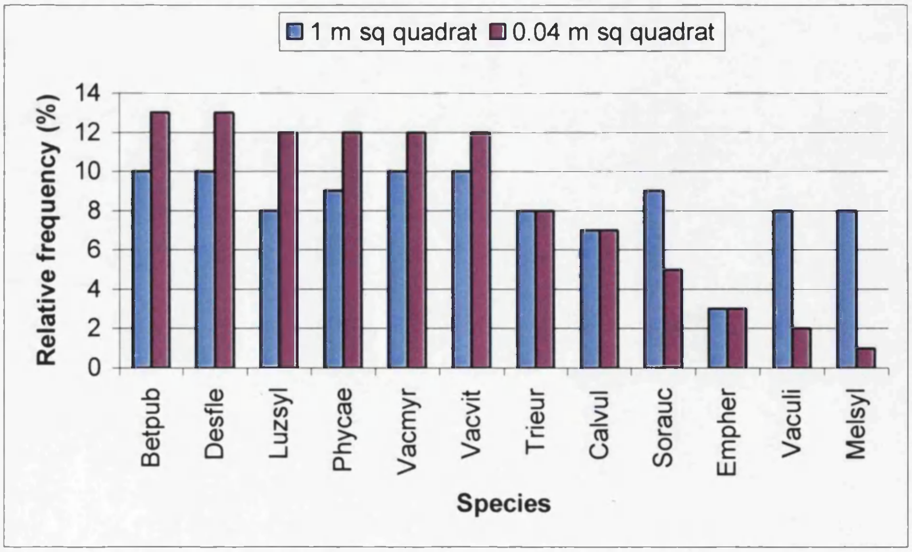


Figure 3-15. Relative frequency of climax vegetation adjacent to Fåbergstølsbreen glacier foreland using two quadrat sizes.

The test shows that the two quadrat sizes produced only minor differences in the species recorded and their relative frequencies. However, it is based on a small sample size and allowances were therefore made for the possible effects of quadrat size when analyzing the main data sets. Only after the data sets had first been described and analyzed separately were they combined in a single analysis for direct comparison and comparisons between the data sets were initially made on the basis of indicator species values rather than relative frequencies.

3.2.5 Species identification and nomenclature

Identification was carried out in the field based on field guides (Fitter et al. 1978, Schauer 1982, Fitter et al. 1984, Wischmann 2000, Gjaerevoll and Jorgensen 2002) and taxonomic keys (Rose 1981, Hayward 1995, Stace 1999). Nomenclature conforms with Lid and Lid (1994). Only vascular species were recorded on roadsides and in additional pioneer habitats, in conformity with the glacier foreland data set. Information on key dispersal agents was obtained from an online database at the University of York (Peat and Fitter 2007).

3.3 Data analysis

All analysis was carried out using PC-ORD Version 4.33 software (McCune and Mefford 1999b), Canoco for Windows version 4.54 (ter Braak and Smilauer 2006) and Microsoft Excel 2002.

3.3.1 Distance coefficients

The use of a distance measure is an integral part of all ordination and classification methods, the first step in multivariate analysis being the calculation of a matrix of distances between sites in multidimensional space in terms of their species composition. The choice of distance measure involves several considerations. A major factor is that all distance measures, to varying degrees, lose sensitivity to differences between sites when beta-diversity is high, thus introducing errors into the analysis. Furthermore, some distance measures treat joint absences of a species (double-zeros) as evidence of similarity between two sites, which can lead to distortion of information on compositional relationships. Coefficients which retain sensitivity to diversity and ignore double zeros when computing distance (asymmetrical coefficients) are therefore considered preferable (Legendre and Legendre 1998).

The Sørensen similarity proportion coefficient (also known as the Bray-Curtis or Czekanowski coefficient) converted to percentage dissimilarity retains greater sensitivity in heterogeneous data sets and gives less weight to outliers compared to Euclidean distance (McCune and Grace 2002). It has also performed well in comparisons with other distance measures (Faith et al. 1987). The Sørensen coefficient is a semimetric, which avoids the paradox inherent in many metric distance measures, where two sites without species in common can be considered closer in composition than two sites that share species. For this reason, Legendre and Legendre (1998) consider Euclidean distance unsuitable for comparing sites on the basis of species abundances. City-block or Manhattan distance on the other hand, into which Sørensen similarity can be converted, creates a gradient of distance that is proportional to the number of species responding to it. Proportional similarity coefficients applied to quantitative data have been shown by Roberts (1986) to be mathematically explained as the intersection between two fuzzy sets. The Sørensen dissimilarity equation can be written as:

$$1 - [2W/(A+B)]$$

where W is the sum of shared abundances and A and B are the sums of abundances in individual sample units. It therefore gives double weight to double presences, according more importance to the presence of a species as this is considered more informative than its absence.

Chi-squared distance also needs to be considered, as it is incorporated into several ordination methods including detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). (DCA is used in this thesis to provide a comparison with the main ordination method). Faith et al. (1987)

found that this distance measure performed poorly and Minchin (1987) questioned its appropriateness as a measure of compositional dissimilarity in ecology, as it accords high weight to species with low total abundance in the data and tends to exaggerate the distinctiveness of samples containing several rare species. Furthermore, the maximum chi-squared distance for sample pairs with no species in common fluctuates according to general variation in species abundances, rather than reaching a constant value. It was considered by Faith et al. to be acceptable in the analysis of small environmental distances but has the problem that distant site units are often misinterpreted as close together in species space.

A distance coefficient measures the degree to which two samples differ in composition and is initially used to obtain an assessment of the overall variability within the data (i.e. the variability in species composition of pioneer sites within each habitat), and later to compare variability within the pioneer stage with that of later stages of succession. Most methods of multivariate analysis incorporate the use of an inherent distance coefficient. However, for the purposes of this project, ordination and classification methods were used which allow for a choice of distance measure.

3.3.2 Ordination

With the development of ideas of species continua came the methods to analyse vegetation in accordance with this concept. Gradient analysis (Whittaker 1967) describes the two methods of direct and indirect analysis of samples according to environmental gradients. In the former, vegetation samples are arranged along a measured environmental gradient, such as elevation, whereas the latter arranges samples according to their species composition along axes, which may or may not correspond to environmental gradients. Indirect gradient analysis requires measurement of the relative similarity between samples and originally only took account of the number of species shared, rather than abundance values. It can be now used with either qualitative or quantitative data.

Non-metric multidimensional scaling (NMS) is a method of indirect gradient analysis in which sites are mapped in reduced ordination space according to the rank order of compositional distances between them. NMS therefore has an advantage over other ordination methods in that its basis on ranked rather than absolute distances improves its ability to extract information from non-linear relationships. This method also overcomes the inherent limitation of dissimilarity coefficients in expressing large distances when sites with no species in common have a fixed maximum distance. (See Kruskal and Wish (1978) and Mather (1976) for a description of the method and McCune and Grace (2002) for a description of the computational procedure.)

Kenkel and Orloci (1986) compared metric and non-metric multidimensional scaling methods for ordination of artificial data and found that the best strategy tested was NMS. Their study was based on Euclidean distance and did not test other distance measures. Austin (2005) states that, although canonical correspondence analysis (CCA) has become the most frequently used ordination method in vegetation science, it is based on assumptions which are often not met, particularly the niche concept of species partitioning of a resource gradient, which implies that species have equal ranges and amplitudes and are equally spaced along a gradient (ter Braak 1986). Unlike ordination methods based on correspondence analysis, NMS makes no assumptions about the nature of species response to underlying gradients. CCA also assumes that the major variation in vegetation composition is due to the environmental parameters measured rather than other factors such as successional and other historical influences. Although NMS is computationally more complicated than other ordination methods, this no longer constitutes a problem and Austin (2005) therefore considers it to be the preferred method on theoretical grounds. According to Minchin (1987), this method is also relatively robust to noise and non-linearities in the data. Recent examples of the use of NMS can be found in Aikio et al. (2000), Soininen et al. (2004) and Caccianiga et al. (2006).

Sample ordination scores can be regressed onto environmental variables and plotted onto the ordination diagram (McCune and Mefford 1999a), producing a similar analytical tool to canonical correspondence analysis i.e. displaying compositional gradients in relation to environmental variables. However, unlike CCA, NMS is not constrained to finding axes expressed in terms of environmental variables but is based solely on compositional trends.

Detrended correspondence analysis (DCA) (Hill and Gauch 1980) is an ordination technique based on correspondence analysis (CA) but with rescaling of axes to rectify the tendency of CA to produce an arched pattern of sites in ordination space. It is chosen as an alternative method for comparison with NMS as it is frequently used in ecological analysis of plant communities despite criticism for lack of robustness and erratic performance (Minchin 1987) and for the effect of the detrending procedure on representation of complex ecological gradients (Legendre and Legendre 1998). An analysis of papers published from 2003 to 2005 by Kent showed that NMS and DCA are used to comparable extents but that DCA is still the most frequently used method of indirect ordination in terrestrial plant ecology (Kent 2006).

Non-metric multidimensional scaling (NMS) is used to examine the relationship between sites in terms of their species composition by summarising multi-dimensional components (species) in a smaller number of dimensions (axes) which can be more easily understood. The aim of NMS is therefore to find a low-dimensional ordination space in which samples are plotted to reflect their separation in terms of "species space" (Faith et al. 1987). This is achieved by calculating ordination scores that represent the highest possible rank correlation between ordination distance and ecological distance. Ordination of sites rather than species is carried out, as the latter leads to problems in interpretation, as the representation of species as points is misleading when they occur across a range of sites.

NMS is first carried out using the most thorough autopilot option of PC-ORD, which performs 40 runs with real data, 50 randomized runs, a maximum of 400 iterations and an instability criterion of 0.00001. Randomization of the data with a Monte Carlo test allows assessment of whether the NMS ordination axes have lower stress than expected by chance and a *p*-value is calculated to test the significance of the reduction in stress when real data are used. The ordination is assessed by examining the level of stress and the stability of a given solution and the proportion of variance expressed by each axis. Stress levels below 20 are considered by Clarke (1993) to provide a usable solution, although levels approaching 20 are more safely used for providing an overall picture rather than precise details of the relationship between sites. Where only a slight reduction in stress is obtained by using a three-dimensional rather than a two-dimensional solution, the two-dimensional solution is used to illustrate the main features of the ordination. The size of the sample must also be taken into account when interpreting stress levels, as these will tend to increase with a large sample size such as the roadside verge data set. A plot of stress versus iteration number is used to assess the stability of the solution and to avoid solutions that fluctuate around a number of possible solutions or local minima and are therefore unstable. A final instability of 10^{-4} or less is considered acceptable (McCune and Grace 2002) although the autopilot mode outlined above seeks an instability of 10^{-5}.

How well the relationships between sites in the solution represent their relationships in the original dissimilarity matrix is assessed by calculating a coefficient of determination (r^2) between distances in ordination space and distances in the original data (McCune and Grace 2002). This is used to evaluate each ordination, to help assess the optimum number of axes required and to compare NMS ordinations with those obtained from Detrended Correspondence Analysis (DCA).

Although, as outlined above, unconstrained ordination techniques are considered preferable, variance partitioning as a component of Canonical Correspondence Analysis (CCA) is used to measure the relative contributions of each environmental factor to the variation in species composition and to quantify the co-variance of these factors. The total variance explained (TVE) measures the amount of variance in the species data explained by all environmental variables included in the analysis (i.e. the sum of all canonical eigenvalues). Variance partitioning is then used to split the TVE into components enabling assessment of the relative influence of each environmental factor on variation in species composition. Variance partitioning is carried out using Canoco 4.54 software (ter Braak and Smilauer 2006). The technique is described in Økland and Eilertsen (1994) and Lepš and Šmilauer (2003). In variance partitioning, a Monte Carlo permutation test is used to test the null hypothesis that the measured environmental variables are not influencing species composition. The TVE is used primarily to partition explanatory variables, rather than to provide a measure of the amount of total inertia explained by these variables, as recommended by Økland (1999).

3.3.3 Outlier analysis

In order to ensure that sites with unusual species composition (outliers) do not dominate the relationship between sites and thus distort the results of ordination and classification, outlier analysis (Tabachnik and Fidell 1989) was performed using PC-ORD software. This procedure calculates the average distance from each sample unit to every other sample unit and identifies those with averages that fall more the specified number of standard deviations above the mean. For the purposes of this project, Sørensen dissimilarity was used as a distance measure to conform with other analytical methods and three standard deviations ($p < 0.005$) were used as a cut-off point for identification of outliers.

3.3.4 Classification

Classification is generally considered to be a “working hypothesis” involving often arbitrary divisions of intergrading units of vegetation (Miles 1979). However, it is an extremely useful method of identifying sub-units for the purposes of scientific analysis.

Two-way indicator species analysis (TWINSPAN) (Hill et al. 1975) is the most popular method of classification in Britain but has the inherent problems of being based on correspondence analysis (Austin 2005). It has received much criticism, particularly in the North America where it is no longer recommended, and McCune and Grace (2002) categorically state that ecologists should not use TWINSPAN except for analysis of a dataset with a one-dimensional structure where a two-way table is needed. Criticism is directed at the fact that, being based on correspondence analysis, it performs poorly on data with more than one gradient, on its use of pseudospecies rather than truly quantitative data and on the complexity of its algorithm. It is therefore used in this study solely to provide additional results for comparison with cluster analysis groups.

Hierarchical, polythetic, agglomerative classification (cluster analysis) is a particularly useful complement to NMS ordination because, unlike other methods of classification, it can be based on any distance measure. It can therefore be performed using the same proportion coefficient so that the results are directly comparable with the NMS ordination. Ward's minimum variance method (Ward 1963) and the unweighted pairs group average technique (UWPGA) (Williams et al. 1966) are the most often used (Kent 2006) and Kent criticizes use of the former as it is implicitly based on the squared Euclidean distance coefficient. However, the flexible beta linkage method (see below) is considered to produce similar results to Ward's method and is compatible with semi-metric distance coefficients when $\beta = -0.25$ (Lance and Williams 1967, McCune and Grace 2002).

Ordination and classification are used as complementary methods for identifying patterns in vegetation data with classification highlighting discrete groups of sites or discontinuities in ordinated data. The plotting of samples in ordination space, coded according to classification groups using colours or symbols, is an effective means to aid interpretation of vegetation patterns. Groups that are compositionally similar appear as tight clusters in ordination space, whereas a cluster group that is diffused throughout the ordination space indicates that the group's cohesion is expressed on a higher ordination axis or that it has been too finely divided (and is not "real"). This approach is especially powerful when the ordination and classification are based on the same ecological distance measure (Legendre and Legendre 1998). Classification of species rather than sites using a transposed matrix is not carried out as clustering results in frequent and rare species being allocated to separate groups even if they share ecological requirements.

Cluster analysis is performed with PC-ORD software which uses the clustering algorithm described by Wishart (1969) and Post and Sheperd (1974). The choice of linkage method used in cluster analysis can have a major influence on the classification (Legendre and Legendre 1998). A flexible combinatorial linkage method (flexible beta with a value of -0.25) was selected for all cluster analyses in this study. The flexibility is obtained by controlling the value of beta and when $\beta = -0.25$ it performs as a space-conserving method (McCune and Grace 2002). This means that the distances between units are not distorted by the formation of each new group but those of the original distance matrix are retained. Flexible beta linkage with this β-value gives similar results to Ward's method of minimizing increases in the error sum of squares from each unit to the centroid of its group. As Ward's method is not compatible with semi-metric distances such as Sørensen, flexible beta is therefore the method chosen for this study.

One way of evaluating the groups produced by classification is to calculate a value for percentage chaining (McCune and Mefford 1999a). This is a measure of the extent to which single sites are repeatedly added to existing groups and would therefore indicate the existence of a continuum rather than discrete groups. Chaining greater than 25% is considered to be too high to indicate discrete groups (McCune and Grace 2002).

Determining the number of groups at which to analyse a cluster analysis dendrogram is always a compromise between obtaining maximum homogeneity and minimum number of groups. Two methods are used in this study: multi-response permutation procedure (MRPP) described in the next section; and a variation on Dufrene and Legendre's method (Dufrene and Legendre 1997) in which species indicator values are calculated at each stage of clustering and the change in collective indicator values is assessed.

Cluster analysis groups are also assessed by calculating a discreteness index based on the ratio of mean between-group Sørensen distance to mean within-group Sørensen distance; the greater the index, the more discrete the group. A further assessment is obtained by plotting centroids onto the NMS diagram as a measure of the mean score of each group along the ordination axes with ellipses to indicate ± 2 standard deviations from this mean. Thus, ellipses enclose approximately 95% of sites within each group.

Environmental factors associated with groups are identified by superimposing correlation vectors onto the NMS ordination diagrams and by calculating mean values for each group. This approach is used in conjunction with altitude, distance east and mean weighted Ellenberg's indicator values for each site.

3.3.5 Multi-response permutation procedure (MRPP)

MRPP (Mielke and Berry 2001) is a non-parametric procedure for comparing the observed within-group average distances for groups produced by classification techniques with the average distances that would have resulted from all the other possible combinations of the data under the null hypothesis. Examples of recent use of this method include an assessment of 25 years of vegetation change on Mount St. Helens (del Moral and Lacher 2005) and a study of vegetation relationships in Pakistan (Enright et al. 2005).

The method is used in this thesis in order to assess each level of clustering objectively and determine which level produces the most discrete and homogeneous groups of sites. MRPP is also used to compare the effectiveness of cluster analysis at finding discrete groups within the data with that of TWINSPAN. The test statistic, δ, is the average of observed within-group distances weighted by relative group size and a *p*-value is calculated for the hypothesis that the differences between groups are no greater than those expected when sites within the data set are randomly allocated to groups. A smaller delta value indicates higher within group homogeneity and larger between group differences. MRPP does not compute exact probabilities but uses an approximation of the distribution of the test statistic (δ) to estimate the p-value.

A measure of chance-corrected within-group agreement (A-value) is also calculated, which is independent of sample size and allows assessment of within-group homogeneity compared to random expectation. The T-value gives a measure of the separation between groups, calculated as the difference between the observed and expected within-group distances, divided by the square root of the variance in the expected within-group distance.

Sørensen distance is used in MRPP analysis for compatibility with ordination and classification methods. The change in A and T-values at each level of clustering is used as a measure of the effect on within-group homogeneity and between-group separation of adding an additional group. The level at which the maximum change occurs is considered to be an important level at which to analyse group membership.

3.3.6 Indicator species analysis (ISA)

Indicator species analysis (Dufrene and Legendre 1997) is a method of assessing the faithfulness of a species to a particular group of sites and the relative abundance of the species within that group compared to other groups. The percentage indicator value of a species is therefore a measure of its specificity and fidelity to a group of sites. Dufrene and Legendre consider this method to be more sensitive than Two-Way Indicator Species Analysis (TWINSPAN) at identifying indicator species and found that TWINSPAN tended to identify species as indicators when they were present in all sites within a group, irrespective of their relative abundance because the cut-off level of pseudospecies is very low. Furthermore, Dufrene and Legendre's method identified several species with high indicator values which TWINSPAN did not detect and is considered by McGeoch and Chown (1998) to significantly advance the field of bioindication. Recent use of this method has been made, for example, in identifying patterns of vegetation distribution in the Italian Alps (Schmidtlein and Ewald 2003) and for analysing understory vegetation in Arizona pine forests (Abella and Covington 2004).

TWINSPAN is used extensively in vegetation analysis to identify indicator species and has received considerable criticism for its complexity and the use of artificial 'pseudospecies'. For example, McCune and Grace (2002, p 97) categorically state: "Ecologists should not use TWINSPAN, except in the very special case where a two-way ordered table … is needed for a data set with a simple, one-dimensional underlying structure." As this project is attempting to analyse the data set in terms of more than one underlying structure, TWINSPAN is used only as a secondary method for comparison with ISA.

Indicator species analysis (Dufrene and Legendre 1997) is used in this study to identify characteristic species for the description and ecological assessment of cluster analysis groups, to provide a measure of how well key species separate between groups and to provide an additional method of evaluating each level of classification. The proportional abundance of a species in a particular group is calculated relative to its abundance in all groups and this is expressed as a percentage. The proportional frequency of the species in each group is then calculated and expressed as a percentage i.e. the proportion of sample units in each group that contain the species. These two proportions are multiplied to give an indicator value for the species. A perfect indicator with a value of 100% would always be present in a particular group and would also be exclusive to that group. The statistical significance of indicator values is assessed with a Monte Carlo randomization test to test the null hypothesis that the indicator value is no greater than would be expected by chance.

In this study, indicator values are calculated at each level of cluster analysis and the effects on these values and on the combined values of all indicator species at each level of clustering are assessed. This provides an important means of understanding the nature of the groups at different hierarchical levels and also a method of assessing possible ecological interpretations of the groups formed.

3.3.7 Ellenberg's indicator (EI) values

Ellenberg's original list of environmental indicator values for vascular plants (Ellenberg 1974) constitutes a set of values for species found in central Europe which can be used to estimate a number of environmental factors for sites based on vegetation data. The six EI values reflect the environmental preferences of individual species and thus have the potential to provide additional information when the direct measurement of environmental variables is not possible due to time or equipment constraints or in retrospective studies of data sets. Ellenberg's work has received some criticism as his attribution of environmental values to species are seen by some researchers as being subjective (e.g. Wiegleb 1986) but, in practice, they have proved extremely useful, for example in aiding the interpretation of ordination diagrams (Persson 1981). Ellenberg et al. (1991) defend their position, explaining that direct measurements of environmental variables and species distribution data were used where possible to calibrate the original values and that the indicator values are intended to characterize the ecological behaviour of plants rather then their ecological requirements.

Particularly pertinent to this study is Ellenberg's view that pioneer species may behave in a different way to that suggested by their indicator values which describe the ecological behaviour of a species subject to competition and coexistence with other species within mature vegetation. However, Grimm (2000) compared the results of estimating soil pH across a number of successional stages on glacier forelands using Ellenberg indicator values (Ellenberg et al. 1991) with Messer's (1988) direct measurements of soil pH and found significant regression coefficients for the two forelands he examined. (Grimm used Ellenberg's values for central Europe rather than the more local values of Vevle. Furthermore, he used qualitative rather than quantitative vegetation data in the calculations and thus used an unweighted average of the values.) Mean EI values for light, moisture, nitrogen and pH were also used successfully within a successional context in Bossuyt et al.'s (2003) study of dune slacks in Belgium and NW France. Ewald (2003) confirms the robustness of Ellenberg's values, finding them to be fairly resilient to incomplete sampling in an experiment which progressively omitted species.

Southall et al. (2003) in their spatial and temporal analysis of vegetation mosaics in Cornish poor fen communities found weighted EI values for nitrogen, light, reaction and moisture to be an effective method of typifying plant communities. Minor variations in species composition and relative abundance were found to reflect environmental variation. Ertsen et al. (1998) working in the Netherlands found that indicator values for moisture were correlated with mean groundwater levels and that nitrogen values were better described as indicators of overall nutrient availability (N, P and K). Similarly, Hill and Carey (1997) in their study of correlation between EIVs and grassland yield, considered Ellenberg nitrogen values to reflect general productivity or soil fertility, rather than nitrogen levels. Truscott et al. (2005) found that the level of nitrogen deposition adjacent to roadside verges in Scotland was reflected in a decrease in nitrogen EI values with distance from the road, although the values did not have direct correlations with air concentrations of nitrous gases.

For the purposes of this project, a set of indicator values for Norwegian plants adapted from Ellenberg's work was used (Vevle 1985). Indicator values for three climate factors (light, temperature and continentality) and three soil factors (moisture, pH and nitrogen) are listed, but for the majority of plants included in this study, temperature and continentality values were not available. The four values described in Table 3-4 are therefore used to calculate the average environmental conditions for each site.

Table 3-4. Ellenberg's environmental indicators used in this study.

Ellenberg Indicator	**Scale**
Light	1 (deep shade) to 10 (full light)
Moisture	1 (extreme dryness) to 10 (submerged)
pH (soil reaction)	1 (extreme acidity) to 10 (basic reaction, usually calcareous)
Nitrogen (soil fertility)	1 (extremely infertile) to 10 (extremely fertile)

In some cases no values were available for the species recorded and as these were mainly species occurring in low abundances, they were omitted from the calculation and the relative frequencies of remaining species were adjusted accordingly. Only one abundant species could not be included (*Salix glauca*) in the assessment of environmental parameters. For each site, a mean weighted value was calculated for each indicator. The terms in Table 3-4 are used to denote each indicator but the results are discussed in light of the preceding arguments, i.e. nitrogen denotes general fertility, moisture denotes groundwater levels.

3.4 Summary of analytical methods used

- Distance coefficient: Sørensen similarity proportion coefficient converted to percentage dissimilarity
- Outlier analysis
- Ordination: non-metric multidimensional scaling (NMS) with detrended correspondence analysis (DCA) for comparison. Canonical correspondence analysis (CCA) is used to obtain variance partitioning.
- Classification: cluster analysis using flexible beta linkage (β = -0.25) (with TWINSPAN for comparison)
- Multi-response permutation procedure (MRPP)
- Indicator species analysis (ISA)
- Ellenberg's environmental indicator (EI) values

4 THE PIONEER VEGETATION OF ROADSIDE VERGES

4.1 Introduction

This chapter describes the pioneer vegetation of roadside verges and addresses two key questions: (1) how variable is the pioneer stage of succession on roadsides; (2) does pioneer roadside vegetation consist of a number of distinct communities?

Question one is first examined in terms of overall species composition and abundance. Then the mean Sørensen distance between sites is used to obtain an overall measure of variability within the pioneer stage. Outlier analysis is used to identify atypical sites and to enable the effects of these sites on subsequent analyses to be assessed. Sites are considered outliers if their average distance to other sites is greater than 3 standard deviations from the mean.

Question two is addressed using ordination and classification methods to identify patterns between sites (gradients and/or groups) within the pioneer stage. Non-metric multidimensional scaling (NMS) is used to examine the relationship between sites in terms of their species composition and to look for areas within the ordination diagram where clusters and/or discontinuities in the distribution of sites occur. This could indicate the existence of distinct plant communities. This approach is complemented by the use of cluster analysis to classify sites according to species composition and to define possible clusters identified on the ordination diagram. Multi-response permutation procedure (MRPP) is carried out to obtain a measure of the degree of separation between groups of sites and of agreement within groups at each level of cluster analysis. This allows a more objective assessment of the level of classification at which the most discrete groups of sites are formed and these groups are then described using indicator species analysis (ISA). The results of NMS ordination and cluster analysis are compared with detrended correspondence analysis (DCA) and two-way indicator species analysis (TWINSPAN) respectively, to ensure that the results obtained are not an artefact of the method used.

4.2 Species composition and abundance at roadside pioneer sites

A total of 152 species were recorded on the 300 roadside verge pioneer sites included in the study (Table 4-1). Four species were recorded on more than 50% of sites, 22 species on at least 20% of sites and 105 species on less than 5% of sites.

Table 4-1. Species recorded on roadside pioneer sites.

Abbreviation	*Species*	% Sites	Mean abundance
Fesovi	*Festuca ovina*	72.00	11.50
Salgla	*Salix glauca*	63.00	3.64
Agrcap	*Agrostis capillaris*	54.67	6.48
Desces	*Deschampsia cespitosa*	54.00	9.37
Poaalp	*Poa alpina*	46.33	5.29
Desfle	*Deschampsia flexuosa*	44.67	10.89
Luzspi	*Luzula spicata*	40.33	4.40
Betpub	*Betula pubescens*	37.00	3.63
Omasup	*Omalotheca supina*	34.00	1.43
Rumlla	*Rumex acetosella*	34.00	3.50
Taragg	*Taraxacum* aggregate	33.33	1.52
Cercer	*Cerastium cerastoides*	31.00	3.05
Sagsag	*Sagina saginoides*	29.33	2.40
Trirep	*Trifolium repens*	26.00	2.32
Salher	*Salix herbacea*	25.00	0.85
Polviv	*Polygonum viviparum*	23.67	1.22
Phlalp	*Phleum alpinum*	23.33	0.79
Poapra	*Poa pratensis*	22.67	3.14
Plamaj	*Plantago major*	22.00	3.45
Hiealp	*Hieracium alpinum*	21.00	0.46
Carbig	*Carex bigelowii*	20.67	0.54
Luzarc	*Luzula arcuata*	20.33	2.11
Ranacr	*Ranunculus acris*	18.67	0.64
Ceralp	*Cerastium alpinum*	18.33	1.46
Desalp	*Deschampsia alpina*	18.33	1.09
Juntrf	*Juncus trifidus*	16.00	0.73
Oxydig	*Oxyria digyna*	15.67	0.56
Omanor	*Omalotheca norvegica*	14.33	0.55
Trispi	*Trisetum spicatum*	14.00	0.84
Rumace	*Rumex acetosa*	13.33	0.80
Saxste	*Saxifraga stellaris*	13.00	0.32
Luzcon	*Luzula arcuata ssp confusa*	12.67	0.48
Antodo	*Anthoxanthum odoratum*	12.00	0.39
Camrot	*Campanula rotundifolia*	12.00	0.28
Empher	*Empetrum hermaphroditum*	12.00	0.40
Leoaut	*Leontodon autumnalis*	11.33	0.30
Solvir	*Solidago virgaurea*	10.33	0.17
Sibpro	*Sibbaldia procumbens*	9.67	0.21
Vacmyr	*Vaccinium myrtillus*	9.67	0.21
Chaang	*Chamerion angustifolium*	9.00	0.28
Minbif	*Minuartia biflora*	8.67	0.34

Abbreviation	***Species***	**% Sites**	**Mean abundance**
Silaca	*Silene acaulis*	8.67	0.31
Epiana	*Epilobium anagallidifolium*	7.67	0.27
Achmil	*Achillea millefolium*	7.33	0.19
Alcalp	*Alchemilla alpina*	7.33	0.12
Antdio	*Antennaria dioeca*	7.33	0.17
Potcra	*Potentilla crantzii*	7.00	0.13
Stegra	*Stellaria graminea*	7.00	0.35
Cerfon	*Cerastium fontanum*	6.67	0.20
Verser	*Veronica serpyllifolia*	6.33	0.21
Chasua	*Chamaemelum suaveolens*	6.00	0.35
Fraves	*Fragaria vesca*	5.67	0.18
Sorauc	*Sorbus aucuparia*	5.67	0.14
Tripra	*Trifolium pratense*	5.67	0.26
Eupagg	*Euphrasia* aggregate	5.33	0.12
Visalp	*Viscaria alpina*	5.33	0.12
Equsci	*Equisetum scirpoides*	4.67	0.37
Rangla	*Ranunculus glacialis*	4.67	0.43
Pinsyl	*Pinus sylvestris*	4.33	0.14
Vacvit	*Vaccinium vitis-idaea*	4.33	0.08
Veroff	*Veronica officinalis*	4.33	0.13
Calvul	*Calluna vulgaris*	4.00	0.07
Narstr	*Nardus stricta*	4.00	0.12
Pruvul	*Prunella vulgaris*	4.00	0.16
Sagpro	*Sagina procumbens*	4.00	0.23
Saxces	*Saxifraga cespitosa*	4.00	0.12
Carbel	*Cardamine bellidifolia*	3.67	0.14
Cerarv	*Cerastium arvense*	3.67	0.10
Veralp	*Veronica alpinum*	3.67	0.07
Hieumb	*Hieracium umbellatum*	3.33	0.09
Phycae	*Phyllodoce caerulea*	3.33	0.12
Saxcer	*Saxifraga cernua*	3.33	0.18
Astalp	*Astragalus alpinus*	3.00	0.04
Lotcor	*Lotus corniculatus*	3.00	0.15
Melsyl	*Melampyrum sylvaticum*	3.00	0.04
Rubida	*Rubus idaeus*	3.00	0.03
Stenem	*Stellaria nemorum*	3.00	0.16
Vaculi	*Vaccinium uliginosum*	3.00	0.03
Viopal	*Viola palustris*	3.00	0.04
Hypmac	*Hypericum maculatum*	2.67	0.05
Pinvul	*Pinguicula vulgaris*	2.67	0.03
Alcglo	*Alchemilla glomerulans*	2.33	0.05
Crecap	*Crepis capillaris*	2.33	0.15
Gersyl	*Geranium sylvaticum*	2.33	0.03
Saualp	*Saussurea alpine*	2.33	0.03
Vioriv	*Viola riviniana*	2.33	0.05
Crycri	*Cryptogramma crispa*	2.00	0.02
Equsyl	*Equisetum sylvaticum*	1.67	0.05
Ortsec	*Orthilia secunda*	1.67	0.02
Saxopp	*Saxifraga oppositifolia*	1.67	0.02
Arapet	*Arabidopsis petraea*	1.33	0.04
Betnan	*Betula nana*	1.33	0.02
Carova	*Carex ovalis*	1.33	0.09

Abbreviation	*Species*	% Sites	Mean abundance
Equsp	*Equisetum sp*	1.33	0.07
Eriace	*Erigeron acer*	1.33	0.07
Junbuf	*Juncus bufonius*	1.33	0.05
Oxaace	*Oxalis acetosella*	1.33	0.05
Polavi	*Polygonum aviculare*	1.33	0.05
Saxriv	*Saxifraga rivularis*	1.33	0.04
Sildio	*Silene dioica*	1.33	0.05
Viobif	*Viola biflora*	1.33	0.03
Alninc	*Alnus incana*	1.00	0.01
Araalp	*Arabis alpina*	1.00	0.01
Athdis	*Athyrium distentifolium*	1.00	0.01
Calpur	*Calamagrostis purpurea*	1.00	0.03
Cretec	*Crepis tectorum*	1.00	0.05
Junfil	*Juncus filiformis*	1.00	0.02
Linbor	*Linnaea borealis*	1.00	0.03
Luzsyl	*Luzula sylvatica*	1.00	0.01
Parpal	*Parnassia palustris*	1.00	0.03
Sallan	*Salix lanata*	1.00	0.02
Salmyr	*Salix myrsinites*	1.00	0.02
Trieur	*Trientalis europea*	1.00	0.03
Astnor	*Astragalus norvegicus*	0.67	0.01
Filuli	*Filaginella uliginosa*	0.67	0.03
Galtet	*Galeopsis tetrahis*	0.67	0.01
Gerrob	*Geranium robertianum*	0.67	0.01
Gymdry	*Gymnocarpium dryopteris*	0.67	0.01
Harhyp	*Harrimanella hypnoides*	0.67	0.01
Juntrg	*Juncus triglumis*	0.67	0.03
Loipro	*Loiseleuria procumbens*	0.67	0.01
Luzcam	*Luzula campestris*	0.67	0.03
Luzmul	*Luzula multiflora*	0.67	0.01
Maibif	*Maianthemum bifolia*	0.67	0.01
Plamed	*Plantago media*	0.67	0.02
Salcap	*Salix caprea*	0.67	0.01
Stemed	*Stellaria media*	0.67	0.01
Tofpus	*Tofieldia pusilla*	0.67	0.01
Urtdio	*Urtica dioica*	0.67	0.01
Antvul	*Anthyllis vulneraria*	0.33	0.02
Carfla	*Carex flava*	0.33	0.02
Epilac	*Epilobium lactiflorum*	0.33	0.02
Eriuni	*Erigeron uniflorus*	0.33	0.00
Fesviv	*Festuca vivipara*	0.33	0.00
Galsax	*Galium saxatile*	0.33	0.00
Galver	*Galium verum*	0.33	0.01
Homalp	*Homogyne alpina*	0.33	0.00
Hupsel	*Huperzia selago*	0.33	0.00
Hypper	*Hypericum perforatum*	0.33	0.00
Junbig	*Juncus biglumis*	0.33	0.01
Luzpil	*Luzula pilosa*	0.33	0.00
Pedsce	*Pedicularis sceptrum-carolinum*	0.33	0.00
Petfri	*Petasites frigidus*	0.33	0.01
Pulver	*Pulsatilla vernalis*	0.33	0.00
Pyrmin	*Pyrola minor*	0.33	0.00

Abbreviation	*Species*	% Sites	Mean abundance
Ranpyg	*Ranunculus pygmaeus*	0.33	0.00
Saxniv	*Saxifraga nivalis*	0.33	0.00
Senvul	*Senecio vulgaris*	0.33	0.00
Thaalp	*Thalictrum alpinum*	0.33	0.00
Trices	*Trichophorum cespitosum*	0.33	0.01
Tusfar	*Tussilago farfara*	0.33	0.00
Viccra	*Vicia cracca*	0.33	0.00

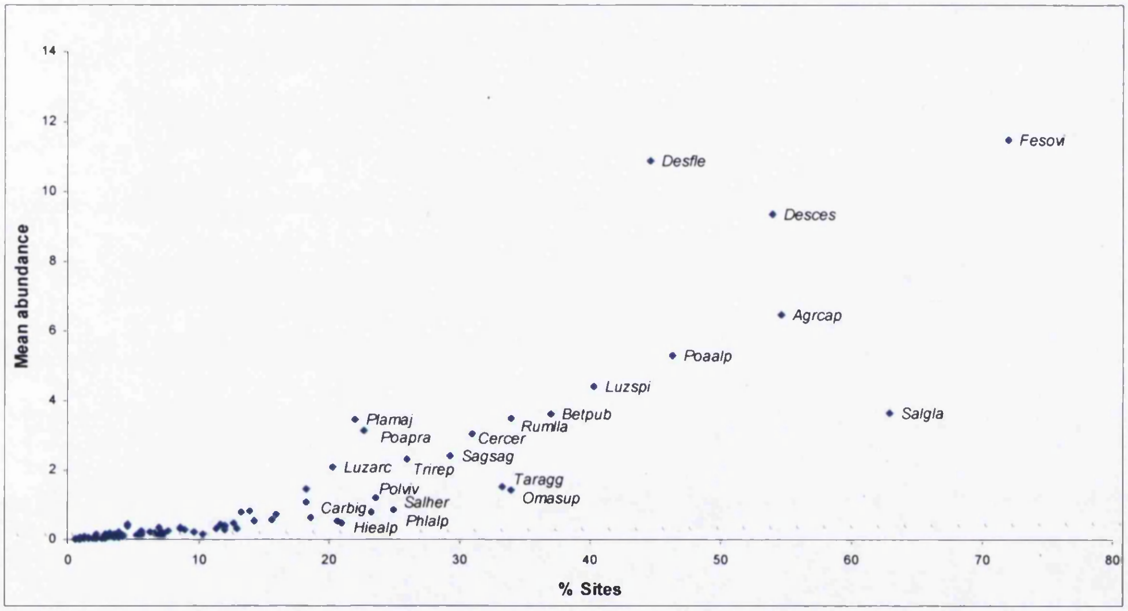


Figure 4-1. Mean abundance of roadside pioneer species and the percentage of sites on which each species occurs. Species occurring on ≥ 20% sites are labelled. Abbreviated species names are listed in full in Table 4.1.

Figure 4-1 illustrates the relationship between percentage frequency (the percentage of sites containing each species) and mean abundance (the mean relative frequency of that species per site), with species occurring on ≥ 20% sites labelled. The grass *Festuca ovina* has the highest frequency and mean abundance, occurring on 72% of roadside pioneer sites with a mean abundance on those sites of 11.5%. Other Poaceae occurring with high frequency are *Agrostis capillaris, Deschampsia cespitosa, Poa alpina, D. flexuosa, Phleum alpinum* and *Poa pratensis*, the first four being the only other species to have a mean abundance greater than 5%. The shrub *Salix glauca* has the second highest frequency of 63%, but with a relatively low mean abundance of 3.6%, and *S. herbacea* is also frequent at 25% with a low mean abundance of 0.85%. Seedlings of the pioneer tree species *Betula pubescens* occur on 37% of sites and have a mean abundance of 3.6%. Other species with a percentage frequency of ≥ 20% include members of the Asteraceae (*Omalotheca supina, Taraxacum* aggregate and *Hieracium alpinum*), Caryophyllaceae (*Cerastium cerastoides* and *Sagina saginoides*), Cyperaceae (*Carex bigelowii*), Fabaceae (*Trifolium repens*), Juncaceae (*Luzula spicata* and *L. arcuata*) , Plantaginaceae (*Plantago major*) and Polygonaceae (*Rumex acetosella* and *Polygonum viviparum*) families.

The roadside pioneer stage is therefore primarily herbaceous with a large number of grasses and forbs but it includes a small number of shrub species that attain comparable abundances. The majority of the most frequent species are perennials adapted for wind-dispersal but which can also propagate vegetatively. However, two of the most common species, *Agrostis capillaris* and *Rumex acetosella*, do not have specific dispersal adaptations (Peat and Fitter 2007).

4.3 Variability of roadside pioneer sites

The overall variability of roadside pioneer sites, measured by calculating the mean Sørensen distance between all sites, is 0.811 (± 0.004) with a standard deviation of 0.0377. Figure 4-2 shows that the frequency distribution of mean distances between sites is apparently normal and a D'Agostino-Pearson test for normality confirms this (*p* = 0.182, indicating that the null hypothesis of normally distributed data cannot be rejected).

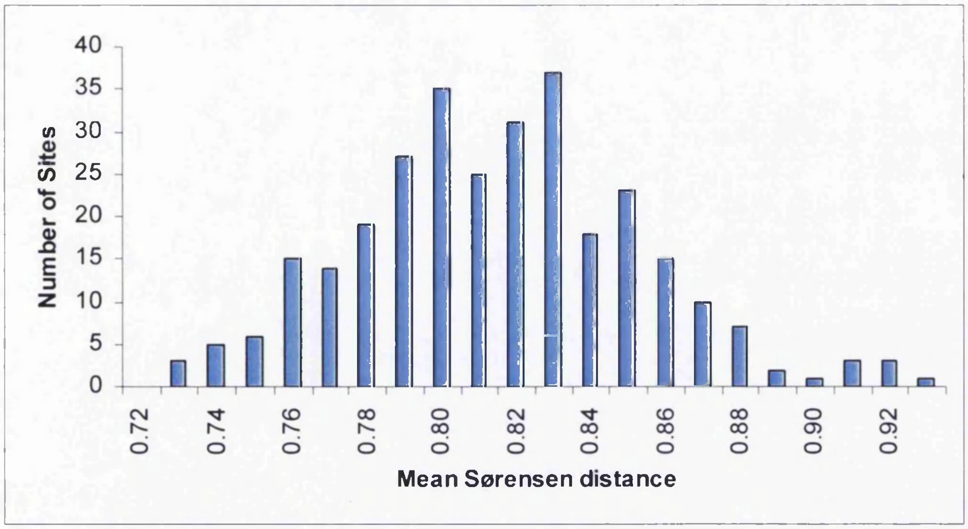


Figure 4-2. Frequency distribution of mean Sørensen distances between roadside pioneer sites.

Outlier analysis was carried out to discover which sites have the greatest mean distances from all other sites and this identified no sites with a mean distance of more than 3 standard deviations from the grand mean. Eight sites have mean Sørensen distances from all other sites ≥ 0.9 (2.3 standard deviations) and of these, three are sites from the highest altitude road sampled (Juvasshytte road at 1800, 1820 and 1840 m). These sites are therefore the most dissimilar to the majority of other sites in terms of species composition. These three sites all have an unusually high abundance (≥ 24%) of *Rancunculus glacialis*. Of the other sites identified, the highest point of the Fortundalen road at 1260 m has a particularly high abundance of *Poa alpina* and *Luzula arcuata* and a complete absence of *Festuca ovina* and *Deschampsia flexuosa*. Two sites on the Storevatnet road at 1320 and 1340 m similarly have high relative frequencies of single species: the 1320 m site has a high abundance of *Omalotheca supina* (28%) and the 1340 m site has the highest abundance of *D. alpina* (31%). Late-lying snow was present on ground adjacent to all of these six sites when recording took place during August 2005. Two lower altitude sites on the Vetlestølsdalen road also have mean Sørensen distances ≥ 0.9: the 400 m site is unusual in having a high relative frequency of *Betula pubescens* seedlings (62%) and *Lotus corniculatus* (13%); the 680 m site has a high relative frequency of *Salix glauca* (71%). An outlier analysis using Euclidean distance gave almost identical results, the only difference being the inclusion of the site at 1280 m on Storevatnet road instead of the 1260 m site on Fortundalen road as one of the most dissimilar eight sites. Thus sites with the highest mean distances from other sites have unusually high abundances of one or two species rather than rare species or unusual combinations of species and are considered to be extremes of the normal range rather than outliers.

4.4 Ordination of roadside pioneer sites

In order to investigate the relationship between sites in terms of their species composition, NMS ordination of roadside pioneer sites was carried out with all species included in the analysis. This resulted in stress levels of 27.5% (p = 0.0196) for two dimensions and 24.3% (p = 0.0196) for three dimensions. Although statistically significant, these stress levels are only 1% lower than the levels obtained for randomized data. Furthermore, the final instability for this ordination after 400 iterations was 0.021, a level which is considered too high to produce a reliable ordination (McCune and Grace 2002).

In order to search for a more stable solution, the 23 species which were only recorded at single sites were excluded from the analysis and the ordination was repeated. This resulted in lower stress levels of 16.3% for three dimensions and 21.5% for two dimensions (p = 0.0196) compared with the values of 25.2% and 34.0% respectively for randomized data. However, examination of the three-dimensional solution revealed an instability of 0.007 after 400 iterations, whereas the two-dimensional solution has a much lower instability of 0.00007 after 112 iterations. Although the stress level of 16% for a three-dimensional solution is lower than that of the two-dimensional solution, the reduction in stress is only 5%. Little benefit is gained, therefore, from using the higher dimension solution which is less stable. Furthermore, instability can be due to using a dimensionality that is too high for the data (McCune and Grace 2002). This must also be considered in the light of Clarke's (1993) caution against reliance on over-simplified guidelines regarding acceptable stress levels with a large sample size.

The ordination was assessed further by calculating coefficients of determination for the correlation between ordination distances and distances in the original n-dimensional space. The cumulative r^2 for the three-dimensional ordination is 0.77, while that for two-dimensional ordination is 0.67. The use of two dimensions rather than three therefore results in a loss of only 10% of the representation of the original distances between sites. As the two-dimensional ordination is considerably more stable, and results in an increase in stress of only 5% and a decrease of only 10% in the correlation between ordination distances and original distances, it is considered to be the most appropriate alternative for assessing the relationship between sites.

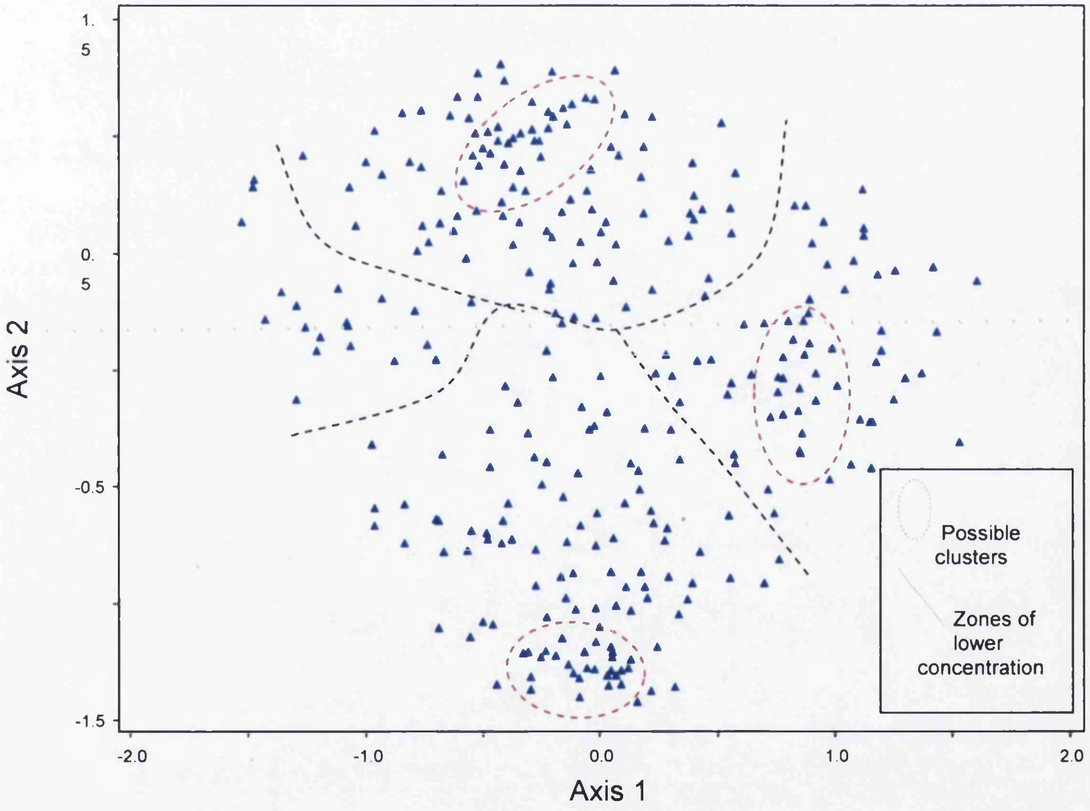


Figure 4-3. NMS ordination of roadside pioneer sites.

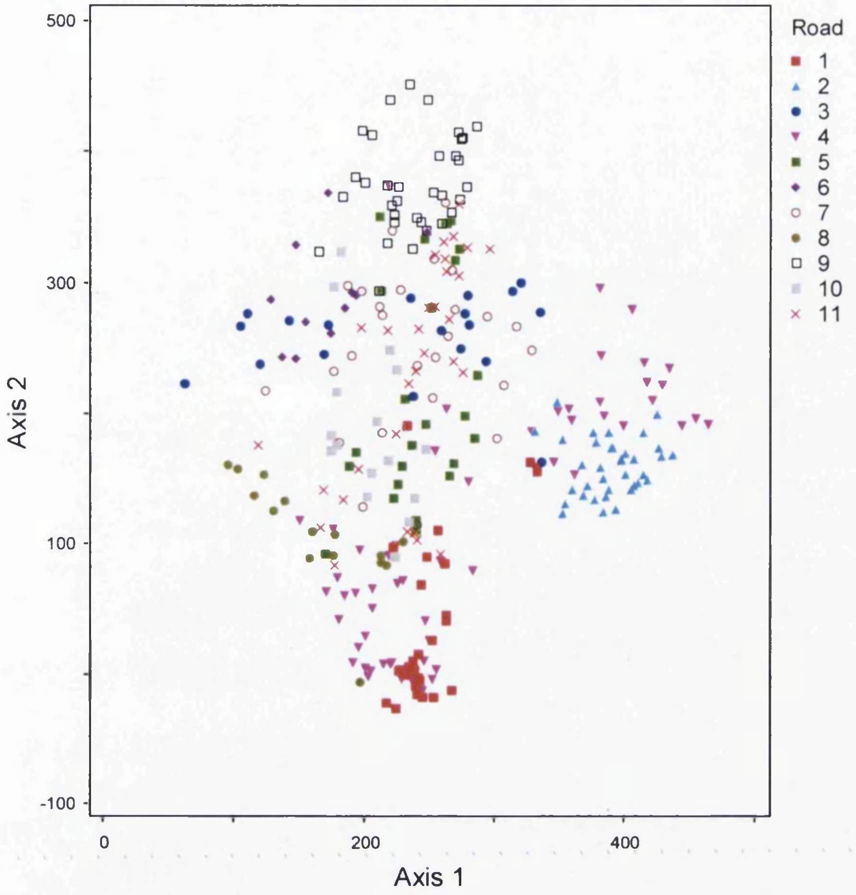
Examination of the two-dimensional ordination diagram (Figure 4-3) shows that the overall distribution of sites in ordination space is fairly even. However, certain areas of ordination space appear to have a lower concentration of sites (indicated by black dashed lines) whereas other areas appear to have a higher concentration of sites (indicated by red dashed lines). These features could indicate discontinuities and clusters, respectively, and possibly form the basis for division into groups. No sharp divisions between groups of sites are discernible at this stage.

In order to compare the NMS results with another ordination method, DCA was performed on all roadside pioneer sites. To facilitate comparison of Figures 4-4(a) which shows the results of DCA ordination and 4-4(b) which shows the NMS ordination, each road is colour-coded so that its relative position in each ordination diagram can be assessed. Only the first two axes of the DCA ordination are displayed as these show relatively high coefficients of determination with the original distance matrix (Table 4-2). Axis 3 of the DCA has a coefficient of determination of only 4%, which contributes little to the ordination as a whole. The two-dimensional DCA ordination diagram is also more directly comparable with the two-dimensional NMS ordination diagram.

Examination of Figure 4-4 reveals that both methods produce a similar pattern of site distribution in ordination space. For example, road 2 sites and a proportion of road 4 sites have high scores on axis 1, road 9 sites have high scores on axis 2, sites forming part of road 1 have low scores on axis 2 and sites belonging to roads 3, 6 and 8 have low scores on axis 1.

However, analysis of the coefficients of determination between distance in ordination space and that of the original distance matrix for the DCA ordination shows a lower correlation for the DCA ordination of 49% for axes 1 and 2 (53% for three axes) compared with 67% for the two-dimensional NMS ordination (Table 4-2). Thus, although both DCA and NMS ordinations show the same broad picture, the NMS ordination reflects the relationships between sites more accurately. In further analyses, therefore, the NMS ordination is used as the primary ordination method, with the DCA ordination as a back-up to ensure that the results are not an artefact of using one particular method.

a) DCA ordination



b) NMS ordination

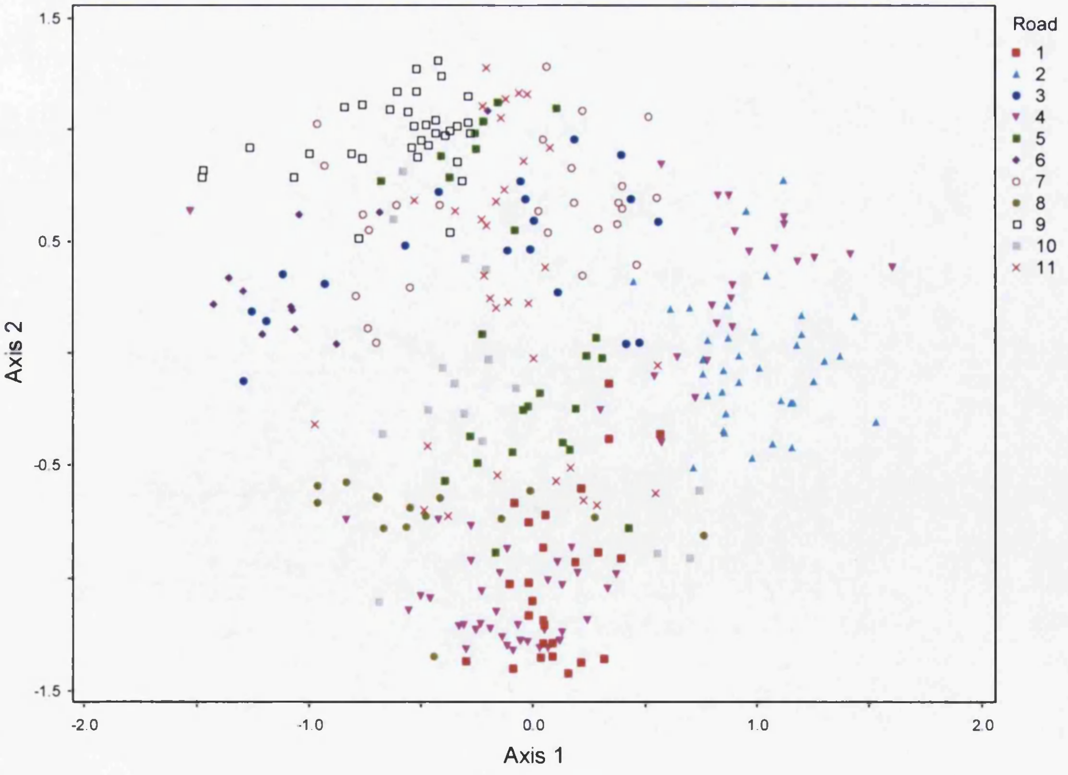


Figure 4-4. Comparison of (a) DCA and (b) NMS ordination of roadside pioneer sites.

Table 4-2. Coefficients of determination (r^2) for roadside pioneer ordination axes.

Axis	Incremental r2	Cumulative r2
NMS 1	0.399	0.399
NMS 2	0.273	0.672
DCA 1	0.289	0.289
DCA 2	0.197	0.486
DCA 3	0.042	0.529

4.5 Classification and indicator species analysis of roadside pioneer sites

Classification of the roadside pioneer sites was carried out to identify groups of sites with similar species composition. These groups are plotted onto the NMS ordination diagram to assess whether sites appear to form separate groups or are part of a continuum of variation. This is compared with the initial assessment of site distribution in ordination space shown in Figure 4-3. MRPP is used to assess the level of within-group agreement and between-group separation at each level of clustering, while indicator species analysis identifies the most important species within each group.

4.5.1 Assessment of the optimum level for roadside pioneer site classification

Cluster analysis of all roadside pioneer sites was performed (including all species recorded on more than one site) and the resulting dendrogram is included as Appendix I. The degree of chaining in the dendrogram was calculated as 0.5% which is well below the acceptable limit of 25% (McCune and Grace 2002).

In order to assess objectively the different levels of clustering, multiple response permutation procedure (MRPP) was carried out on the twelve highest levels to test the null hypothesis of no difference between groups. The test statistic (T) measures the amount of separation between groups, a more negative T-value indicating relatively greater separation. The agreement statistic (A) measures within-group homogeneity compared to random expectation and is independent of group size. The results are used to detect the point at which the greatest change in T and A values occurs when additional clusters are added. The high statistical significance (p < 0.001) for all levels of clustering levels is partly related to the large sample size. The ecological significance of the groups is not considered at this stage of the analysis.

Table 4-3 and Figure 4-5 show a sharp decrease in the T statistic (from -104 to -143), when the data are clustered into three groups rather than two, indicating that the three-group level produces the greatest degree of separation between clusters in terms of their species composition. There is also a considerable increase in the A statistic at this level from 0.094 to 0.182. At the four-group level, the T statistic becomes less negative and subsequent levels show relatively little change while there is a relatively small increase in the A statistic, a pattern which continues for additional clusters. After the three-group level, therefore, there is no specific level of clustering which produces a marked increase in separation between groups or agreement within groups, while the four-group level produces decreased separation and agreement.

Table 4-3 MRPP statistics for cluster analysis of roadside pioneer sites.

Number of Clusters	T	A	Observed δ	p
2	-104.342	0.094	0.735	< 0.001
3	-142.576	0.182	0.664	< 0.001
4	-133.341	0.208	0.642	< 0.001
5	-132.402	0.239	0.617	< 0.001
6	-128.808	0.261	0.599	< 0.001
7	-126.371	0.282	0.583	< 0.001
8	-121.994	0.294	0.573	< 0.001
9	-119.398	0.308	0.562	< 0.001
10	-117.368	0.321	0.551	< 0.001
11	-113.326	0.330	0.543	< 0.001
12	-110.159	0.339	0.536	< 0.001

Expected δ = 0.811

Figure 4-5. Change in MRPP statistics at each level of roadside pioneer cluster analysis.

The number of significant indicator species ($p \leq 0.05$) and the sum of significant indicator values were also calculated for each stage as an additional method of assessing appropriate levels of clustering (Dufrene and Legendre 1997). The greatest increase in the number of significant indicator species occurred at the three-, five- and ten-group levels and the greatest increase in the sum of significant indicator values occurred at the three-, six- and eleven-group levels (Figure 4-6).

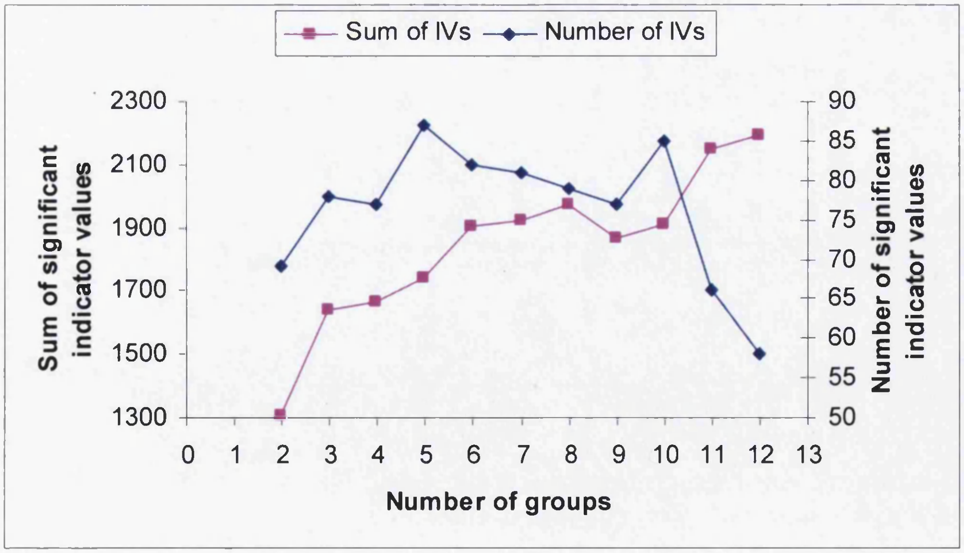


Figure 4-6. Indicator value (IV) statistics for each level of roadside pioneer cluster analysis.

The results therefore point to the three-group level as a consistently important level of clustering but suggest that further subdivision is more arbitrary. It was therefore decided to focus on the three-group level but to also examine six groups and nine groups in order to provide additional detail.

In the detailed analysis of the three-, six- and nine-group levels, each level of clustering is first superimposed onto the NMS diagram to assess visually the degree of separation between groups. Indicator species values are then listed for each group and compared across all groups with the aid of bar charts. For the three-group level, the patterns of abundance of individual indicator species with a value ≥ 25% are examined in more detail by superimposing individual species abundance values on the NMS. This approach enables further interpretation of indicator values and illustrates ways in which patterns of indicator species distributions can vary. An indicator value of 25% is used as the cut-off point for key species, as it signifies a species which is present at a large number of sites within that group and at a high relative abundance compared with other groups. As the group indicator value is the product of these two measurements, a group indicator value greater than 25%, for example, means that a species has a proportional abundance of at least 50% in a particular group and is present on at least 50% of sites within that group.

4.5.2 Three roadside pioneer groups

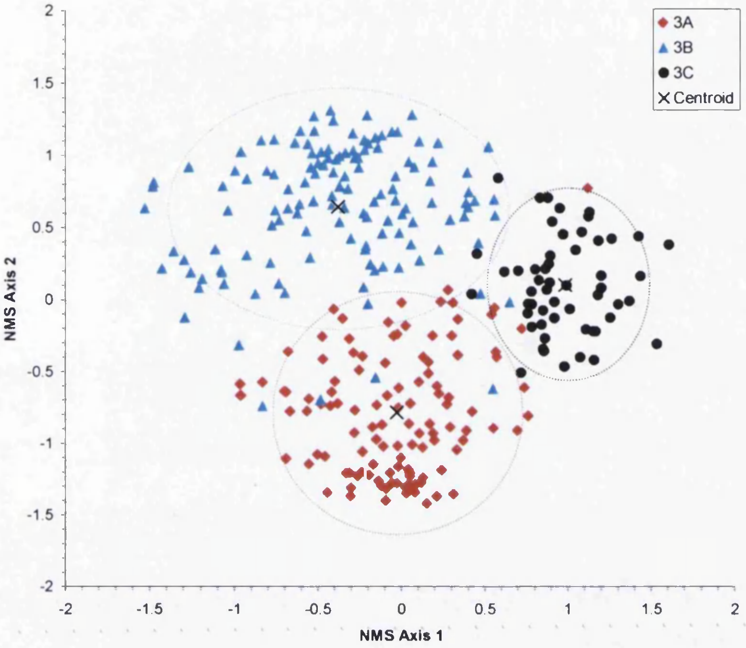


Figure 4-7. NMS ordination of roadside pioneer sites with three colour-coded cluster analysis groups superimposed. Dashed ellipses indicate ±2 standard deviations from each group centroid.

As shown in Figure 4-7, groups 3A and 3B are separated along axis 2 with only a small amount of overlap, while group 3C is concentrated towards the higher end of axis 1 and again is well separated from the other two groups. These groupings are along the lines predicted from visually assessing the original NMS ordination diagram (Figure 4-3). The number of sites, mean within-group distance (mean Sørensen distance) and number of significant indicator species ($p \leq 0.05$) for each group are listed in Table 4-4.

Table 4-4. Descriptive statistics for three roadside pioneer cluster analysis groups.

Group	**n**	**Mean within-group distance**	**No. of significant indicator spp.**
3A	115	0.678	38
3B	131	0.723	26
3C	54	0.448	14

These analyses confirm the degree of clustering anticipated from examination of the NMS ordination diagram. Group 3C, the smallest group, is the most tightly clustered (mean within-group distance 0.45) and group 3B (the largest group) is the most diffuse (mean within-group distance 0.72). As an additional measure, mean between-group dissimilarities are given in Table 4-5 which enable calculation of a value quantifying the discreteness of a group in terms of the ratio between mean between-group distance and mean within-group distance. This Discreteness Index (DI) confirms that group 3C is the most discrete with a DI of 1.94, followed by group 3A with a DI of 1.29 and group 3B with a DI of 1.23.

Table 4-5. Mean between- and within-group distances and the Discreteness Index (DI) for the three roadside pioneer cluster analysis groups.

	Mean b-g distance	**Mean w-g distance**	**DI**
3A	0.876	0.678	1.292
3B	0.890	0.723	1.231
3C	0.870	0.448	1.942

4.5.2.1 Indicator species analysis of three roadside pioneer groups

Statistically significant indicator species ($p \leq 0.05$) for each group are listed in Table 4-6. Bar charts based on Table 4-6 are also included to illustrate the indicator values for species within each group (Figures 4-8 to 4-10).

Table 4-6. Significant indicator values for the three roadside pioneer groups.

	Indicator Value (%)			
Species	**Group 3A**	**Group 3B**	**Group 3C**	***p***
Desces	**86**	1	2	0.001
Trirep	**60**	0	0	0.001
Plamaj	**57**	0	0	0.001
Agrcap	**43**	2	30	0.001
Ranacr	**41**	0	0	0.001
Taragg	**34**	2	0	0.001
Poapra	**34**	8	0	0.001
Achmil	**19**	0	0	0.001
Sagsag	**19**	16	0	0.027
Verser	**17**	0	0	0.001
Cerfon	**16**	0	0	0.001
Chasua	**16**	0	0	0.001
Fraves	**15**	0	0	0.001
Chaang	**15**	1	0	0.002
Tripra	**14**	0	0	0.001

	Indicator Value (%)			
Species	Group 3A	Group 3B	Group 3C	*p*
Potcra	**12**	0	0	0.004
Veroff	**11**	0	0	0.001
Stegra	**11**	0	0	0.004
Pruvul	**10**	0	0	0.001
Eupagg	**10**	0	0	0.003
Sagpro	**9**	0	0	0.004
Rubida	**8**	0	0	0.001
Stenem	**8**	0	0	0.007
Hypmac	**7**	0	0	0.006
Pinsyl	**7**	0	0	0.021
Viopal	**7**	0	0	0.011
Crecap	**6**	0	0	0.004
Alcglo	**6**	0	0	0.008
Gersyl	**6**	0	0	0.01
Vioriv	**6**	0	0	0.012
Vacvit	**6**	0	0	0.034
Equsyl	**4**	0	0	0.029
Eriace	**4**	0	0	0.028
Viobif	**4**	0	0	0.031
Junbuf	**4**	0	0	0.034
Polavi	**4**	0	0	0.043
Oxaace	**4**	0	0	0.045
Fesovi	4	**70**	13	0.001
Luzspi	2	**55**	2	0.001
Poaalp	6	**54**	1	0.001
Cercer	1	**52**	0	0.001
Desalp	0	**41**	0	0.001
Ceralp	0	**38**	0	0.001
Trispi	0	**32**	0	0.001
Rumlla	10	**26**	2	0.003
Luzarc	1	**24**	2	0.001
Polviv	8	**22**	0	0.002
Phlalp	5	**19**	2	0.007
Silaca	0	**19**	0	0.001
Oxydig	0	**17**	0	0.004
Antdio	1	**17**	2	0.001
Rumace	1	**16**	1	0.002
Saxste	2	**13**	1	0.017
Sibpro	0	**11**	3	0.007
Camrot	3	**10**	0	0.045
Epiana	0	**10**	1	0.012
Rangla	0	**10**	0	0.002
Saxces	0	**9**	0	0.004
Carbel	0	**8**	0	0.005
Visalp	0	**8**	0	0.013
Saxcer	0	**7**	0	0.014
Saualp	0	**5**	0	0.02
Desfle	4	1	**87**	0.001
Salgla	14	9	**50**	0.001
Betpub	8	0	**49**	0.001
Empher	0	0	**41**	0.001

Species	Indicator Value (%)			*p*
	Group 3A	Group 3B	Group 3C	
Vacmyr	1	0	**28**	0.001
Hiealp	1	6	**26**	0.001
Juntrf	0	5	**21**	0.001
Salher	0	18	**21**	0.001
Phycae	0	0	**19**	0.001
Carbig	1	13	**14**	0.045
Vaculi	0	0	**12**	0.001
Calvul	0	0	**8**	0.006
Harhyp	0	0	**4**	0.033
Loipro	0	0	**4**	0.043

Group 3A has seven species with an indicator value greater than 25%, the most important being *Deschampsia cespitosa* (85%), followed by *Trifolium repens* (60%) and *Plantago major* (57%) (Figure 4-8). There are a further 13 species with indicator values ≥ 10%. It should be noted that these are all species commonly found at relatively low altitudes associated with agricultural activity or disturbed woodland sites. Only three of these species have appreciable indicator values in either of the other two groups: *Agrostis capillaris* has an indicator value of 30% in group 3C compared to 43% in group 3A; *Sagina saginoides* has an indicator value of 16% in group 3B compared to 19% in group 3A; and *Taraxacum* agg. has an indicator value of 8% in group 3B compared to 34% in group 3A. Fourteen of the indicators are not found in either of the other two groups and the remaining species have indicator values of 1 or 2% outside of group 3A.

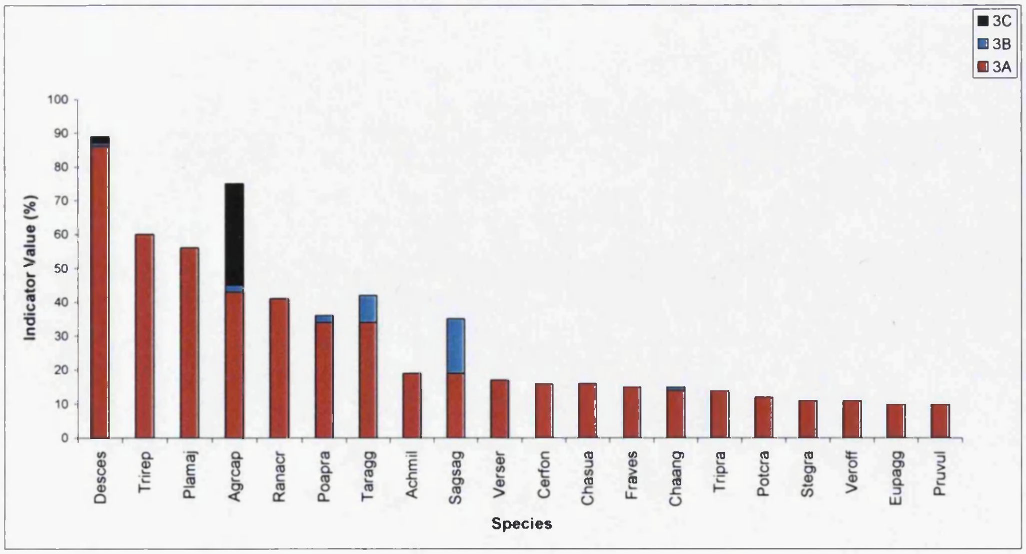


Figure 4-8. Group 3A indicator species (with values ≥ 10%) showing indicator values across the three roadside pioneer cluster analysis groups.

Group 3B has a total of eight species with indicator values ≥ 25% and a further 12 species with indicator values ≥ 10% (Figure 4-9). The majority of these are species typically found on disturbed ground at relatively high altitudes. The most important indicator for this group is *Festuca ovina* (70%), with *Luzula spicata* (55%), *Poa alpina* (54%) and *Cerastium cerastoides* (52%) also having values above 50%. As indicated in Table 4-6 and Figure 4-9, only six species are completely absent from the other two groups but of these almost all species have a very low indicator value (< 5%) within the other groups.

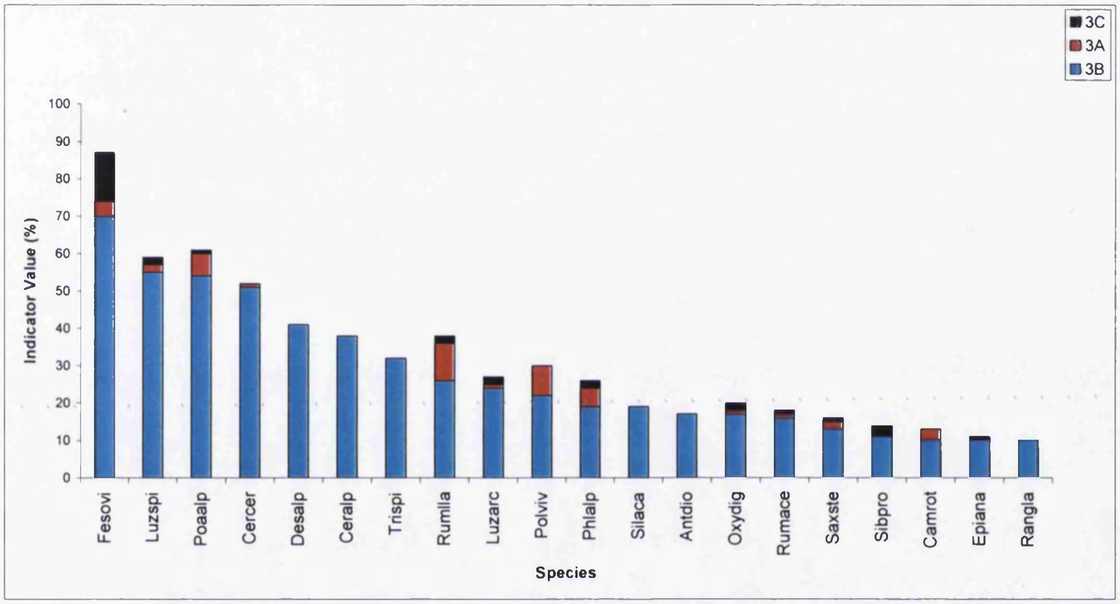


Figure 4-9. Group 3B indicator species (with values ≥ 10%) showing indicator values across the three roadside pioneer cluster analysis groups.

Group 3C has six species with an indicator value ≥ 25% and a further five ≥ 10% (Figure 4-10). *Deschampsia flexuosa* (87%), *Salix glauca* (50%) and *Betula pubescens* (49%) are the most important indicators and nine of the indicator species are shrubs, all species which are more usually associated with later stages of succession. These include *Empetrum hermaphroditum, Vaccinium myrtillus* and *Phyllodoce caerulea,* which are either absent from or have an indicator value of 1% in another group. Five species have indicator values greater than 5% in one or both of the other two groups: *Salix glauca, Betula pubescens, Hieracium alpinum, S. herbacea* and *Carex bigelowii.*

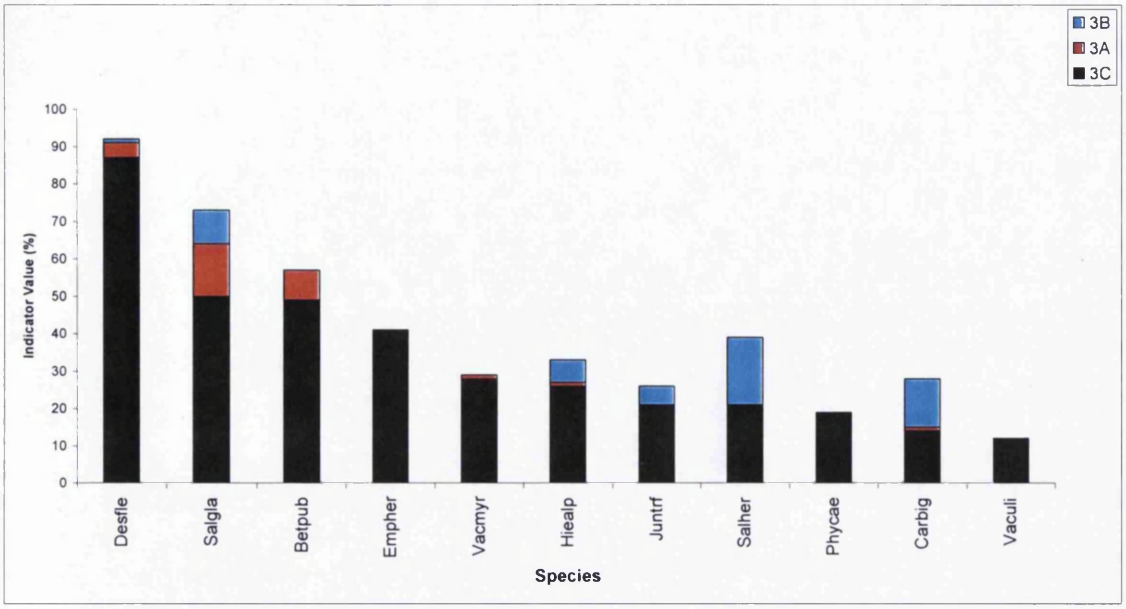


Figure 4-10. Group 3C indicator species (with values ≥ 10%) showing indicator values across the three roadside pioneer cluster analysis groups.

At this level of clustering, all but one species (*Omalotheca supina*) which occur on at least 30% of roadside pioneer sites (Table 4-1) have an indicator value of ≥ 25%. The most important indicators therefore include widespread species.

Scores calculated for species by weighted averaging are plotted onto the NMS ordination diagram in Figure 4-11 and indicator species with a value ≥ 25% are labelled. Envelopes enclosing the indicator species for each group have been superimposed onto the diagram to show that three clear groups are defined by the position of these indicators. The grouping of indicator species in this way provides further evidence to support the existence of three unambiguous groups of roadside pioneer sites.

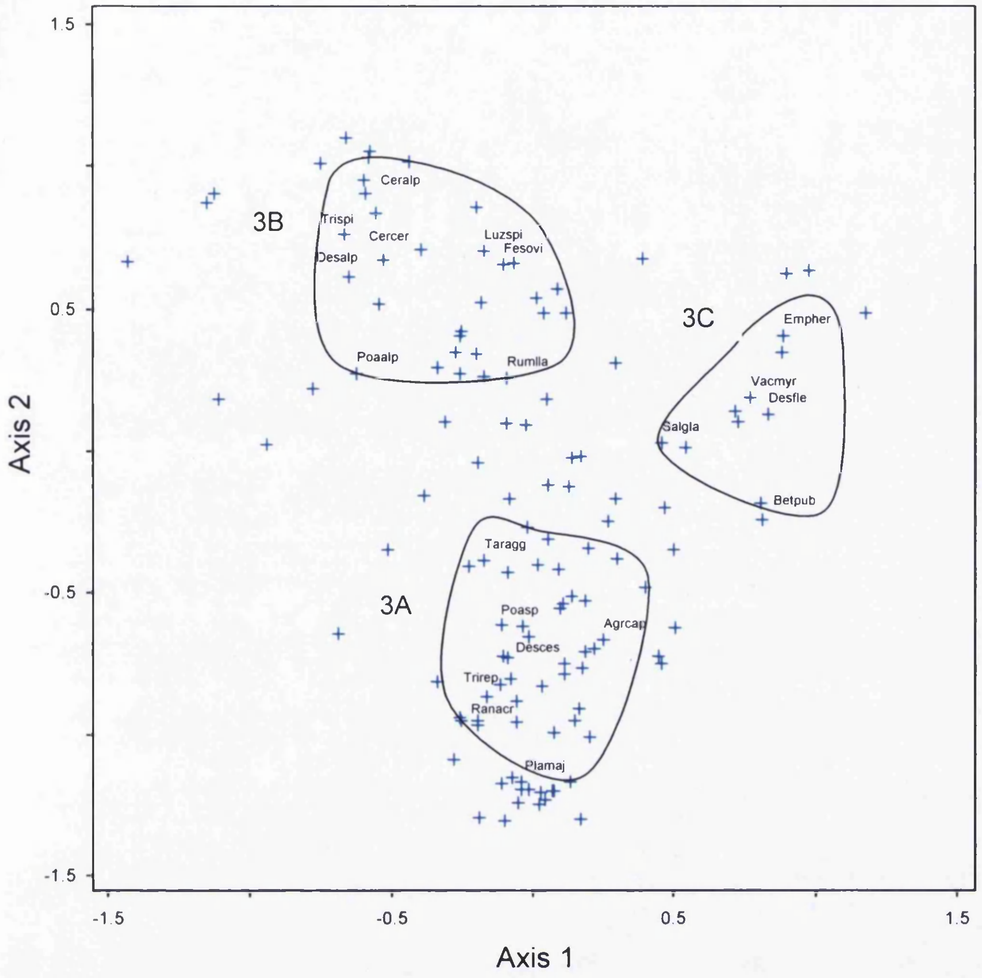


Figure 4-11. NMS ordination of roadside pioneer sites at the three-group level showing weighted scores for indicator species with an indicator value of ≥ 25% . Envelopes indicate the three separate groups.

The positions of the key indicator species in relation to each of the three groups are clear, with species that are indicators for more than one group being placed between those groups. For example, *Salix glauca*, a species which is present at 63% of all roadside pioneer sites, has a high indicator value in group 3C (50%) but also occurs in group 3A (14%) and group 3B (9%). In contrast, species which are indicators of only one group are placed at a greater distance from the other two groups e.g. *Plantago major* in group 3A and *Cerastium alpinum* in group 3B.

4.5.2.2 Relative abundance of indicator species within the three roadside pioneer groups

Examination of variability in the relative abundance of indicator species for the three cluster analysis groups shows whether sharp or gradual changes in relative abundance occur at the boundaries between groups in ordination space. This approach also illustrates whether indicator species within a group have similar patterns of variability and helps to show which levels of indicator value are most useful. In order to achieve this, NMS ordination diagrams are presented with the three groups colour-coded and the relative abundances of individual species represented by the size of the symbol for each site (Figures 4-12 to 4-32).

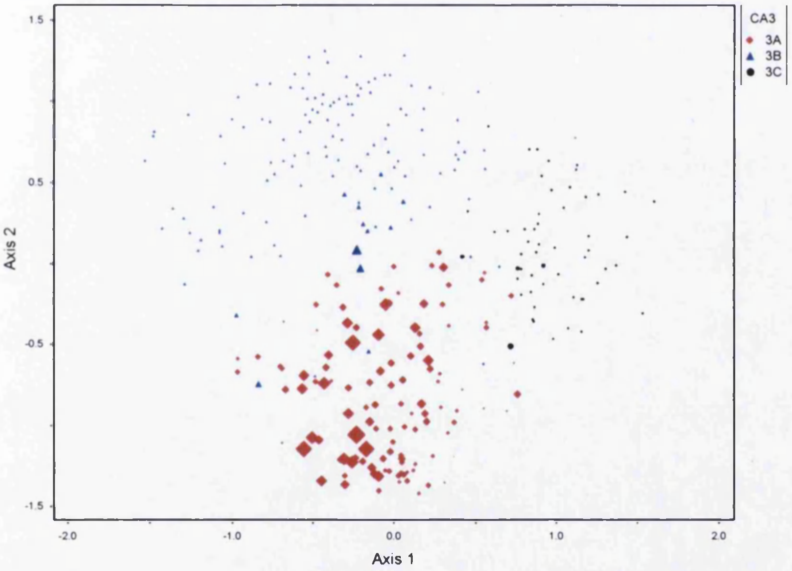


Figure 4-12. Relative abundance of *Deschampsia cespitosa.*

Deschampsia cespitosa is the species with the highest indicator value within group 3A (86%). As illustrated in Figure 4-12, it is present in a high percentage of sites within that group (relative frequency, 97%) and its mean abundance within that group is also high compared to other groups (89%). Its abundance shows a tendency to decrease towards group borders. A similar pattern is shown by *Trifolium repens* in Figure 4-13 (indicator value, 60%; relative abundance, 96%; relative frequency, 63%).

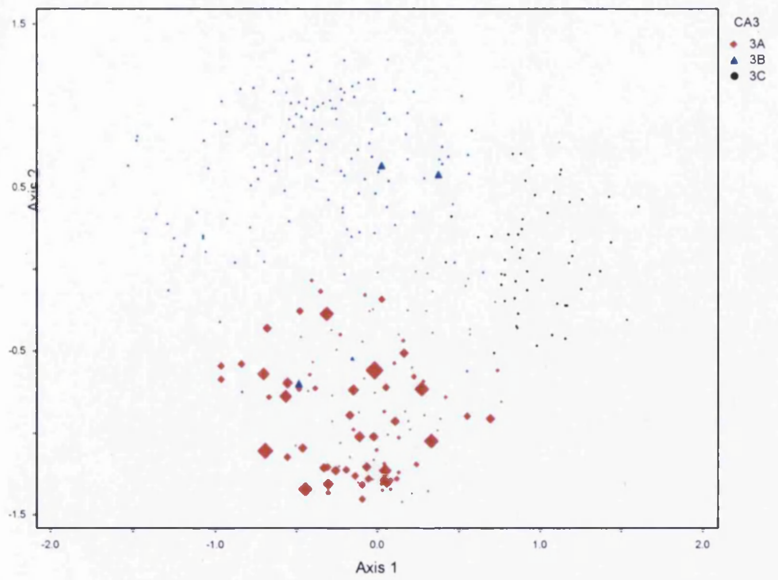


Figure 4-13. Relative abundance of *Trifolium repens*.

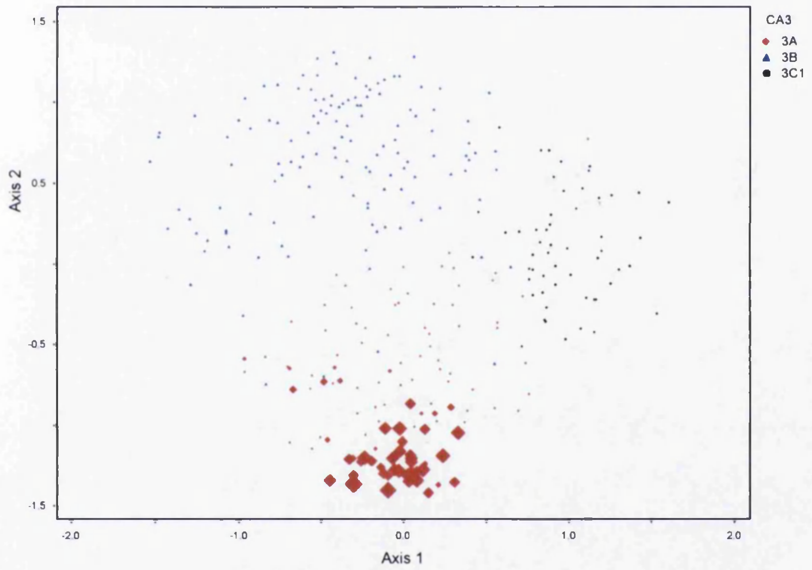


Figure 4-14. Relative abundance of *Plantago major*.

In contrast, *Plantago major* (Figure 4-14), with an indicator value of 56% has a relative abundance of 100% but is only present in 56% of group 3A sites. As these sites are clustered together, this may indicate the existence of a sub-group when further levels of clustering are considered. A similar pattern but with a smaller subset of sites is exhibited by *Ranunculus acris* (Figure 4-15). Again, this may be indicative of a sub-group. This pattern is typical of the majority of species with indicator values below 25%. These indicators are useful in supporting the need to examine more clusters than the three-group level, illustrating the nested nature of cluster analysis, and emphasising the value of ordination as a supplement to classification.

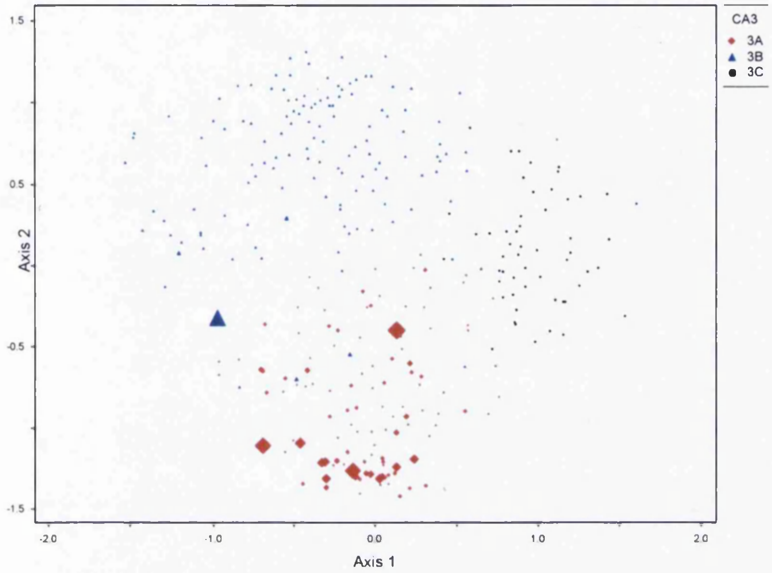


Figure 4-15. Relative abundance of *Ranunculus acris.*

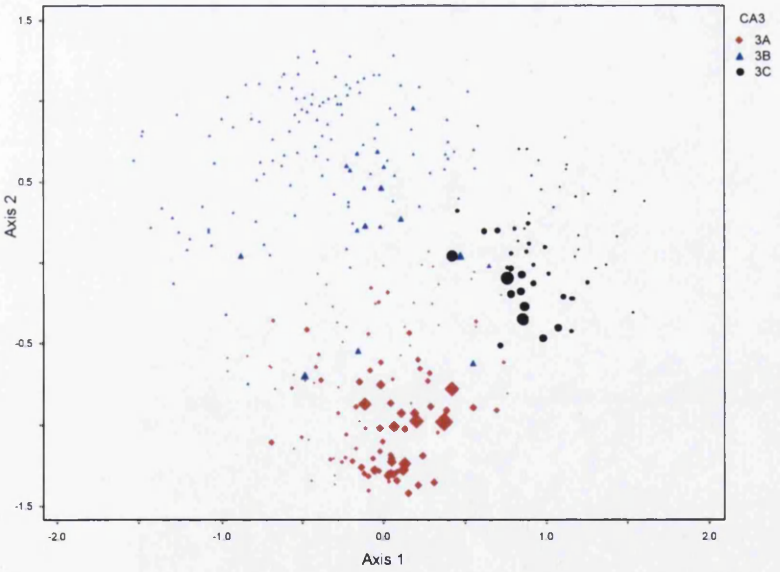


Figure 4-16. Relative abundance of *Agrostis capillaris.*

The next three species show less clear fidelity to one particular group and, although having higher indicator values for group 3A than the other two groups, their values within one of the other two groups reflect their intermediate nature.

Figure 4-16 clearly illustrates that *Agrostis capillaris* with an indicator value of 43% is present at a high percentage of sites (83%) within group 3A but its relative abundance is only 52% reflecting its occurrence in group 3C where it has an indicator value of 30%. Species are also found which, although significant indicators of a particular group, have values which are only slightly lower within another group e.g. *Sagina saginoides* which has a value of 19% in group 3A and 16% in group 3B. The usefulness of such a species in characterising a single group is questionable but the absence of such species from a group or groups, in this case group 3C, may be important.

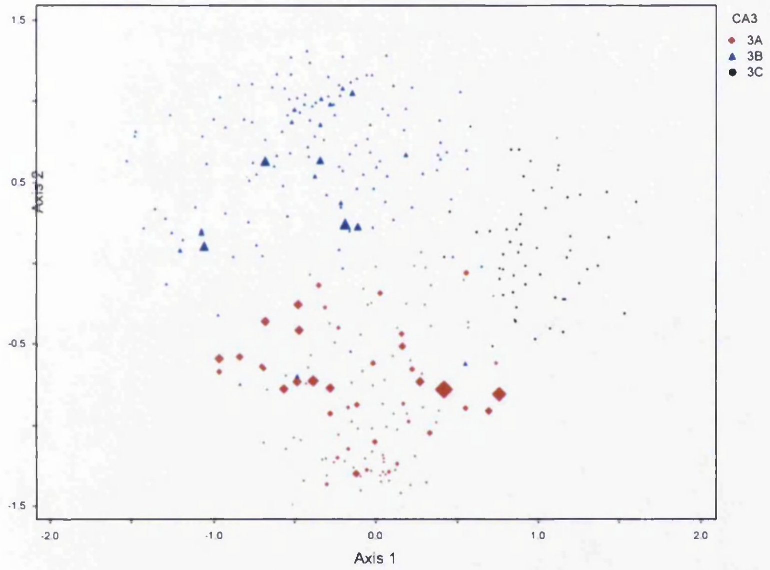


Figure 4-17. Relative abundance of *Taraxacum* agg.

Figure 4-17 shows the occurrence of *Taraxacum* agg. in group 3A (indicator value 34%) where it is present at 47% of sites and has a relative abundance of 73%, and in group 3B, where it is present at 31% of sites and has a relative abundance of only 25%. Its distribution in group 3A is concentrated on a different subset of sites from *P. major* and *R. acris*. The *Taraxacum* aggregate includes many similar microspecies which are impossible to distinguish in the field. It is therefore possible that the species recorded in groups 3A and 3B are different microspecies which occur in contrasting habitats. *Taraxacum* is virtually absent from group 3C. *Poa pratensis* (figure 4-18) also occurs only in these two groups but with an indicator value of only 2% in group 3B compared with 34% in group 3A.

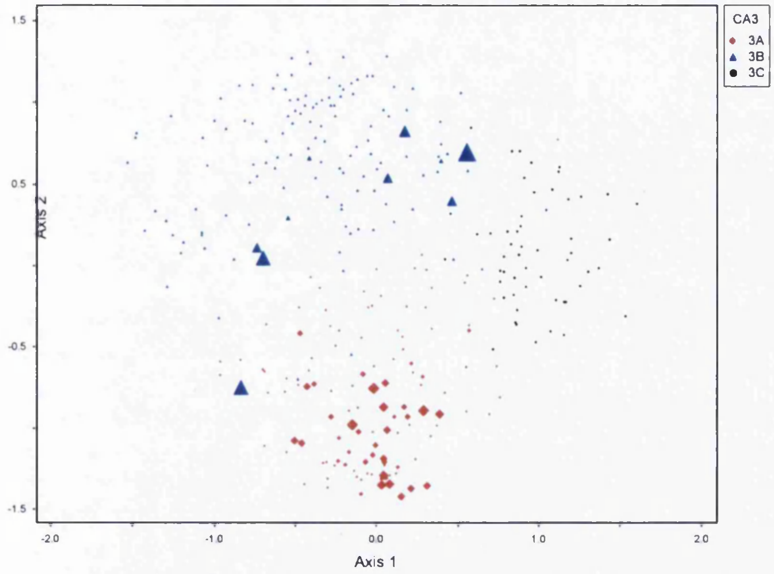


Figure 4-18. Relative abundance of *Poa pratensis*.

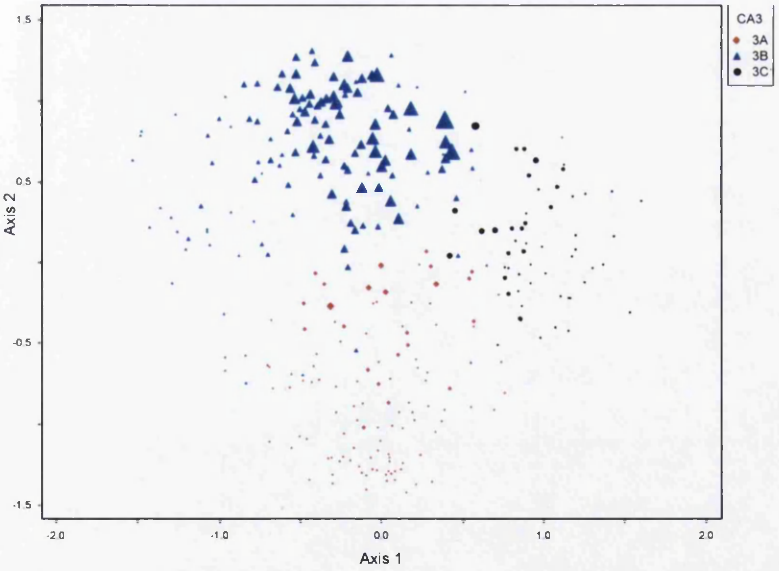


Figure 4-19. Relative abundance of *Festuca ovina*.

Festuca ovina (Figure 4-19) is the species recorded on the highest number (72%) of pioneer roadside sites and has the highest mean relative frequency (11.5%) of all species recorded. Within group 3B, it occurs on 93% of sites and its mean abundance compared to other groups is 75%, giving an indicator value of 70%. This compares with a mean relative abundance of 8% in group 3A and 16% in group 3C, and a relative frequency of 44% in group 3A and 80% in group 3C. The high abundance on sites in group 3B, compared to the other two groups, is clearly illustrated in Figure 4-19. It also appears that the highest abundance of *F. ovina* occurs in a subset of this group towards the centre of axis 1, perhaps indicating further division of this group with higher numbers of clustering. Its relative abundance in group 3B appears to increase as site scores on axis 1 increase and decrease sharply at the border with group 3C.

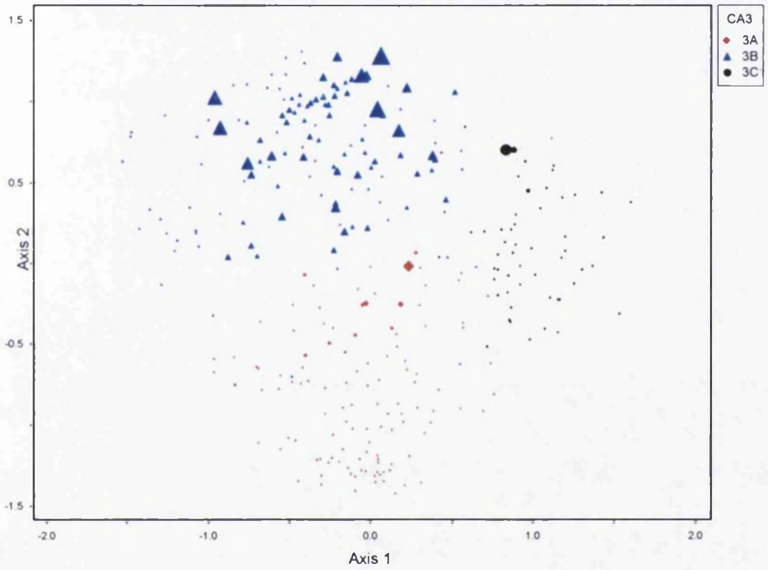


Figure 4-20. Relative abundance of *Luzula spicata*.

Figure 4-20 shows the distribution of *Luzula spicata*, primarily within group 3B where it has an indicator value of 55%, the product of a relative abundance of 80% and a relative frequency of 69%. Its highest levels of abundance do not appear to be concentrated in any one area of group 3B.

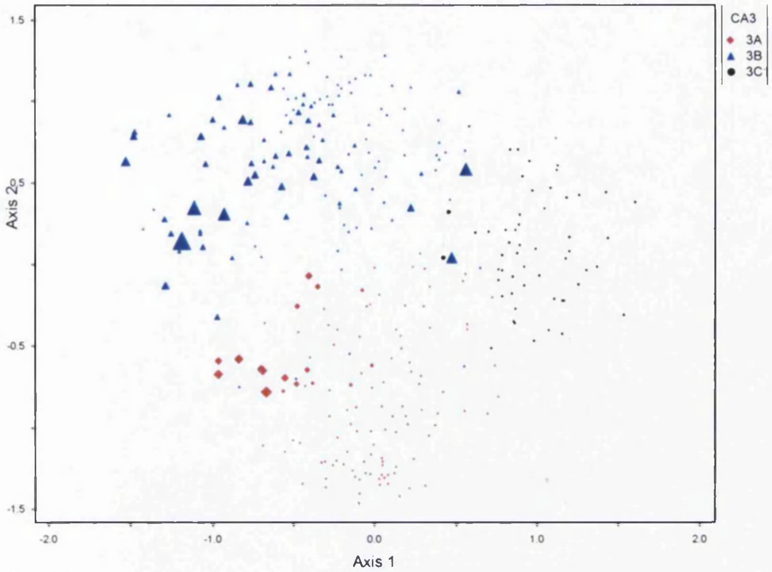


Figure 4-21. Relative abundance of *Poa alpina*.

Poa alpina (Figure 4-21), which occurs on 46% of all roadside pioneer sites and has a mean abundance of 5%, is present on 77% of sites in group 3B and has a relative abundance of 69% within this group. It was recorded on 24% and 19% of sites in groups 3A and 3C, with a mean abundance of 26% and 5% respectively. It is also interesting to note that the highest abundance of *P. alpina* on sites within group 3B appears to occur where the abundance of *F. ovina* is lowest (Figure 4-19). Its presence in group 3A sites is concentrated in one area where *P. pratensis* was absent or has low relative abundance.

The two Cerastium species (Figures 4-22 and 4-23), *C. cerastoides* (indicator value 52%) and *C. alpinum* (indicator value 38%) are both examples of species which appear to occur in a subset of sites within group 3B. Their relative abundances in this group are similar at 92% and 97% respectively. However, *C cerastoides* is present in a greater number of sites than *C. alpinum* (56% as opposed to 39%). The sites with a higher relative abundance of *C. alpinum* appear to occur at a higher position on axis 2 than those where *C. cerastoides* is most abundant.

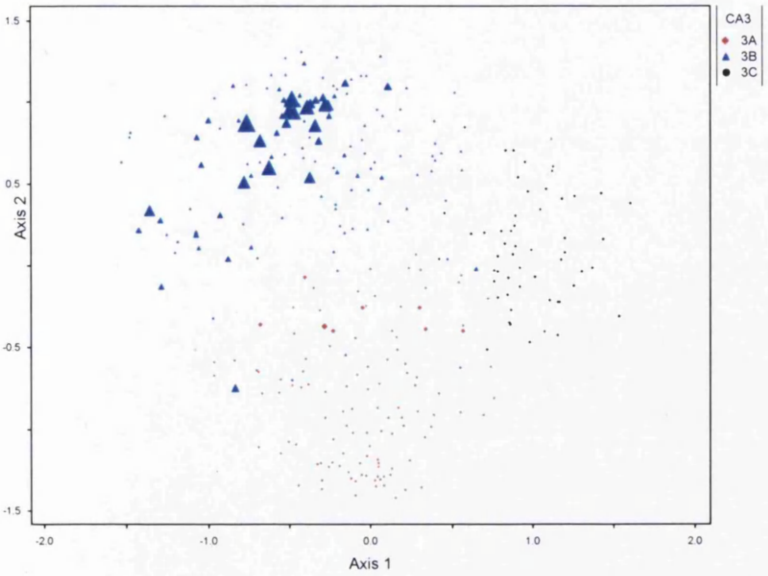


Figure 4-22. Relative abundance of *Cerastium cerastoides*.

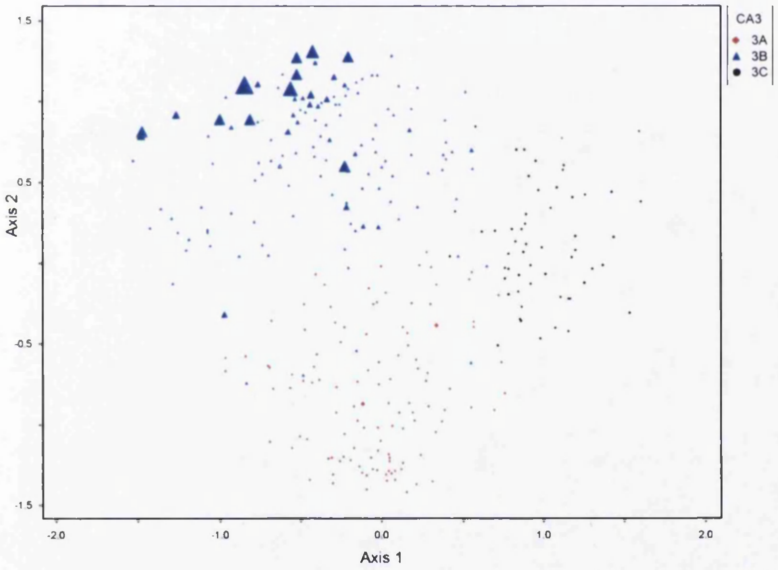


Figure 4-23. Relative abundance of *Cerastium alpinum*.

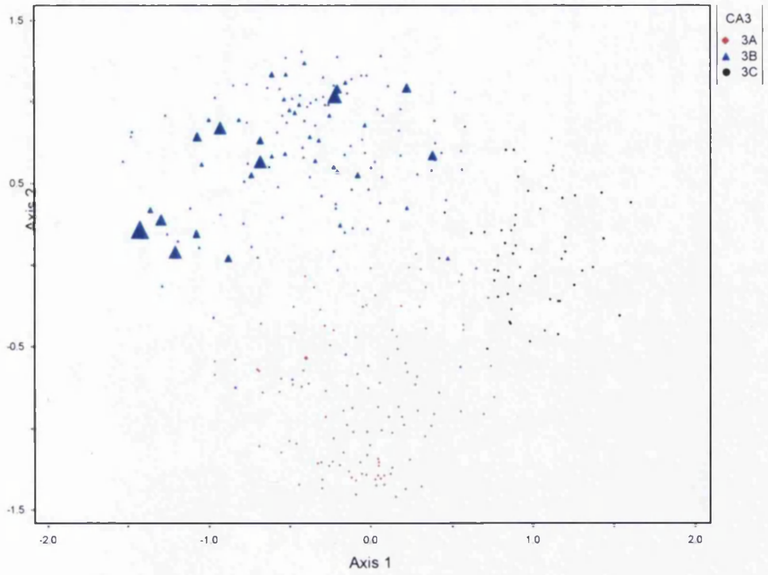


Figure 4-24. Relative abundance of *Deschampsia alpina.*

Deschampsia alpina (Figure 4-24) has an indicator value 41% for group 3B, is virtually absent from the other two groups and it therefore has a relative abundance of 99% within this group. It is present at 41% of sites in group 3B and Figure 4-24 shows that its abundance is not concentrated in any particular subsection of sites.

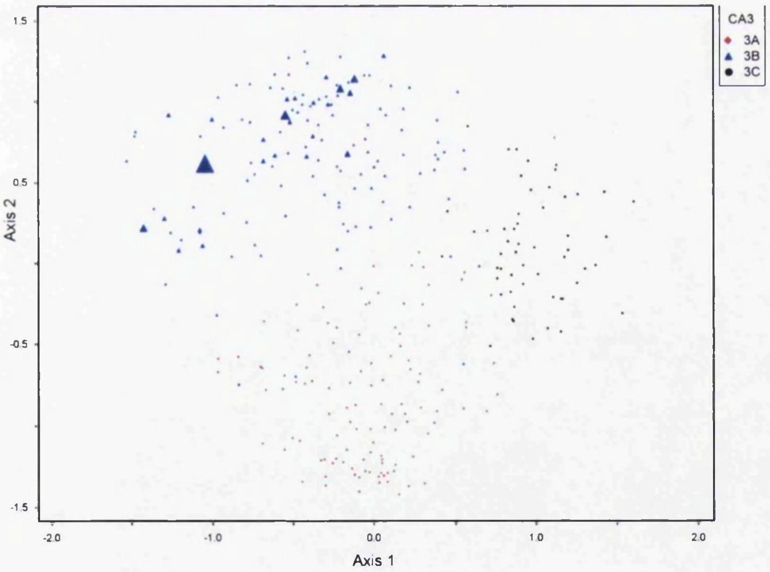


Figure 4-25. Relative abundance of *Trisetum spicatum.*

Trisetum spicatum has an indicator value of 32% and again is completely absent from the other two groups of sites, having 100% relative abundance within group 3B. It is recorded at 32% of sites within this group and its distribution does not appear to be concentrated in any one area (Figure 4-25).

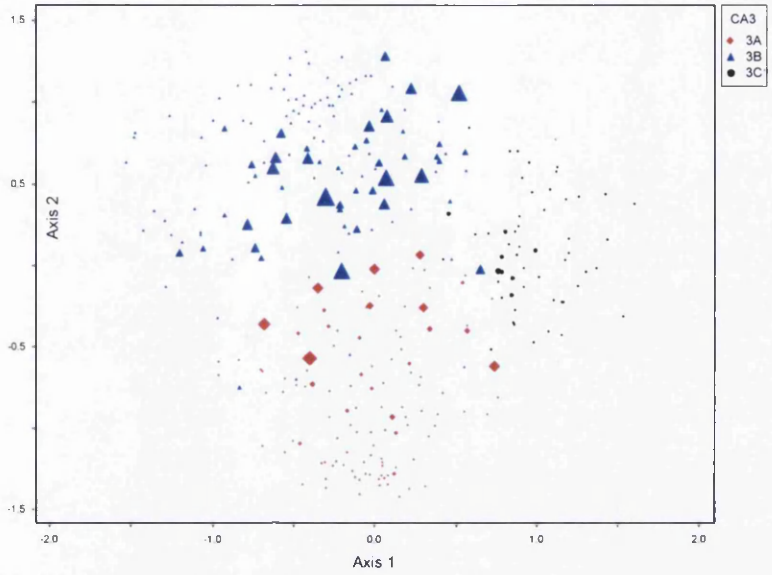


Figure 4-26. Relative abundance of *Rumex acetosella.*

Rumex acetosella (indicator value 26%) is the indicator species for group 3B, which has the highest occurrence in group 3A. Its relative frequency is 34% in group 3A and 40% in group 3B, whereas its relative abundance in group 3A is only 28%, compared to 64% in group 3B. Its distribution overlaps the borders between the three groups and its abundance is higher in the group 3B sites, which are closest to the other two groups in the ordination diagram (Figure 4-26).

Figure 4-27 shows the relative abundance of *Deschampsia flexuosa,* the species with the highest indicator value in group 3C (87%). Although this species occurs in the other two groups, particularly in sites on the borders between groups in the NMS diagram, (44% of group 3A and 22% of group 3B), its relative abundance in these two groups is only 8% and 5% respectively. This is another widespread species occurring on 45% of all roadside pioneer sites, but its relative abundance is considerably higher in group 3C.

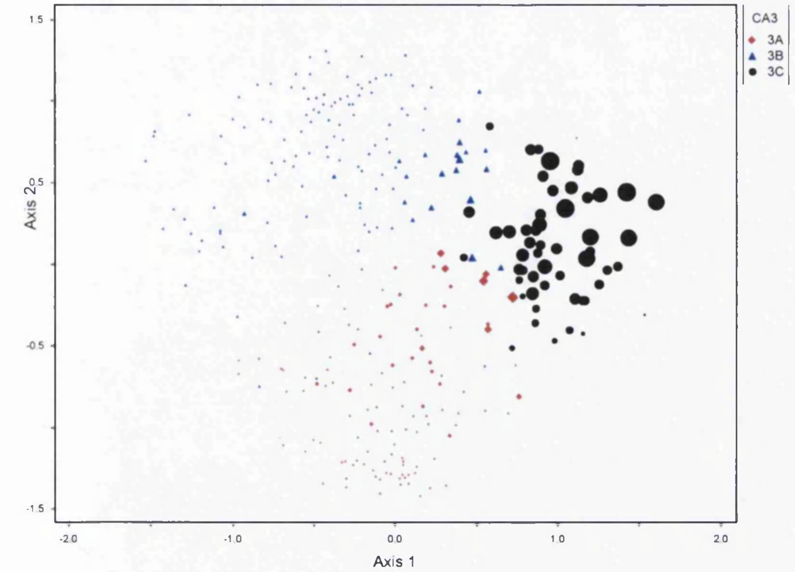


Figure 4-27. Relative abundance of *Deschampsia flexuosa.*

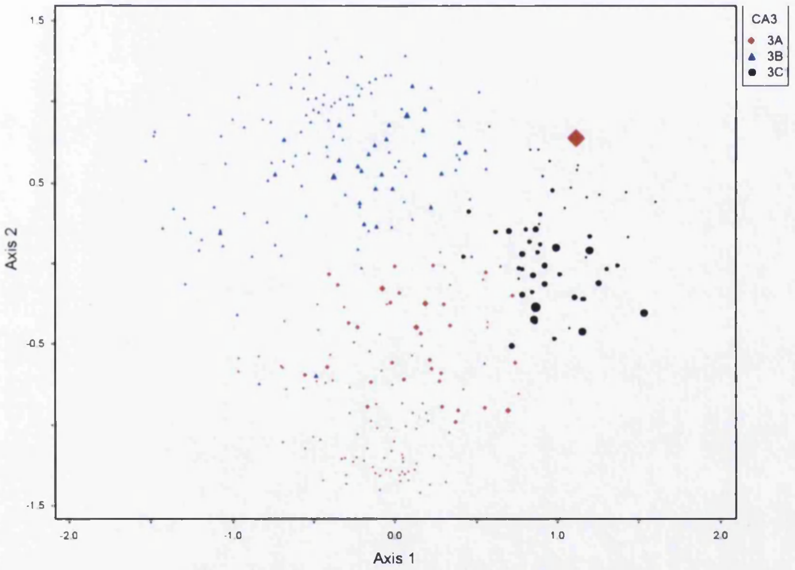


Figure 4-28. Relative abundance of *Salix glauca.*

Salix glauca (Figure 4-28) is a very widespread species, second only to *Festuca ovina* and recorded on 63% of roadside pioneer sites (81% of sites in group 3C, 58% of sites in group 3A and 60% of sites in group 3B). However, its mean abundance across all sites is only 4% and it is here that the difference between sites in the three groups occurs, with a relative abundance of 61% in group 3C but only 23% and 16% in groups 3A and 3B respectively. The highest abundance is on an outlying site within group 3A (B680) but situated on the ordination diagram above group 3C. Within group 3C, its relative abundance is highest on sites with lower scores on axis 2.

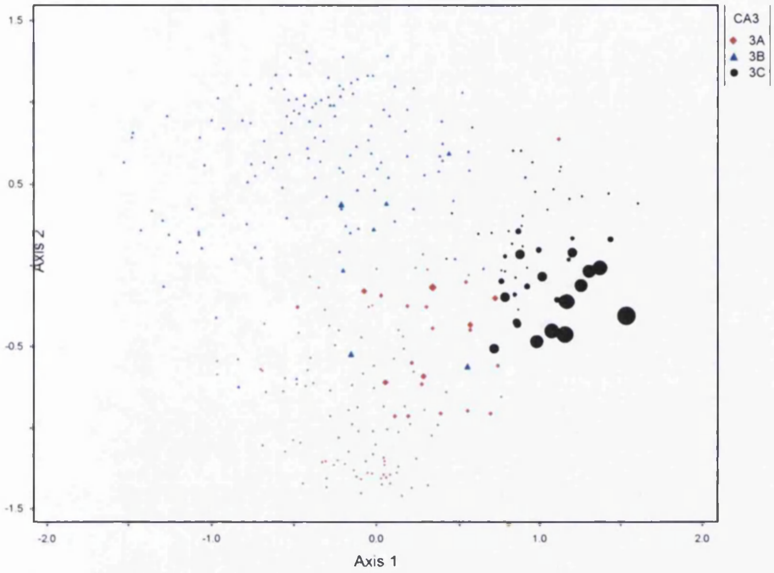


Figure 4-29. Relative abundance of *Betula pubescens*.

The relative abundance of *Betula pubescens* (Figure 4-29) on sites within group 3C, compared to other groups is high at 83%. However, it only occurs on 59% of sites within this group and may form the basis of a sub-group at a lower stage of clustering. Its abundance decreases gradually towards the border between groups. A similar pattern is found for *Empetrum hermaphroditum* (Figure 4-30) but with a higher abundance in a different subset of sites where *Salix glauca* and *Betula pubescens* are absent or in low abundance and with a sharp decrease in abundance at the border between groups 3C and 3B..

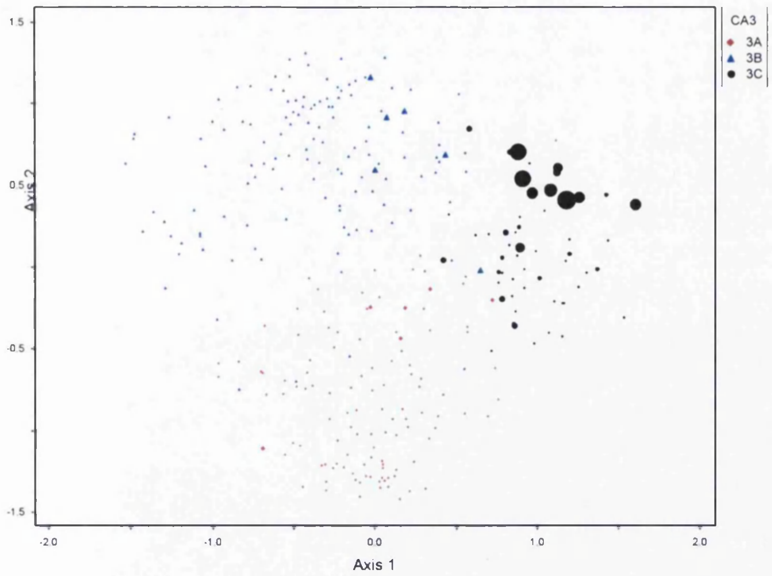


Figure 4-30. Relative abundance of *Empetrum hermaphroditum*.

Vaccinium myrtillus (indicator value 28%) occurs at a small number of sites within groups 3A and 3B (< 5% compared with 35% in group 3C) and its relative abundance in group 3C is 80%. The sites where it occurs in greatest relative abundance (Figure 4-31) are more scattered than those for *E. hermaphroditum*.

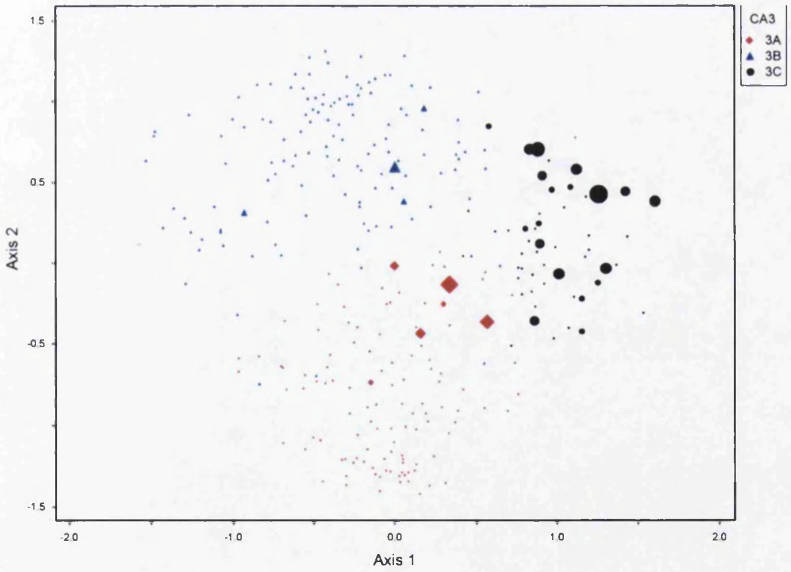


Figure 4-31. Relative abundance of *Vaccinium myrtillus*.

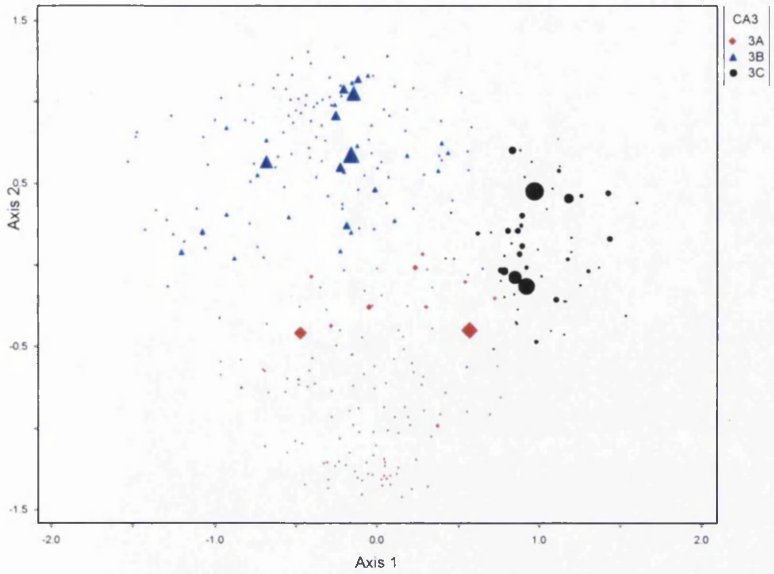


Figure 4-32. Relative abundance of *Hieracium alpinum.*

Hieracium alpinum (Figure 4-32) is recorded at 61% of sites within group 3C (27% of group 3B and 12% of group 3A). Its relative abundance is 43%, 22% and 10% respectively. It is therefore not such a clear indicator for this group and its distribution is not concentrated at sites on the borders between the three groups.

4.5.2.3 Summary and naming of three roadside pioneer groups

This section has demonstrated the usefulness of indicator species in characterising groups at the three-group level of cluster analysis. However, it also demonstrates the considerable variability in the patterns of abundance exhibited by indicator species in relation to the borders between groups where there may be sharp or gradual changes in indicator species abundances. There may also be discrete areas of high abundance, which possibly form the focus of sub-groups at the six- or nine-group level of clustering. The key indicators at the three-group level of clustering are widespread species which have a high relative abundance within a particular group. It is possible to name the groups based on these indicators: group 3A, *Deschampsia cespitosa-Trifolium repens* (Desces-Trirep); group 3B, (*Festuca ovina-Luzula spicata* (Fesovi-Luzspi); group 3C, (*Deschampsia flexuosa-Salix glauca* (Desfle-Salgla).

Variability in species composition is assessed at a more detailed scale in the next two sub-sections by examining the six- and nine-group levels of cluster analysis and their indicator species.

4.5.3 Six roadside pioneer groups

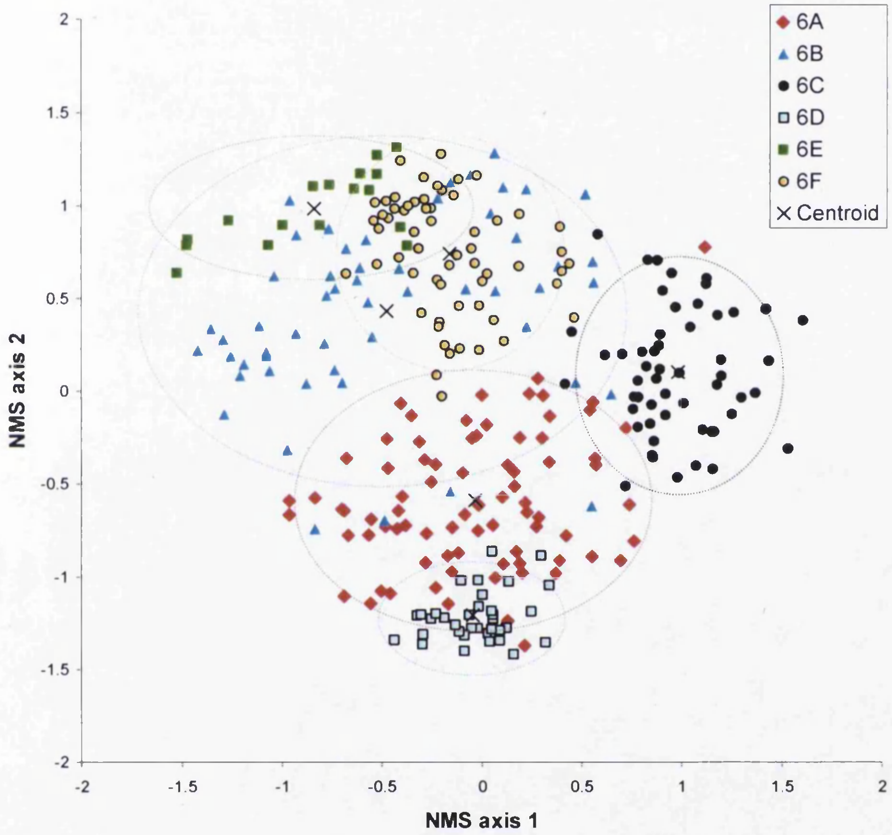


Figure 4-33. NMS ordination of roadside pioneer sites with six colour-coded cluster analysis groups superimposed. Dashed ellipses indicate ±2 standard deviations from each group centroid.

Figure 4-33 illustrates the site groupings obtained from the six-group level of cluster analysis superimposed onto the NMS ordination diagram. Part of former group 3A now forms a separate sub-group (group 6D), which appears to be centred on an area of the diagram characterized by abundant *Plantago major* as was predicted in the previous section (Figure 4-14). Group 3B of the three-group level now forms three sub-groups (6B, 6E and 6F). A clear division between groups 6B and 6F is not obvious on examination of the NMS diagram, although group 6F appears more tightly clustered than group 6B and it occurs where sites in group 6B are most diffuse. Group 6E is composed of sites towards the upper end of axis two. Group 3C remains undivided and becomes group 6C.

The number of sites, mean within-group Sørensen distance and number of significant indicator species ($p \leq 0.05$) for each of these six groups are listed in Table 4-7.

Table 4-7. Descriptive statistics for six roadside pioneer cluster analysis groups.

Group	n	Mean Within-Group Distance	No. of Significant Indicator Spp
6A	79	0.693	14
6B	54	0.748	15
6C	54	0.448	10
6D	36	0.437	22
6E	17	0.525	13
6F	60	0.559	7

Group 6D is now the most tightly clustered with a mean within-group distance of 0.437 and it also has the highest number of significant indicator species at 22. Group 6E is a fairly small cluster with only 17 sites but has 13 significant indicator species and a relatively low mean within-group distance of 0.525. Group 6F, a large group which includes 60 sites has only seven significant indicator species. Group 6B is the least tightly clustered of the groups with a mean within-group distance of 0.748. The total number of significant indicator species is now 81, only three more than at the three-group level of clustering. As an additional measure, mean between-group dissimilarities and Discreteness Indices are given in Table 4-8. This confirms that group 6D is the most discrete with a DI of 1.99, followed by group 6C with a DI of 1.97 and group 6E with a DI of 1.75. The other three groups have lower DI values, 6F at 1.46, 6A at 1.21 and 6B at 1.15. The mean DI is 1.6, showing only a marginal increase from the mean value of 1.5 obtained from the three-group level.

Table 4-8 Mean between- and within-group distances and the Discreteness Index (DI) for the six roadside pioneer cluster analysis groups.

	Mean b-g distance	Mean w-g distance	DI
6A	0.841	0.693	1.214
6B	0.859	0.748	1.148
6C	0.882	0.448	1.970
6D	0.869	0.437	1.988
6E	0.921	0.525	1.754
6F	0.818	0.559	1.463

4.5.3.1 Indicator species analysis of six roadside pioneer cluster analysis groups

In order to investigate the species composition of these six groups, indicator species analysis was carried out (Table 4-9 and Figures 4-34 to 4-39).

Table 4-9. Significant indicator values for the six roadside pioneer cluster analysis groups.

	Indicator Value (%)						
Species	6A	6B	6C	6D	6E	6F	*p*
Desces	**46**	1	1	41	0	1	0.001
Taragg	**29**	4	0	4	0	7	0.002
Stegra	**13**	1	0	0	0	0	0.007
Eupagg	**12**	0	0	0	0	0	0.007
Veroff	**10**	0	0	1	0	0	0.015
Achmil	**10**	0	0	10	0	0	0.022
Pinsyl	**9**	0	0	0	0	1	0.021
Vacvit	**9**	0	0	0	0	1	0.018
Cerfon	**8**	0	0	7	0	0	0.034
Potcra	**8**	0	0	4	0	0	0.044
Equsyl	**6**	0	0	0	0	0	0.036
Gersyl	**6**	0	0	1	0	0	0.049
Viobif	**5**	0	0	0	0	0	0.034
Eriace	**5**	0	0	0	0	0	0.039
Cercer	1	**28**	0	0	10	16	0.001
Desalp	0	**27**	0	0	13	5	0.001
Sagsag	12	**25**	0	4	0	1	0.001
Phlalp	4	**24**	1	0	2	2	0.001
Rumlla	8	**23**	1	0	0	12	0.004
Omasup	2	**22**	6	4	0	7	0.003
Oxydig	1	**20**	1	0	1	5	0.002
Saxste	2	**19**	1	0	0	1	0.002
Rumace	1	**16**	0	0	0	5	0.005
Omanor	5	**14**	1	0	0	0	0.013
Epiana	0	**13**	0	0	0	2	0.017
Sibpro	0	**12**	1	0	0	4	0.012
Veralp	1	**11**	0	0	0	0	0.008
Equsci	1	**8**	0	0	0	1	0.022
Sildio	0	**7**	0	0	0	0	0.015

	Indicator Value (%)						
Species	6A	6B	6C	6D	6E	6F	*p*
Desfle	5	2	**79**	0	0	1	0.001
Betpub	12	0	**44**	1	0	1	0.001
Empher	0	0	**38**	0	0	1	0.001
Salgla	18	6	**37**	1	0	12	0.001
Vacmyr	1	0	**25**	0	0	0	0.001
Hiealp	2	2	**19**	0	0	11	0.004
Phycae	0	0	**19**	0	0	0	0.001
Juntrf	0	8	**14**	0	3	1	0.023
Vaculi	0	0	**11**	0	0	0	0.006
Calvul	3	0	**7**	0	0	0	0.037
Plamaj	2	0	0	**95**	0	0	0.001
Trirep	19	0	0	**50**	0	0	0.001
Ranacr	10	1	0	**40**	0	0	0.001
Agrcap	20	1	18	**39**	0	2	0.001
Fraves	0	0	0	**35**	0	0	0.001
Poapra	8	4	0	**34**	0	0	0.001
Pruvul	0	0	0	**22**	0	0	0.001
Sagpro	0	0	0	**20**	0	0	0.001
Crecap	0	0	0	**19**	0	0	0.001
Verser	5	0	0	**17**	0	0	0.001
Chasua	5	0	3	**15**	0	0	0.003
Chaang	4	1	0	**12**	0	0	0.016
Alcglo	0	0	0	**11**	0	0	0.007
Hypmac	1	0	0	**10**	0	0	0.008
Tripra	5	0	0	**10**	0	0	0.016
Cretec	0	0	0	**8**	0	0	0.014
Carova	0	0	0	**8**	0	0	0.02
Rubida	2	0	0	**7**	0	0	0.015
Filuli	0	0	0	**6**	0	0	0.014
Galtet	0	0	0	**6**	0	0	0.014
Gerrob	0	0	0	**6**	0	0	0.016
Junbuf	0	0	0	**5**	0	0	0.047
Luzarc	0	1	0	0	**86**	1	0.001
Rangla	0	0	0	0	**64**	0	0.001
Saxces	0	0	0	0	**56**	0	0.001
Ceralp	0	1	0	0	**52**	6	0.001
Saxcer	0	0	0	0	**41**	0	0.001
Poaalp	5	31	0	0	**37**	6	0.001
Carbel	0	0	0	0	**35**	1	0.001
Salher	0	7	9	0	**35**	4	0.001
Silaca	0	0	0	0	**25**	8	0.001
Saxopp	0	0	0	0	**16**	0	0.001
Trispi	0	11	0	0	**13**	11	0.024
Araalp	0	0	0	0	**11**	0	0.005
Saxriv	0	0	0	0	**8**	1	0.017
Fesovi	3	10	5	0	20	**52**	0.001
Antdio	0	0	0	0	0	**34**	0.001
Luzspi	2	29	1	0	1	**32**	0.001
Polviv	8	2	0	0	3	**27**	0.001
Camrot	2	0	0	1	0	**21**	0.004
Visalp	1	0	0	0	0	**19**	0.001
Antodo	1	2	1	0	0	**13**	0.018

Many of the indicators for new sub-groups e.g. *Plantago major* and *Fragaria vesca* in group 6D, *Luzula arcuata* and *Ranunculus glacialis* in group 6E and *Antennaria dioica* and *Polygonum viviparum* in group 6F now have higher values than they had at the three-group level of cluster analysis. However, the majority of the most common roadside pioneer species, which had high indicator values at the three-group level, now have lower values, e.g. the indicator value for *Deschampsia cespitosa* has fallen from 86% to 46% and that for *Festuca ovina* from 70% to 52%. This is to be expected because, as the number of groups increases, the composition of these smaller sub-groups is less likely to be characterised by the most widespread species.

Group 6A (Figure 4-34) has only two indicator values greater than 25% and only four with a value between 10 and 25%. *D. cespitosa* is still the species with the highest indicator value (46%) but it is clearly not a good discriminator between groups 6A and 6D, where it has an indicator value of 41%. Similarly, *Achillea millefolium* has equal values (to two significant figures) for groups 6A and 6D even though indicator analysis suggests it as an indicator for group 6A. *Taraxacum* agg. is therefore a more reliable indicator as, although present in other groups, it has a much higher value in group 6A. This was anticipated from examination of its distribution at the three-group level. Many of the species with lower indicator values are informative, for example *Veronica officinalis* (10%), *Geranium sylvaticum* (6%) and *Equisetum sylvaticum* (6%) are typical woodland species, while *Pinus sylvestris* seedlings (9%) are also indicative of this group.

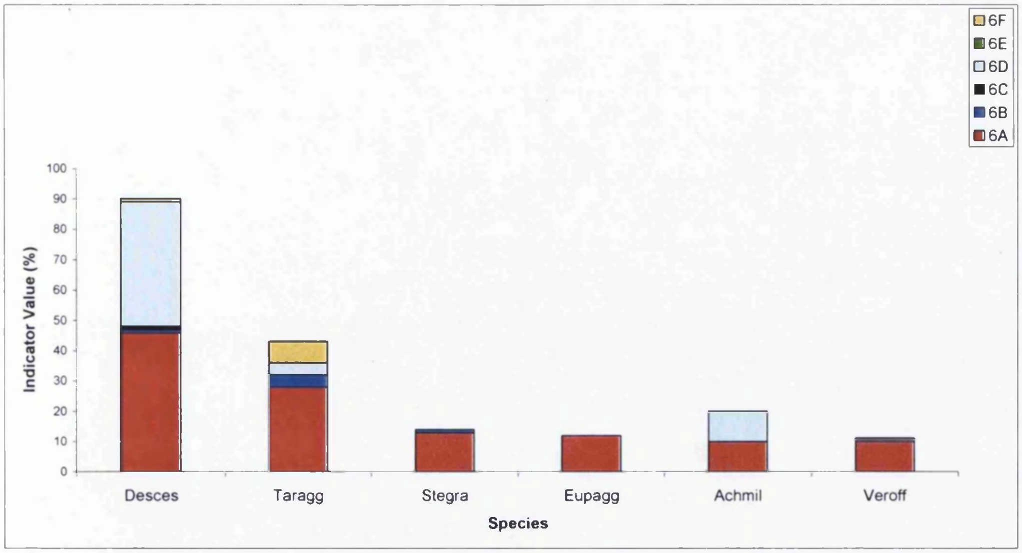


Figure 4-34. Group 6A indicator species (with values ≥ 10%) showing indicator values across the six roadside pioneer cluster analysis groups.

Group 6B (Figure 4-35) has only three indicator values greater than 25% and a further 10 species with values between 10 and 25%. Examination of the species which have significant indicator values for this group reveals a high proportion of species which are expected to be more abundant on sites at higher altitudes than groups 6A and 6D and with a relatively high moisture level e.g. *Cerastium cerastoides*, *Deschampsia alpina, Phleum alpinum, Oxyria digyna* and *Saxifraga stellaris*.

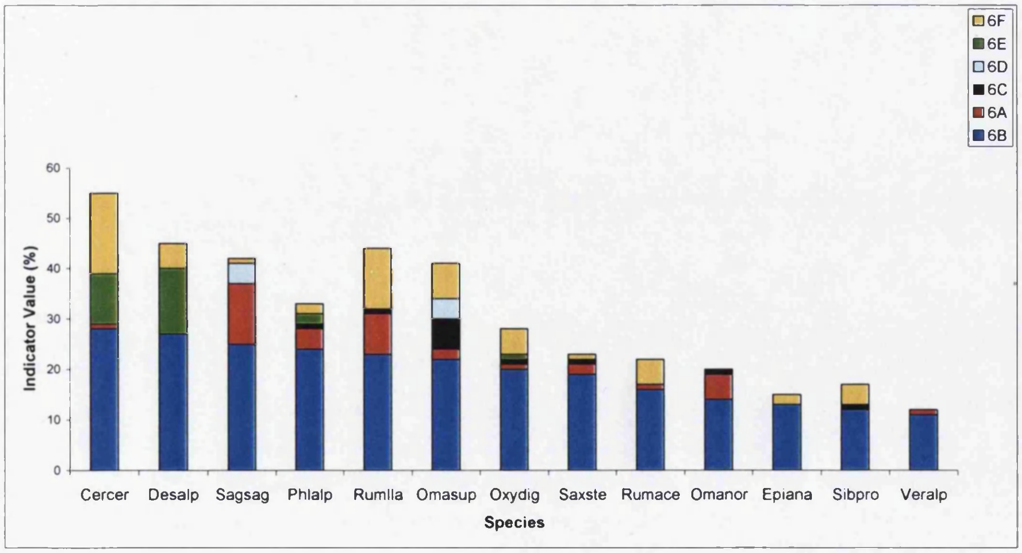


Figure 4-35. Group 6B indicator species (with values ≥ 10%) showing indicator values across the six roadside pioneer cluster analysis groups.

Group 6C indicator species (Figure 4-36) are the same as for group 3C except for the loss of *Salix herbacea* and *Carex bigelowii*.

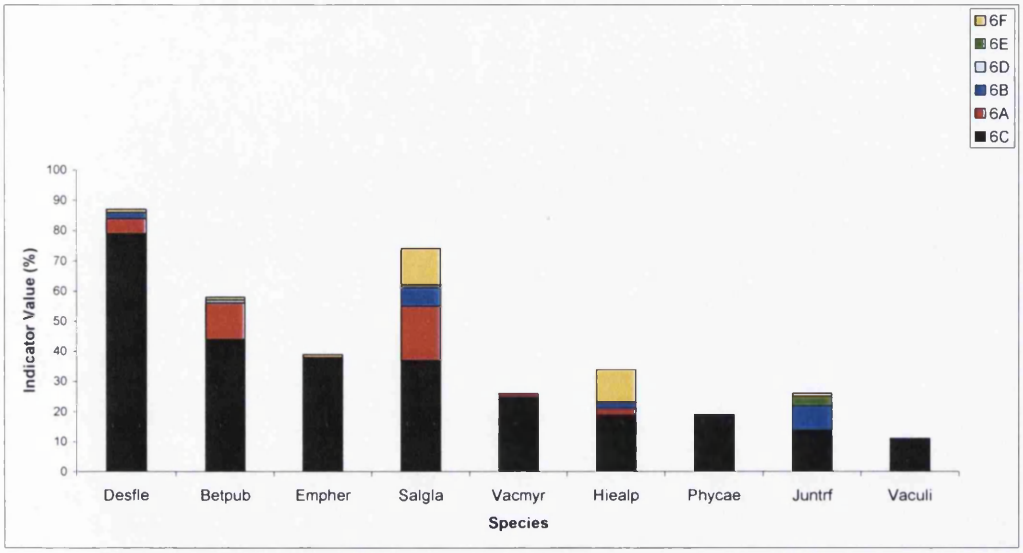


Figure 4-36. Group 6C indicator species (with values ≥ 10%) showing indicator values across the six roadside pioneer cluster analysis groups.

Group 6D has six indicator values greater than 25% (Figure 4-37), including a value of 95% for *Plantago major*, the highest obtained so far in the analysis. As anticipated from analysis at the three-group level, *P. major* is therefore an extremely good indicator species; it is present in 100% of sites within group 6D and its relative abundance is 95%. *Trifolium repens* has an indicator value of 50% for group 6D and only 19% for group 6A. Species such as this, while useful for detecting differences between groups, are clearly stronger indicators when the two sub-groups are combined. (*T. repens* has an indicator value of 60% when sub-groups 6A and 6D are combined to form group 3A.) There are an additional nine indicator values greater than 10% in group 6D and the indicator species for this group are typical of grassland and areas dominated by human activity.

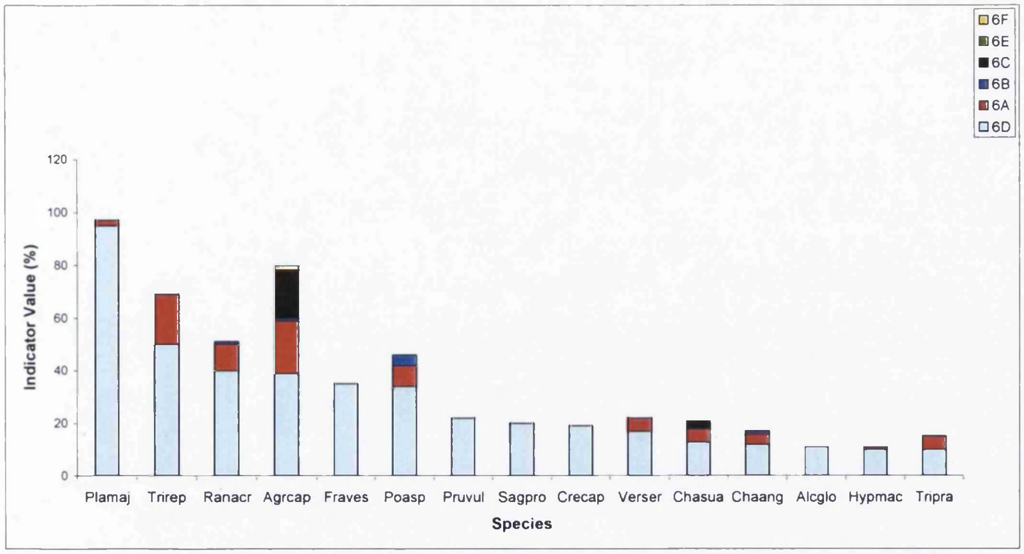


Figure 4-37. Group 6D indicator species (with values ≥ 10%) showing indicator values across the six roadside pioneer cluster analysis groups.

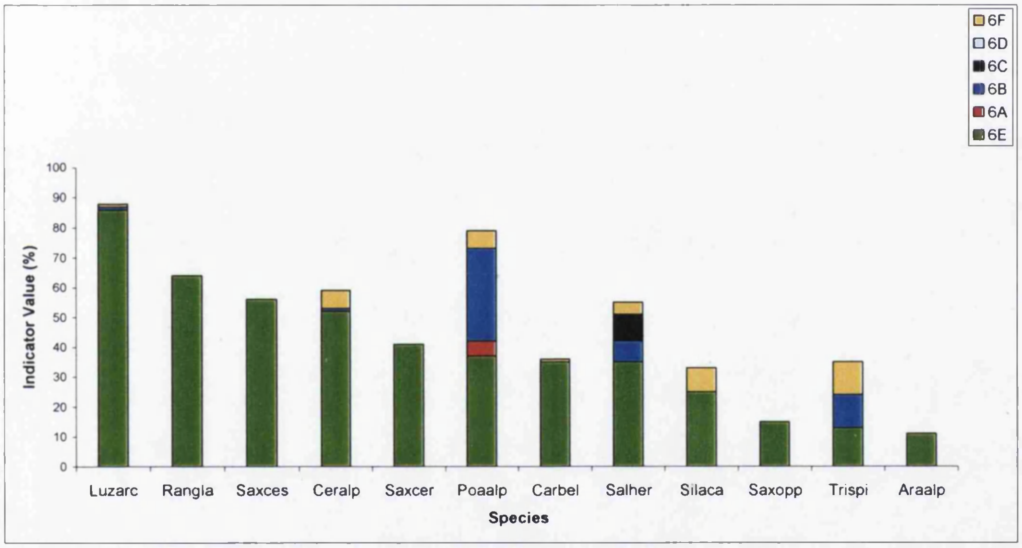


Figure 4-38. Group 6E indicator species (with values ≥ 10%) showing indicator values across the six roadside pioneer cluster analysis groups.

Group 6E (Figure 4-38) has a number of high value indicator species which are virtually absent from other groups of sites, for example *Luzula arcuata* is present at 100% of sites in group 6E with a relative abundance of 86%, whereas in other groups, although it is present, its relative abundance is extremely low. *Ranunculus glacialis* is almost exclusive to group 6E but is only present at 65% of sites within this group, a pattern also seen in the two saxifrage species *Saxifraga cespitosa* with an indicator value of 56% and *S. cernua* with an indicator value of 41%. These species all had much lower indicator values at the three-group level. The formation of a subset of group 3B based partly on the relative abundance of *Cerastium alpinum,* which has an indicator value of 52%, was anticipated when examining species distributions at the three group level. These and the other group 6E indicator species (e.g. *Cerastium alpinum*, *Cardamine bellidifolia, Salix herbacea* and *Arabis alpina*) are characteristic of the more extreme conditions found in the mid to high alpine vegetation zones and the highest altitude sites are included in this group. *Poa alpina* is not such a useful indicator for group 6E, where it has a value of 37%, as it has a value of 31% in group 6B.

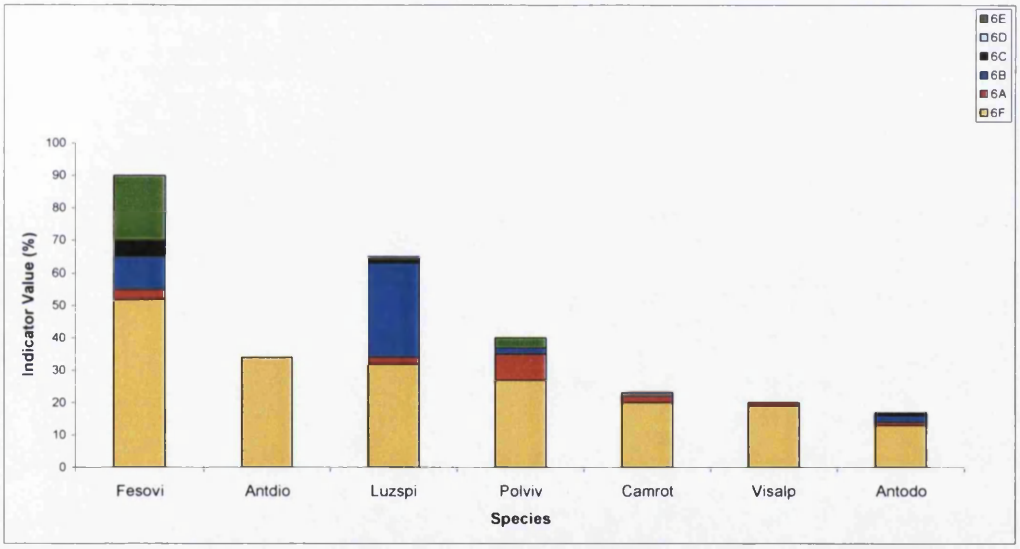


Figure 4-39. Group 6F indicator species (with values ≥ 10%) showing indicator values across the six roadside pioneer cluster analysis groups.

Species which are now significant indicators for group 6F (Figure 4-39) include those which are generally characteristic of drier conditions e.g. *Luzula spicata*, *Polygonum viviparum* and *Campanula rotundifolia*. *Festuca ovina* is now the strongest indicator for group 6F with a value of 52% and also tends to be more abundant in drier conditions. It is present at a high percentage (80-90%) of sites in groups 6B, 6C and 6E, but its relative abundance in these groups is lower. Analysing sites according to six clusters rather than three has reduced its indicator value by 18%. However, examination of its distribution and abundance at the three-group level anticipated the formation of a possible subset based on its relative abundance at sites now forming group 6F. *Antennaria dioica* is only present at 35% of sites in group 6F (compared with 2% of sites in group 6B) but its relative abundance is 98% (2% in group 6B) giving an indicator value of 34%. Like *F. ovina*, its highest abundance is concentrated towards the centre of axis 1 and towards the top of axis 2 and it is also a characteristic species of drier habitats.

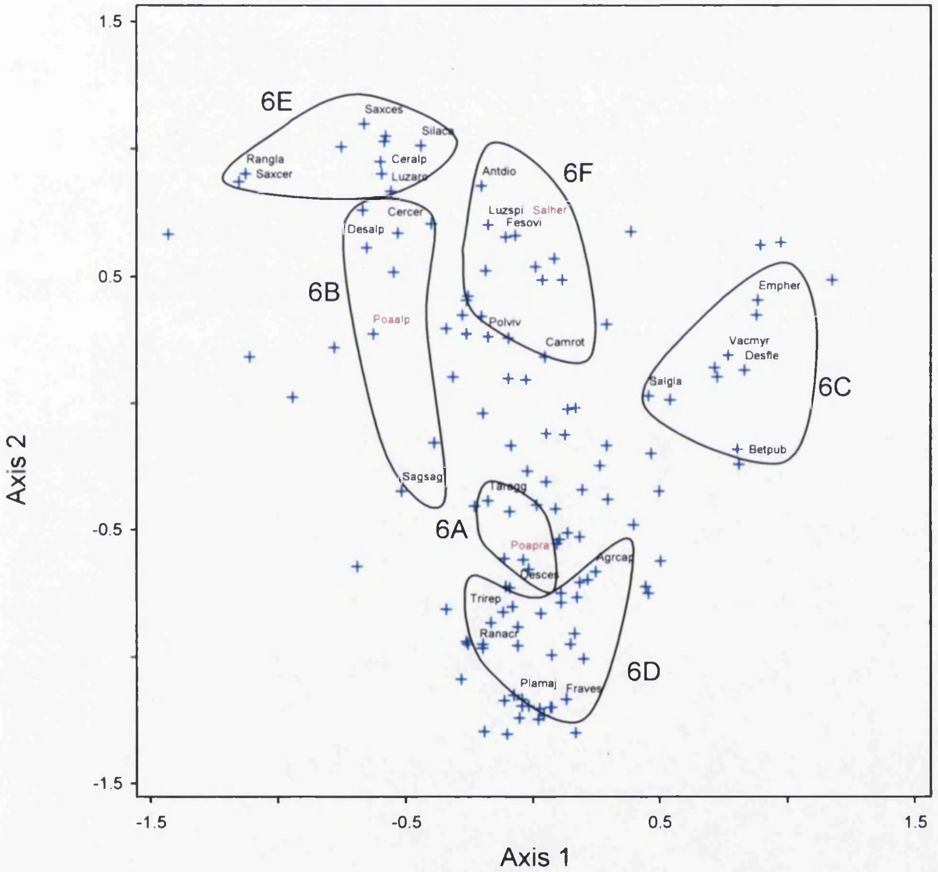


Figure 4-40. NMS ordination of roadside pioneer sites at the six-group level showing weighted scores for indicator species with a value of ≥ 25%. (Species which occur outside the clusters of indicators are shown in red.)

Figure 4-40 shows the weighted NMS scores of species with an indicator value of ≥ 25% at the six-group level of cluster analysis. Species which are strong indicators for group 6E (e.g. *Saxifraga cespitosa, S. cernua* and *Ranunculus glacialis*) are positioned within that group. Species which are now indicators for group 6F appear to have higher scores on axis 1 than those which are indicators for group 6B. Species which characterise group 6D (e.g. *Plantago major, Fragaria vesca, Ranunculus acris* and *Trifolium repens*) occur towards the lower end of axis 2.

4.5.3.2 Summary and naming of six roadside pioneer sub-groups

In the light of earlier analysis, it seems appropriate to refer to clusters of sites formed at the six- and nine-group levels as sub-groups. The six-group level of cluster analysis seems to summarise the variability in pioneer vegetation well, as these sub-groups occupy distinct areas of ordination space (Figure 4-33) and the indicator species are clearly separated (Figure 4-40). The general ecological requirements of the indicator species also suggest that these sub-groups can be interpreted in terms of environmental differences, which will be tested in the next chapter. However, the general decrease in indicator values for most species which were indicators at the three-group level suggests the less discrete nature of groups at the six-group level. Notable exceptions are the increase in indicator value for *Plantago major* in group 6D and for indicator species in group 6E. The Discreteness Index (DI) gives a mean value for the six-group level of 1.6 which is only marginally higher than the value when the data is classified into only three groups (1.5). As a higher mean DI would be expected as the data are further sub-divided, this does not therefore indicate a great improvement in the discreteness of each group.

The sub-groups can be renamed on the basis of their indicator species as follows: group 6A, *Deschampsia cespitosa-Taraxacum* agg. (Desces-Taragg); group 6B, *Cerastium cerastoides-Deschampsia alpina* (Cercer-Desalp); group 6C, *Deschampsia flexuosa-Betula pubescens* (Desfle-Betpub); group 6D, *Plantago major-Trifolium repens* (Plamaj-Trirep); group 6E, *Luzula arcuata-Ranunculus glacialis* (Luzarc-Rangla); group 6F, *Festuca ovina-Antennaria dioica* (Fesovi-Antdio).

4.5.4 Nine roadside pioneer groups

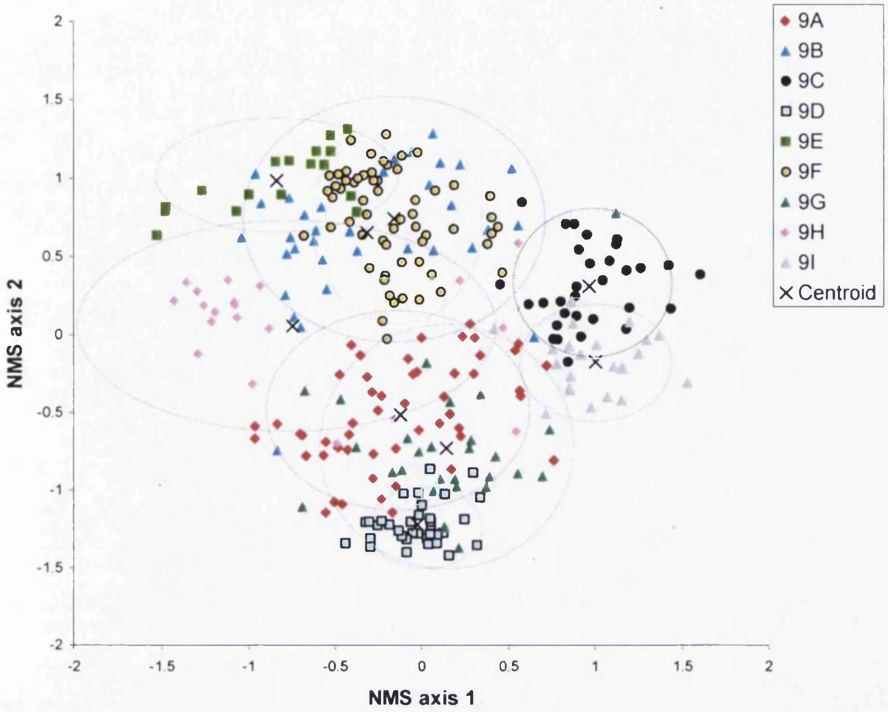


Figure 4-41. NMS ordination of roadside pioneer sites with nine colour-coded cluster analysis groups superimposed. Dashed ellipses indicate ±2 standard deviations from each group centroid.

Division of the roadside pioneer sites into nine sub-groups results in the pattern illustrated in Figure 4-41, with at least one additional sub-group being formed from each of the three original groups. Groups 9A and 9G are subsets of group 6A and no clear division between these two groups can be seen although the majority of group 9G sites have a higher score on axis 1. Group 9H and 9B are subsets of group 6B with the majority of sites (13 sites) within group 9H forming a cluster towards the lower end of axis 1 and approximately half way up axis 2 and the remaining seven sites being distributed in a diffuse pattern with a range of axis scores. For the first time, group 3C/6C has split along axis 2 into an upper (group 9C) and a lower sub-group (group 9I).

Table 4-10 confirms that group 9G, with a mean within-group distance of 0.667 is not a tightly clustered group. It has 14 significant indicator species but only one of these has a value ≥ 25%. Group 9A has only seven indicators and only one species with a value ≥ 25%. Indicator values for group 9D have tended to decrease slightly but apart from the loss of one species there is little change.

There is also little change in groups 6E (now 9E) and 6F (now 9F). Group 9H, a sub-group of group 6B is now the least tightly clustered of the groups, with a mean within-group distance of 0.7, and has 11 significant indicator species, six of which have values ≥ 25%. Group 9B how has only three significant indicator species rather than the 15 it had as group 6B at the six-group level and these are all greater than 20%. Group 9I is the most tightly clustered group with a mean within-group distance of 0.378 and two significant indicator species both with values over 35%. Group 9C has the same number of significant indicator species as group 6C at the six-group level but now has only four with a value ≥ 25%.

Table 4-10. Descriptive statistics for nine roadside pioneer cluster analysis groups.

Group	n	Mean Within-Group Distance	No. of Significant Indicator Spp
9A	52	0.642	7
9B	34	0.690	3
9C	31	0.411	10
9D	36	0.437	14
9E	17	0.525	11
9F	60	0.559	6
9G	27	0.667	14
9H	20	0.700	11
9I	23	0.378	2

Table 4-11. Mean between- and within-group distances and the Discreteness Index (DI) for the nine roadside pioneer cluster analysis groups.

	Mean b-g distance	Mean w-g distance	DI
9A	0.824	0.642	1.283
9B	0.857	0.690	1.242
9C	0.840	0.411	2.044
9D	0.873	0.437	1.998
9E	0.892	0.525	1.699
9F	0.841	0.559	1.504
9G	0.839	0.667	1.258
9H	0.862	0.700	1.231
9I	0.838	0.378	2.218

The Discreteness Index (Table 4-11) confirms that sub-groups 9I and 9C are the most discrete with values of 2.2 and 2.1 respectively. Sub-groups 9B and 9H are the least discrete with values of 1.2. The mean DI of 1.6 is the same as that for the six-group level, showing that further sub-division has not improved the discreteness of the groups.

4.5.4.1 Indicator species analysis of nine roadside pioneer sub-groups

Table 4-12. Significant indicator values for the nine roadside pioneer sub-groups.

	Indicator Value (%)									
Species	**9A**	**9B**	**9C**	**9D**	**9E**	**9F**	**9G**	**9H**	**9I**	**p**
Desces	**43**	0	0	29	0	1	15	1	1	0.001
Veroff	**10**	0	0	1	0	0	2	0	0	0.025
Solvir	**9**	0	1	0	0	2	0	0	4	0.021
Hieumb	**7**	0	0	0	0	0	0	1	0	0.038
Linbor	**6**	0	0	0	0	0	0	0	0	0.047
Parpal	**6**	0	0	0	0	0	0	0	0	0.048
Salmyr	**6**	0	0	0	0	0	0	0	0	0.053
Luzspi	3	**43**	2	0	1	24	0	1	0	0.001
Rumlla	5	**29**	1	0	0	8	6	1	0	0.001
Cercer	1	**23**	0	0	7	12	0	15	0	0.001
Desfle	5	1	**53**	0	0	0	0	1	29	0.001
Empher	0	0	**42**	0	0	0	0	0	4	0.001
Phycae	0	0	**32**	0	0	0	0	0	0	0.001
Juntrf	1	11	**25**	0	2	1	0	0	0	0.001
Vacmyr	1	0	**21**	0	0	0	0	0	7	0.001
Hiealp	1	1	**16**	0	0	7	0	2	7	0.002
Vaculi	0	0	**14**	0	0	0	0	0	1	0.003
Carbig	1	5	**12**	0	5	7	0	0	0	0.019
Harhyp	0	0	**6**	0	0	0	0	0	0	0.028
Loipro	0	0	**6**	0	0	0	0	0	0	0.032
Plamaj	1	0	0	**89**	0	0	3	0	0	0.001
Trirep	11	0	0	**35**	0	0	19	0	0	0.001
Fraves	0	0	0	**33**	0	0	0	0	0	0.001
Ranacr	6	0	0	**28**	0	0	8	3	0	0.001
Poapra	2	7	0	**23**	0	0	16	0	0	0.001
Crecap	0	0	0	**19**	0	0	0	0	0	0.001
Sagpro	0	0	0	**18**	0	0	1	0	0	0.002
Pruvul	0	0	0	**18**	0	0	2	0	0	0.002
Verser	1	0	0	**12**	0	0	8	0	0	0.006
Alcglo	0	0	0	**10**	0	0	0	0	0	0.012
Chasua	4	0	1	**9**	0	0	2	0	3	0.046
Cretec	0	0	0	**8**	0	0	0	0	0	0.034
Carova	0	0	0	**8**	0	0	0	0	0	0.017
Hypmac	0	0	0	**7**	0	0	3	0	0	0.032
Luzarc	0	1	1	0	**80**	1	0	0	0	0.001
Rangla	0	0	0	0	**64**	0	0	0	0	0.001
Saxces	0	0	0	0	**56**	0	0	0	0	0.001

Species	**Indicator Value (%)**									**p**
	9A	**9B**	**9C**	**9D**	**9E**	**9F**	**9G**	**9H**	**9I**	
Ceralp	0	2	0	0	**49**	6	0	0	0	0.001
Saxcer	0	0	0	0	**40**	0	0	0	0	0.001
Carbel	0	0	0	0	**35**	1	0	0	0	0.001
Salher	0	4	14	0	**26**	3	0	7	0	0.001
Silaca	0	1	0	0	**24**	8	0	0	0	0.001
Saxopp	0	0	0	0	**15**	0	0	0	0	0.002
Araalp	0	0	0	0	**9**	0	0	1	0	0.009
Saxriv	0	0	0	0	**8**	1	0	0	0	0.031
Fesovi	2	12	6	0	17	**44**	2	3	3	0.001
Antdio	0	0	0	0	0	**34**	0	0	0	0.001
Polviv	3	1	0	0	2	**18**	9	1	0	0.004
Visalp	1	0	0	0	0	**17**	0	0	0	0.002
Camrot	1	0	0	0	0	**15**	2	1	0	0.004
Antodo	1	1	3	0	0	**9**	1	3	0	0.046
Agrcap	3	0	3	22	0	1	**31**	2	24	0.001
Taragg	13	0	0	2	0	4	**24**	7	0	0.001
Stenem	0	0	0	1	0	0	**16**	0	0	0.001
Viobif	0	0	0	0	0	0	**15**	0	0	0.001
Minbif	1	0	0	0	0	1	**13**	2	0	0.011
Chaang	0	0	0	7	0	0	**12**	6	0	0.01
Eriace	0	0	0	0	0	0	**10**	0	0	0.013
Equsyl	1	0	0	0	0	0	**9**	0	0	0.013
Vioriv	0	0	0	1	0	0	**9**	0	0	0.035
Achmil	5	0	0	6	0	0	**8**	0	0	0.041
Cerfon	4	0	0	4	0	0	**7**	0	0	0.036
Maibif	0	0	0	0	0	0	**7**	0	0	0.019
Gersyl	2	0	0	0	0	0	**7**	0	0	0.041
Oxaace	0	0	0	1	0	0	**6**	0	0	0.05
Phlalp	3	3	1	0	1	1	1	**44**	0	0.001
Sagsag	7	3	0	2	0	1	5	**43**	0	0.001
Poaalp	5	12	0	0	24	4	0	**35**	0	0.001
Epiana	0	0	0	0	0	0	0	**31**	0	0.001
Veralp	0	0	0	0	0	1	0	**31**	0	0.001
Omanor	2	1	0	0	0	0	2	**28**	1	0.001
Desalp	0	14	0	0	8	3	0	**21**	0	0.001
Sildio	0	0	0	0	0	0	0	**20**	0	0.001
Saxste	1	6	1	0	0	1	0	**19**	0	0.002
Rumace	1	6	0	0	0	3	0	**17**	0	0.001
Oxydig	1	10	2	0	0	3	0	**16**	0	0.003
Betpub	4	0	2	0	0	0	7	1	**65**	0.001
Salgla	7	4	9	0	0	6	14	2	**37**	0.001

Significant indicator values for the nine sub-groups are listed in Table 4-12. Group 9A (formerly 6A) is now mainly characterised by *Deschampsia cespitosa* with an indicator value of 43%. The other indicator species for this group, with values of 10% and below, are characteristic of a range of habitats including damp woods, dry heaths and marshes and would not therefore form a single community. Group 9B only has three indicator species: *Luzula spicata, Rumex* *acetosella* and *Cerastium cerastoides*. Group 6C has split into two subgroups: within the new group 9C, *Deschampsia flexuosa* has dropped its indicator value considerably from 79% to 53% while the values for *Phyllodoce caerulea* and *Juncus trifidus* have risen to 32% and 25% respectively; group 9H has high indicator values for *Betula pubescens* (65%) and *Salix glauca* (37%).

There is little difference in the species characterising group 9D (6D) except for a general lowering of values and the loss of *Agrostis capillaris* as an indicator. This is now the species with the highest indicator in group 9G at 31%, but has values of 22% in group 9D and 24% in group 9I. *Taraxacum* agg. is also now an indicator for group 9G with a value of 24%. On preliminary examination, the five other species with indicator values of 10% and above include a number of species often found in woods e.g. *Stellaria nemorum* and *Viola biflora* as well as *Chamerion angustifolium* which may be found in a variety of disturbed habitats including within woodland. *Minuartia biflora* is normally found in mountains but was particularly abundant at one site within this group.

Group 9E is virtually unchanged from 6E. The main change to group 9F from 6F is the loss of *Luzula spicata* to group 9B. The new group 9H appears to have species typical of wetter sites including *Phleum alpinum* and *Sagina saginoides*.

Figure 4-42 shows good separation between the weighted scores for sub-group indicator species, except for those characterizing groups 9B and 9F, which are indicated by overlapping areas on the ordination diagram. Figure 4-41 confirms that these two groups, along with groups 9D and 9G, are indeed indistinct. Examination of Figure 4-41 also suggests that the clustering of roadside pioneer sites into nine groups does not produce clear divisions in ordination space between the new groups. It therefore seems likely that this level of cluster analysis produces groups which are based on subdivisions of a continuum rather than distinct groups. This is supported by the fact that indicator values for individual species have again tended to decrease compared to the six group level with the exception of a number of species indicating groups 9C, 9H and 9I.

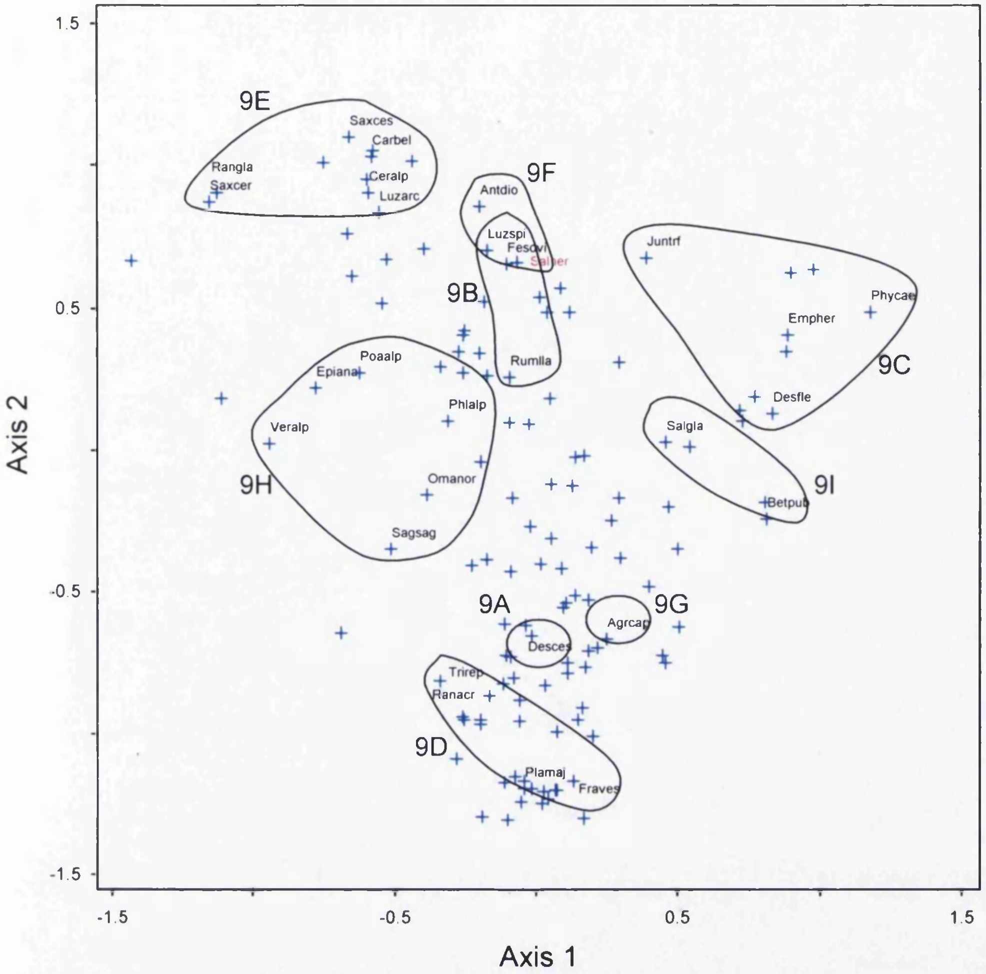


Figure 4-42. NMS ordination of roadside pioneer sites at the nine group level showing weighted scores for indicator species with a value of ≥ 25%. (Species which occur outside the clusters of indicators are shown in red.)

The sub-groups formed at the nine-group level of cluster analysis will not therefore be renamed, as it is unlikely that they will prove useful in further analyses.

4.5.5 Summary of differences in indicator values for roadside pioneer groups

In order to provide an overview of all three levels of cluster analysis, Table 4-13 shows all species which reach a value of ≥ 25% and their indicator values at each level of clustering with the maximum value reached shown in bold type. At the three-group level, widespread species are the main indicators, while at subsequent levels, species with progressively narrower ranges reach their highest indicator values.

Table 4-13. Species indicator values at each stage of clustering. Maximum values for each species are indicated in bold. Only values reaching ≥ 25% are included.

Species	**Indicator Values (%)**		
	3 Groups	**6 Groups**	**9 Groups**
Agrcap	**43**	39	31
Antdio	17	**34**	34
Betpub	49	44	**65**
Carbel	8	**35**	35
Ceralp	38	**52**	50
Cercer	**52**	28	23
Desalp	**41**	27	21
Desces	**86**	46	43
Desfle	**87**	79	53
Empher	41	38	**42**
Epiana	10	13	**32**
Fesovi	**70**	52	44
Fraves	15	**35**	33
Hiealp	**26**	19	16
Juntrf	21	14	**25**
Luzarc	24	**86**	80
Luzspi	**55**	32	43
Omanor		14	**28**
Phlalp	19	24	**44**
Phycae	19	19	**32**
Plamaj	57	**95**	89
Poaalp	**54**	37	35
Poapra	**34**	34	23
Polviv	22	**27**	18
Ranacr	**41**	40	28
Rangla	10	**64**	64
Rumlla	26	23	**29**
Sagsag	19	25	**43**
Salgla	**50**	37	37
Salher	21	**35**	26
Saxcer	7	**41**	40
Saxces	9	**56**	56
Silaca	19	**25**	24
Taragg	**34**	29	24
Trirep	**60**	50	35
Trispi	**32**	13	
Vacmyr	**28**	25	21
Veralp		11	**31**
No. of maxima	16	12	10
Mean maximum	50	49	37

Each level gives a different amount of detail regarding pioneer community composition but, based on previous analyses and on the number of indicators which reach maxima at each level, the three-group level appears to be optimal with 16 maxima in Table 4-13. The number of maxima decreases to 12 at the six-group level and to 10 at the nine-group level. The average value of the maxima shows little difference between the three- and six-group levels (50% and 49% respectively) but then decreases to 37% at the nine-group level. This evidence supports the usefulness of the six-group level in providing additional detail of pioneer roadside site species composition but not that of the nine-group level.

Thus, the three-group level of cluster analysis produces three relatively distinct communities. Further subdivision at the six-group level makes ecological sense as dissection of a continuum rather than distinct communities. Division into nine groups results in a number of indistinct groups which are not useful.

4.5.6 Comparison of cluster analysis with TWINSPAN roadside pioneer groups

TWINSPAN analysis was carried out to test the results of cluster analysis, to assess how well the two different methods identify groups of sites with similar species composition and to explore further the nature of the groups already identified. [The TWINSPAN two-way ordered table is appended (Appendix II).] Table 4-14 lists the MRPP statistics for different levels of classification with TWINSPAN and this is compared with cluster analysis in Figure 4-43. It is clear that separation between groups at the three-group level is considerably lower for the TWINSPAN classification (T = -96) than the cluster analysis classification (T = -143) and mean within-group agreement is also lower for TWINSPAN (A = 0.123) than for cluster analysis (A = 0.182). At the six-group level the TWINSPAN figures are T = -105 and A = 0.214. Again this does not compare favourably with the cluster analysis figures of T = -129 and A = 0.261. Nine groups give a T-value of -101 and A-value of 0.262 for TWINSPAN compared to -119 and 0.308 for cluster analysis.

Table 4-14. MRPP statistics for roadside pioneer TWINSPAN groups.

Number of groups	T	A	*p*
2	-101	0.09	0
3	-96	0.123	0
4	-114	0.178	0
5	-108	0.195	0
6	-105	0.214	0
7	-104	0.232	0
8	-106	0.256	0
9	-101	0.262	0
10	-100	0.277	0

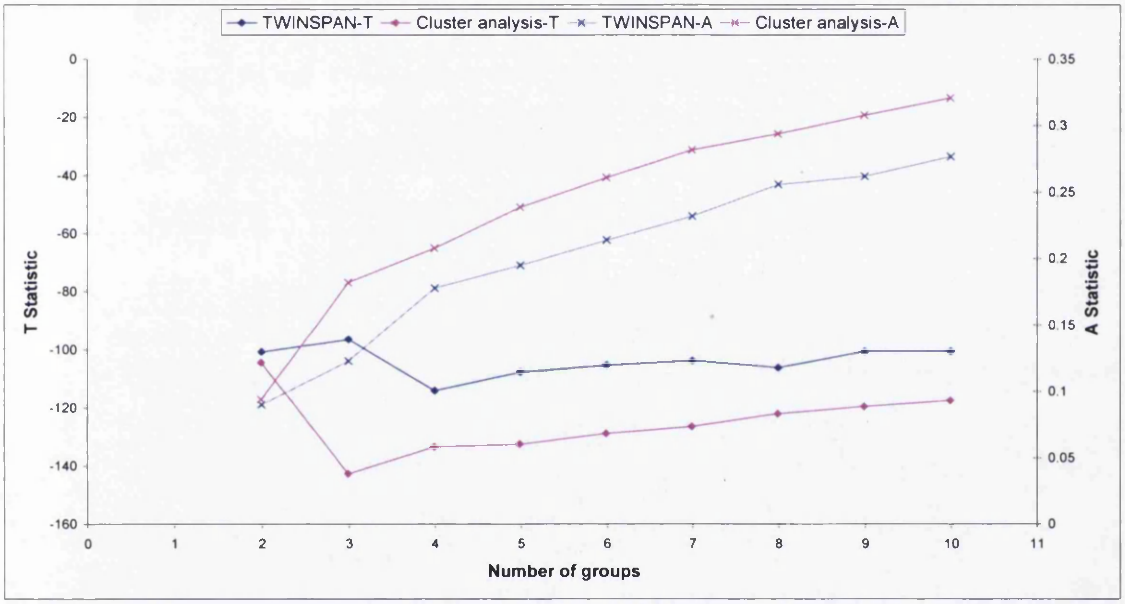


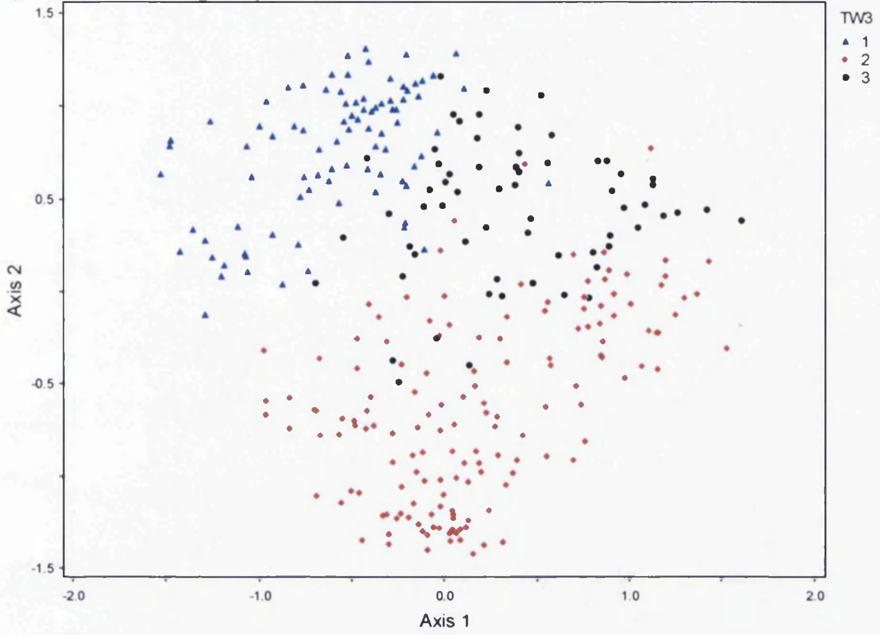
Figure 4-43. Comparison of MRPP T and A statistics for cluster analysis and TWINSPAN analysis of roadside pioneer sites.

It is apparent that, based on these criteria, cluster analysis gives consistently better results than TWINSPAN. However, it is still useful to examine TWINSPAN classifications superimposed onto the NMS ordination diagram to test the conclusions reached from cluster analysis.

Figure 4-44(a) illustrates three TWINSPAN groups superimposed on the NMS diagram and shows, perhaps surprisingly, that the division of sites is not consistent with that of cluster analysis (Figure 4-44-b). The main difference is the presence of an intermediate group between groups 1 and 2, rather than a single group towards the top of axis 2 (cluster analysis group 3C). There is a

72% level of agreement between the two methods based on the number of sites grouped consistently by both methods. It is also evident from this diagram that the groups of sites are not as tightly clustered as the three groups from cluster analysis.

a) TWINSPAN groups



b) Cluster analysis groups

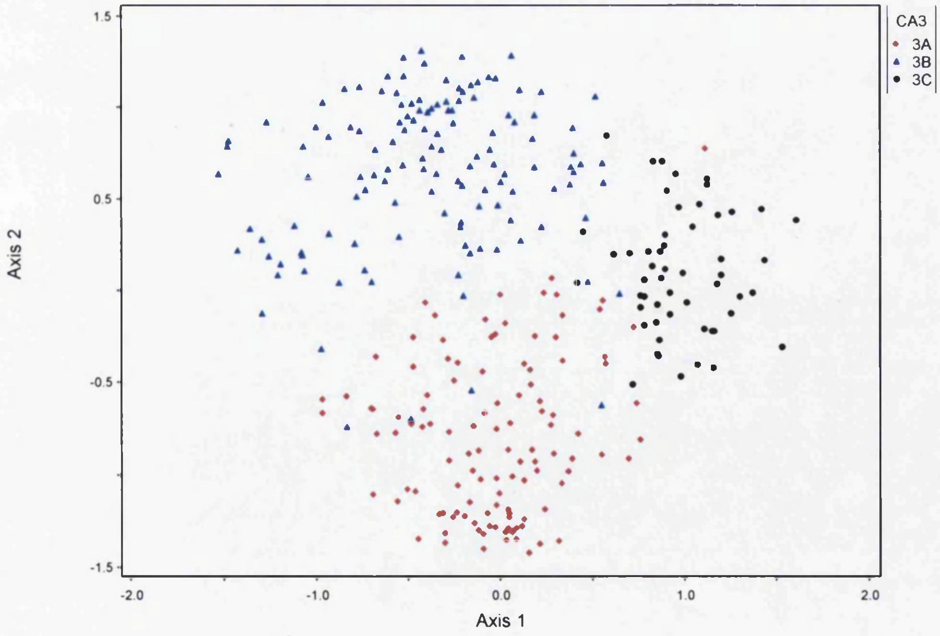


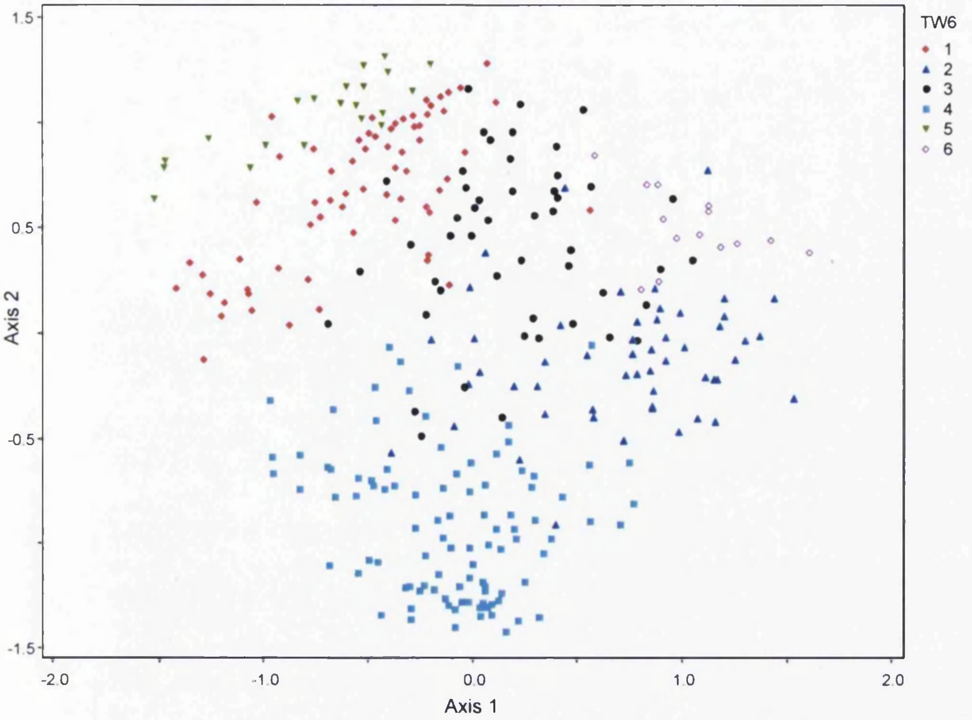
Figure 4-44. NMS ordination of roadside pioneer sites at the three-group level: (a) TWINSPAN groups; (b) cluster analysis groups.

When the six-group stage of TWINSPAN analysis is compared with cluster analysis in Figure 4-45, it is interesting to note that the two methods give a similar general pattern, the main differences being the formation of TWINSPAN group 6 and cluster analysis group 6D. However, when the level of agreement is calculated, it is much lower than at the three-group level at 53%. Again, it can be seen that the TWINSPAN groups are not as tightly clustered as the cluster analysis groups. TWINSPAN group 2 is similar to group 9C at the nine-group level of cluster analysis.

Examination of the results of both methods of classification at the nine-group level (Figure 4-46) again shows a broadly similar pattern of clustering, the most obvious differences being at the boundaries between groups and the formation of TWINSPAN group 5 and cluster analysis group 9H which do not have equivalents in both classifications. The level of agreement between the two methods is similar to that for the six group-level at 52%.

Although the TWINSPAN analysis does not give such good results when analysed with MRPP, its similarity to the cluster analysis does provide supporting evidence for the validity of the cluster analysis groups. Furthermore, the much higher level of agreement between TWINSPAN and cluster analysis at the three-group level supports the conclusion that the three-group level can be regarded as relatively discrete.

a) TWINSPAN groups



b) Cluster analysis groups

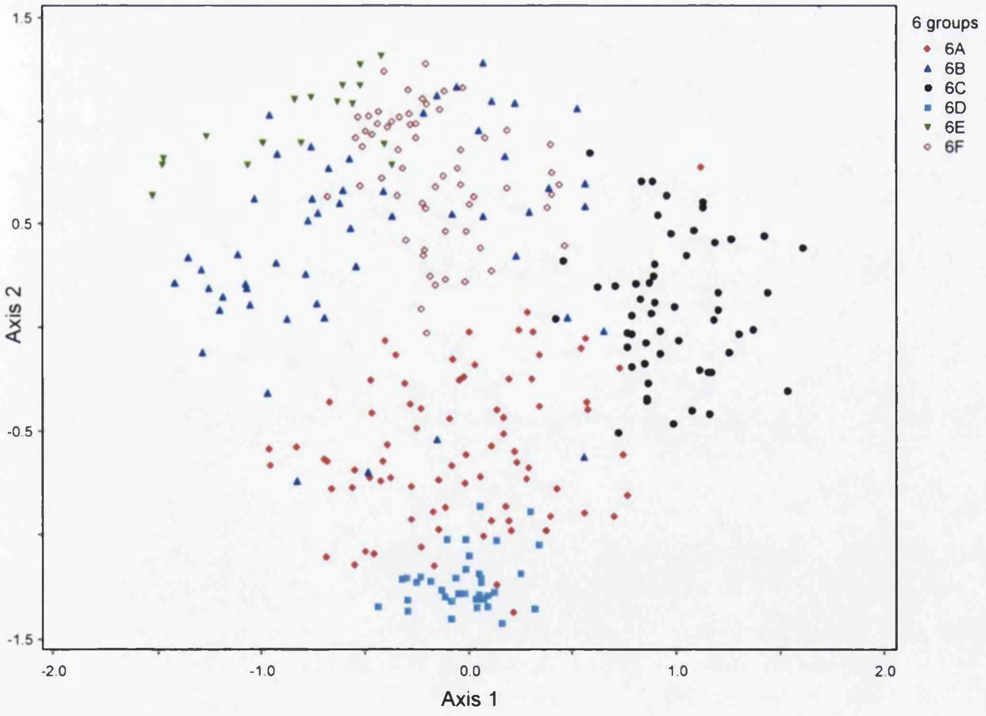
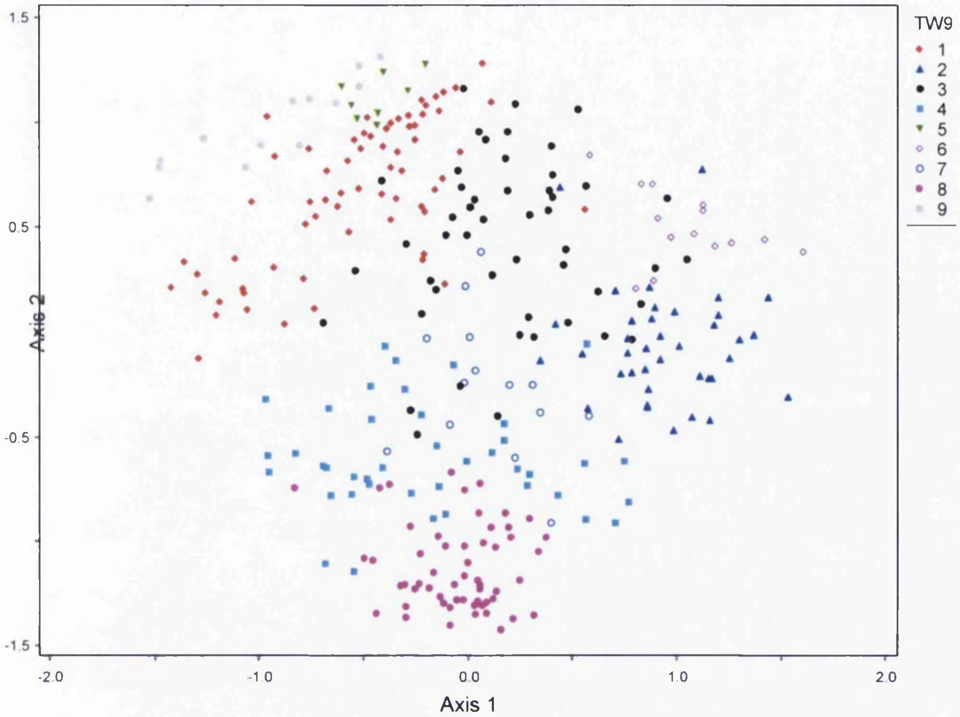


Figure 4-45. NMS ordination of roadside pioneer sites at the six-group level: (a) TWINSPAN groups; (b) cluster analysis groups.

a) TWINSPAN groups



b) Cluster analysis groups

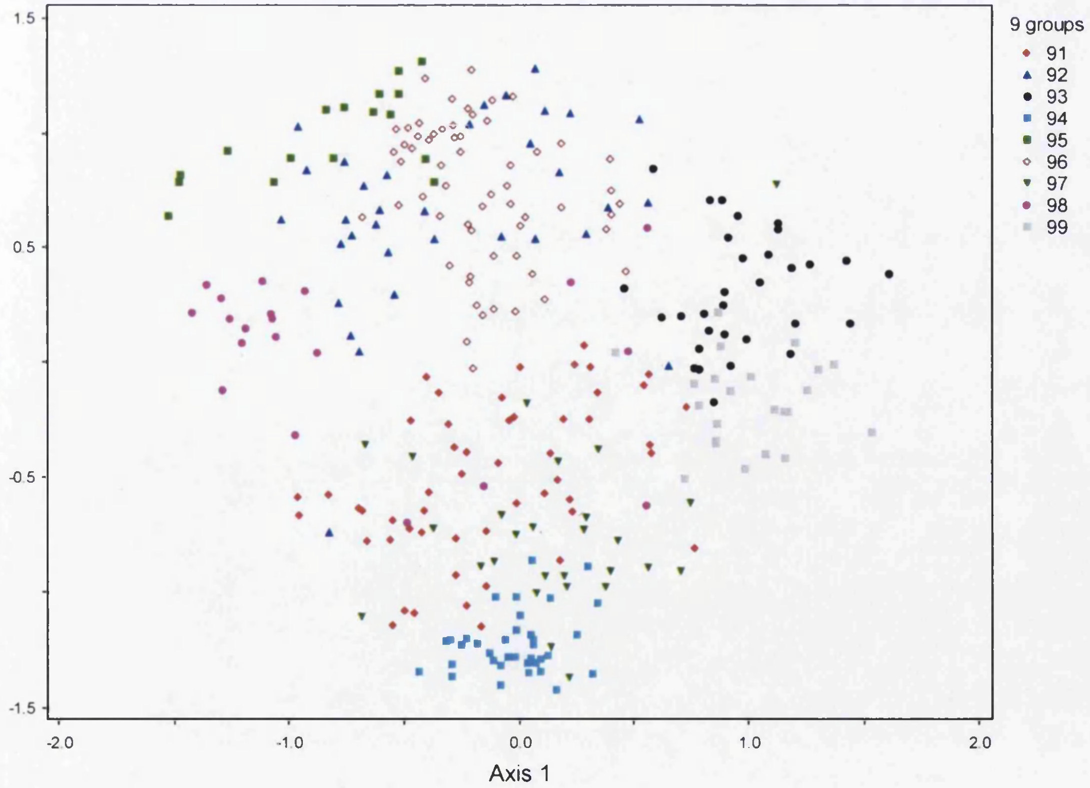


Figure 4-46. NMS ordination of roadside pioneer sites at the nine-group level: (a) TWINSPAN groups; (b) cluster analysis groups.

4.6 Summary

4.6.1 *How variable is the pioneer stage of succession on roadsides?*

1. One hundred and fifty-two species were recorded on the 300 roadside pioneer sites. Only four species were recorded on ≥ 50% sites, 22 species on ≥ 20% sites and 105 species on less than 5% sites. The pioneer stage on roadside verges is therefore highly variable, with only a small percentage of species having a widespread distribution.

2. The species are mainly perennial grasses and forbs. The most frequently occurring species are *Festuca ovina*, *Salix glauca*, *Agrostis capillaris* and *Deschampsia cespitosa.* The majority are adapted for wind dispersal and are also able to propagate vegetatively. These characteristics are typical of pioneer vegetation in general.

3. The mean Sørensen distance as a measure of variability within the pioneer stage on roadside verges is 0.81 (± 0.004), further evidence of a high level of overall variability. However, no sites qualify as statistical outliers (≥ 3 standard deviations from the mean). The sites with the greatest mean Sørensen distance from all other sites include six higher altitude sites (characterised by high relative abundances of one or two species) and two lower altitude sites (characterised by high relative abundances of shrubs and tree seedlings) which support the view that these are extremes of the range of a single population rather than outliers.

4.6.2 *Does pioneer roadside vegetation consist of a number of distinct communities?*

1. The two-dimensional non-metric multidimensional scaling (NMS) ordination diagram (Figure 4-3) shows areas of relatively tightly clustered sites and areas with a lower concentration of sites, suggesting possible divisions into

communities. These communities were investigated further at the three-group level of cluster analysis.

2. MRPP statistics indicate that the optimum separation between cluster analysis groups and the greatest increase in within-group agreement occurs at the three-group level (Section 4.5.1). Indicator analysis of these three groups reveals a *Deschampsia cespitosa-Trifolium repens* community (3A), a *Festuca ovina-Luzula spicata* community (3B) and a *Deschampsia flexuosa-Salix glauca* community (3C). These are ecologically interpretable communities characterized by species typical of relatively low altitude (3A), relatively high altitude (3B) and relatively low disturbance (3C). The weighted ordination scores for indicator species also showed clear separation on the NMS diagram.

3. Variability in the patterns of abundance of the main indicator species for these three communities was explored further by indicating the relative abundance of indicator species within each group (Figures 4-12 to 4-32) as a means of assessing the usefulness of each indicator. This method also detected the existence of possible sub-communities.

4. The six-group level of cluster analysis also shows clear separation between indicator species for most groups but with generally lower indicator values (Table 4-13). These six groups, termed 'sub-groups' or 'sub-communities', are characterized by *Deschampsia cespitosa-Taraxacum* agg. (6A), *Cerastium cerastoides-Deschampsia alpina* (6B), *Deschampsia flexuosa-Betula pubescens* (6C), *Plantago major-Trifolium repens* (6D), *Luzula arcuata-Ranunculus glacialis* (6E) and *Festuca ovina-Antennaria dioica* (6F). The mean discreteness index (DI) (the mean between-group distance divided by the mean within-group distance) for this level of clustering revealed only a marginal increase from the three-group level.

5. The nine-group level of cluster analysis does not produce such clear divisions between groups and the indicator values tend to decrease further. This level of cluster analysis is best regarded as creating sub-divisions of a

continuum of variation rather than identifying natural communities. The mean DI value for the nine-level did not show an improvement on the six-group level. (DI values are 1.5 for the three-group level, 1.6 for the six-group level and 1.6 for the nine-group level.)

6. It is concluded that the pioneer vegetation on roadsides displays a high degree of variability in species composition. Three main communities are recognized, which can be further divided into six sub-communities. The nine-group level represents a more arbitrary division of sites within a continuum of change in species composition.

5 THE PIONEER VEGETATION OF GLACIER FORELANDS AND THE ADDITIONAL DISTURBED HABITATS

5.1 Introduction

This chapter describes the pioneer vegetation of glacier forelands and additional types of disturbed habitat and addresses four key questions, the first two of which are similar to those addressed in relation to the pioneer stage on roadside verges, namely: (1) how variable is species composition and abundance in the pioneer stage of succession on glacier forelands and; (2) does pioneer vegetation on glacier forelands consist of a number of distinct communities? The third question asks whether the characteristics of pioneer vegetation identified for roadside and glacier foreland sites are consistent across a range of additional pioneer habitats. The fourth question asks whether the same pioneer communities characterize different pioneer habitats or are habitat-specific. The data set from glacier forelands provides evidence from a contrasting habitat type for detailed comparison with the roadside data presented in Chapter 4, while the data set from the additional pioneer habitats is used to generalize further. Data analyses follow similar procedures to those outlined in the introduction to Chapter 4.

5.2 Species composition and abundance on glacier foreland pioneer sites

A total of 71 species were recorded on glacier foreland pioneer sites, with seven species occurring on more than 50% of sites, 18 species on at least 20% of sites and 33 on less than 5% of sites. Table 5-1 lists all the species recorded on glacier foreland pioneer sites with their percentage frequency (the percentage of sites containing that species) and mean abundance (the mean relative frequency of that species).

Table 5-1. Species recorded on glacier foreland pioneer sites.

Code	Species	% Sites	Mean abundance
Poaalp	*Poa alpina*	92.86	18.36
Oxydig	*Oxyria digyna*	85.71	13.17
Desalp	*Deschampsia alpina*	83.33	9.93
Fesovi	*Festuca ovina*	80.95	5.41
Ceralp	*Cerastium alpinum*	76.19	8.91
Trispi	*Trisetum spicatum*	59.52	7.55
Rangla	*Ranunculus glacialis*	57.14	7.57
Salgla	*Salix glauca*	47.62	1.95
Araalp	*Arabis alpina*	45.24	4.50
Saxces	*Saxifraga cespitosa*	45.24	1.86
Saxste	*Saxifraga stellaris*	38.10	3.41
Saxopp	*Saxifraga oppositifolia*	38.10	1.71
Silaca	*Silene acaulis*	35.71	0.95
Epiana	*Epilobium anagallidifolium*	28.57	1.52
Luzspi	*Luzula spicata*	26.19	1.14
Salher	*Salix herbacea*	26.19	0.98
Phlalp	*Phleum alpinum*	21.43	0.98
Omanor	*Omalotheca norvegica*	21.43	0.41
Omasup	*Omalotheca supina*	19.05	0.62
Saxriv	*Saxifraga rivularis*	16.67	0.83
Luzarc	*Luzula arcuata*	16.67	0.55
Chaang	*Chamerion angustifolium*	14.29	0.74
Athdis	*Athyrium distentifolium*	14.29	0.55
Arapet	*Arabidopsis petraea*	11.90	0.21
Rumlla	*Rumex acetosella*	9.52	0.48
Alcalp	*Alchemilla alpina*	9.52	0.31
Crycri	*Cryptogramma crispa*	9.52	0.17
Saxniv	*Saxifraga nivalis*	9.52	0.14
Taragg	*Taraxacum* aggregate	9.52	0.14
Rhoros	*Rhodiola rosea*	9.52	0.10
Saxcer	*Saxifraga cernua*	7.14	0.69
Polviv	*Polygonum viviparum*	7.14	0.29
Carbig	*Carex bigelowii*	7.14	0.19
Gymdry	*Gymnocarpium dryopteris*	7.14	0.12
Minbif	*Minuartia biflora*	7.14	0.12
Veralp	*Veronica alpinum*	7.14	0.12
Betpub	*Betula pubescens*	7.14	0.10
Leoaut	*Leontodon autumnalis*	7.14	0.07
Narstr	*Nardus stricta*	4.76	0.26
Agrcap	*Agrostis capillaris*	4.76	0.19
Juntrf	*Juncus trifidus*	4.76	0.12
Saxazo	*Saxifraga azoides*	4.76	0.07
Camrot	*Campanula rotundifolia*	4.76	0.05
Empher	*Empetrum hermaphroditum*	4.76	0.05
Sagsag	*Sagina saginoides*	4.76	0.05
Visalp	*Viscaria alpina*	4.76	0.05
Desces	*Deschampsia cespitosa*	2.38	0.55
Cercer	*Cerastium cerastoides*	2.38	0.31
Ranrep	*Ranunculus repens*	2.38	0.26
Cirhet	*Circium heterophyllum*	2.38	0.19

Code	*Species*	% Sites	Mean abundance
Wooalp	*Woodsia alpina*	2.38	0.17
Viobif	*Viola biflora*	2.38	0.14
Alcglo	*Alchemilla glomerulans*	2.38	0.12
Alninc	*Alnus incana*	2.38	0.12
Phycae	*Phyllodoce caerulea*	2.38	0.07
Lotcor	*Lotus corniculatus*	2.38	0.05
Stearv	*Stellaria arvensis*	2.38	0.05
Antdio	*Antennaria dioeca*	2.38	0.02
Antodo	*Anthoxanthum odoratum*	2.38	0.02
Carbel	*Cardamine bellidifolia*	2.38	0.02
Epihor	*Epilobium hornemannii*	2.38	0.02
Equsci	*Equisetum scirpoides*	2.38	0.02
Hiealp	*Hieracium alpinum*	2.38	0.02
Ortsec	*Orthilia secunda*	2.38	0.02
Petfri	*Petasites frigidus*	2.38	0.02
Sallan	*Salix lanata*	2.38	0.02
Sedvil	*Sedum villosum*	2.38	0.02
Sibpro	*Sibbaldia procumbens*	2.38	0.02
Sildio	*Silene dioica*	2.38	0.02
Solvir	*Solidago virgaurea*	2.38	0.02
Urtdio	*Urtica dioica*	2.38	0.02

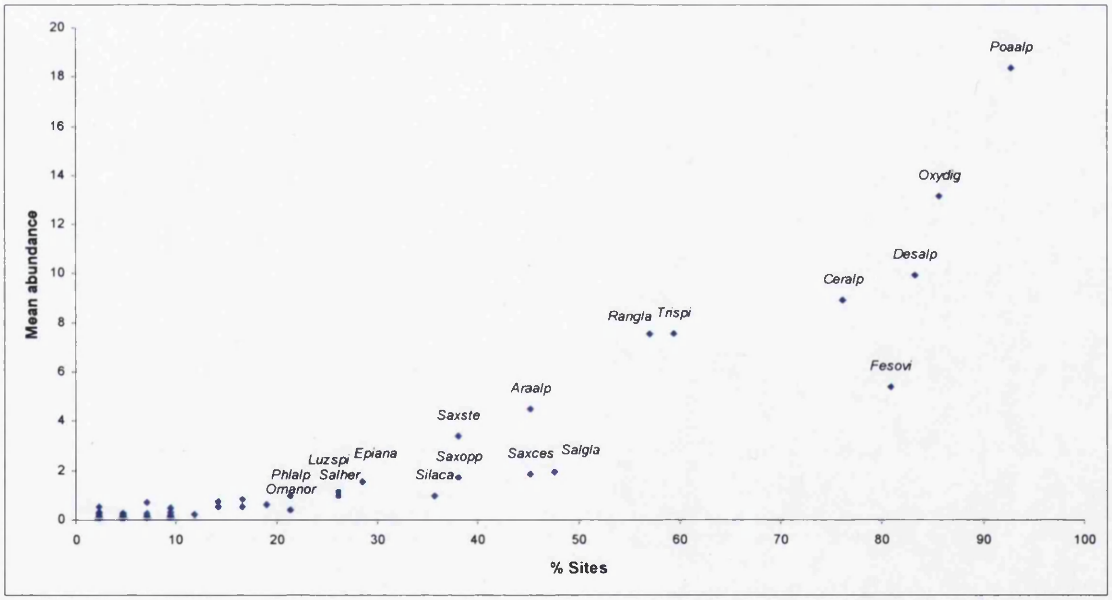


Figure 5-1. Mean abundance of glacier foreland pioneer species and the percentage of sites on which each species occurs. Species occurring on ≥ 20% of sites are labelled. Abbreviated species names are listed in full in Table 5-1.

Figure 5-1 illustrates the relationship between percentage frequency and mean abundance, with species occurring on ≥ 20% sites labelled. *Poa alpina* has the highest frequency and mean abundance of the glacier foreland pioneers, occurring on 93% of sites with a mean abundance of 18%. Three other species occur with a frequency greater than 80%: *Oxyria digyna* (86%), *Deschampsia alpina* (83%) and *Festuca ovina* (81%) and of these *O. digyna* has the highest mean abundance at 13%. Three of the four most frequent species are Poaceae, with two other grasses also occurring at relatively high frequencies: *Trisetum spicatum* (60%) and *Phleum alpinum* (21%). Of the remaining species recorded on more than 20% of foreland pioneer sites, *Cerastium alpinum* has the highest frequency at 76%, followed by *Ranunculus glacialis* (57%), *Salix glauca* (48%) and *Arabis alpina* (45%). *C. alpinum, T. spicatum* and *R. glacialis* also have high mean relative abundances at 9%, 8% and 8% respectively. *S. herbacea* is present on 26% of glacier foreland pioneer sites and three *Saxifraga* spp also occur with high frequency: *S. cespitosa* (45%), *S. oppositifolia* (38%) and *S. stellaris* (38%). The last species has the highest mean abundance at 3%. *Silene acaulis* was recorded on 15 sites out of 42, a frequency of 36%, and *Epilobium anagallidifolium, Luzula spicata* and *Omalotheca norvegica* were also found on more than 20% of sites.

The glacier foreland pioneer community, like that of roadsides, is therefore predominantly herbaceous, consisting of grasses and forbs, with the shrubs *Salix glauca* and *S. herbacea* also attaining high relative abundances. All species are perennials and the majority are adapted for either water- or wind-dispersal and also have the capacity for vegetative propagation. Six species (*Poa alpina, Festuca ovina, Salix glauca, S. herbacea, Luzula spicata* and *Phleum alpinum*) occur on at least 20% of both glacier foreland and roadside sites. However, the total number of species recorded on glacier forelands (71) is considerably lower than that for roadsides (152), while the number of species occurring on at least 50% of sites is higher for the glacier forelands (seven species) than the roadside data set (four species). Both these comparisons suggest a greater degree of uniformity within glacier foreland sites than within roadside sites.

5.3 Variability of glacier foreland pioneer sites

The mean Sørensen distance between glacier foreland sites, as a measure of the overall variability within this data set, is 0.649 (± 0.025) with a standard deviation of 0.0797. Figure 5-2 shows the frequency distribution of mean distances between sites. A D'Agostino-Pearson test for normality showed that the data are not normally distributed (p < 0.001) with a weak positive skew of 1.42. Variability is therefore considerably lower than for the roadside data set (0.811) and the glacier foreland data also differs in having a positively skewed rather than normal distribution.

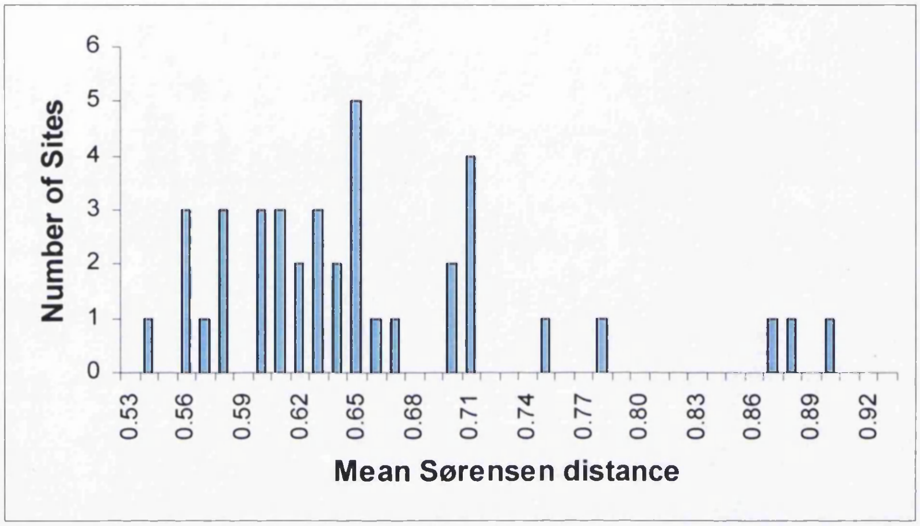


Figure 5-2. Frequency distribution of mean Sørensen distance between glacier foreland pioneer sites.

Outlier analysis was carried out to discover which sites have the greatest mean dissimilarity from other sites and this identified no sites with a mean dissimilarity of more than 3 standard deviations from the grand mean. The three forelands with the greatest mean Sørensen distances from other sites are Vivakulen (P12) (mean distance = 0.88; SD = 2.93) , Bøyabreen (P2) (mean distance = 0.87, SD = 2.79) and Besshobreen (P41) (mean distance = 0.84, SD = 2.45). Vivakulen has only 2 species present (*Luzula arcuata* and *Oxyria digyna*); Bøyabreen has 22 species, 8 of which do not occur on other forelands; and Besshobreen is unusual in having a relative frequency of 86% *Ranunculus glacialis* and only two other species (*Poa alpina* and *Festuca ovina*). As was the case with the roadside data, these are considered to be extremes rather than outliers and will be included in subsequent analyses. Bøyabreen with eight rare species is a possible candidate for exclusion as an outlier, but its mean distance from other sites is lower than that of Vivakulen and its exclusion cannot therefore be justified.

5.4 Ordination of glacier foreland pioneer sites

In order to investigate the relationship between glacier foreland pioneer sites in terms of their species composition, NMS ordination was carried out. Ordination with all sites and species included resulted in a stress of 19.7% for two dimensions (p = 0.0196) and 13.7% for three dimensions (p = 0.0196). Instability reached an acceptable level at 10^{-5} for three dimensions after 112 iterations and 10^{-4} for two dimensions after 50 iterations. The stress levels are fairly high for the relatively small number of sites compared to the roadside data set, suggesting greater randomness or less structure in the variation in species composition between sites.

For comparison with the roadside data set ordination, the 25 species recorded on only one site were excluded and the ordination was repeated. This resulted in a three-dimensional ordination with a stress level of 17.3%, which was not significantly lower than the stress level for randomized data (15.3%, p = 0.226) and a two-dimensional ordination with a significantly lower stress level than for randomized data of 22.4% (p = 0.0323) but with a high level of instability at 0.024 after 400 iterations. Finding a stable solution therefore seems to be dependent on including rare species, which also suggests a relatively weak structure to the data.

The ordination was assessed further by calculating coefficients of determination for the correlation between ordination distances and distances in the original n-dimensional space. The cumulative r^2 for the three-dimensional ordination is 0.81, while that for two-dimensional ordination is 0.76. There is therefore an increase in stress of only 6% and a reduction in the coefficient of determination of only 5% if two axes are used instead of three. Instability is higher for two dimensions than for three but both are within acceptable limits. Two dimensions will therefore be used rather than three, as this facilitates interpretation of the ordination diagram (and comparison with the roadside data).

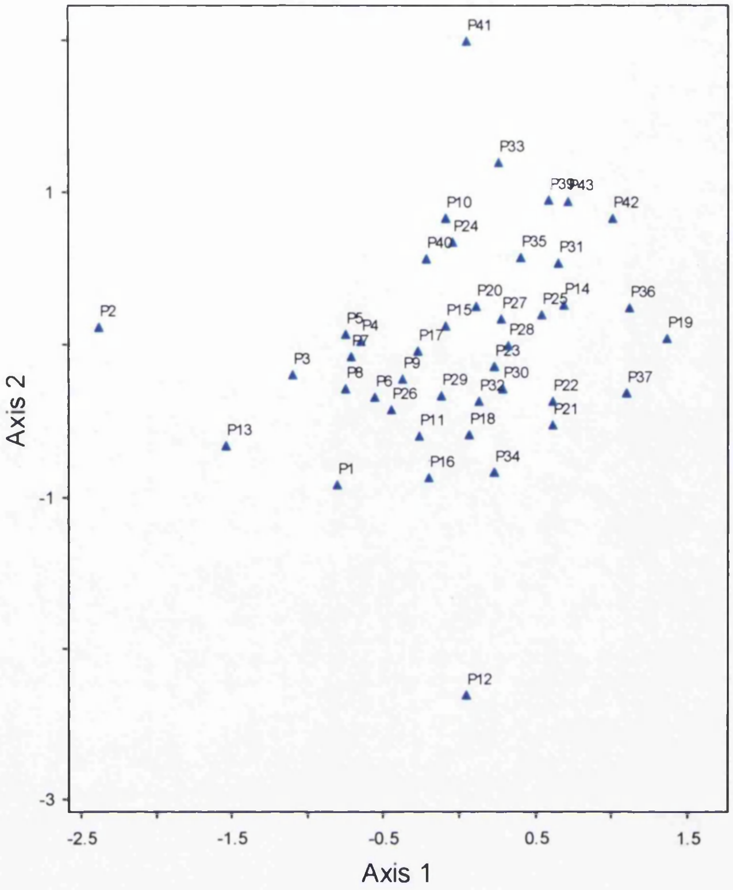
Visual examination of the NMS ordination diagram (Figure 5-3a) does not reveal any obvious clusters or clear divisions between groups of sites which could form the basis for classification. However, the three sites which were identified as extremes, Vivakulen (P12), Bøyabreen (P2) and Besshobreen (P41), are clearly separated from each other and from the majority of other sites on the ordination diagram.

In order to compare the results of NMS with another method of ordination and to ensure that the pattern produced is not an artefact of NMS, DCA was carried out on the glacier foreland pioneer data set. Comparison of Figures 5-3a and b reveals that, although there are differences in the positions of individual sites, the overall pattern is quite similar, particularly when allowance is made for the fact that the DCA analysis is based on the first two axes only. However, the coefficients of determination between distance in ordination space and that of the original distance matrix for the DCA ordination show a lower cumulative correlation for axes 1 and 2 of 51% compared with 76% for the NMS axes (Table 5-2). These values confirm that the NMS ordination more accurately reflects the information in the original distance matrix and hence it will be used as the preferred method in further analyses.

Table 5-2. Coefficients of determination (r^2) for glacier foreland pioneer ordination axes.

Axis	Incremental r2	Cumulative r2
NMS 1	0.356	0.356
NMS 2	0.406	0.763
DCA 1	0.380	0.380
DCA 2	0.129	0.507
DCA 3	0.090	0.597

a) NMS ordination



b) DCA ordination

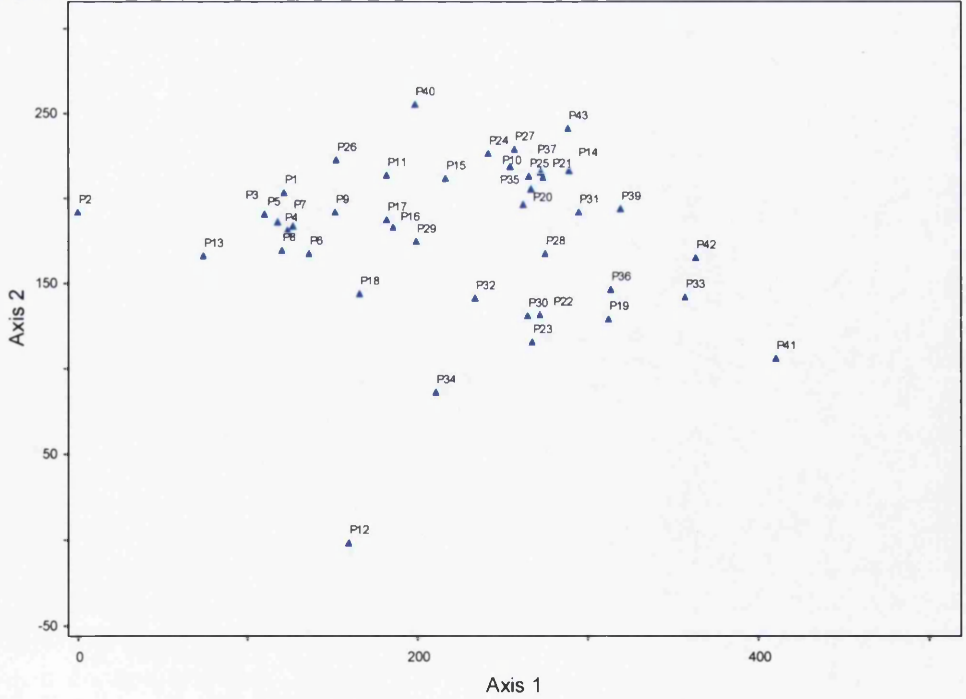


Figure 5-3. Ordination of glacier foreland pioneer sites: a) NMS; b) DCA.

5.5 Classification and indicator species analysis of glacier foreland pioneer sites

5.5.1 Assessment of the optimum level for glacier foreland pioneer site classification

Cluster analysis of all glacier foreland pioneer sites was carried out and the degree of chaining was within acceptable limits at 5.65%. The cluster analysis dendrogram is included in Appendix III. The effects on the classification of including the three most extreme sites (described in section 5.3) should be noted here. At the three-group level, sites P2 (Vivakulen) and P12 (Bøyabreen) form a separate two-site group which subsequently forms two single-site groups at the five-group level. The initial clustering of these two sites clearly reflects their dissimilarity from other sites in terms of species composition rather than any similarity between them. Furthermore, the subsequent formation of single-group sites means that they cannot be used in MRPP and indicator species analysis. It is also worth noting that at the four-group level P41 (Besshobreen) forms a two-site group with P33 (Austabotbreen). Both these forelands have high relative frequencies of *Rancunculus glacialis* but are not otherwise unusual and are therefore not regarded as outliers.

MRPP analysis to identify the level of clustering which provides the greatest separation between groups and agreement within groups was carried out up to the four-group level only with all sites included, as above this level the data split into single-site groups. To check the effects of the three most extreme sites, MRPP was also carried out up to the eight-group level with these sites excluded. The MRPP statistics reveal that separation between groups is generally low (T = -12.1 to -14.3 with all sites included and -11.8 to -15.3 without extreme sites) (Table 5-3) and the T statistic is lower for the three groups than for two or four in both analyses. Further analysis will therefore concentrate on the two and four-group levels of cluster analysis.

Table 5-3. MRPP statistics for cluster analysis of glacier foreland pioneer sites.

a) all sites

Number of Clusters	T	A	Observed δ	p
2	-14.3	0.089	0.591	< 0.001
3	-12.1	0.127	0.566	< 0.001
4	-13.3	0.172	0.528	< 0.001

Expected δ = 0.656

b) with three sites excluded

Number of Clusters	T	A	Observed δ	p
2	-13.7	0.091	0.574	< 0.001
3	-11.8	0.132	0.548	< 0.001
4	-13.6	0.179	0.518	< 0.001
5	-14.1	0.213	0.496	< 0.001
6	-15.0	0.252	0.472	< 0.001
7	-15.3	0.282	0.453	< 0.001
8	-15.1	0.306	0.438	< 0.001

Expected δ = 0.631

The two-group level may be considered most appropriate given the relatively small number of sites. Furthermore, as ordination did not reveal a strong structure in the data, it is likely that none of the groups is a natural group and therefore that division of the sites into groups is arbitrary at all levels. Assessment of the relative numbers of indicator species and the sum of significant indicator values at each level of clustering (Table 5-4) also show that the three-group level gives a lower value for both factors than the two- and four-groups levels.

Table 5-4. The number and sum of significant indicator values (IVs) for glacier foreland cluster analysis groups.

Number of groups	No. of significant IVs	Sum of significant IVs
2	16	806
3	6	433
4	15	937

5.5.2 Two glacier foreland pioneer groups

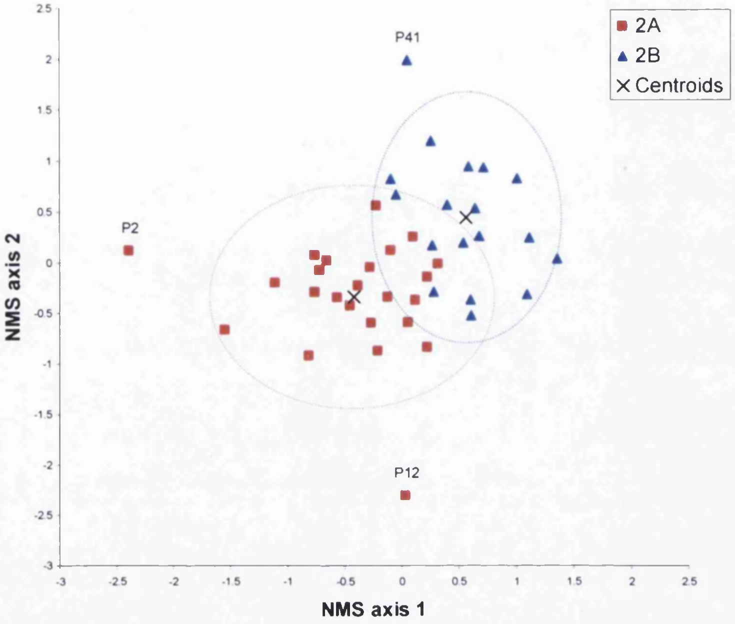


Figure 5-4. NMS ordination of glacier foreland pioneer sites with two colour-coded cluster analysis groups superimposed. Dashed ellipses indicate ±2 standard deviations from each group centroid.

Figure 5-4 shows that sites in group 2A tend to have lower scores on both axes than sites in group 2B. The ordination distance between sites at the border between the two groups does not show any discontinuity and there do not appear to be areas of tighter clustering within either of the two groups. The three extreme sites (P2, P12 and P41) are clearly at some considerable distance from other sites. Table 5-5 confirms that the mean within-group distance for both groups is comparable, with group 2A being slightly larger with 24 sites as opposed to 18 sites in group 2B. The number of significant indicator species in each group is similar (9 for group 2A and 7 for group 2B) and these are investigated in the next sub-section. The Discreteness Index (DI) for each of the two groups (Table 5-6) gives a similarly low value of approximately 1.2. Cluster and indicator species analyses with the three extreme sites excluded results in division of the two groups at the same coordinates in ordination space and the same species being indicators for the two groups.

Table 5-5. Descriptive statistics for two glacier foreland pioneer groups.

Group	n	Mean Within-Group Distance	No. of Significant Indicator Spp
2A	24	0.583	9
2B	18	0.602	7

Table 5-6. Mean between- and within-group distances for the two glacier foreland groups and the Discreteness Index (DI).

Group	Mean b-g distance	Mean w-g distance	DI
2A	0.711	0.583	1.220
2B	0.711	0.602	1.181

5.5.2.1 Indicator species analysis of two glacier foreland pioneer groups

Table 5-7. Significant indicator values (IV) for the two glacier foreland pioneer groups.

	Observed IV (%)		
Species	2A	2B	*p*
Desalp	**77**	13	0.001
Oxydig	**72**	17	0.003
Saxste	**62**	0	0.001
Epiana	**40**	0	0.011
Omasup	**33**	0	0.013
Phlalp	**32**	0	0.021
Omanor	**31**	0	0.029
Chaang	**25**	0	0.043
Athdis	**25**	0	0.045
Saxces	2	**69**	0.001
Trispi	6	**68**	0.003
Poaalp	29	**67**	0.003
Araalp	4	**58**	0.002
Rangla	11	**57**	0.012
Saxopp	3	**56**	0.002
Saxriv	0	**33**	0.01

Figures 5-5 and 5-6 graphically display the values in Table 5-7 for ease of assessment. The two most important indicator species for group 2A (*Deschampsia alpina* and *Oxyria digyna*) are also present in group 2B with lower values but the remaining seven species are absent from group 2B. With the exception of *Poa alpina* and *Ranunculus glacialis*, group 2B indicators have values < 10% in group 2A. *Saxifraga cespitosa* and *Trisetum spicatum* are the two most important indicators for group 2B. *D. alpina, O. digyna* and *P. alpina* are the most frequent and abundant pioneers on glacier foreland sites.

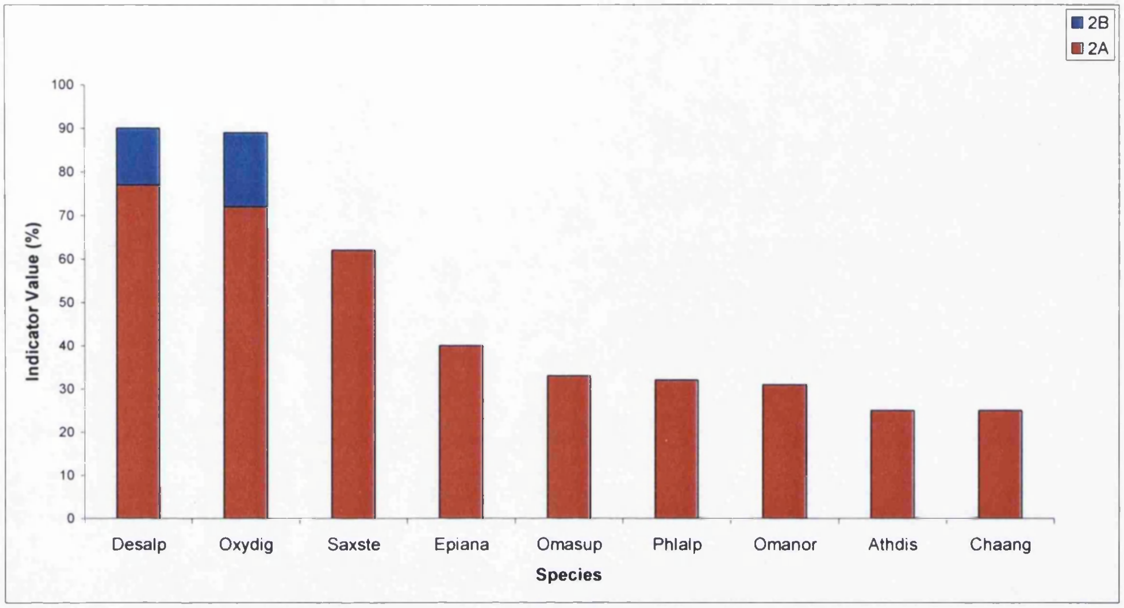


Figure 5-5. Group 2A indicator species showing indicator values across the two glacier foreland pioneer groups.

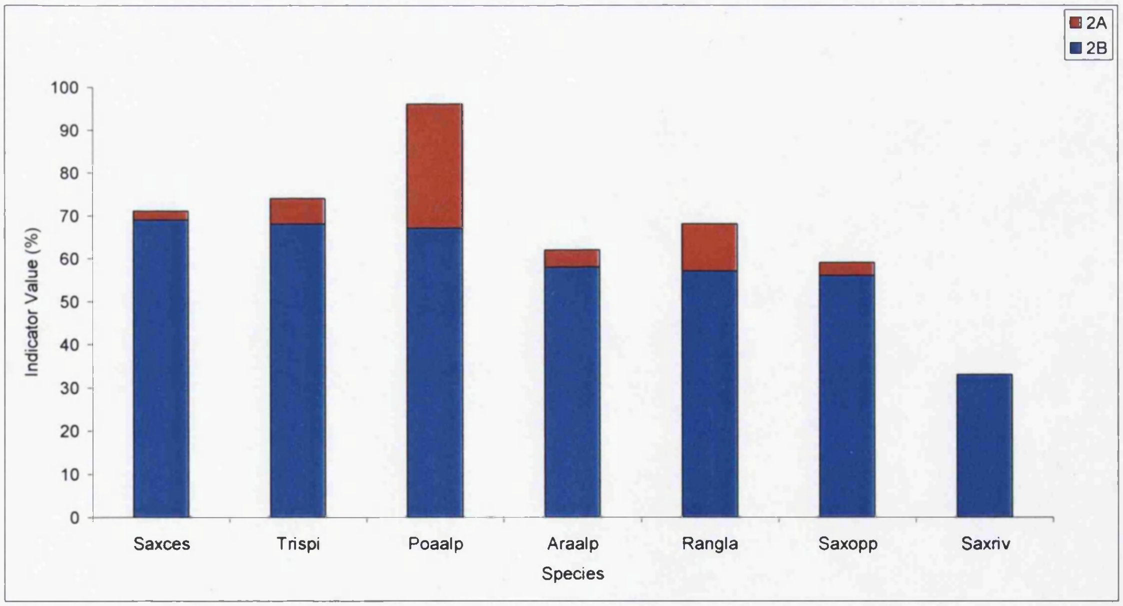


Figure 5-6. Group 2B indicator species showing indicator values across the two glacier foreland pioneer groups.

Preliminary assessment of the other indicator species for these two groups suggests that those indicative of group 2B may be species which are more often found at higher altitudes. However, all indicators identified for glacier foreland pioneer sites are species which tend to occur above the treeline, although a number of glacier foreland sites are at lower altitudes. The majority of group 2A indicators, with the exception of *Chamerion angustifolium* and *Athyrium distentifolium*, are species which characterize roadside group 6B, while group 2B has species in common with roadside group 6E.

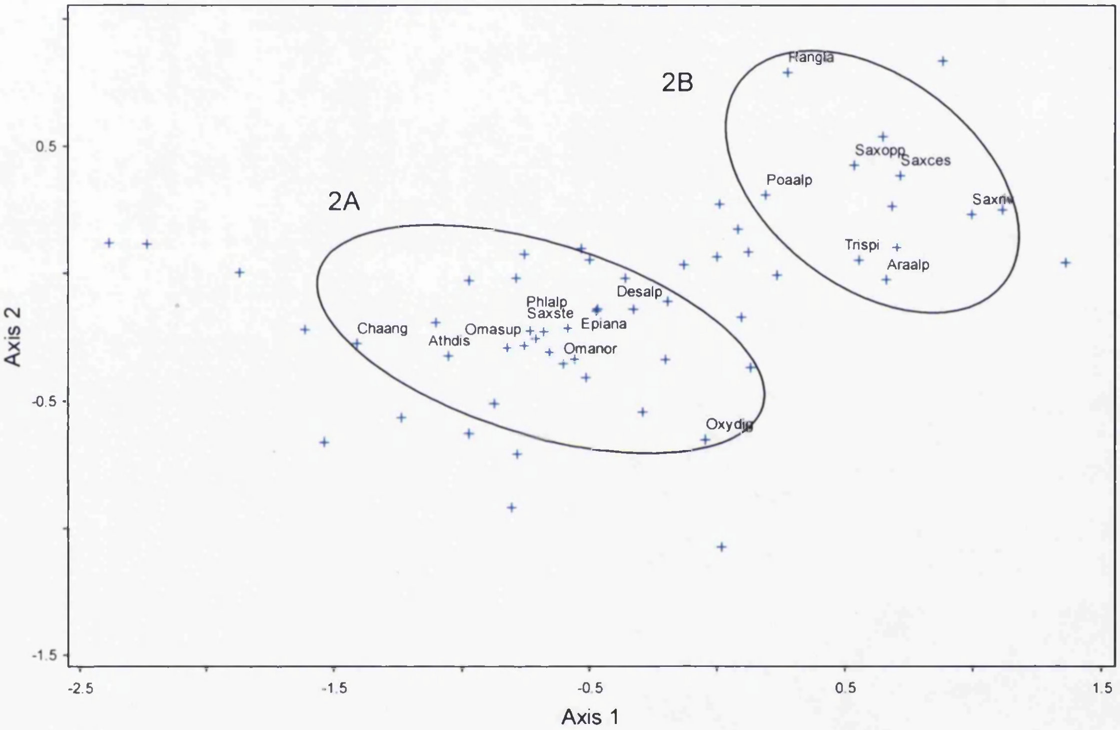


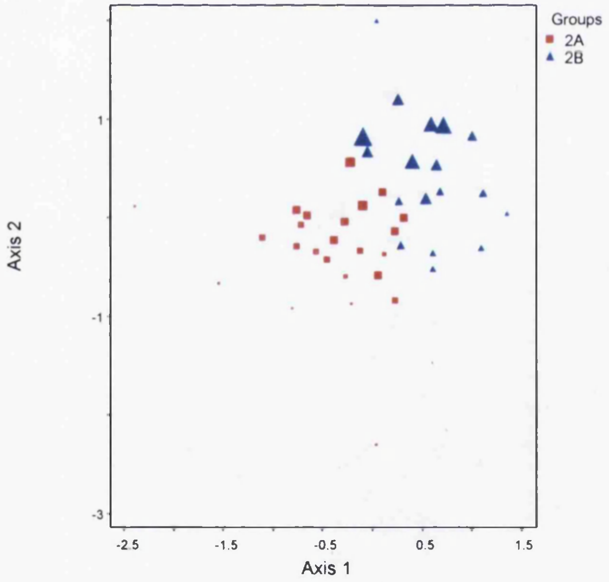
Figure 5-7. NMS ordination of glacier foreland pioneer sites at the two-group level showing weighted scores for indicator species. Envelopes indicate the two separate groups.

The position of indicator species on the ordination diagram (Figure 5-7) shows that they fall into two distinct groups. However, in the light of previous conclusions, they may be better considered as two ends of a gradient. The three most widespread species (*Poa alpina, Oxyria digyna* and *Deschampsia alpina*) are located towards the centre, which could be interpreted as a feature of the whole gradient, but their relative abundances place them within a specific group.

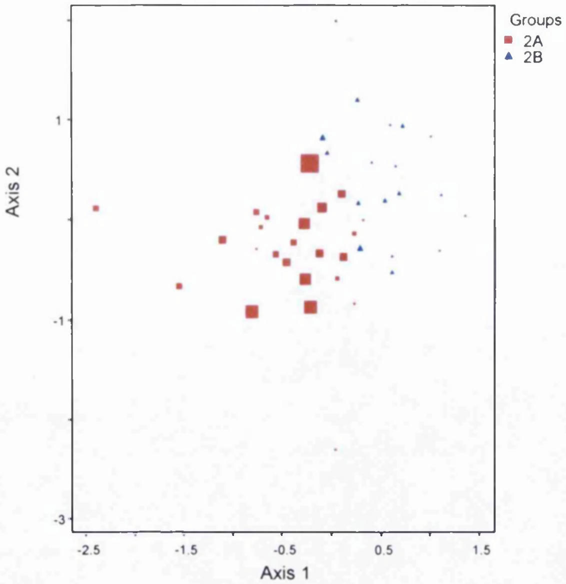
5.5.2.2 Relative abundance of indicator species for the two glacier foreland pioneer groups

Examination of the relative abundances of the three most widespread species at individual sites on the ordination diagrams in Figure 5-8 shows a gradual gradient across the group boundary for *P. alpina* and a relatively sharp boundary change for *D. alpina* and *O. digyna*. The other indicators species show similar distributions within group 2A, with the exception of *Athyrium distentifolium,* which is concentrated towards the lower end of axis 1 as indicated by its position on Figure 5-7. Group 2B indicators also show a similar pattern and their occurrences in group 2A tend to be at the sites with the highest scores on axis 1. There is reasonably good separation between these two groups but the border between them is determined by the absence of group 2A indicators from group 2B rather than *vice versa*. The separation is not therefore considered good enough to confer group status.

a)*Poa alpina*



b) *Deschampsia alpina*



c) *Oxyria digyna*

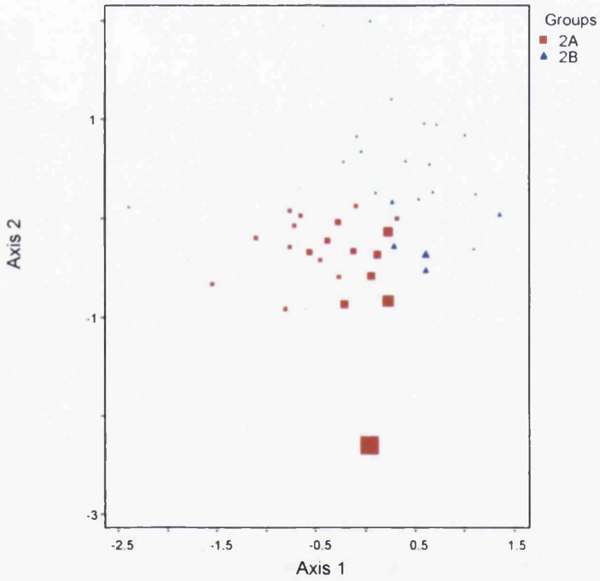


Figure 5-8. Relative abundance of a) *Poa alpina, b) Deschampsia alpina and c) Oxyria digyna* on glacier foreland pioneer sites.

5.5.2.3 Summary and naming of the two glacier foreland pioneer groups

There is reasonably good separation between glacier foreland sites at the two-group level but the evidence suggests that these groups are part of a continuum of variation. The gradient of relative abundance in a number of indicator species suggests that these are sub-groups, rather than having group status. It is possible to name the two sub-groups on the basis of the most important indicator species: sub-group 2A *Deschampsia alpina-Oxyria digyna* (Desalp-Oxydig); sub-group 2B, *Saxifraga cespitosa-Trisetum spicatum* (Saxces-Trispi).

5.5.3 Four glacier foreland pioneer groups

Clustering of the glacier foreland pioneer sites into four groups (Figure 5-9) produces a group of seven sites (group 4C), which were formerly part of group 2A and a small group of two sites (group 4D), which previously belonged to group 2B, P41 (Besshobreen) and P33 (Austabotbreen). Group 4C consists of sites with relatively low scores on axis 1, while the two sites in group 4D have high scores on axis 2.

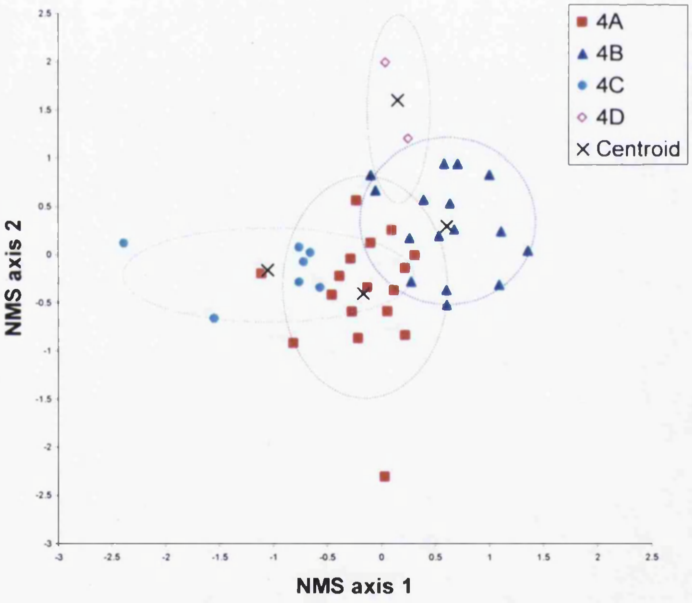


Figure 5-9. NMS ordination of glacier foreland pioneer sites with four colour-coded cluster analysis groups superimposed. Dashed ellipses indicate ±2 standard deviations from each group centroid.

Table 5-8 shows that group 4D, the smallest group is, not surprisingly, the most tightly clustered, Group 4C has a mean within-group distance of 0.48, followed by group 4A at 0.50, and group 4B is the least tightly clustered group with a mean within-group distance of 0.57. Groups 4A to 4C appear to be divided along a continuum of change rather than being separate clusters of sites, while group 4D is based on a very small number of sites.

Table 5-8. Descriptive statistics for the four glacier foreland pioneer cluster analysis groups.

Group	n	Mean within-group distance	No. of significant indicator spp
4A	17	0.552	2
4B	16	0.570	3
4C	7	0.553	9
4D	2	0.370	1

The DI for each of the four groups (Table 5-9) shows that the smallest group (4D) is the most discrete with a value of 2.2 and the two main groups, 4A and 4B have similar values of 1.27 and 1.28 respectively.

Table 5-9. Mean between- and within-group distances for the four glacier foreland groups and the Discreteness Index (DI).

Group	Mean b-g distance	Mean w-g distance	DI
4A	0.703	0.552	1.274
4B	0.729	0.570	1.279
4C	0.770	0.553	1.392
4D	0.802	0.370	2.168

5.5.3.1 Indicator species analysis of four glacier foreland pioneer sub-groups

Table 5-10. Significant indicator values (IV) for the four glacier foreland pioneer sub-groups.

	Observed IV (%)				
Species	**4A**	**4B**	**4C**	**4D**	*p*
Oxydig	**53**	12	23	1	0.043
Desalp	**52**	9	27	2	0.023
Trispi	8	**74**	0	0	0.004
Araalp	6	**64**	0	0	0.027
Saxces	3	**58**	0	9	0.035
Salgla	6	5	**71**	0	0.003
Chaang	0	0	**71**	0	0.019
Epiana	4	0	**69**	0	0.012
Omasup	3	0	**66**	0	0.022
Saxste	14	0	**63**	0	0.018
Phlalp	2	0	**62**	0	0.025
Crycri	0	0	**57**	0	0.011
Athdis	1	0	**53**	0	0.019
Omanor	7	0	**39**	0	0.047
Rangla	4	4	0	**87**	0.001

Table 5-10 presents the results of indicator species analysis for the four glacier foreland pioneer sub-groups. Group 4A has only two significant indicator species: *Oxyria digyna* (53%) which is also a fairly high indicator of group 4C (23%), and *Deschampsia alpina* (52%) which has a value of 27% in group 4C. Group 4C has the largest number of indicators (9), all of which are either absent from or have values of 10% or less in other groups with the exception of *Saxifraga stellaria,* which has a value of 14% in group 4A. Group 4B has three indicator species: *Trisetum spicatum* (74%), *Arabis alpina* (64%) and *Saxifraga cespitosa* (58%), none of which has a value of more than 10% in another group. Group 4D is characterised by one species, *Ranunculus glacialis* (87%), which has low indicator values within two of the other groups.

On the basis of this evidence, there seems little justification for subdivision into four sub-groups. Group 4A is characterized solely on the relative abundance of only two widespread species, while group 4D consists of only two sites and is characterized by a single species. Groups 4A, 4B and 4C appear to be part of a continuum of change, rather than distinct communities. Figure 5-10 illustrates the weighted species ordination scores for these indicators.

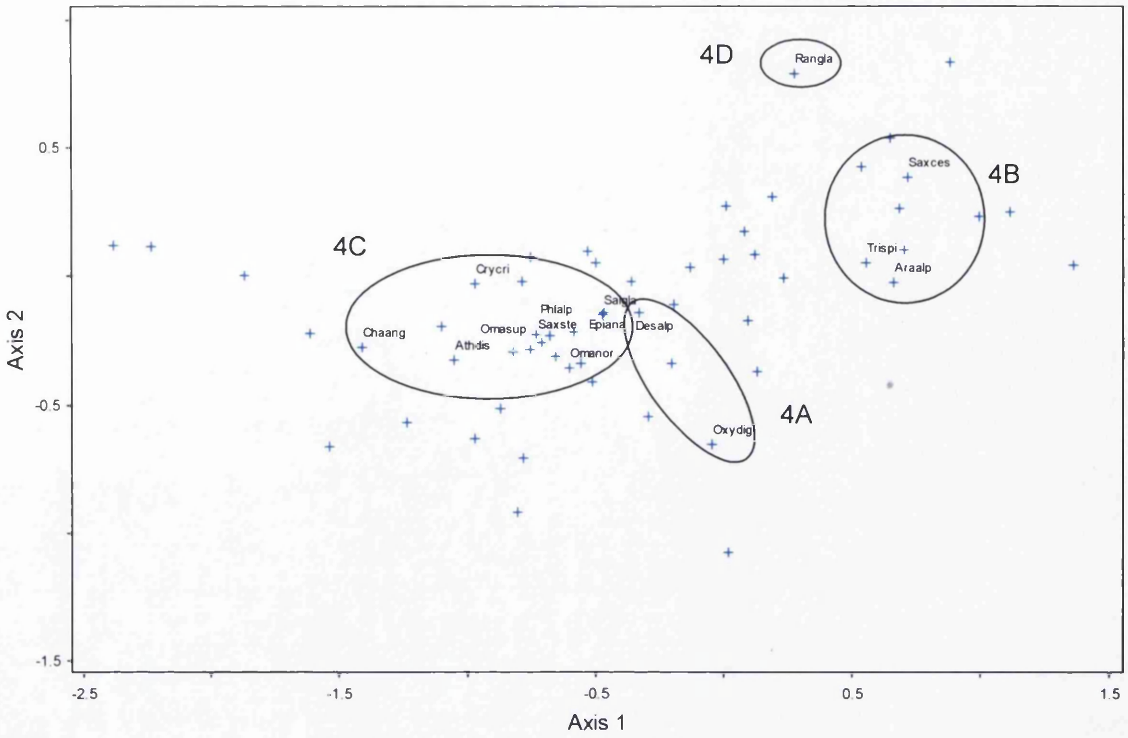


Figure 5-10. NMS ordination of glacier foreland pioneer sites at the four-group level showing weighted scores for indicator species. Envelopes indicate the four separate groups.

5.5.4 Summary of differences in indicator values for glacier foreland pioneer groups

Table 5-11 shows indicator species and their values at the two- and four-group levels of cluster analysis with the maximum value reached shown in bold type. As expected, the two-group level gives higher values for widespread species, while the four-group level introduces a number of new indicator species which have narrower ranges. The number of maxima increases to 11 at the four-group stage and the mean maximum increases to 67. This differs from the pattern observed for the roadside data set, in which the number of maxima and the mean maximum value both decreased slightly as additional groups were added.

Table 5-11. Species indicator values at each stage of glacier foreland pioneer cluster analysis. Maximum values for each species are indicated in bold.

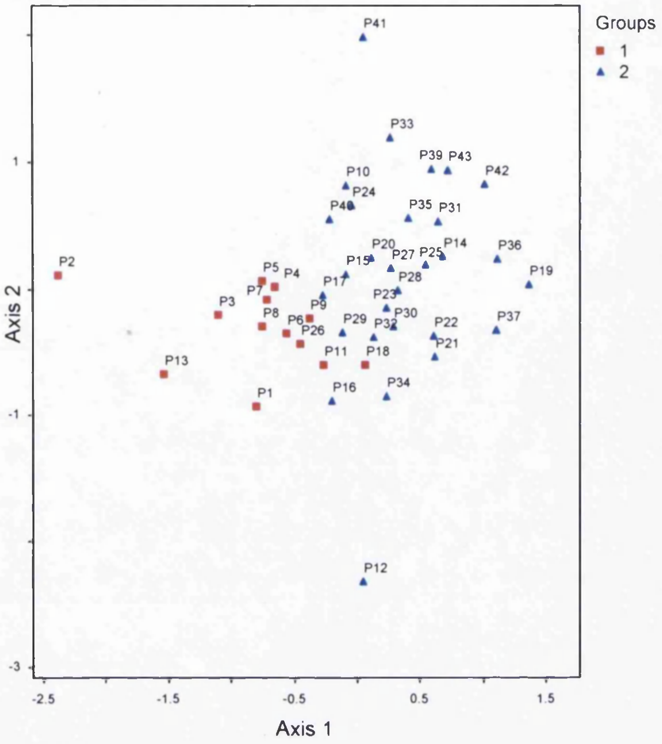
Species	Indicator Value (%)	
	2 groups	**4 groups**
Araalp	58	**64**
Athdis	25	**53**
Chaang	25	**71**
Crycri		**57**
Desalp	**77**	52
Epiana	40	**69**
Omanor	**31**	
Omasup	33	**66**
Oxydig	**72**	53
Phlalp	32	**62**
Poaalp	**67**	
Rangla	57	**87**
Salgla		**71**
Saxces	**69**	58
Saxopp	**56**	
Saxriv	**33**	
Saxste	62	**63**
Trispi	68	**74**
No. maxima	7	11
Mean maximum	58	67

5.5.5 Comparison of cluster analysis with TWINSPAN glacier foreland pioneer groups

Comparison of MRPP statistics for cluster analysis and TWINSPAN groups was only possible at the two-group level of classification, as the addition of further groups results in single-site clusters with TWINSPAN analysis. For this level, however, TWINSPAN gives a slightly less negative T-value (-13.3 compared with -14.3) and a slightly lower A-value (0.083 compared with 0.089) than cluster analysis. The TWINSPAN results therefore lend further justification for not considering classifications above the two-group level. (The TWINSPAN two-way ordered table is included in Appendix IV.)

Figure 5-11 shows that at the two-group level, both classification methods split the sites into groups primarily along axis one but at different points along this axis, supporting the hypothesis of continuous variation rather than groups with sharp boundaries. This lends further weight to the argument for considering these two groups to be sub-groups. Movement of the boundary between groups to a lower position on axis 1 results in a higher number of indicator species being exclusive to group 2B/2 rather than 2A/1.

a) TWINSPAN



b) Cluster analysis

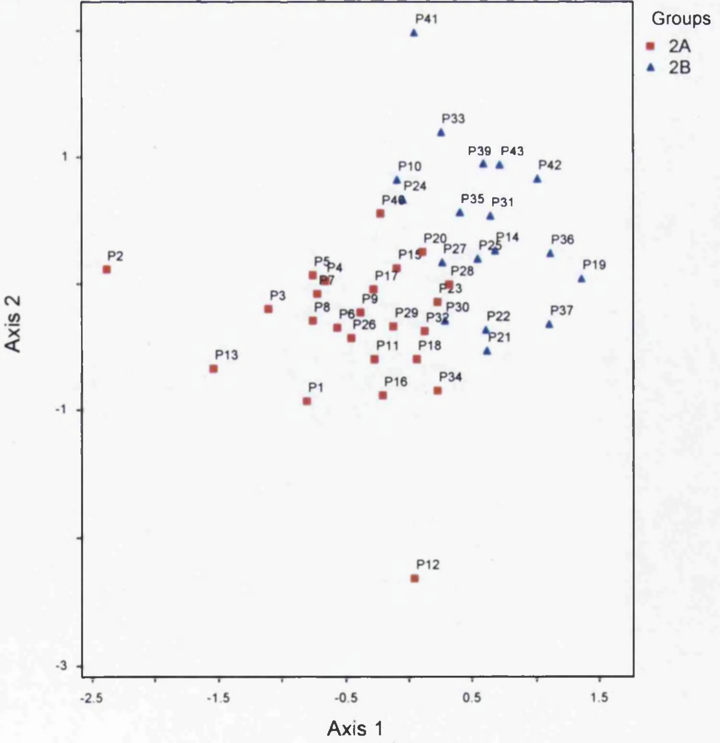


Figure 5-11. NMS ordination of glacier foreland pioneer sites showing: a) 2 TWINSPAN groups; b) 2 cluster analysis groups.

These findings support the argument for a single group of glacier foreland pioneer sites, which classification splits into sub-groups at arbitrary points along a continuum of variation. However, the sub-groups produced by cluster analysis show consistently greater separation and within-group agreement than those produced by TWINSPAN classification.

5.6 Comparison of pioneer vegetation across habitat types

This section uses data from a variety of pioneer habitats including avalanche tracks, frost-patterned ground, debris flows, gravel tips, gravel tips, river levées and river outwash plains for comparison with the findings already presented for roadside and glacier foreland pioneer sites. It addresses a single key question: are the characteristics of pioneer vegetation identified from roadside and glacier foreland sites consistent across a range of pioneer habitats? The generality of conclusions regarding variability in the composition of pioneer vegetation is tested by analysing a data set that includes a variety of pioneer habitats rather than a single habitat type.

In sections 5.6.1 to 5.6.3, the data set of additional pioneer habitats is first analysed independently to identify groups of sites and their indicator species across this range of habitats. Similarities between the indicator species for groups identified in this analysis and those identified previously for roadsides and glacier forelands are then highlighted in section 5.6.4.

The conclusions reached from the above analysis are tested further by combining data from the additional pioneer habitats with the roadside and glacier foreland sites in a single cluster and indicator species analysis (section 5.6.5). This provides additional information on the way in which sites from different habitat types are grouped together and on the similarities in species composition between habitat types.

5.6.1 Species composition and abundance in other pioneer habitats

A total of 94 species were recorded on the 34 sites comprising the data set of additional pioneer habitats (Table 5-12). Eleven species were recorded on at least 50% of sites, 47 species on at least 20% of sites and 19 on only one site. The most frequently recorded species is the shrub *Salix glauca* at 97% which also has a relatively high mean abundance at 10%. *S. glauca* was only absent from one high altitude patterned ground site. The species recorded on at least 50% of sites include four grasses, four forbs, two shrubs and one tree. All but one of these species (*Oxyria digyna*) also occur on more than 30% of roadside sites and five of them occur on more than 25% of glacier foreland sites. Again the main species are all perennials and are dominated by species with adaptations for wind or water dispersal and vegetative reproduction.

Table 5-12. Species occurring in additional pioneer habitats.

Code	**Species**	**% Sites**	**Mean abundance**
Salgla	*Salix glauca*	97.06	9.57
Fesovi	*Festuca ovina*	82.35	10.63
Desfle	*Deschampsia flexuosa*	82.35	6.48
Luzspi	*Luzula spicata*	73.53	4.49
Poaalp	*Poa alpina*	70.59	4.86
Cercer	*Cerastium cerastoides*	61.76	2.71
Betpub	*Betula pubescens*	55.88	8.11
Oxydig	*Oxyria digyna*	55.88	2.58
Agrcap	*Agrostis capillaris*	52.94	1.57
Empher	*Empetrum hermaphroditum*	52.94	1.04
Carbel	*Cardamine bellidifolia*	50.00	1.23
Salher	*Salix herbacea*	47.06	6.04
Saxste	*Saxifraga stellaris*	47.06	1.38
Rumace	*Rumex acetosa*	44.12	0.65
Desces	*Deschampsia cespitosa*	41.18	1.68
Omasup	*Omalotheca supina*	41.18	1.31
Desalp	*Deschampsia alpina*	38.24	2.24
Solvir	*Solidago virgaurea*	38.24	0.64
Luzarc	*Luzula arcuata*	35.29	1.74
Camrot	*Campanula rotundifolia*	35.29	0.61
Phlalp	*Phleum alpinum*	32.35	3.67
Rumlla	*Rumex acetosella*	32.35	1.61
Vacmyr	*Vaccinium myrtillus*	32.35	0.65
Ceralp	*Cerastium alpinum*	32.35	0.45
Juntrf	*Juncus trifidus*	32.35	0.32
Hiealp	*Hieracium alpinum*	29.41	0.76
Lotcor	*Lotus corniculatus*	29.41	0.72
Gymdry	*Gymnocarpium dryopteris*	29.41	0.63
Antdio	*Antennaria dioeca*	29.41	0.61
Taragg	*Taraxacum* aggregate	29.41	0.52

Code	Species	% Sites	Mean abundance
Sorauc	*Sorbus aucuparia*	29.41	0.21
Rangla	*Ranunculus glacialis*	26.47	2.31
Calvul	*Calluna vulgaris*	26.47	1.26
Crycri	*Cryptogramma crispa*	23.53	3.40
Epiana	*Epilobium anagagallidifolium*	23.53	1.87
Chaang	*Chamerion angustifolium*	23.53	0.65
Antodo	*Anthoxanthum odoratum*	23.53	0.61
Carbig	*Carex bigelowii*	23.53	0.44
Omanor	*Omalotheca norvegica*	23.53	0.43
Alcalp	*Alchemilla alpina*	23.53	0.38
Sibpro	*Sibbaldia procumbens*	23.53	0.36
Silaca	*Silene acaulis*	23.53	0.33
Vaculi	*Vaccinium uliginosum*	23.53	0.22
Stegra	*Stellaria graminea*	20.59	1.10
Arapet	*Arabidopsis petraea*	20.59	0.67
Polviv	*Polygonum viviparum*	20.59	0.38
Veralp	*Veronica alpinum*	20.59	0.24
Vacvit	*Vaccinium vitis-idaea*	17.65	0.45
Minbif	*Minuartia biflora*	17.65	0.40
Sallan	*Salix lanata*	17.65	0.22
Leoaut	*Leontodon autumnalis*	17.65	0.10
Visalp	*Viscaria alpina*	14.71	0.68
Equsci	*Equisetum scirpoides*	14.71	0.38
Athdis	*Athyrium distentifolium*	14.71	0.34
Trispi	*Trisetum spicatum*	14.71	0.25
Saxopp	*Saxifraga oppositifolia*	11.76	0.38
Sagsag	*Sagina saginoides*	11.76	0.28
Betnan	*Betula nana*	11.76	0.25
Phycae	*Phyllodoce caerulea*	11.76	0.19
Gersyl	*Geranium sylvaticum*	11.76	0.07
Pinsyl	*Pinus sylvestris*	11.76	0.05
Araalp	*Arabis alpina*	8.82	0.15
Saxces	*Saxifraga cespitosa*	8.82	0.12
Rubida	*Rubus idaeus*	8.82	0.11
Hievul	*Hieracium vulgatum*	8.82	0.10
Rhoros	*Rhodiola rosea*	8.82	0.09
Drasp	*Draba* sp	5.88	0.29
Pinvul	*Pinguicula vulgaris*	5.88	0.09
Hupsel	*Huperzia selago*	5.88	0.05
Ortsec	*Orthilia secunda*	5.88	0.04
Narstr	*Nardus stricta*	5.88	0.04
Arcuva	*Arctostaphylos uva-ursi*	5.88	0.03
Eupagg	*Euphrasia* aggregate	5.88	0.03
Saualp	*Saussurea alpina*	5.88	0.02
Juncom	*Juniperus communis*	5.88	0.01
Melsyl	*Melampyrum sylvaticum*	2.94	0.12
Alninc	*Alnus incana*	2.94	0.09
Pyrnor	*Pyrola norvegica*	2.94	0.06
Saxazo	*Saxifraga azoides*	2.94	0.04
Veroff	*Veronica officinalis*	2.94	0.03
Luzcon	*Luzula arcuata ssp confusa*	2.94	0.02
Luzsyl	*Luzula sylvatica*	2.94	0.02

Code	Species	% Sites	Mean abundance
Baralp	*Bartsia alpina*	2.94	0.02
Potcra	*Potentilla crantzii*	2.94	0.02
Salcap	*Salix caprea*	2.94	0.01
Tusfar	*Tussilago farfara*	2.94	0.01
Wooalp	*Woodsia alpina*	2.94	0.01
Astalp	*Astragalus alpinus*	2.94	0.01
Carsp	*Carex species*	2.94	0.01
Dipalp	*Diphasiastrum alpinum*	2.94	0.01
Junbig	*Juncus biglumis*	2.94	0.01
Naross	*Narthecium ossifragum*	2.94	0.01
Ranacr	*Ranunculus acris*	2.94	0.01
Viopal	*Viola palustris*	2.94	0.01

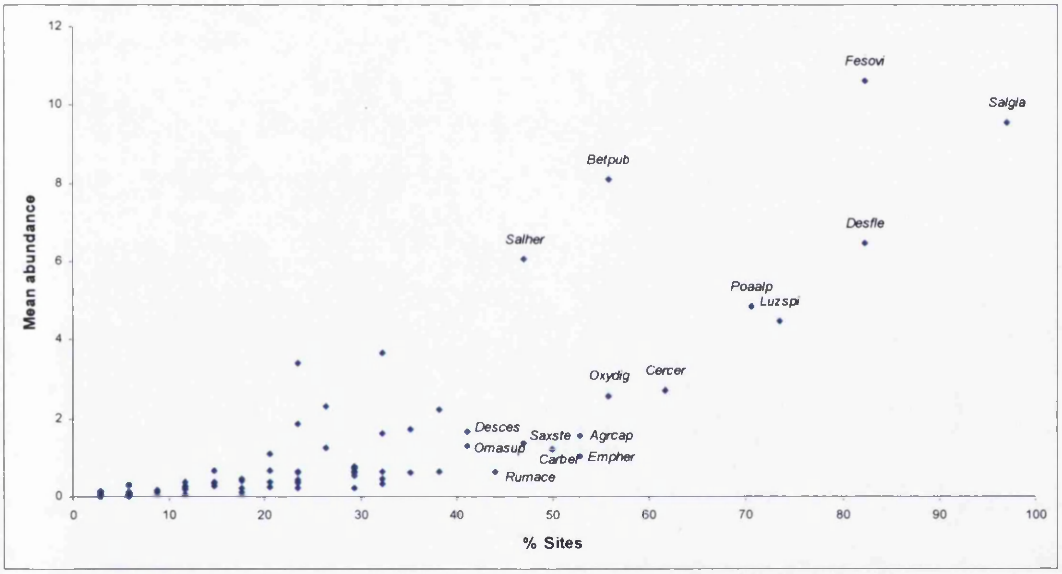


Figure 5-12. Mean abundance of pioneer species in additional habitats and the percentage of sites on which each species occurs. Species occurring on ≥ 40% sites are labelled. Abbreviated species names are listed in full in Table 5-10.

Figure 5-12 shows the relationship between percentage frequency and mean abundance for the species found in additional pioneer habitats and reveals a similar pattern to that found for the roadside and glacier foreland pioneer species, with a small number of species having a high frequency and mean abundance but the majority being infrequent and in low abundance.

5.6.2 Variability of sites in additional pioneer habitats

The mean Sørensen distance between sites in additional pioneer habitats is 0.772 (± 0.019) with a standard deviation of 0.054. Figure 5-13 shows the frequency distribution of mean distances between sites. The data are normally distributed (D'Agostino-Pearson test for normality $p = 0.559$) with a skewness of 0.41.

The sites with the greatest mean distance from all other sites in this data set were both recorded in high altitude patterned ground habitats and had unusually high abundances of *Luzula arcuata*. However, no sites are more than 3 standard deviations from the mean. A high abundance of *L. arcuata* was also found on one of the more extreme roadside sites and one of the glacier forelands.

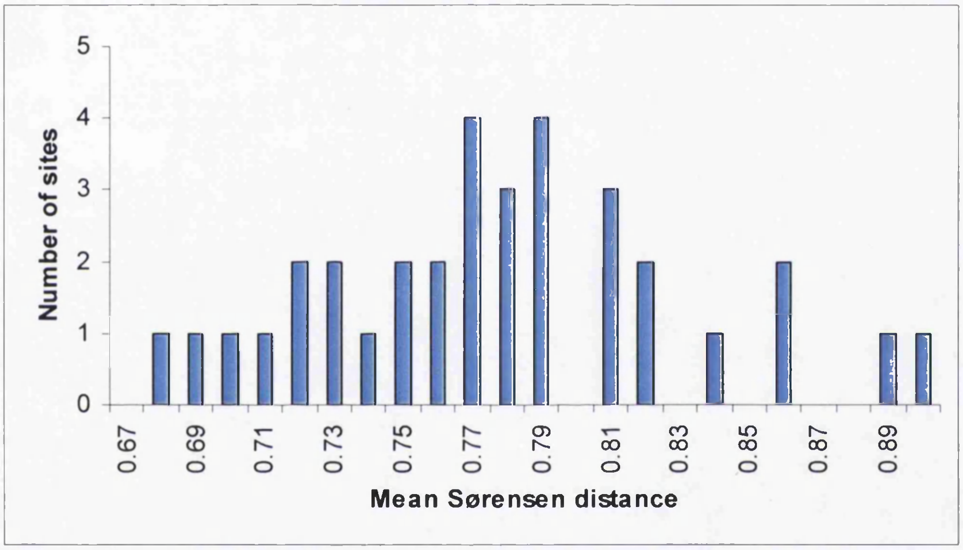


Figure 5-13. Frequency distribution of mean Sørensen distance between sites in additional pioneer habitats.

5.6.3 *Ordination and classification of sites from additional pioneer habitats*

NMS ordination of the 34 sites from additional pioneer habitats reached a stable solution of 0.0001 after 36 iterations, with a final stress of 16% for two dimensions. Cluster analysis resulted in a low level of chaining (9.05%) and MRPP analysis indicated that the four-group level is optimum for maximum separation between groups (T = -16.77) and greatest increase in within-group agreement (A = 0.259) (Figure 5-14).

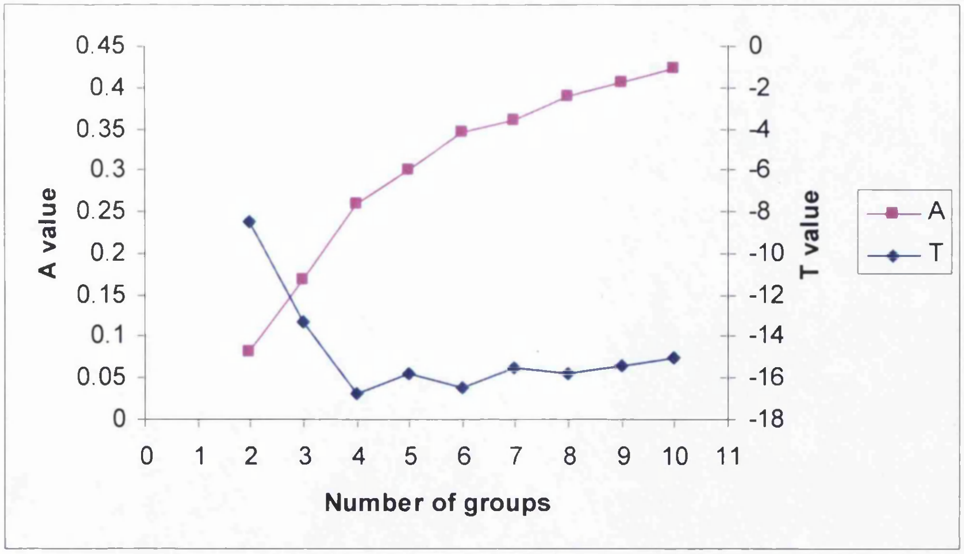
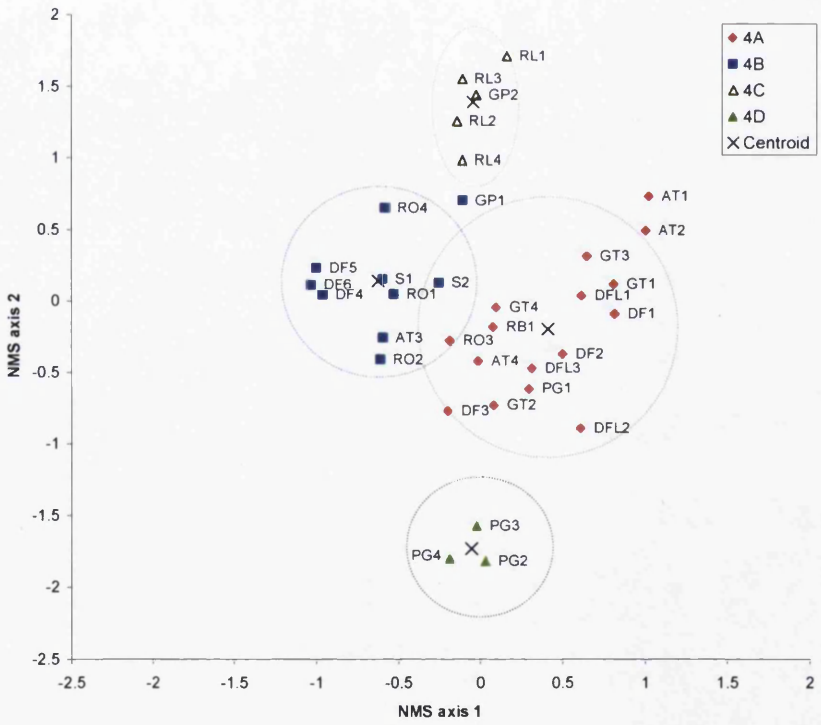


Figure 5-14. MRPP A and T statistics for cluster analysis of the other pioneer habitats data set.



Key to habitats
AT = avalanche track
DF = debris flow
DFL = debris flow levée
GP = gravel pit
GT = gravel tip
PG = patterned ground
RB = river bar
RL = river levée
RO = river outwash
S = sandur

Figure 5-15. NMS ordination of additional pioneer sites with four colour-coded cluster analysis groups superimposed. Dashed ellipses indicate ±2 standard deviations from each group centroid.

Figure 5-15 shows the four cluster analysis groups superimposed onto the two-dimensional NMS ordination diagram. Cluster analysis splits the sites into two groups along a line at an approximately 45° angle to the two axes (groups 4A and 4B) and two groups of sites (groups 4C and 4D) which form clusters at the upper and lower ends of axis 2. The descriptive statistics for these four groups are given in Table 5-13 and the mean between- and within-group distances and DI values in Table 5-14. Groups 4C and 4D have the lowest mean within-group distance and greatest mean between-group distance, giving them comparatively high DI values of 2.5 and 3.3 respectively. These two groups also have the highest number of significant indicator species. Groups 4A and 4B both have a DI value of 1.3 (to 2 significant figures) based on similar mean between- and within-group distances. On the basis of this evidence, these four clusters would appear to be genuine groups rather than sub-groups.

Table 5-13. Descriptive statistics for the four additional pioneer habitats cluster analysis groups.

Group	n	Mean w-g distance	No. significant indicator spp
4A	16	0.680	3
4B	10	0.649	6
4C	5	0.369	7
4D	3	0.289	7

Table 5-14. Mean between- and within-group distances for the four additional pioneer habitats groups and the Discreteness Index (DI).

Group	Mean b-g distance	Mean w-g distance	DI
4A	0.867	0.680	1.275
4B	0.865	0.649	1.333
4C	0.922	0.922	2.499
4D	0.943	0.943	3.263

Group 4D (n = 3) consists of three of the four frost-patterned ground sites, while group 4C (n = 5) consists of the four river levée sites plus one gravel pit. Group 4B (n = 10) consists of three debris flows, two sandurs, three river outwash sites, one avalanche track and one gravel pit, whereas group 4A (n = 16) is the most diverse with sites from three avalanche tracks, four gravel tips, three debris flows, three debris flow levées, one river outwash, one river bar and one frost-patterned ground site. Apart from group 4D, the cluster analysis groups therefore consist of sites from more than one pioneer habitat rather than being clustered according to habitat type. This indicates that habitat type does not generally determine pioneer species composition. Indicator species for these four groups are listed in Table 5-13.

Table 5-15. Significant indicator values (IV) for the four additional pioneer habitats groups.

	Observed IV (%)				
Species	**4A**	**4B**	**4C**	**4D**	*p*
Fesovi	**91**	4	1	2	0.001
Antdio	**53**	1	0	0	0.019
Juntrf	**51**	0	1	0	0.038
Phlalp	1	**74**	0	0	0.002
Stegra	0	**70**	0	0	0.006
Desfle	14	**56**	26	0	0.029
Epiana	0	**56**	0	0	0.011
Oxydig	14	**55**	5	0	0.028
Desalp	9	**53**	0	0	0.024
Betpub	1	5	**93**	0	0.001
Gymdry	1	2	**69**	0	0.008
Vaculi	6	2	**68**	0	0.005
Vacmyr	0	3	**68**	0	0.007
Solvir	6	1	**66**	0	0.011
Sorauc	0	12	**63**	0	0.01
Empher	11	10	**57**	0	0.02
Saxces	0	0	0	**100**	0.001
Saxopp	0	0	0	**100**	0.001
Luzarc	0	1	0	**96**	0.001
Rangla	2	0	0	**92**	0.001
Salher	7	0	0	**88**	0.001
Ceralp	10	3	0	**52**	0.032
Silaca	6	0	0	**51**	0.014

Group 4A is characterized by three indicator species, *Festuca ovina* (92%), *Antennaria dioica* (53%) and *Juncus trifidus* (51%) all of which are absent or have very low indicator values in the other three groups. Roadside group 6F is also characterized by the first two species. Group 4B has a number of indicator species in common with glacier foreland pioneer group 2A and roadside group 3B/6B e.g. *Phleum alpinum* and *Oxyria digyna.* The indicator species for group 4C are mainly tree seedlings and shrubs including *Betula pubescens* (93%), *Vaccinium uliginosum* (68%) and *V. myrtillus* (68%) and *Sorbus aucuparia* (63%). This group shares a number of indicator species with roadside pioneer group 3C/6C and appears to consist of sites that have reached a later stage of colonization and are possibly less disturbed. Group 4D indicator species are those typical of higher altitude sites, such as *Saxifraga cespitosa* and *Ranunculus glacialis* and this group has a number of indicator species in common with roadside pioneer group 6E and glacier foreland pioneer group 2B. There is therefore a degree of consistency between different pioneer habitat types in terms of the combinations of species which characterize them and this will be explored further in the next sub-section.

5.7 Comparison of pioneer vegetation from roadsides, glacier forelands and other disturbed habitats

This section addresses the question: do the same pioneer communities characterize different pioneer habitats or are they habitat-specific? As the previous sub-section seemed to show commonalities in terms of indicator species between the six-group level for roadsides, the two-group level for glacier forelands and the four-group level for additional pioneer habitats, this is investigated here in more detail.

Table 5-14 gives indicator values for all indicator species at these levels of cluster analysis and confirms that roadside group 6D has indicator species which are exclusive to that group while group 6A shares only one indicator species (*Stellaria graminea*) with group 4B of the additional pioneer habitats. Roadside group 6B has nine indicator species in common with glacier foreland group 2A and four species in common with additional pioneer habitats group 4B. These four species, are common to all three groups: *Deschampsia alpina*, *Phleum alpinum, Oxyria digyna* and *Epilobium anagallidifolium.* Roadside group 6C has four species in common with additional pioneer habitats group 4C (*Betula pubescens, Empetrum hermaphroditum, Vaccinnium myrtillus* and *V. uliginosum*). However, its main indicator *Deschampsia flexuosa* is an indicator for group 4B and *Juncus trifidus* is an indicator for group 4A. Roadside group 6E has seven species in common with additional pioneer habitats group 4D and seven species in common with glacier forelands group 2B. However, only three of these species are indicators for all three data sets: *Ranunculus glacialis*, *Saxifraga cespitosa* and *S. oppositifolia.* Roadside group 6F has two species in common with additional pioneer habitats group 4A but none with the two glacier foreland groups. *Festuca ovina* is a very widespread species on glacier forelands but cannot be used to separate the two groups. Where the three data sets have indicator species in common, they can have very different indicator values. For example, *S. cespitosa* has a value of 56% in roadside group 6E, 69% in glacier foreland group 2B and 100% in additional pioneer habitats group 4D.

Table 5-16. Indicator species values (%) for roadsides (6 groups), glacier forelands (2 groups) and additional pioneer habitats (4 groups).

	Roadsides						**Glacier Forelands**		**Additional Pioneer Habitats**			
Species	**6A**	**6B**	**6C**	**6D**	**6E**	**6F**	**2A**	**2B**	**4A**	**4B**	**4C**	**4D**
Desces	**46**	1	1	41		1						
Taragg	**29**	4		4		7						
Stegra	**13**	1								**70**		
Eupagg	**12**											
Veroff	**10**			1								
Achmil	**10**			10								
Pinsyl	**9**					1						
Vacvit	**9**					1						
Cerfon	**8**			7								
Potcra	**8**			4								
Equsyl	**6**											
Gersyl	**6**			1								
Viobif	**5**											
Eriace	**5**											
Cercer	1	**28**			10	16						
Desalp		**27**			13	5	**77**	13	9	**53**		
Sagsag	12	**25**		4		1						
Phlalp	4	**24**	1		2	2	**32**		1	**74**		
Rumlla	8	**23**	1			12						
Omasup	2	**22**	6	4		7	**33**					
Oxydig	1	**20**	1		1	5	**72**	17		**55**		
Saxste	2	**19**	1			1	**62**					
Rumace	1	**16**				5						
Omanor	5	**14**	1				**31**					
Epiana		**13**				2	**40**			**56**		
Sibpro		**12**	1			4						
Veralp	1	**11**										
Equsci	1	**8**				1						
Sildio		**7**										
Athdis							**25**					
Chaang							**25**					
Minbif												
Veralp												
Hievul												
Lotcor												
Desfle	5	2	**79**			1			14	**56**	26	
Betpub	12		**44**	1		1			1	5	**93**	

Empnig			**38**			1			11	10	**57**	
Salgla	18	6	**37**	1		12						
Vacmyr	1		**25**							3	**68**	
Hiealp	2	2	**19**			11						
Phycae			**19**									
Juntrf		8	**14**		3	1			**51**		1	
Vaculi			**11**						6	2	**68**	
Calvul	3		**7**									
Sorauc										12	**63**	
Solvir									6	1	**66**	
Gymdry									1	2	**69**	
Plamaj	2			**95**								
Trirep	19			**50**								
Ranacr	10	1		**40**								
Agrcap	20	1	18	**39**		2						
Fraves				**35**								
Poasp	8	4		**34**								
Pruvul				**22**								
Sagpro				**20**								
Crecap				**19**								
Verser	5			**17**								
Chasua	5		3	**15**								
Chaang	4	1		**12**								
Alcglo				**11**								
Hypmac	1			**10**								
Tripra	5			**10**								
Cretec				**8**								
Carova				**8**								
Rubida	2			**7**								
Filuli				**6**								
Galtet				**6**								
Gerrob				**6**								
Junbuf				**5**								
Luzarc		1			**86**	1				1		**96**
Rangla					**64**		11	**57**	2			**92**
Saxces					**56**		2	**69**				**100**
Ceralp		1			**52**	6			10	3		**52**
Saxcer					**41**							
Poaalp	5	31			**37**	6	29	**67**				
Carbel					**35**	1						
Salher		7	9		**35**	4			7			**88**
Silaca					**25**	8			6			**51**
Saxopp					**16**		3	**56**				**100**
Trispi		11			**13**	11	6	**68**				
Araalp					**11**		4	**58**				
Saxriv					**8**	1		**33**				
Fesovi	3	10	5		20	**52**			**91**	4	1	2
Antdio						**34**			**53**	1		
Luzspi	2	29	1		1	**32**						
Polviv	8	2			3	**27**						
Camrot	2			1		**21**						
Visalp	1					**19**						
Antodo	1	2	1			**13**						

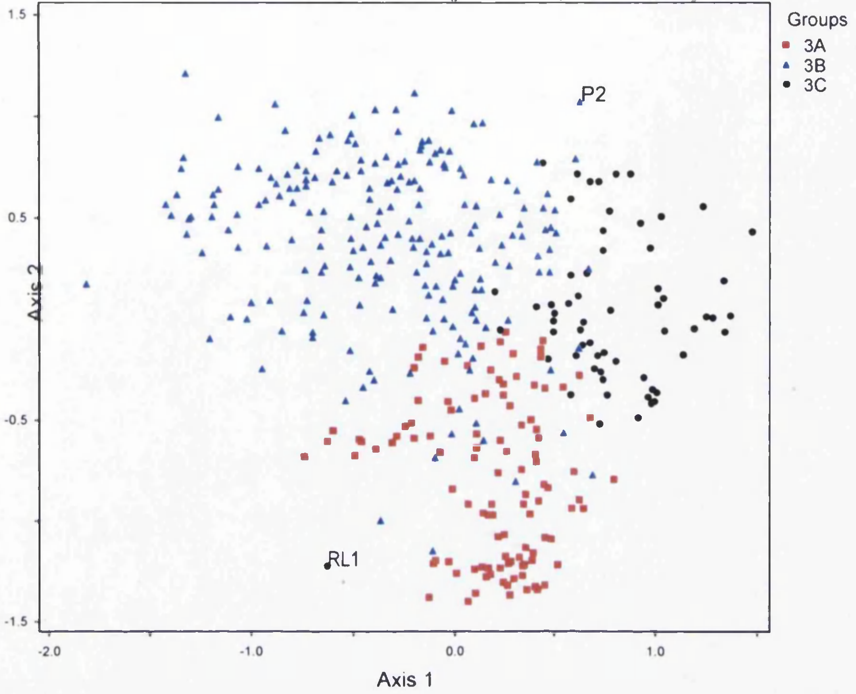
The evidence generally supports the existence of six pioneer communities or sub-communities in the habitats investigated. Two communities are virtually unique to roadsides: *Deschampsia cespitosa-Taraxacum* agg. (6A) and *Plantago major-Trifolium repens* (6D); two occur on roadsides and in additional pioneer habitats: . *Festuca ovina-Antennaria dioica* (6F/4A) and *Betula pubescens-Empetrum hermaphroditum* (6C/4C); and two are identified in all three data sets: *Deschampsia alpina-Phleum alpinum* (6B/2A/4B) and *Ranunculus glacialis-Saxifraga cespitosa* (6E/2B/4D). However, in the additional pioneer habitats *Deschampsia flexuosa* and *Juncus trifidus* indicate two separate groups, which are distinguished from the group characterized by *Betula pubescens* and *Empetrum hermaphroditum*, whereas on the roadside verges these four species characterize a single group. A number of species which were recorded on glacier forelands do not appear in this analysis as glacier foreland indicators as they do not distinguish between groups. These are predominantly indicator species for the *Ranunculus glacialis-Saxifraga cespitosa* community and include *Cerastium alpinum, Silene acaulis* and *Salix herbacea*, all of which occur on at least 25% of glacier forelands. Festuca ovina is also a very frequent pioneer colonizer of glacier forelands, occurring on 81% of sites.

As these conclusions are reached by seeking optimum matches between groups which result from three independent cluster analyses, they are tested in the next section by performing a single cluster analysis on all three data sets together.

5.7.1 Cluster analysis of all three data sets together

In order to confirm whether sites with similar indicator species are grouped together when classified in a single analysis, a cluster analysis was performed of the roadside, glacier foreland and additional pioneer habitats data sets. Although the different quadrat size used for the glacier foreland data set means that the three data sets are not directly comparable, the prior independent analysis of each data set can be used to assess the effects of conducting a single analysis. The cluster dendrogram is included in Appendix V. NMS ordination of all pioneer sites was also carried out but failed to reach a stable solution (instability = 0.005 after 400 iterations).

a) NMS ordination: stress = 27.72% (*p* = 0.03), instability = 0.005 after 400 iterations.



b) NMS ordination: stress = 25.73% (*p* = 0.03), instability = 0.004 after 400 iterations

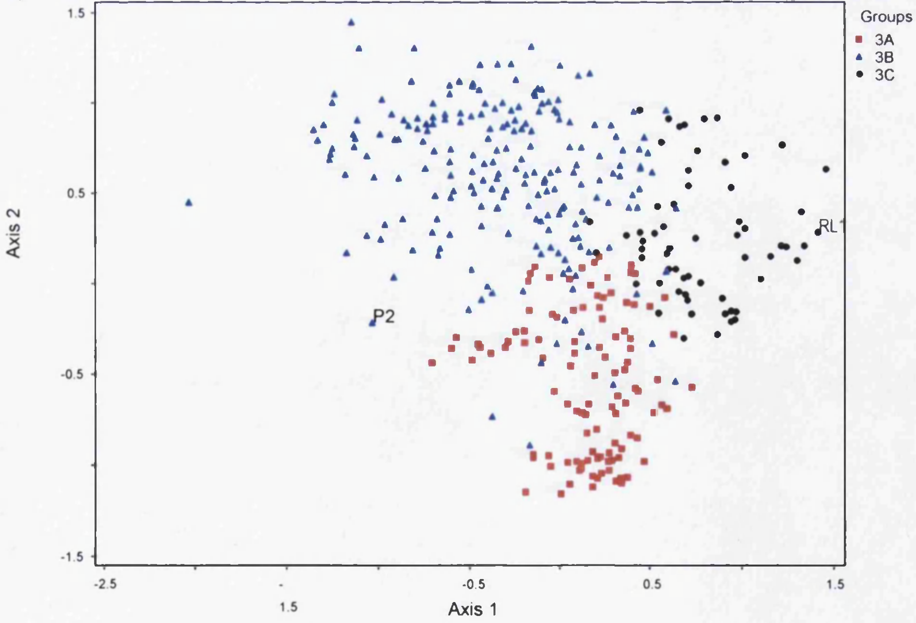


Figure 5-16. Two alternative NMS ordination diagrams for combined pioneer sites showing three cluster analysis groups.

The ordination was repeated and the two final results are presented in Figure 5-16, with the three cluster analysis groups superimposed to aid comparison. (NMS ordination with the exclusion of species recorded at less than three sites also failed to find a stable solution.) Although the solutions are unstable, the majority of sites have similar relative positions in both diagrams, the main difference between the two results being the positioning of glacier foreland P2 and river levée RL1. Figure 5-17(b) will therefore be used for purposes of illustration, as it has the lowest level of stress and instability.

5.7.1.1 Three combined groups

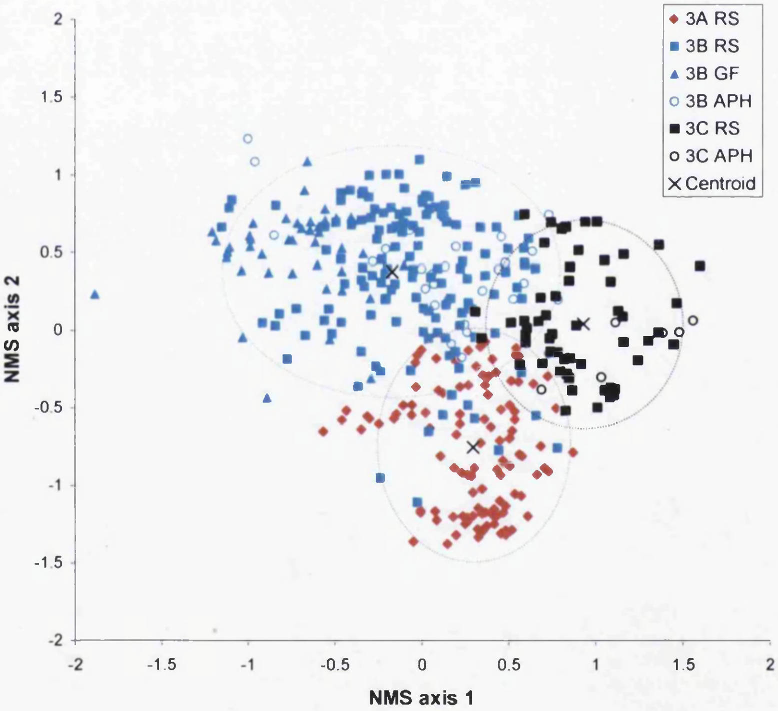


Figure 5-17. NMS ordination of all pioneer sites with three colour-coded cluster analysis groups superimposed (RS = roadsides, GF = glacier foreland, APH = additional pioneer habitat). Dashed ellipses indicate ±2 standard deviations from each group centroid.

Classification of all pioneer sites into three groups (Figure 5-17) results in the three original roadside groups 3A, 3B and 3C, with the exception that six roadside sites now in group 3B and one site now in 3C were classified in group 3A in the original roadside data set analysis. All glacier forelands belong to group 3B and all sites from the additional pioneer habitat data set are also classified with group 3B, except for the group of five sites characterized by tree seedlings and shrubs (group 4C), plus one river outwash site which are part of group 3C.

The MRPP statistics for these three groups are A = 0.153, T = -166 ($p < 0.001$) which compare with values of A = 0.182 and T = -142 for the three groups of roadside sites. There is therefore a slightly lower level of within-group agreement and less separation between groups when all data sets are combined. The DI values (Table 5-17) are comparable with those for the three roadside pioneer communities (Table (4-5), with a slightly lower value for group 3C (1.65 compared with 1.94) reflecting the greater mean within-group distance. The mean DI is 1.4, slightly lower than the mean DI of 1.5 for the three roadside communities.

Table 5-17 Mean between- and within-group distances and the Discreteness Index (DI) for the three combined pioneer cluster analysis groups.

Group	n	No. Significant Indicator Spp.	Mean b-g distance	Mean w-g distance	DI
3A	108	34	0.883	0.659	1.340
3B	207	31	0.897	0.774	1.159
3C	61	15	0.879	0.534	1.646

The indicator species and their values within these three groups (Table 5-18) are very similar to those identified for the three roadside groups (Table 4-6), the main differences occurring in group 3B, which reflects the addition of the glacier foreland sites. Of the species with high indicator values, the main difference is that *Salix herbacea* is now an indicator for group 3B rather than group 3C. There are also a number of changes to indicator values within each group (e.g. the value for *Luzula spicata* in group 3B has decreased from 55% to 45%) and a number of species with relatively low indicator values are added to group 3B, the most important of which are *Saxifraga oppositifolia* and *Arabis alpina* with values of 12%.

Table 5-18. Indicator values for the three combined pioneer groups.

	Indicator Value (%)			
Species	**3A**	**3B**	**3C**	*p*
Desces	**90**	1	2	0.001
Plamaj	**60**	0	0	0.001
Trirep	**57**	0	0	0.001
Agrcap	**45**	2	28	0.001
Ranacr	**40**	0	0	0.001
Poapra	**39**	1	0	0.001
Taragg	**34**	7	0	0.001
Sagsag	**25**	9	0	0.002
Achmil	**17**	0	0	0.001
Cerfon	**17**	0	0	0.001
Chasua	**17**	0	0	0.001
Verser	**16**	0	0	0.001
Fraves	**16**	0	0	0.001
Tripra	**15**	0	0	0.001
Potcra	**12**	0	0	0.001
Veroff	**12**	0	0	0.001
Pruvul	**11**	0	0	0.001
Eupfri	**11**	0	0	0.002
Stegra	**11**	1	0	0.002
Sagpro	**10**	0	0	0.001
Chaang	**9**	4	0	0.039
Hypmac	**7**	0	0	0.001
Viopal	**7**	0	0	0.004
Crecap	**6**	0	0	0.003
Alcglo	**6**	0	0	0.003
Vioriv	**5**	0	0	0.018
Stenem	**5**	0	0	0.013
Rubida	**5**	0	0	0.028
Hieumb	**4**	0	0	0.048
Carova	**4**	0	0	0.012
Polavi	**4**	0	0	0.016
Oxaace	**4**	0	0	0.018
Junbuf	**4**	0	0	0.021
Salmyr	**4**	0	0	0.052
Fesovi	5	**63**	14	0.001
Poaalp	6	**57**	1	0.001
Desalp	0	**47**	0	0.001
Ceralp	0	**45**	0	0.001
Luzspi	2	**45**	2	0.001
Cercer	1	**41**	0	0.001
Oxydig	0	**38**	1	0.001
Trispi	0	**35**	0	0.001
Silaca	0	**24**	0	0.001
Saxste	1	**23**	0	0.001
Salher	0	**23**	15	0.005
Polviv	5	**22**	0	0.001
Rangla	0	**22**	0	0.001
Rumlla	9	**22**	2	0.005
Luzarc	1	**20**	3	0.004
Phlalp	5	**19**	2	0.007

	Indicator Value (%)			
Species	**3A**	**3B**	**3C**	*p*
Saxces	0	**16**	0	0.001
Antdio	0	**16**	0	0.001
Epiana	0	**15**	1	0.001
Carbel	0	**14**	0	0.001
Rumace	2	**13**	1	0.009
Saxopp	0	**12**	0	0.002
Araalp	0	**12**	0	0.003
Sibpro	0	**9**	3	0.04
Visalp	0	**9**	0	0.012
Equsci	0	**7**	0	0.037
Saxcer	0	**6**	0	0.013
Arapet	0	**6**	0	0.025
Veralp	1	**6**	0	0.046
Saxriv	0	**5**	0	0.017
Saualp	0	**4**	0	0.046
Desfle	4	1	**85**	0.001
Salgla	8	11	**56**	0.001
Betpub	6	1	**54**	0.001
Empher	0	1	**44**	0.001
Vacmyr	1	0	**32**	0.001
Hiealp	1	5	**22**	0.001
Juntrf	0	4	**21**	0.001
Vaculi	0	0	**18**	0.001
Phycae	0	0	**17**	0.001
Carbig	1	10	**15**	0.022
Calvul	1	1	**9**	0.008
Lotcor	0	1	**8**	0.028
Sorauc	4	0	**8**	0.01
Harhyp	0	0	**3**	0.024
Loipro	0	0	**3**	0.025

Combining the three data sets has not, therefore, had a great effect on the key indicator species for these three groups, suggesting that these groups can be considered general pioneer communities.

5.7.1.2 Six combined groups

At the six-group level (Figure 5-18), the roadside sites fall into six groups, with two groups (6A and 6D) consisting only of roadside sites. The main changes from the individual data set analyses are that 34 roadside sites, which were classified in group 6B when the roadside data set was analyzed separately, are now in group 6F. These two groups were the least well-separated in the roadside data set analysis. Five sites have been classified in group 6B rather than 6A and one site has moved from 6B to 6E. Together, these reclassifications constitute a 13% difference between the combined data set analysis and the original roadside data set cluster analysis.

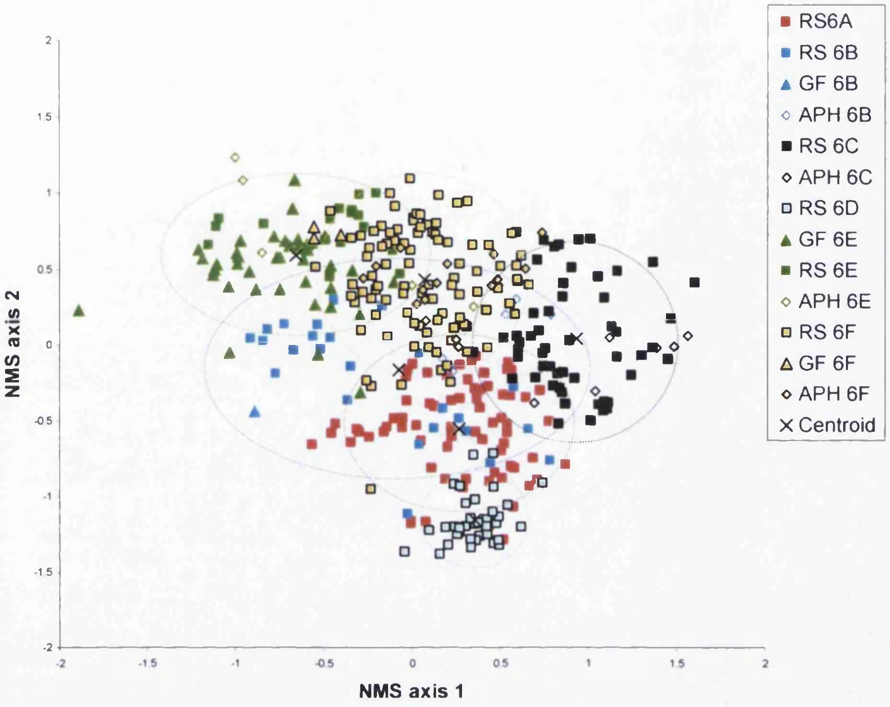


Figure 5-18. NMS ordination of all pioneer sites with six colour-coded cluster analysis groups superimposed (RS = roadsides, GF = glacier foreland, OS = other site). Dashed ellipses indicate ±2 standard deviations from each group centroid.

All but four of the glacier foreland sites are now classified in a single group (6E), with three forelands belonging to group 6F and one to group 6B. This supports the evidence presented in section 5.5.1, where the validity of classifying the glacier foreland sites into separate groups was questioned. The additional pioneer habitats data set is classified into four groups as was the case when it was analysed independently. However, the classification of six of these sites has changed: three sites which were in group 4A (S1, S2 and RO1) are now in 6B, two from 4A (AT3 and RO2) are now in 6E and one from group 4C (GP1) is now in 6B.

The MRPP statistics for these six groups are A = 0.227 and T = -154. This compares with values of A = 0.261 and T = -129 for the six-group level of classification for the roadside data set and indicates a lower level of overall within-group agreement when all sites are included but a higher level of separation between groups. All groups, with the exception of groups 6A and 6D are less discrete (Table 5-17) than the corresponding roadside groups (Table 4-8) reflecting the addition of sites from other habitats. 6B, the smallest group (n = 34) is the least discrete with a value of 1.108, reflecting its high mean within-group distance (0.779). The mean DI for this level of classification is 1.4, compared with a value of 1.6 for six roadside groups.

Table 5-19. Mean between- and within-group distances and the Discreteness Index (DI) for the six combined pioneer cluster analysis groups.

Group	n	No. Significant Indicator Spp.	Mean b-g distance	Mean w-g distance	DI
6A	72	11	0.834	0.668	1.249
6B	34	19	0.863	0.779	1.108
6C	61	10	0.888	0.534	1.663
6D	36	22	0.891	0.438	2.034
6E	61	18	0.908	0.697	1.303
6F	112	11	0.872	0.666	1.309

Table 5-20 shows the indicator values for the combined analysis at the six-group level. If the five species with the highest values within each group are compared with their values in Tables 5-14, groups 6A, 6C and 6D are the most consistent, with the loss of *Stellaria graminea* from group 6A to 6B and the increased indicator value of *Poa pratensis* in group 6D. The differences in indicator species for group 6E mainly reflect the influence of the glacier foreland sites, 38 of which are now classified in this group. *Cerastium alpinum* is the main indicator for group 6E and has a frequency of 76% on glacier foreland sites as whole. It was not an indicator species for either of the two glacier foreland groups, due to its widespread occurrence. *Luzula arcuata,* which had a high value (86%) within the roadside sites in this group, has a relatively low indicator value, reflecting its frequency of only 17% on glacier forelands, while *Saxifraga cernua* only occurs on the roadside sites within this group. *Oxyria digyna* and *Deschampsia alpina* are now important indicators for group 6E, reflecting their high percentage frequency on glacier forelands (86% and 83% respectively).

Groups 6B and 6F display the most marked changes in indicator species compared with those identified for the roadside sites alone. This is not surprising, as the most differences in site classification have involved movement of roadsides between these two groups. Group 6B (26 roadside sites, 7 additional pioneer habitat sites, one glacier foreland) is characterized by *Phleum alpinum* (43%) and *Sagina saginoides* (29%), having lost *Cerastium cerastoides* and *Rumex acetosella* to group 6F and *Deschampsia alpina* to group 6E. Group 6F (93 roadside sites, 16 additional pioneer habitat sites and 3 glacier foreland sites) still has all five indicator species from the roadside group 6F but has gained *Cerastium cerastoides* and *Rumex acetosella* from group 6B as indicated above.

Table 5-20. Indicator values for the six combined pioneer groups.

	Indicator Value (%)						
Species	**6A**	**6B**	**6C**	**6D**	**6E**	**6F**	**p**
Desces	**51**	1	1	39	0	1	0.001
Tarsp	**25**	11	0	4	0	4	0.001
Eupspp	**14**	0	0	0	0	0	0.001
Veroff	**11**	0	0	1	0	0	0.001
Cerfon	**9**	0	0	7	0	0	0.004
Potcra	**9**	0	0	4	0	0	0.014
Hieumb	**6**	1	0	0	0	0	0.015
Viopal	**5**	1	0	5	0	4	0.054
Parpal	**4**	3	0	0	0	0	0.047
Linbor	**4**	0	0	1	0	0	0.048
Calpur	**4**	0	0	0	0	0	0.054
Phlalp	3	**43**	0	0	3	2	0.001
Sagsag	13	**29**	0	4	0	2	0.001
Epiana	0	**26**	0	0	5	0	0.001
Omanor	4	**23**	1	0	2	0	0.001
Veralp	0	**22**	0	0	1	0	0.001
Minbif	1	**21**	0	0	0	1	0.001
Omasup	2	**15**	5	4	1	10	0.002
Rumace	1	**15**	0	0	0	9	0.017
Chaang	2	**14**	0	7	1	0	0.002
Stegra	8	**13**	0	0	0	0	0.001
Sildio	0	**11**	0	0	0	0	0.001
Lotcor	0	**9**	4	0	0	0	0.012
Sibpro	0	**9**	1	0	0	6	0.017
Viobif	0	**8**	0	0	0	0	0.002
Athdis	0	**7**	1	0	0	0	0.006
Equsci	0	**7**	0	0	0	5	0.032
Alcalp	4	**6**	0	0	1	1	0.011
Petfri	0	**6**	0	0	0	0	0.011
Calvul	1	**5**	4	0	0	0	0.018

	Indicator Value (%)						
Species	**6A**	**6B**	**6C**	**6D**	**6E**	**6F**	**p**
Desfle	6	3	**73**	0	0	2	0.001
Betpub	9	6	**45**	0	0	0	0.001
Salgla	11	10	**39**	0	3	10	0.001
Empher	0	1	**37**	0	0	1	0.001
Vacmyr	1	0	**27**	0	0	1	0.001
Juntrf	1	0	**16**	0	1	8	0.003
Phycae	0	0	**16**	0	0	0	0.001
Hiealp	2	4	**15**	0	0	8	0.002
Vaculi	0	0	**15**	0	0	0	0.001
Solvir	7	0	**7**	0	0	3	0.001
Plamaj	2	0	0	**94**	0	0	0.001
Trirep	15	3	0	**45**	0	0	0.001
Poapra	11	0	0	**39**	0	2	0.001
Agrcap	18	8	15	**36**	0	1	0.001
Ranacr	8	5	0	**35**	0	0	0.001
Fraves	0	0	0	**34**	0	0	0.001
Pruvul	1	0	0	**22**	0	0	0.001
Sagpro	0	0	0	**20**	0	0	0.001
Crecap	0	0	0	**19**	0	0	0.001
Verser	4	0	0	**15**	0	0	0.001
Chasua	5	0	0	**14**	0	0	0.001
Hypmac	1	0	0	**10**	0	0	0.001
Tripra	6	0	0	**10**	0	0	0.005
Achmil	7	1	0	**8**	0	0	0.002
Alcglo	0	1	0	**8**	0	0	0.017
Carova	0	0	0	**8**	0	0	0.002
Cretec	0	0	0	**8**	0	0	0.005
Filuli	0	0	0	**6**	0	0	0.019
Galtet	0	0	0	**6**	0	0	0.023
Gerrob	0	0	0	**6**	0	0	0.024
Junbuf	0	0	0	**5**	0	0	0.027
Rubida	1	0	0	**5**	0	0	0.031
Ceralp	0	0	0	0	**59**	7	0.001
Rangla	0	0	0	0	**57**	0	0.001
Saxces	0	0	0	0	**47**	0	0.001
Oxydig	0	7	0	0	**44**	3	0.001
Desalp	0	12	0	0	**38**	6	0.001
Trispi	0	3	0	0	**38**	4	0.001
Poaalp	5	22	0	0	**36**	12	0.001
Araalp	0	0	0	0	**33**	0	0.001
Luzarc	1	1	1	0	**32**	2	0.001
Saxopp	0	0	0	0	**31**	0	0.001
Salher	0	3	7	0	**22**	8	0.001
Silaca	0	0	0	0	**20**	9	0.001
Saxcer	0	0	0	0	**16**	0	0.001
Saxste	0	15	0	0	**16**	2	0.002
Saxriv	0	0	0	0	**13**	0	0.001
Carbel	0	1	0	0	**10**	4	0.015
Astnor	0	0	0	0	**9**	0	0.006
Saxniv	0	0	0	0	**6**	0	0.021
Fesovi	4	3	8	0	13	**58**	0.001
Luzspi	3	3	1	0	2	**58**	0.001

Species	Indicator Value (%) 6A	6B	6C	6D	6E	6F	p
Antdio	0	0	0	0	0	**26**	0.001
Cercer	1	22	0	0	3	**26**	0.001
Rumlla	8	9	1	0	0	**23**	0.001
Camrot	3	1	0	1	0	**14**	0.005
Polviv	4	12	0	0	1	**14**	0.017
Visalp	0	0	0	0	0	**13**	0.001
Carbig	1	1	9	0	3	**12**	0.015
Antodo	2	2	1	0	0	**11**	0.006
Luzcon	6	3	0	0	0	**7**	0.028

This analysis has confirmed the existence of largely consistent groups of pioneer species across a range of habitat types. The three-group level can be described as a *Deschampsia cespitosa-Plantago major* community (3A) restricted to 108 roadside sites, a *Festuca ovina-Poa alpina* (3B) community which occurs on all 42 glacier foreland sites, 28 additional pioneer habitats and 137 roadside sites, and a *Deschampsia flexuosa-Salix glauca* (3C) community which occurs on 55 roadside sites and 6 additional pioneer sites.

At the six-group level, cluster analysis of all pioneer sites also confirms the conclusions reached from independent data set analyses. The roadside sites are classified into six groups, the majority of glacier forelands are classified into a single group and the additional pioneer habitats are classified into four groups. Groups 6A and 6D consist solely of roadside sites and the other four groups include sites from a variety of pioneer habitats, confirming that pioneer species colonization is not primarily dependent on habitat type. Indicator species analysis of the combined data set shows some consistency with the findings for the six roadside groups, with the influence of the glacier foreland and additional habitat sites which, as shown in Table 5-14, often have the same indicator species but with different indicator values.

The six pioneer groups can therefore be summarized as: two sub-communities which are unique to roads, *Deschampsia cespitosa-Taraxacum* agg. (6A) and *Plantago major-Trifolium repens* (6D); a *Deschampsia flexuosa-Betula pubescens* community (6C) occurring on 55 roadside and 6 additional pioneer habitat sites; a *Cerastium alpinum-Ranunculus glacialis* sub-community (6E) which occurs on 38 glacier forelands,15 roadside sites and 5 additional pioneer habitat sites; and two further sub-communities which are the least well-differentiated, *Festuca ovina-Luzula spicata* (6F) on 93 roadside sites, 3 forelands and 16 additional pioneer habitats; *Phleum alpinum-Sagina saginoides* (6B) on 26 roadside sites, one glacier foreland and 7 additional pioneer habitat sites.

The geographical distribution and environmental parameters of these communities and sub-communities will be examined in the next chapter.

5.8 Summary

5.8.1 How variable is the pioneer stage of succession on glacier forelands?

1. Glacier foreland pioneer sites are colonized primarily by perennial grasses and forbs. The most frequently occurring species are *Poa alpina, Oxyria digyna, Deschampsia alpina* and *Festuca ovina.* The majority of species are adapted for wind or water dispersal and many can also propagate vegetatively. This is largely consistent with the findings for the roadside pioneer species, the exception being that adaptations for water dispersal were not a feature of the roadside species.

2. 71 species were recorded at pioneer sites on 42 glacier forelands: seven species occurred on ≥ 50% sites, 18 species on ≥ 20% sites, and 33 on < 5% sites. Species richness is therefore considerably lower than on the roadside sites but the number of species occurring on ≥ 50% sites is higher than for the roadside data set, both of which point to a more uniform pioneer vegetation on glacier forelands.

3. The mean Sørensen distance of 0.65 (+/- 0.025) also points to lower variability than on roadside sites. Like the roadside data set, no sites are regarded as statistical outliers. The extreme sites have either unusually high or low species richness: two sites have only two or three species present

and one site has 22 species (eight of which are not recorded in the pioneer zone of other forelands).

5.8.2 Does glacier foreland pioneer vegetation consist of a number of distinct communities?

1. The two-dimensional NMS ordination (Figure 5-3) shows no obvious clusters of sites or divisions between groups of sites and the MRPP statistics indicate relatively low separation between cluster analysis groups and little within-group agreement. Finding a stable ordination is dependent on including rare species, which suggests a relatively weak structure to the data.

2. The two-group level of cluster analysis (Figure 5-4) produces groups that appear to be sub-divisions of a continuum of change but with reasonably good separation between indicator species. Group 2A is characterized by key species *Deschampsia alpina-Oxyria digyna* and group 2B by *Saxifraga cespitosa-Trisetum spicatum.* The patterns of abundance of key indicator species suggest gradual rather than sharp gradients in species composition across these two groups. These are therefore considered to represent sub-groups rather than discrete communities.

3. At the four-group level of cluster analysis (Figure 5-9), one of the groups consists of only two sites characterized by a single indicator species, another is characterized by widespread species and two groups are more appropriately interpreted as part of a continuum of change. There seems to be little or no justification for considering this level of classification even on the basis of sub-communities.

4. It is likely, therefore, that the glacier foreland sites consist of a single community which can be sub-divided along a continuum of change.

5.8.3 Are the characteristics of pioneer vegetation consistent across a range of additional pioneer habitats?

1. The 34 sites in additional pioneer habitats are also characterized mainly by perennial grasses and forbs, the most frequent species being *Salix glauca, Festuca ovina, Deschampsia flexuosa* and *Luzula spicata.* The majority of species are adapted for wind dispersal and can also reproduce vegetatively and, like the glacier foreland species, some are adapted for water dispersal. These characteristics are therefore consistent across habitat types.

2. 94 species were recorded on the 34 sites, with eleven species occurring on ≥ 50% sites, 47 species on ≥ 20% sites and 19 on < 5% sites. Of the eleven most frequently recorded species, all but one occur on > 30% of the roadside sites and five occur on > 25% of the glacier foreland sites, suggesting a degree of consistency across habitats in relation to the most frequent species.

3. The mean Sørensen distance between all sites in additional pioneer habitats is 0.77 (± 0.019) and no sites have dissimilarities more than three standard deviations from the mean. The sites with the greatest mean Sørensen distance from all other sites are two of the high altitude patterned-ground sites with high relative abundances of *Luzula arcuata.* This species was also found in high abundance at extreme sites in the other two data sets.

4. NMS ordination (Figure 5-15) showed the three high altitude patterned-ground sites to be clustered together and the four river-levée sites to be clustered together with the two gravel-pit sites. However, the other site types were distributed more widely across ordination space suggesting that, at these sites, pioneer species composition is not habitat-specific.

5. Cluster analysis and MRPP of the additional pioneer habitats data set (Figure 5-14) showed the four-group level to be optimum in terms of within-group agreement and between-group separation. This produced two groups

consisting of sites from a range of habitats, one group of sites from two habitat types and one group of single-habitat sites.

5.8.4 Do the same pioneer communities characterize different habitats or are they habitat-specific?

1. Comparison of indicator species for all three data sets from separate analyses (Table 5-14) showed a reasonable level of agreement and led to support for the six-group level of cluster analysis for roadsides, the two-group level for glacier forelands and the four-group level for additional pioneer habitats. These groups have species in common but show variation in their indicator values according to habitat.

2. At the three-group level of the combined cluster analysis (Figure 5-17) the roadside sites fall into three distinct groups, the additional pioneer habitats into two groups and the glacier forelands into one group.

3. At the six-group level of the combined cluster analysis (Figure 5-16), roadside sites are classified into six groups of which two groups consist solely of roadside sites: additional pioneer habitats are included in four groups and the majority of glacier forelands are in one group. At this level, the combined cluster analysis predominantly recreates (and hence supports the validity of) the site groupings obtained from analyses of each of the three data sets separately.

4. Pioneer species colonization therefore has relatively low habitat dependence. However, the species that are common to different data sets such as *Deschampsia alpina, Oxyria digyna* and *Festuca ovina* do have indicator values which vary according to habitat.

5. The pioneer vegetation can be said to form three communities: a *Deschampsia cespitosa-Plantago major* community restricted to roadside sites; a *Festuca ovina-Poa alpina* community which occurs on all glacier

foreland sites, 28 additional-habitat sites and 137 roadside sites; and a *Deschampsia flexuosa-Salix glauca* community which occurs on 55 roadside sites and 6 additional-habitat sites.

6. The communities can be further divided into six sub-communities. Two are unique to roads: *Deschampsia cespitosa-Taraxacum* agg. and *Plantago major-Trifolium repens. Deschampsia flexuosa-Betula pubescens* occurs on 55 roadside and 6 additional pioneer habitat sites. *Cerastium alpinum-Ranunculus glacialis* occurs on 38 glacier forelands, 15 roadside sites and 5 additional pioneer habitat sites. The last two sub-communities are the least well-differentiated: *Festuca ovina-Luzula spicata* on 93 roadside sites, 3 forelands and 16 additional pioneer habitats; and *Phleum alpinum-Sagina saginoides* on 26 roadside sites, one glacier foreland and 7 additional pioneer habitat sites.

6 GEOGRAPHICAL PATTERNS AND ENVIRONMENTAL INFLUENCES ON PIONEER COMMUNITIES

6.1 Introduction

This chapter explores the spatial distribution of the cluster analysis groups identified in Chapters 4 and 5, focussing on altitudinal and regional patterns and also examining a range of environmental influences using Ellenberg's indicator values for light, moisture, pH and nitrogen. The three key questions addressed are: (1) does pioneer vegetation exhibit altitudinal and/or regional patterns of distribution; (2) does the use of Ellenberg's indicator values to quantify environmental factors provide further explanation of spatial patterns; and (3) what are the relative influences of habitat type and altitude/continentality on pioneer colonization?

The height above sea-level and continentality (distance east from a baseline 5km to the west of Haugabreen glacier foreland) of each site are used to identify altitudinal and regional patterns in the data. Altitudinal and regional patterns in the distribution of roadside (section 6.2) and glacier foreland (section 6.4) pioneer vegetation are first analysed separately using four approaches. First, correlations between the altitude and continentality of each site on the one hand, and its position in ordination space on the other, are used to assess the strength of the relationship between pioneer species composition and these two variables. Second, site groups identified by classification as communities and sub-communities in Chapters 4 and 5, are ordinated using NMS and the relationship between groups in terms of altitude and distance east are assessed visually in ordination diagrams. Third, a graph of groups plotted according to their altitude and distance east provides a direct gradient analysis of communities in relation to geographical coordinates. Fourth, the mean altitude and distance east (with 95% confidence intervals) are calculated for each group in order to assess the degree of separation between communities in terms of their altitude and continentality.

Further explanation for the distribution of pioneer communities is sought for the roadside (section 6.3) and glacier foreland (section 6.5) pioneer data sets using

Ellenberg's indicator values (EI values). The second key question is thus addressed using the following strategy. First, correlations between the mean weighted EI values for each site and its position in ordination space are analyzed using a joint plot with EI value vectors superimposed on the ordination diagram. This allows assessment of the relationship between trends in EI values and ordination scores. Second, mean EI values are calculated for cluster analysis groups at each level of classification, in order to identify possible environmental factors influencing the species composition of each community. Variance partitioning is also carried out to quantify the relative contributions of each environmental factor to an explanation of species composition.

Section 6.6 continues to address question one in relation to the additional pioneer habitats and a combined analysis of all three data sets respectively. These analyses enable conclusions to be reached regarding question three, i.e. the relative importance of habitat type versus altitude/continentality in influencing pioneer species colonization.

6.2 Altitudinal and regional patterns in the distribution of roadside pioneer vegetation

6.2.1 Indirect gradient analysis of roadside pioneer sites in relation to altitude and continentality

In order to assess whether the positions of roadside pioneer sites in the NMS ordination diagram are related to altitude (Figure 4-3), Figure 6-1 shows the same diagram rotated to maximize correlation between the altitudes of sites and their ordination scores on axis 1. This provides a method of examining the relationship between the altitude of a site and its relative species composition. Figure 6-1 and Table 6-1 show a strong positive correlation between axis 1 and altitude ($r = 0.897$, $p \leq 0.01$) suggesting that the relative species composition of the roadside pioneer sites is strongly influenced by altitude.

Table 6-1. Pearson's r coefficients for correlations between NMS axes of roadside pioneers and altitude and distance east ($p < 0.01$).

	Axis 1	Axis 2
Altitude	0.897	n.s.
Distance east	0.468	0.210

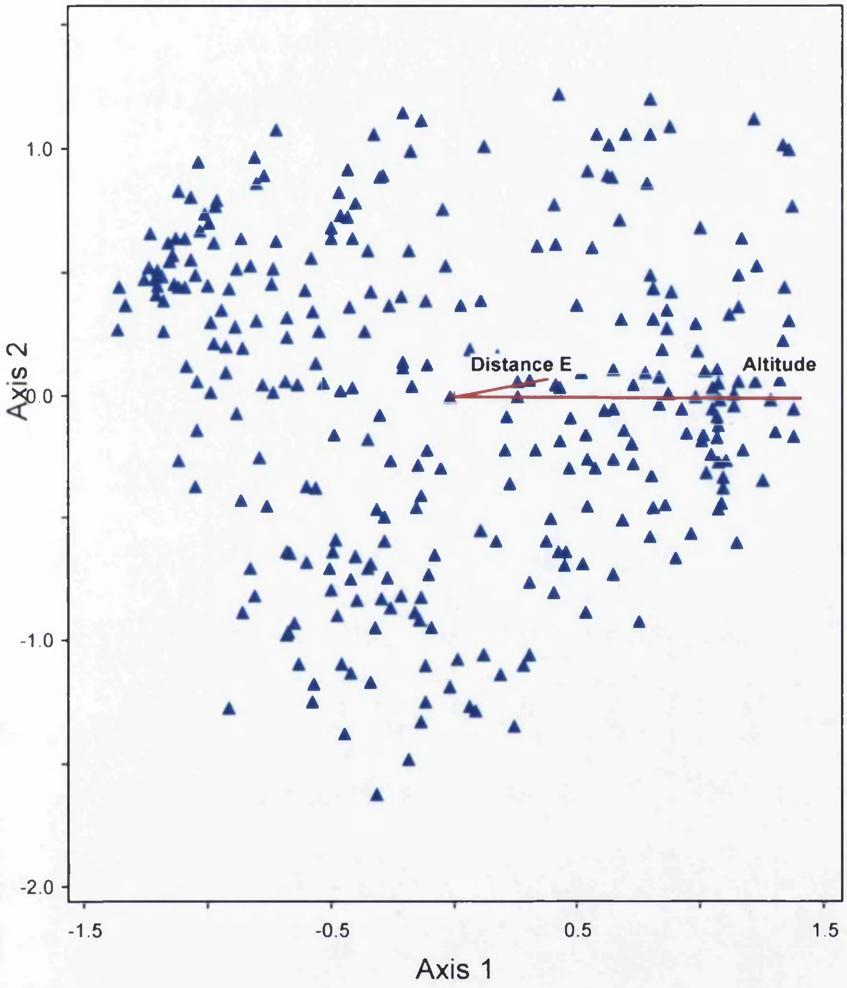


Figure 6-1. NMS ordination of roadside pioneer sites showing correlation between axis 1 and altitude and distance east (rotated axes).

When axis 1 is rotated to maximize correlation with altitude, it also shows a moderate correlation with distance east of r = 0.468 (Table 6-1). Axis 2 and distance east have a weak positive correlation of r = 0.210, suggesting that only a small proportion of the change along this axis (r^2 = 4%) can be explained by regional effects independent of altitude. The correlation between altitude and distance east is r = 0.551 ($p < 0.01$), a result that reflects the general regional topography of the study area with higher elevations occurring towards the east. Partitioning of the variance (Table 6-2) shows that, of the variation in species composition explained by these two factors, the fraction explained by altitude which is not shared with distance east (A|E) is 64%, that explained by distance east not shared with altitude (E|A) is 25%, and the variability shared between the two factors (A∩E) is 11%. Although these two factors tend to co-vary within the study region, the effects of altitude are therefore more than twice as important than the effects of continentality. However, continentality does have an appreciable independent influence.

Table 6-2 Variance explained (VE) by altitude and distance east for the roadside pioneer data set. TVE = total variance explained, A = altitude, E = distance east. All values are significant at $p = 0.002$.

Variable	VE (% TVE)
TVE	0.73 (1.00)
A	0.55 (0.75)
E	0.26 (0.36)
A∩E	0.08 (0.11)
A|E	0.47 (0.64)
E|A	0.18 (0.25)

6.2.2 Geographical distribution of roadside pioneer communities

6.2.2.1 Distribution of three roadside pioneer communities

When the three roadside pioneer communities identified in Chapter 4 (Figure 4-7) are superimposed onto the NMS ordination diagram rotated for maximum correlation between axis 1 and altitude (Figure 6-2), a clear altitudinal gradient can be seen between communities 3A and 3B, group 3A sites having lower scores on this axis than those in group 3B. The area of greatest discontinuity between these two communities now occurs along a line which is almost perpendicular to axis 1, emphasizing the pronounced difference in species composition related to altitude. Community 3C appears to occur mainly at low to intermediate altitudes but is differentiated from community 3A by factors other than altitude.

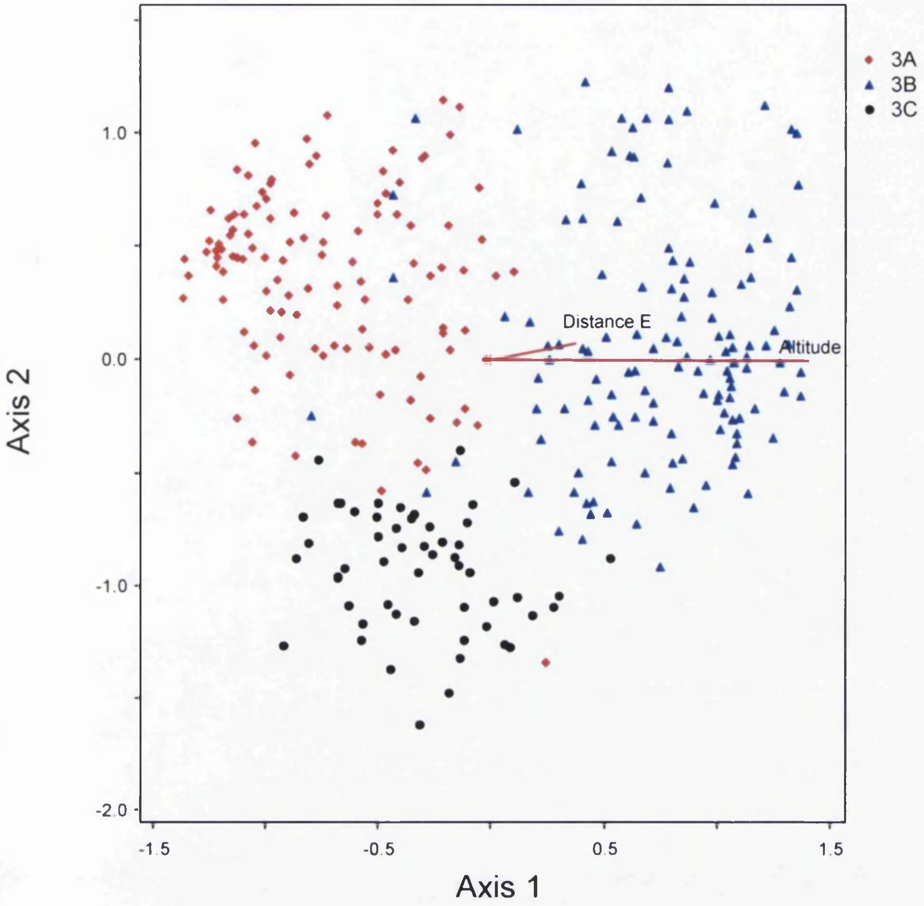


Figure 6-2. NMS ordination diagram rotated for maximum correlation between axis 1 and altitude showing three roadside pioneer cluster analysis groups.

To consider the position of roadside pioneer sites in geographical space, the sites are plotted onto a graph of altitude versus distance east (direct gradient analysis) and colour coded according to their community membership (Figure 6-3).

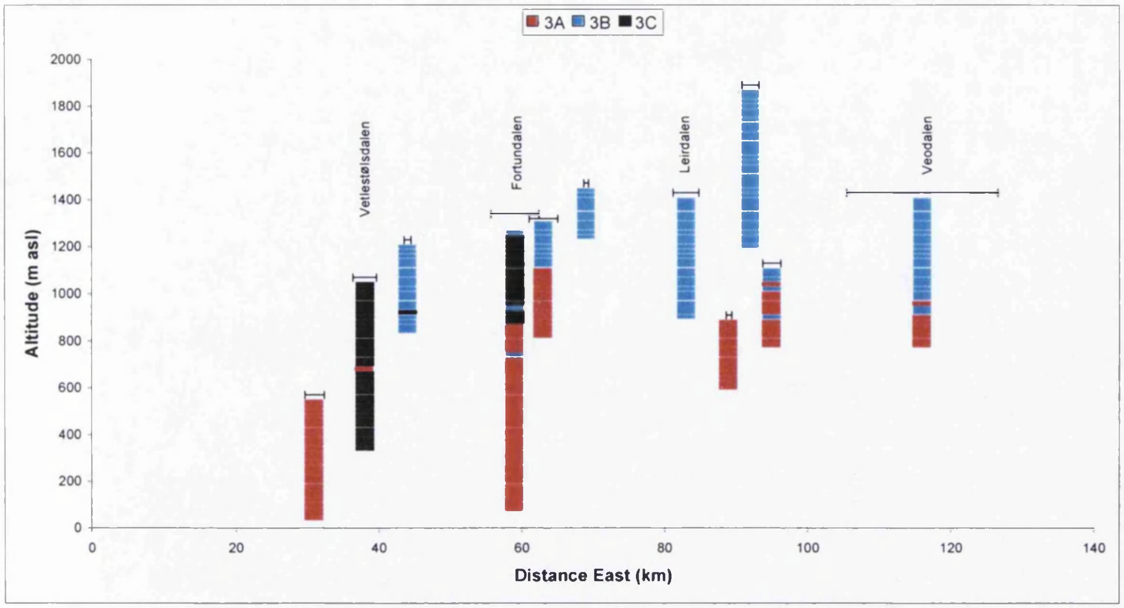


Figure 6-3. Altitude and distance east of three roadside pioneer communities. Coloured vertical columns represent the altitudinal range of individual roads; horizontal bars represent their west-east range. The column at 59 km east has been displaced slightly from 61 km to avoid overlap of columns.

This graph confirms the clear altitudinal distribution of communities 3A and 3B, with 3C sites at intermediate altitudes. The boundary between 3A and 3B occurs between 740 and 1100 m but only one community 3B site is below 800 m. Table 6-3 and Figure 6-4 provide statistical confirmation of the pattern of altitudinal zonation described, with mean altitudes of 597 m for community 3A and 1247 m for 3B. The figures also show that sites within 3C exhibit a more restricted regional distribution pattern, being present on only three roads which are all towards the oceanic west of the study area. Vetlestølsdalen road is almost entirely community 3C over an altitudinal range of 340 to 1040 m The mean distances east of the three communities are 46 km for 3C, 65 km for 3A and 83 km for 3B, which also confirms that the higher altitude 3B sites tend to occur further east. These findings support the conclusions reached from examination of the ordination diagram. However, examination of Figures 6-3 and 6-4 also reveals that 3C sites tend to be found at higher altitudes (mean = 819 m) than 3A sites within the same sub-region. The predominantly contiguous nature of the communities in Figure 6-3, suggests that pioneer vegetation on roadsides follows a consistent geographical pattern of colonization, primarily in relation to altitude but with an additional regional influence. It does not indicate a random distribution of species or even a strong influence of local habitat features, both of which would lead to a much lower level of contiguity.

Table 6-3. Mean altitude and distance east of the three roadside pioneer groups.

Community	Mean ± 95% confidence interval Altitude (m a.s.l.)	Distance east (km)
3A	597 ± 54	64 ± 5
3B	1247 ± 41	83 ± 4
3C	819 ± 68	45 ± 3

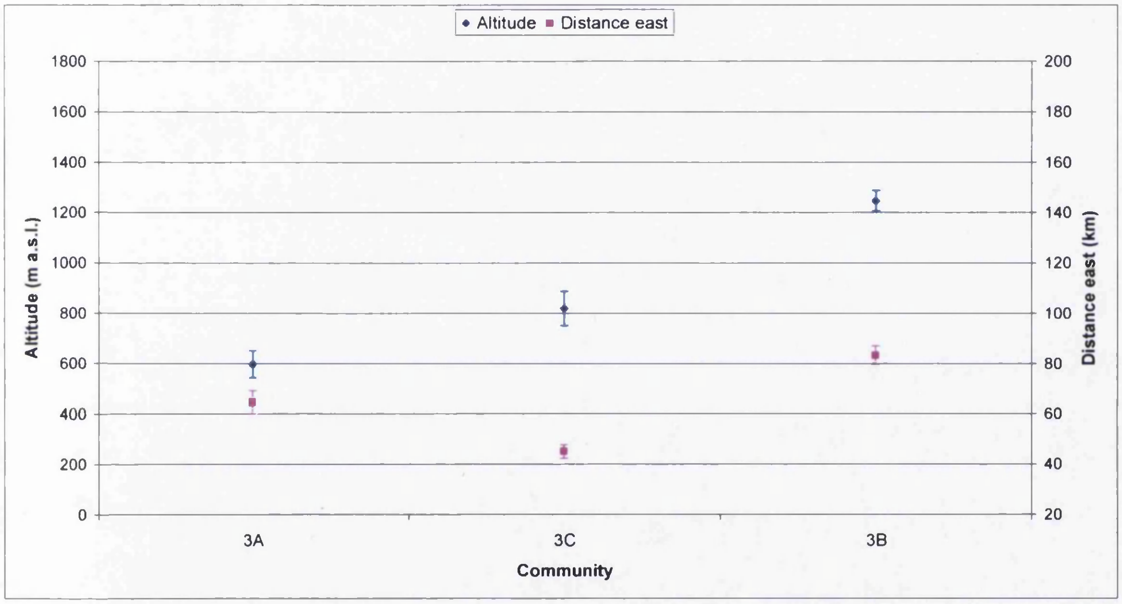


Figure 6-4. Mean altitude and distance east of three roadside pioneer communities.

6.2.2.2 Distribution of six roadside pioneer sub-communities

Indirect ordination of the six pioneer roadside sub-communities identified in Chapter 4 (Figure 4-33) using the rotated NMS axes (Figure 6-5) reveals that the majority of sites comprising sub-community 6D now occur at the lower end of axis 1, below 6A, but with a degree of overlap along axis 1. Sites within sub-community 6E have the highest scores on axis 1, above 6B and 6F and there is the possibility of a sharper variation in species composition between sites in 6B and 6E at the higher end of axis 2. The boundaries between 6A and 6D and between groups 6E and 6F are suggestive of a continuum of variation with altitude, although the degree of variation is large. There is relatively poor separation between 6B and 6F along axis 1, suggesting that factors other than altitude are having an important influence on their species composition. Sub-community 6F sites have relatively low positions on axis two, whereas 6B sites have a broader distribution along this axis but with the majority of sites having higher scores than those in 6F.

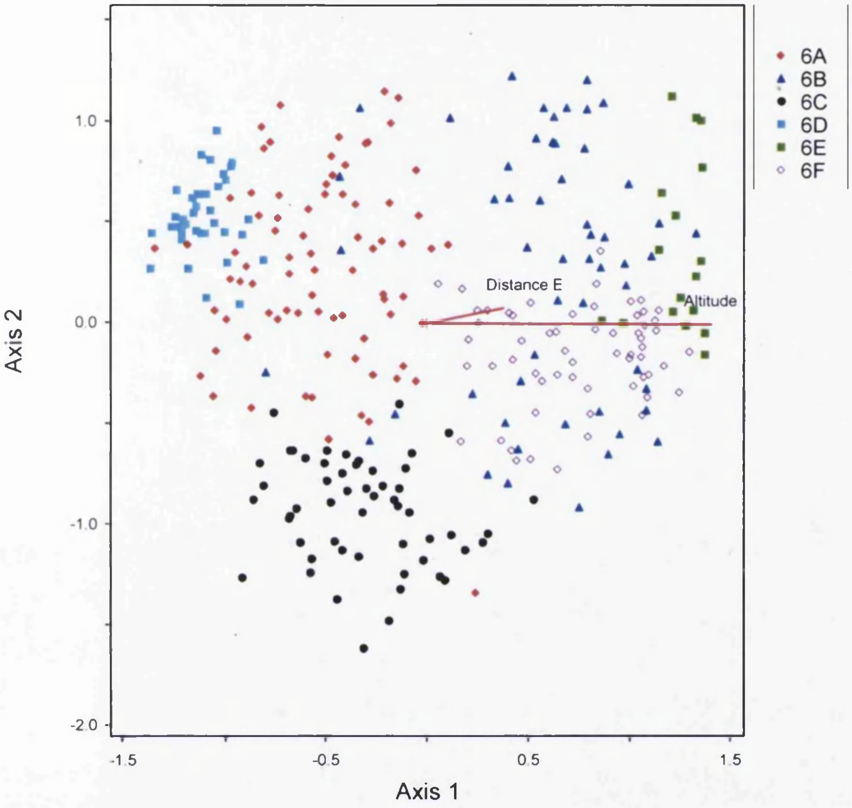


Figure 6-5. NMS ordination diagram rotated for maximum correlation between axis 1 and altitude showing six roadside pioneer cluster analysis groups.

In the direct gradient analysis (Figure 6-6), altitudinal zonation is less clear-cut than for the three communities. Sub-community 6D sites occur at the lowest altitudes, with a number of 6A sites also occurring within this low altitude zone. The upper altitudinal limit of 6D appears to increase with distance east from 440 m at 31 km east to 620 m at 89 km east. The upper boundary of 6A lies between 880 and 1100 m, and above this it is most often replaced by 6B or 6F sites except for one road (Fortundalen) at 61 km east where 6C sites replace it. As anticipated from examination of the indirect ordination diagram (Figure 6-5), there is no clear relationship between 6B and 6F in terms of altitude, with these two sub-communities showing different altitudinal patterns on different roads. This is possibly a reflection of habitat factors operating a t a local scale Figure 6-6 clearly indicates that 6E sites occupy the highest altitudes.

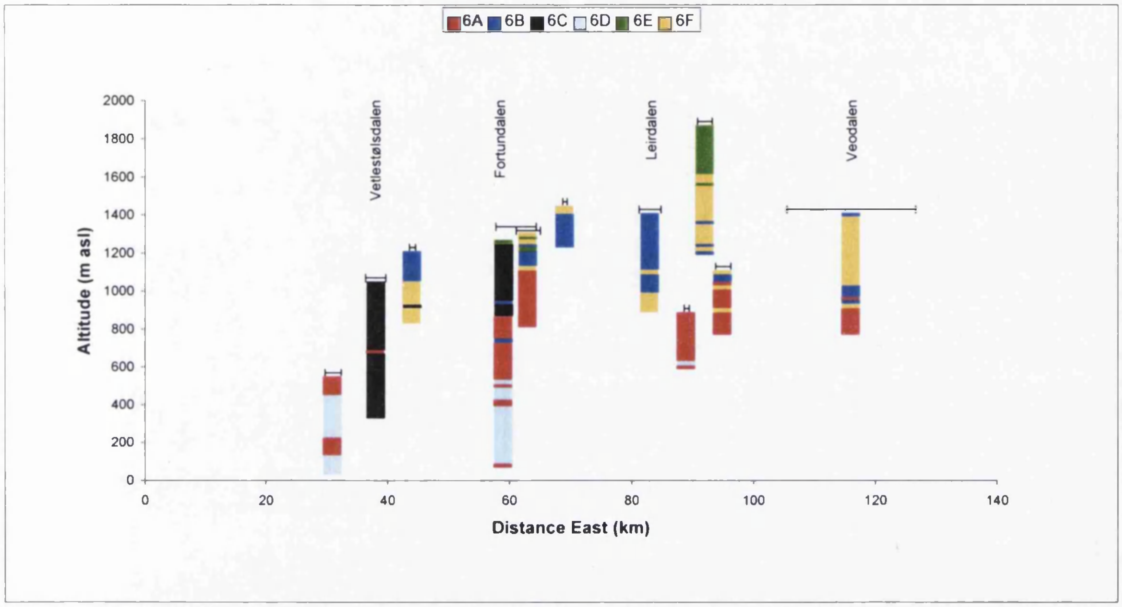


Figure 6-6. Altitude and distance east of six roadside pioneer sub-communities. Coloured vertical columns represent the altitudinal range of individual roads; horizontal bars represent their west-east range. The column at 59 km east has been displaced slightly from 61 km to avoid overlap of columns.

Table 6-4. Mean altitude and distance east of the six roadside pioneer sub-communities.

	Mean ± 95% confidence interval	
Sub-community	**Altitude (m a.s.l.)**	**Distance east (km)**
6A	740 ± 52	72 ± 6
6B	1169 ± 42	76 ± 5
6C	827 ± 71	47 ± 4
6D	326 ± 61	47 ± 5
6E	1644 ± 97	87 ± 6
6F	1192 ± 53	89 ± 6

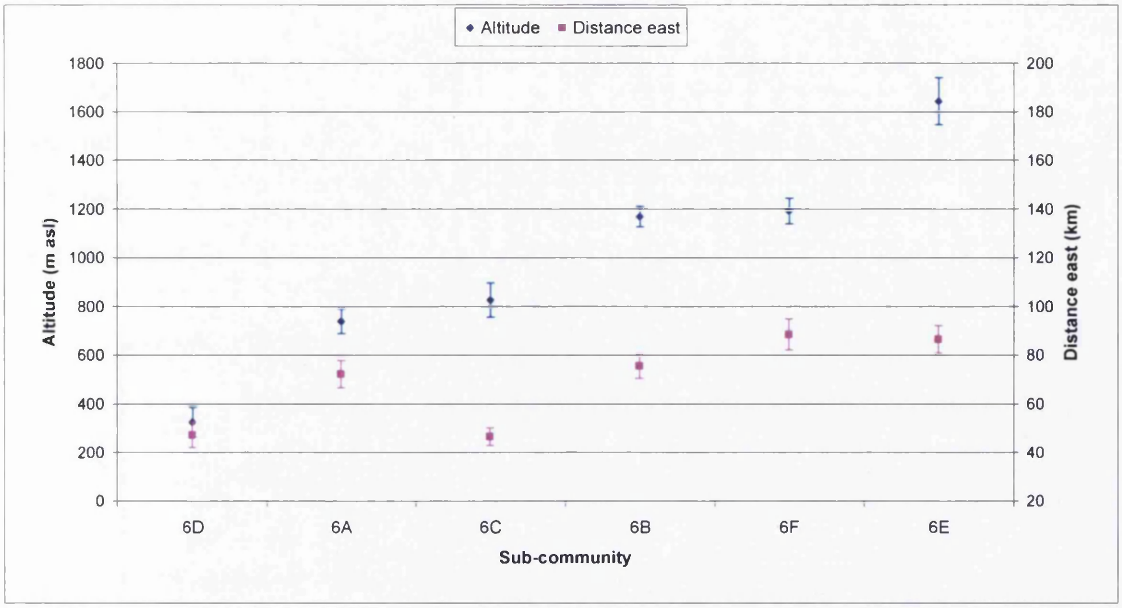


Figure 6-7. Mean altitude and distance east of six roadside pioneer sub-communities.

Calculation of the mean altitudes and 95% confidence intervals for these six sub-communities (Table 6-4 and Figure 6-7) confirms the degree of altitudinal separation discussed above. Sub-community 6D has a mean altitude of 298 m, 6A and 6C have overlapping 95% confidence intervals with means of 739 m and 819 m respectively, as do 6B and 6F at 1183 m and 1192 m, while the mean altitude of 6E is the highest at 1643 m. The regional zonation in relation to continentality is also clarified, with 6D and 6C being furthest east (mean distances east are 48 km and 46 km, respectively), and sub-communities 6E and 6F being more continental (87 km and 89 km east). Sub-communities 6A and 6B have greater mean distances east than 6C and 6D and shorter mean distances east than 6E and 6F but overlap with each other. 6B and 6F differ in their mean distances east (76 km and 89 km respectively). The difference between these two sub-communities therefore appears to be influenced more by continentality than by altitude. However, the general relationship between altitude and distance east is confirmed at this level of cluster analysis with mean altitude and mean distance east co-varying predictably.

6.2.2.3 Distribution of nine roadside pioneer cluster analysis groups

In Chapter 4, the nine-group level of cluster analysis for the roadside pioneer sites was considered likely to consist of sub-divisions of a continuum, rather than distinct groups. The geographical distribution of these groups is examined here in order to confirm or disprove this conclusion.

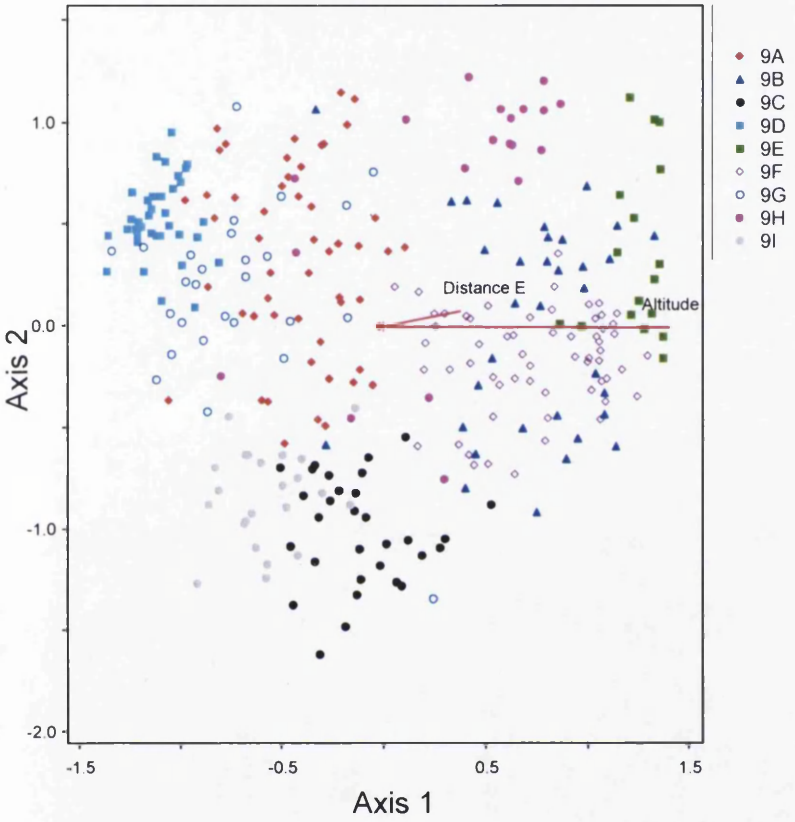


Figure 6-8. NMS ordination diagram rotated for maximum correlation between axis 1 and altitude showing nine roadside pioneer cluster analysis groups.

Indirect gradient analysis at the nine-group level of cluster analysis (Figure 6-8) shows that group 9D sites have the lowest scores on axis 1 and the majority of sites within group 9G appear to have lower scores than those within group 9A, suggesting that this group has an intermediate altitude between groups 9A and 9D. Group 9I sites are distributed at lower positions along axis 1 than those within group 9C, suggesting that these sites occur at lower altitudes than group 9C. Groups 9E and 9F are the same as groups 6E and 6F. The majority of sites within group 9H occur towards the upper end of axis 1, but have lower scores than sites within group 9E, and the ordination suggests that the mean altitude of group 9H is comparable with groups 9B and 9F. The positions of groups 9H and 9I in relation to the vector for distance east may reflect a regional influence on these two groups.

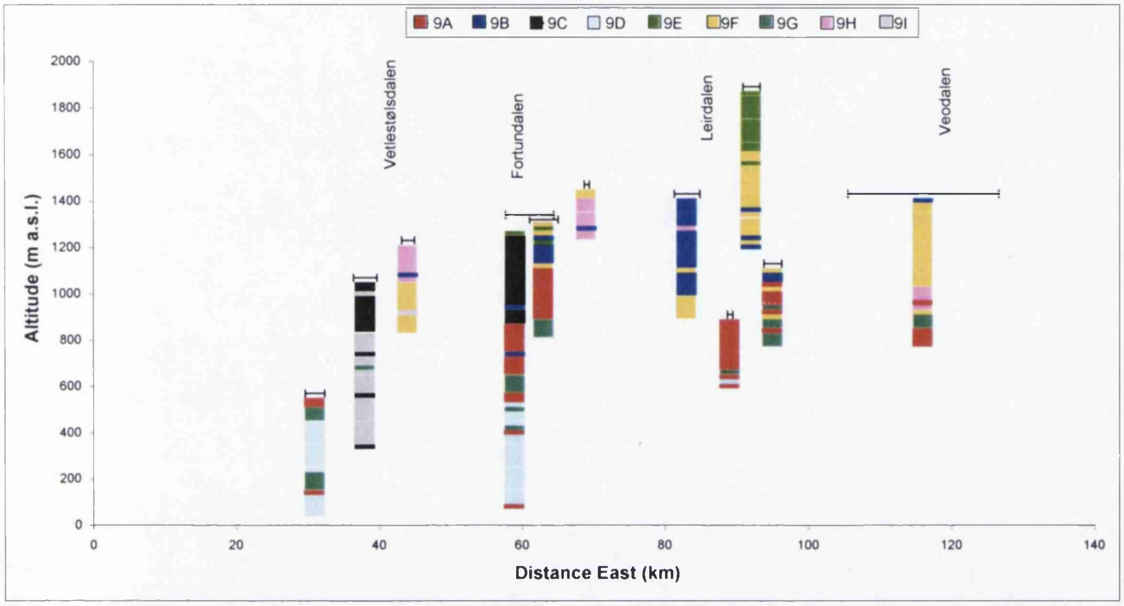


Figure 6-9. Altitude and distance east of nine roadside pioneer cluster analysis groups. Coloured vertical columns represent the altitudinal range of individual roads; horizontal bars represent their west-east range. The column at 59 km east has been displaced slightly from 61 km to avoid overlap of columns.

In the direct gradient analysis of the nine groups (Figure 6-9), group 9I occurs on only one road towards the west of the region and is clearly at a lower altitude than group 9C from which it has split. The altitudinal distribution of group 9G is not as clear cut but it most often occurs below group 9A and the majority of sites within this group lie above group 9D sites. However, unlike group 9D, it occurs across the whole region. As anticipated in analysis of the ordination diagram (Figure 6-8), group 9H does not have a clear altitudinal relationship with groups 9B and 9F and it is interesting to note that the majority of group 9B sites are concentrated along a single road (Leirdalen) at 83 km east.

The mean altitudes for the nine roadside pioneer cluster analysis groups (Table 6-5 and Figure 6-10) clarify the conclusions reached regarding their altitudinal distributions. In order of mean altitude from lowest to highest, group 9D has a mean altitude of 285 m, followed by groups 9G and 9I at 637 m and 612 m respectively; group 9A has a mean altitude of 792 m, group 9C a mean altitude of 974 m, groups 9B, 9F and 9H have very similar mean altitudes (1180 m, 1192 m and 1189 m respectively), and group 9E has the highest at 1643 m. The mean distance east for each group reveals that group 9I sites are on average the furthest west (38 km east) followed by groups 9D and 9C (48 km and 51 km respectively), groups 9A, 9G, 9B and 9H have overlapping 95% confidence intervals and mean distances east of 76 km, 66 km, 80 km and 70 km respectively, while the upper 95% confidence interval for group 9B also overlaps that of groups 9E and 9F. The altitudinal influence on pioneer vegetation is therefore still clear at this level of cluster analysis, with mean altitude being a factor which can be used to distinguish six altitudinal zones. There is some evidence that the groups which are not distinguishable by altitude (i.e. groups 9G and 9I and groups 9B, 9F and 9H) have different regional distributions in relation to continentality but the differences between groups 9B and 9F and between groups 9B and 9H cannot be accounted for by differences in mean distance east.

Table 6-5 Mean altitude and distance east of the nine roadside pioneer groups.

	Mean ± 95% confidence interval	
Group	**Altitude (m a.s.l.)**	**Distance east (km)**
9A	792 ± 57	75 ± 6
9B	1154 ± 51	81 ± 5
9C	994 ± 74	54 ± 6
9D	305 ± 46	47 ± 5
9E	1595 ± 115	84 ± 8
9F	1200 ± 57	88 ± 6
9G	711 ± 103	67 ± 11
9H	1189 ± 62	70 ± 12
9I	613 ± 73	38 ± 1

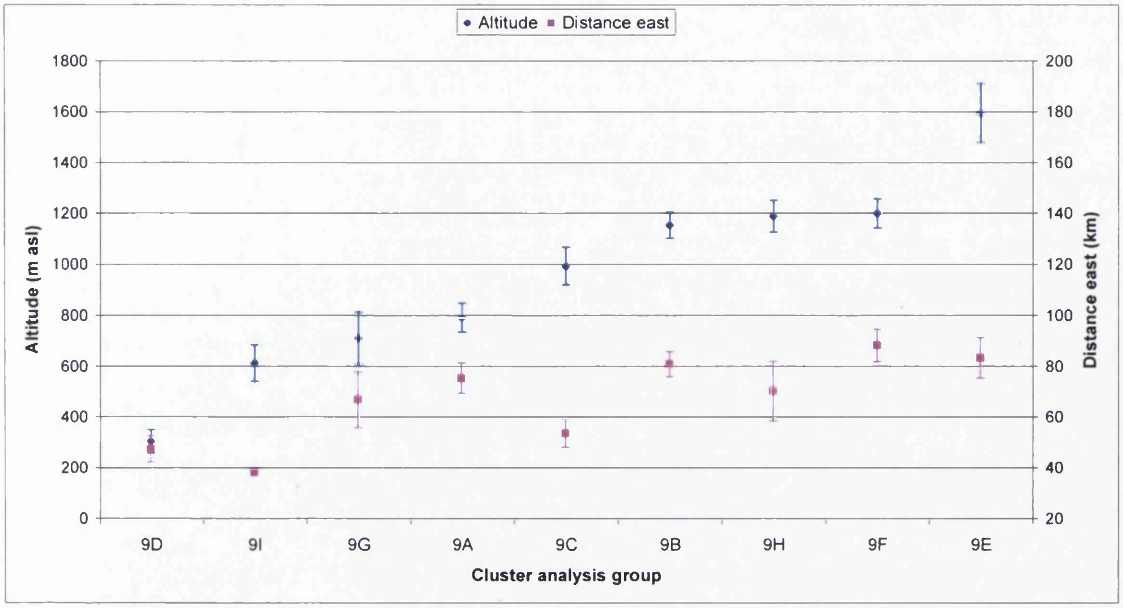


Figure 6-10 Mean altitude and distance east of nine roadside pioneer groups.

Altitudinal factors therefore appear to have a major influence on the distribution of pioneer roadside vegetation, with the majority of communities, sub-communities and groups at the three-, six- and nine-group levels of cluster analysis being distinguishable by differences in their mean altitudes. The effect of continentality is also evident and differences between mean distances east can in some cases be identified for communities which are not distinguished by altitude. In order to seek further clarification of these geographical influences and to investigate ecological factors which may be important in differentiating communities not distinguished by altitudinal or regional distribution, Ellenberg's indicator values are used in section 6.3 to characterise sites within each cluster analysis group and analyse changes in these values in both vegetational and geographical space.

6.3 The use of Ellenberg indicator (EI) values to detect environmental differences between roadside pioneer communities

Weighted mean EI values for light, moisture, pH and nitrogen were calculated for all roadside pioneer sites to enable assessment of trends in these variables in relation to altitude and continentality and to seek possible environmental interpretations of axis 2 of the NMS ordination diagram. Trends in EI values in relation to vegetational space are first assessed for the data set as a whole by analysing correlations between ordination axes and EI values and by examining variations in EI values for individual sites along each axis. Mean EI values and 95% confidence intervals are then calculated for groups of sites at each of the three levels of cluster analysis to determine whether the communities and sub-communities can be distinguished on this basis.

6.3.1 The relationship between mean EI values of roadside pioneer sites and NMS axes.

Figure 6-11 shows the relationship between weighted mean EI values and the NMS ordination axis scores when the diagram is rotated for maximum correlation between axis 1 and altitude and Table 6-6 lists the correlation coefficients between the two ordination axes and the four EI values.

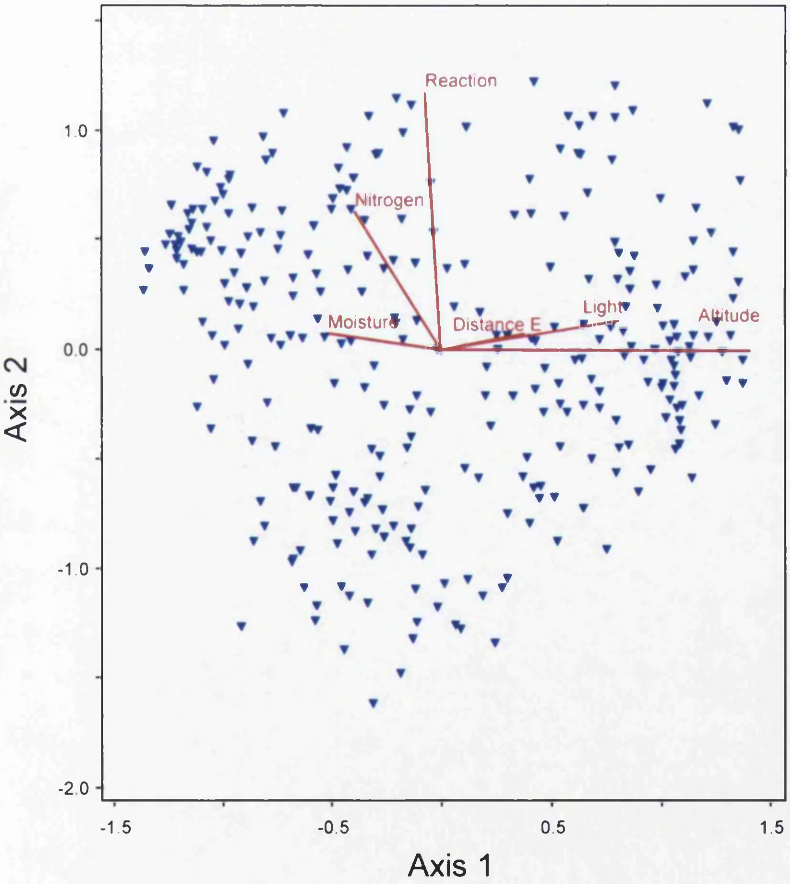


Figure 6-11. NMS ordination of roadside pioneer sites rotated for maximum correlation between axis 1 and altitude showing vectors for mean weighted Ellenberg indicator values.

Table 6-6. Pearson's r coefficients for correlations between rotated roadside pioneer NMS axes and EI values ($p < 0.01$).

	Axis 1	**Axis 2**
Light	+0.655	+0.361
Moisture	-0.556	n.s.
pH	-0.272	+0.794
Nitrogen	-0.521	+0.538

Examination of the correlations between NMS axis 1 and EI values (when the axes are rotated for maximum correlation between axis 1 and altitude) reveals that the value for light has a moderate positive correlation of r = +0.655, while values for moisture (r = -0.556) and nitrogen (r = -0.521) have moderate negative correlations. Both these correlations can be understood in terms of their relationship with altitude. Light levels would be expected to increase with altitude, due to the effect of moving from forest to sub-alpine and alpine vegetation zones, where shading of pioneers would be limited. The effect of increasing cloud cover with altitude is not reflected in this result. The decrease in moisture levels with altitude can be interpreted in four ways: firstly, the higher wind speed at higher altitudes has a drying effect on vegetation; secondly the lower temperatures at higher altitudes mean that the ground is frozen for the majority of the year; thirdly, greater soil depths and better developed soils at lower altitudes increase the moisture-holding capacity of the substrate; and, fourthly, the relationship between altitude and distance east means that the lower altitude sites are concentrated in the western region which has higher precipitation rates. However, the last is probably not so important, as there is no relationship demonstrated between moisture levels and distance east.

Nitrogen levels would be expected to increase in areas of intensive agriculture. However, this is not likely to have a significant effect within the study area, except at very low altitudes where fertilizers may be used. The value for pH has a weak negative correlation with axis 1 of r = -0.272 but a strong positive correlation with axis 2 of r = +0.794. Axis 2 also has a moderate positive correlation with nitrogen (r = +0.538) and a weak positive correlation with light (r = +0.361). The evidence therefore points to a possible explanation of axis 2 in terms of the level of substrate pH which in turn would affect the availability of nitrogen to pioneer vegetation, low pH levels decreasing nitrogen uptake in most plant species. This may therefore be a nutrient axis. An alternative interpretation would be that disturbance levels decrease at the lower end of axis 2 and shrubs such as *Vaccinium* spp, which are more typical of later stages of succession, are able to colonize earlier and have an acidifying effect on the substrate. The presence of coniferous trees below the tree line would also be expected to have an acidifying effect. Decreased disturbance would have the effect of increasing nutrient concentration by promoting accumulation rather than dispersal. The latter interpretation would be supported by the weak positive correlation of axis 2 with mean EI value for light, succession leading to increased shading.

Table 6-7 lists the correlations between all six variables (the four EI values plus altitude and distance east) and shows significant correlations between altitude and the other five factors and between distance east and the Ellenberg values for light and moisture. The correlation between the mean EI values is strongest between nitrogen and reaction (r = +0.748), is moderately positive between nitrogen and moisture (r = +0.497), moderately negative between light and moisture (r = -0.411) and is weakly positive between moisture and pH (r = +0.201).

Table 6-7. Pearson's r coefficient values for correlations between roadside pioneer site environmental variables ($p < 0.01$).

	Altitude	**Distance East**	**Light**	**Moisture**	**pH**
Altitude					
Distance East	0.551				
Light	0.570	0.476			
Moisture	-0.449	-0.382	-0.411		
pH	-0.215	n.s.	n.s.	0.201	
Nitrogen	-0.458	n.s.	n.s.	0.497	0.748

In order to examine the relationship between EI values and ordination space more closely, the following four figures (6-12 to 6-15) show the NMS ordination diagram with the size of the symbol representing each site indicating its relative mean weighted EI value, and side scatter-plots showing how mean weighted EI values change along each axis.

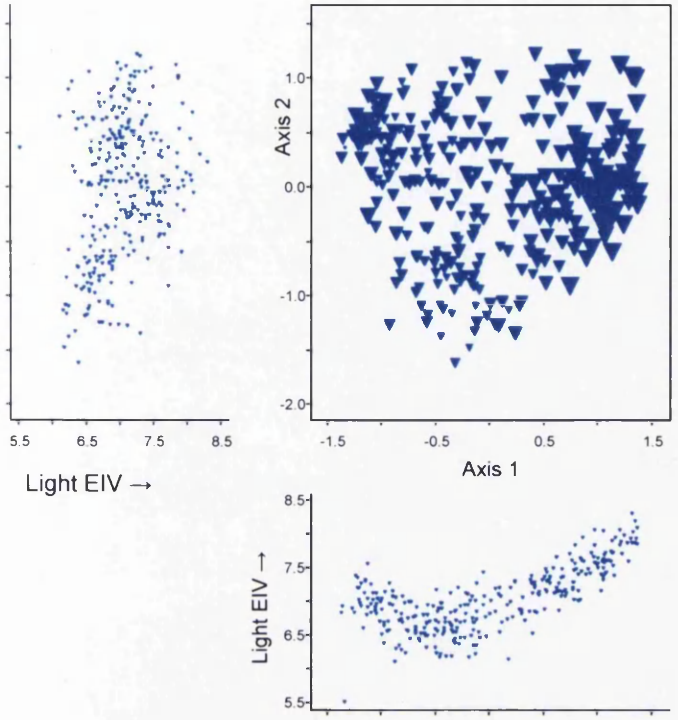


Figure 6-12 NMS ordination and scatter-plots showing mean weighted EI values for light on roadside pioneer sites. The size of each site symbol in the ordination diagram is relative to its mean EI value.

Figure 6-12 clearly shows an increase in the mean EI value for light for sites at the upper end of axis 1 and the scatter-plot for axis 1 confirms this trend. Although, as the positive correlation with axis 1 indicated, there is a tendency for the mean value for light to increase along axis 1, the situation is more complex. The mean EI value for light tends to decrease from values of 6.8 to 7.5 at the lower end of axis 1 to values between 6.2 and 7 at approximately -0.5 on axis 1, before increasing to values of 7.7 to 8.4 at -1.5 on axis 1. This would reflect the change with increasing altitude from open agricultural land to forest and then to the alpine zone above the tree-line.

The pattern of mean EI values for moisture (Figure 6-13) is also more complicated than a simple decrease along axis 1 suggested by the negative correlation. The mean value for moisture first increases and then tends to decrease until about 0.2 on axis 1, after which there is a much wider range of values. The point on axis 1 where the change to a wider range of values occurs appears to coincide with the discontinuity in site ordination scores (i.e. between groups 3A and 3B), which reflects the change in species composition between lower and upper altitude sites. Furthermore, if we examine the values along the upper half of axis 1, we can see that this is where an additional trend occurs, with higher values for moisture towards the top of axis 2. It would therefore seem that the variation between sites in their mean moisture values is greater at higher altitudes. The pattern of site EI values for moisture along axis 1 probably reflects increasing precipitation with altitude, followed by a decrease due to extreme windiness and frozen ground, where water is not available for uptake by plants, whereas the pattern at higher altitudes along axis 2 is possibly related to snowbed gradients.

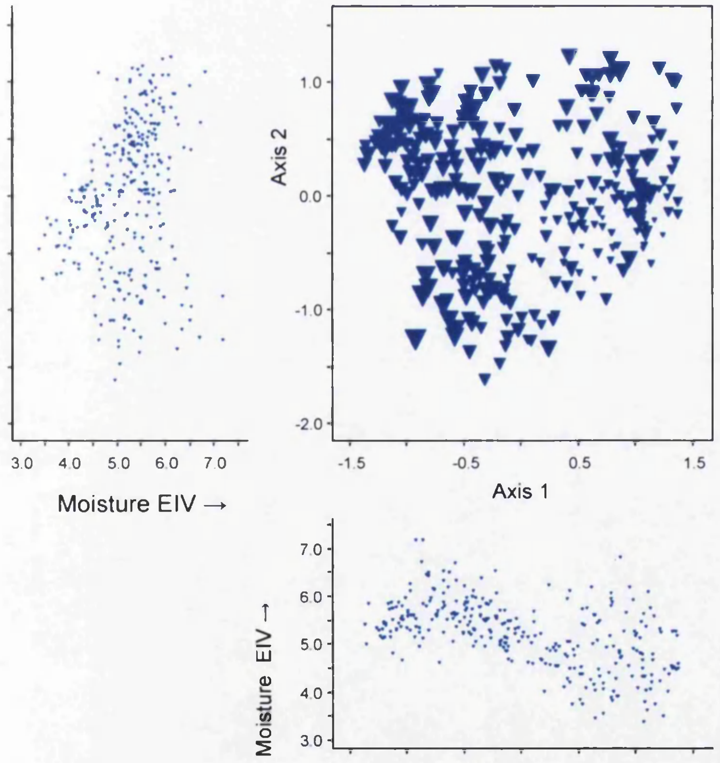


Figure 6-13 NMS ordination and scatter-plots showing mean weighted EI values for moisture on roadside pioneer sites. The size of each site symbol in the ordination diagram is relative to its mean EI value.

The mean values for pH, which show the strongest correlation with axis 2, reveal a very clear trend in Figure 6-14 with values increasing steadily along axis 2. The values for pH along axis 1 are most variable towards the middle of this axis, but with generally higher values at the lower end than the higher end.

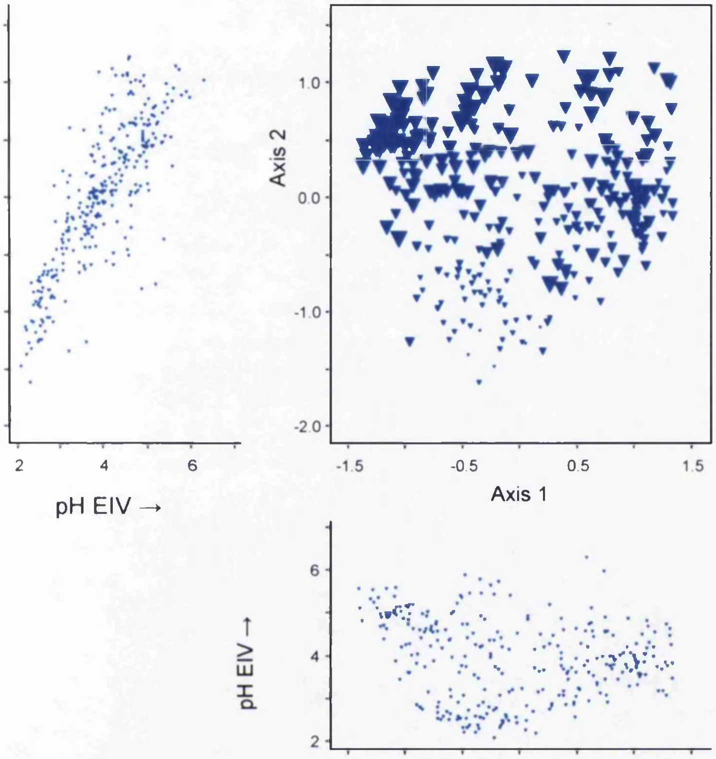


Figure 6-14 NMS ordination and scatter-plots showing mean weighted EI values for pH on roadside pioneer sites. The size of each site symbol in the ordination diagram is relative to its mean EI value.

The mean values for nitrogen (Figure 6-15) follow similar overall trends to those for described for pH but most of its variation along axis 2 is towards the upper end of the axis, with little change towards the lower end. It also shows a clearer general decrease along axis 1 and appears to vary more at higher than at lower altitudes. The overall co-variation in pH and nitrogen values is to be expected and is consistent with natural variation due to local nutrient conditions, which are affected by factors such as acidification by shrubs and conifers and disturbance regimes.

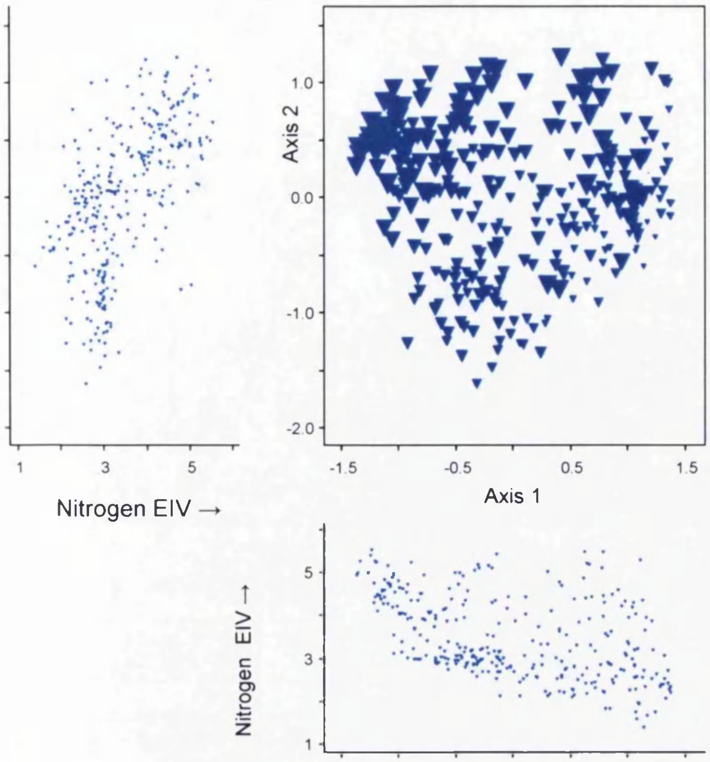


Figure 6-15 NMS ordination and scatter-plots showing mean weighted EI values for nitrogen on roadside pioneer sites. The size of each site symbol in the ordination diagram is relative to its mean EI value.

The more complex variation in mean EI values according to the position of sites in ordination space described above therefore add useful detail to the simple linear trends obtained from analysis of correlation coefficients. Variation in mean EI values for light and moisture are consistent with altitudinal effects as the major factor influencing axis 1 of the site ordination. EI values for pH and nitrogen provide further detail which supports this hypothesis. Trends in pH and nitrogen values also contribute to a possible explanation of variation in pioneer vegetation along axis 2, as does the trend in values for moisture at higher altitudes. Nutrient levels may be influenced by the effects of wet and dry flushes, both of which may increase the availability of nutrients to plants, through the redistribution of minerals.

Variance partitioning is used to quantify the relative contributions of each EI value to variation in species composition and to calculate the covariance between EI values and altitude and distance east. Table 6-8 lists the variance explained (VE) by each environmental factor and the variance explained when that factor is partitioned out, enabling shared variance between factors to be quantified. Altitude and soil pH are confirmed as the dominant factors, explaining 32% and 28% of the total variance explained (TVE), respectively. When altitude is factored out, the values for all other factors decrease indicating co-variance with altitude, the lowest co-variance being with pH which decreases from 28% to 27%. When pH is factored out, the value for nitrogen (24%) decreases to 18%, indicating that 25% of the effect of nitrogen is shared with pH. Distance east explains the smallest fraction of TVE (15% non-independent, 6% independent variance) and is shown to co-vary with altitude, light and moisture. The values for moisture and light both co-vary slightly more with altitude than with distance east (by 3% and 2% respectively). It is interesting to note that moisture shares 32% of its effect with altitude but only 21% with distance east, indicating that the effect of altitude on moisture levels is greater than the effect of continentality. Figure 6-16 summarizes the independent and non-independent variance explained by each environmental factor.

Table 6-8. Variance explained by altitude (A), distance east (E) and mean EI values for light (L), moisture (M), pH and nitrogen (N) for the roadside pioneer data set. TVE = total variance explained. VE| = variance explained with factor partitioned out. a) VE, b) VE expressed as percentages of TVE. All values are significant at $p = 0.002$.

a)

Variable	VE	VE|A	VE|E	VE|AE	VE|L	VE|M	VE|pH	VE|N
TVE	1.72	1.17	1.62	0.99	1.26	1.38	1.24	1.30
A	0.55	N/A	0.47	N/A	0.39	0.48	0.53	0.47
E	0.26	0.18	N/A	N/A	0.13	0.19	0.26	0.25
L	0.46	0.30	0.32	0.27	N/A	0.37	0.46	0.45
M	0.34	0.23	0.27	0.23	0.25	N/A	0.34	0.29
pH	0.48	0.46	0.48	0.40	0.48	0.48	N/A	0.37
N	0.42	0.34	0.41	0.32	0.41	0.37	0.31	N/A

b)

Variable	VE	VE|A	VE|E	VE|AE	VE|L	VE|M	VE|pH	VE|N
TVE	1.00	0.68	0.94	0.58	0.73	0.80	0.72	0.76
A	0.32	N/A	0.27	N/A	0.23	0.28	0.31	0.27
E	0.15	0.10	N/A	N/A	0.08	0.11	0.15	0.15
L	0.27	0.17	0.19	0.16	N/A	0.22	0.27	0.26
M	0.20	0.13	0.16	0.13	0.15	N/A	0.20	0.17
pH	0.28	0.27	0.28	0.23	0.28	0.28	N/A	0.22
N	0.24	0.20	0.24	0.19	0.24	0.22	0.18	N/A

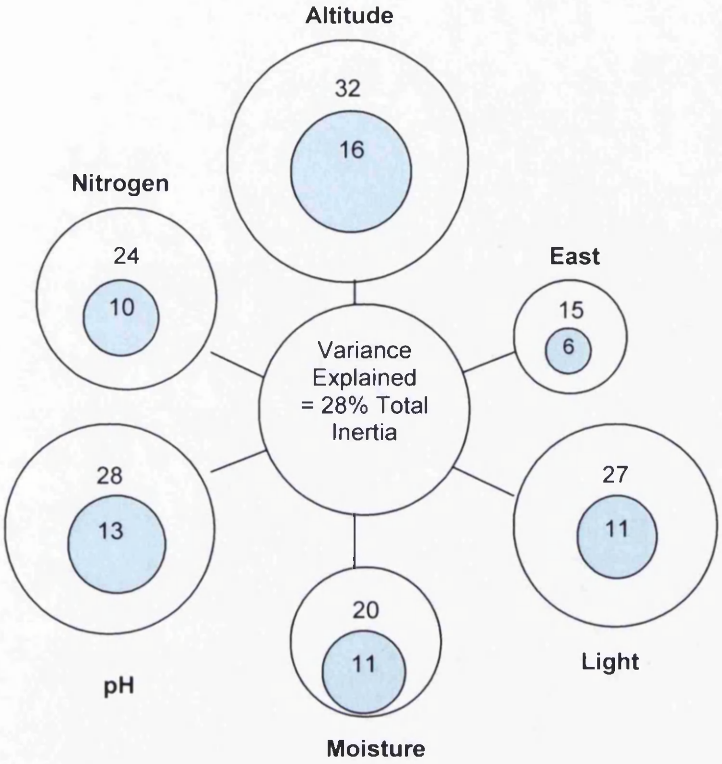


Figure 6-16. Variance explained by measured environmental factors for roadside pioneer sites. Large circles represent % non-independent variance explained, smaller shaded circles represent % independent variance explained.

EI values are next used to investigate possible environmental differences between roadside pioneer communities. All three levels of clustering previously examined are analysed, using mean weighted EI values and 95% confidence intervals for each group. Possible explanations are particularly sought for the differences between groups which were not separated along axis 1 and could not therefore be distinguished on the basis of their mean altitudes.

6.3.2 EI values of roadside pioneer communities and sub-communities

6.3.2.1 EI values at the three-group level

At the three group level of cluster analysis (Table 6-9 and Figure 6-17), the means and 95% confidence intervals show a distinct difference between all three communities for light, pH and nitrogen EI values, whereas the mean EI values for moisture show a difference between 3A and 3B but have overlapping confidence intervals between 3A and 3C. Table 6-9 confirms that 3A and 3C have similar mean EI values for moisture (5.6 and 5.5 respectively) compared to 4.8 for 3B. They also have similar mean light values (6.8 and 6.6 respectively) compared to the higher value of 7.4 for 3B, but the 95% confidence intervals are narrow enough for them to be distinct. Communities 3A and 3C can also be distinguished on the basis of their mean pH and nitrogen EI values: the mean pH value for 3C at 2.6 is considerably lower than the value for 3A at 4.6 while the mean nitrogen value is also lower for 3C at 2.6 than 3A at 4.1. Community 3B has intermediate values for both these indicators. Clear environmental differences are therefore reflected in mean EI values at this level of clustering.

Table 6-9. Mean EI values for the three roadside pioneer communities.

	Mean EIV ± 95% confidence intervals			
Community	**Light**	**Moisture**	**pH**	**Nitrogen**
3A	6.8 ± 0.06	5.6 ± 0.07	4.6 ± 0.13	4.1 ± 0.14
3B	7.4 ± 0.06	4.8 ± 0.12	3.9 ± 0.11	3.2 ± 0.16
3C	6.6 ± 0.06	5.5 ± 0.18	2.6 ± 0.07	2.9 ± 0.07

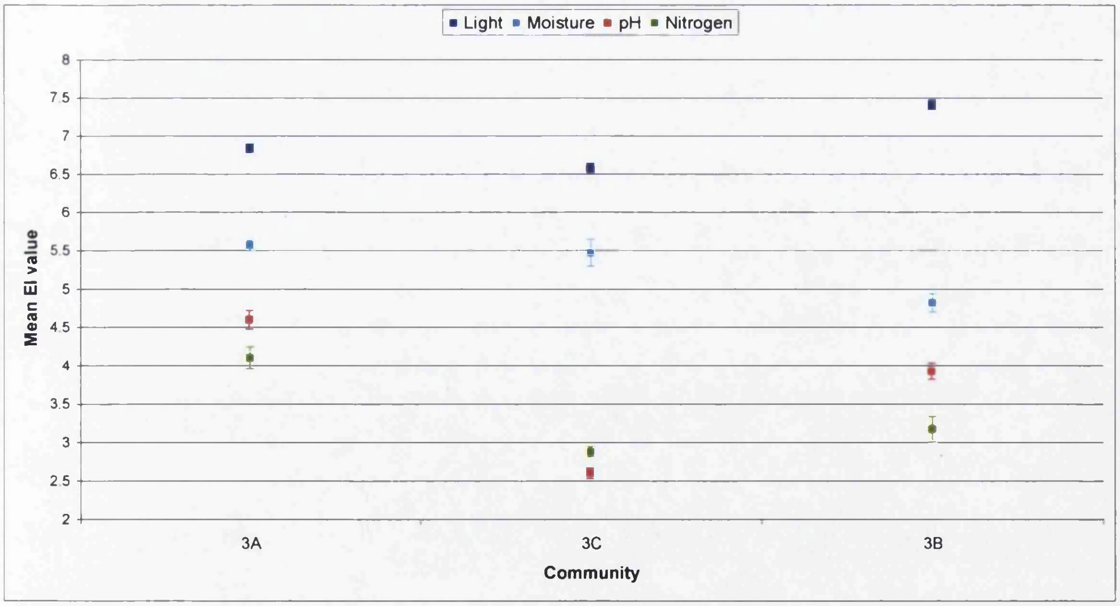


Figure 6-17. Mean EI values for the three roadside pioneer communities.

6.3.2.2 EI values at the six-group level

Analysis of mean El values for six roadside pioneer cluster analysis groups (Table 6-10 and Figure 6-18) reveals that the El values for light vary between all clusters except 6B and 6F which both have a mean value of 7.3. This is consistent with the relationship between altitude and light values, as these two sub-communities also have similar mean altitudes. Sub-communities 6A, 6D and 6C are not distinguishable in terms of their mean El values for moisture (5.6, 5.5 and 5.5 respectively) and the values for 6D and 6C also overlap with that of 3B (5.3). 6E and 6F differ in their mean moisture El value (4.8 and 4.4 respectively) and have lower levels than the other four sub-communities. The mean El values for pH show similar values for 6A, 6B and 6E (4.4, 4.3 and 4.1 respectively) and these values are clearly different to the other three sub-communities, the lowest being 2.6 for 6C and the highest 5.0 for 6D. Mean nitrogen El values are the same for 6A and 6B (3.8) and for 6E and 6F (2.8) and the latter two are similar to 6C which has a value of 2.9. 6D has the highest mean value at 4.7.

The two sub-communities which were not separated along axis 1 of the ordination diagram, groups 6B and 6F, have therefore been shown to vary in their mean values for moisture, pH and nitrogen, 6F being drier, having a lower mean pH and lower mean nitrogen value than 6B. 6A and 6C, which did not have significantly different mean altitudes are distinguishable in terms of mean El values for light, pH and nitrogen, 6A having higher mean values for all three variables.

Table 6-10. Mean El values for the six roadside pioneer sub-communities.

Sub-Community	Mean EIV ± 95% confidence intervals			
	Light	Moisture	pH	Nitrogen
6A	6.8 ± 0.07	5.6 ± 0.09	4.4 ± 0.16	3.8 ± 0.16
6B	7.3 ± 0.09	5.3 ± 0.16	4.3 ± 0.19	3.8 ± 0.27
6C	6.6 ± 0.07	5.5 ± 0.18	2.6 ± 0.08	2.9 ± 0.08
6D	7.0 ± 0.07	5.5 ± 0.09	5.0 ± 0.15	4.7 ± 0.15
6E	7.9 ± 0.10	4.8 ± 0.22	4.1 ± 0.26	2.8 ± 0.27
6F	7.3 ± 0.07	4.4 ± 0.14	3.6 ± 0.11	2.8 ± 0.17

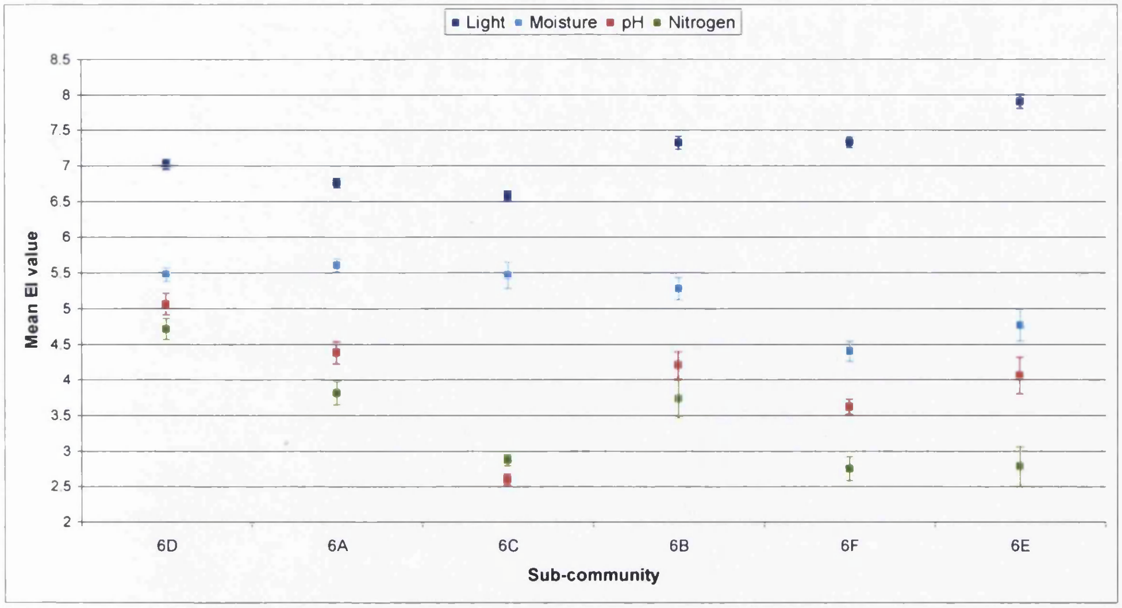


Figure 6-18. Mean EI values for the six roadside pioneer sub-communities.

6.3.2.3 EI values at the nine-group level

When the nine-group level of clustering is analysed in this way (Table 6-11 and Figure 6-19) there is much more of a continuum of variation in mean EI values between groups. For example, with the exception of 9E, the mean EI values for light vary by only 0.1 to 0.2 units along a continuum of values with overlapping 95% confidence intervals. It is still possible at this level of clustering, however, to identify differences in mean EI values for the groups which could not be distinguished in terms of their mean altitudes or mean distances east. Groups 9G and 9I have very similar mean altitudes (637m and 612m respectively), but they differ in all four mean EI values, 9G having higher values for light, pH and nitrogen and a lower value for moisture. Groups 9B, 9F and 9H have similar mean altitudes ranging from 1180 to 1192 m and, although 9F and 9H were found to differ in their mean distance east (88km and 70km respectively), no difference was found between 9B and 9F or 9B and 9H. However, when the mean EI values of these groups are examined, 9B is found to have higher values for light and lower values for moisture, pH and nitrogen than 9H and higher values for moisture, pH and nitrogen than 9F.

Table 6-11. Mean EI values for the nine roadside pioneer groups.

	Mean EIV ± 95% confidence intervals			
Group	**Light**	**Moisture**	**pH**	**Nitrogen**
9A	6.7 ± 0.08	5.7 ± 0.08	4.5 ± 0.22	3.7 ± 0.22
9B	7.4 ± 0.12	5.1 ± 0.12	4.0 ± 0.20	3.3 ± 0.35
9C	6.6 ± 0.16	5.1 ± 0.16	2.5 ± 0.19	2.8 ± 0.14
9D	7.0 ± 0.07	5.5 ± 0.07	5.1 ± 0.10	4.7 ± 0.13
9E	7.9 ± 0.15	4.8 ± 0.15	4.1 ± 0.23	2.8 ± 0.20
9F	7.3 ± 0.14	4.4 ± 0.14	3.6 ± 0.21	2.8 ± 0.32
9G	6.9 ± 0.10	5.4 ± 0.10	4.2 ± 0.14	4.0 ± 0.17
9H	7.2 ± 0.09	5.6 ± 0.09	4.6 ± 0.29	4.4 ± 0.22
9I	6.6 ± 0.06	6.0 ± 0.06	2.7 ± 0.11	3.0 ± 0.04

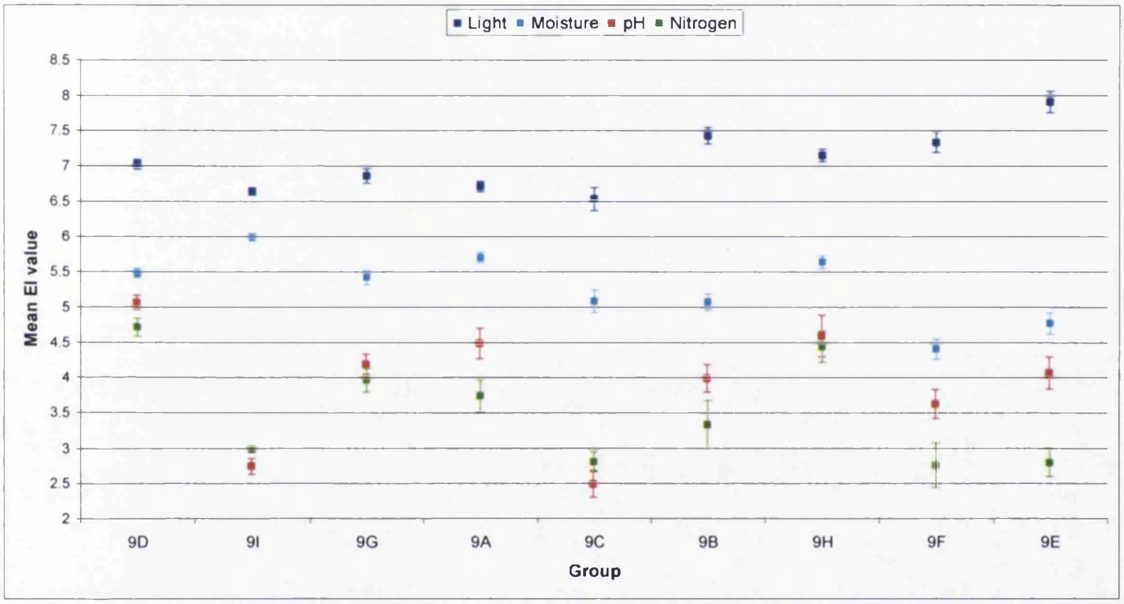


Figure 6-19. Mean EI values for the nine roadside pioneer groups.

The overall trend in the relationship between the mean altitude of a group i.e. its position on axis 1 and its mean values for light and moisture is still evident at the nine group level, and the trend of increasing moisture along axis 2 is evident from groups 9B, 9F and 9H. The position of groups along axis 2 can also be explained by their mean EI values for pH and nitrogen both at lower and higher altitudes, with both values increasing as site scores on axis 2 increase.

Thus, EI values, which were devised specifically for analysis of climax vegetation, clearly also have a use in quantifying environmental factors in relation to the pioneer stage of succession. The absolute values of these indicators may not be as accurate as for climax vegetation but their relative values appear useful in analysing differences between pioneer communities and teasing out complex environmental controls on sub-communities.

A clear altitudinal pattern in the distribution of pioneer vegetation has been identified with distance east (continentality) constituting an additional, though secondary, influence. Analysis of mean EI values has shown that the differences between individual sites and groups of sites along the second major ordination axis can be described primarily in terms of their pH and nitrogen levels, with moisture levels related to axis 2 scores at higher altitudes. Axis 2 is therefore interpreted as primarily a nutrient axis.

6.4 Altitudinal and regional patterns in the distribution of glacier foreland pioneer vegetation

The following two sections present the results of investigation of the glacier foreland pioneer sites, following a similar analytical strategy to that of the roadside pioneer data set. Section 6.4 looks for evidence of geographical patterns in glacier foreland pioneer vegetation and section 6.5 analyzes possible environmental influences.

6.4.1 Indirect gradient analysis in relation to altitude and continentality

To assess the relationship between altitude and continentality of glacier foreland pioneer sites and their positions in NMS ordination space, the ordination diagram has been rotated to obtain maximum correlation between the altitude of each site and its score on axis 1 (Figure 6-20). The resulting correlation coefficient between these two variables is r = 0.753 ($p < 0.01$) (Table 6-12), showing a moderately strong relationship between the species composition of a site and its altitude. The rotated ordination diagram also shows an almost identical level of correlation between the distance east of a site and its position on axis 1 (r = 0.764); and the correlation between altitude and distance east, as expected, is high at r = 0.889 (r^2 = 79%). This suggests that 56% of the variation in species composition along this axis is related to altitudinal and regional influences. For the rotated ordination, the coefficients of determination for correlations between ordination distances and distances in the original n-dimensional space are: axis 1, r = 0.692; axis 2, r = 0.532. Therefore, axis 1 now represents 48% of the original distances between sites and axis 2 represents 28%.

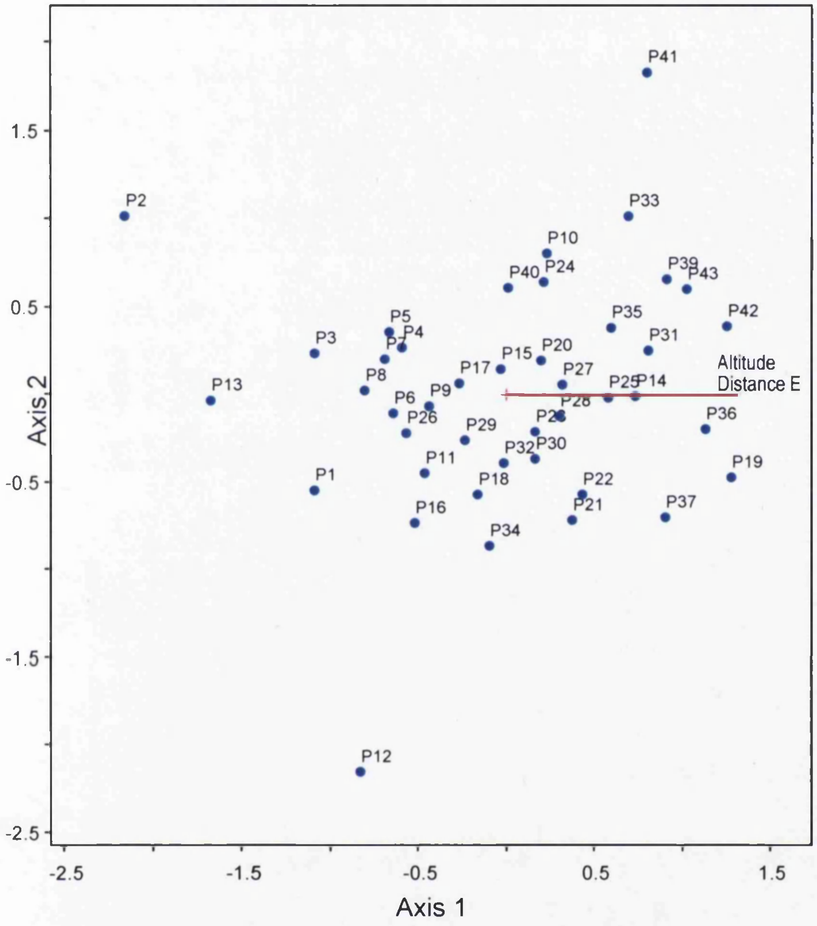


Figure 6-20. NMS ordination of glacier foreland pioneer sites showing correlation between axis 1 and altitude and distance east.

Table 6-12. Pearson's r coefficients for correlations between glacier foreland pioneer NMS axes and altitude and distance east ($p < 0.01$).

	Axis 1	**Axis 2**
Altitude	0.753	n.s.
Distance east	0.764	n.s.

Variance partitioning of the glacier foreland pioneer data set confirms that the total variance in species composition within the data is relatively low at 0.011 and the variance explained by altitude and distance east is 0.007. Table 6-13 shows that within this low variance, altitude alone accounts for 37%, distance east for 29% and the component shared by altitude and distance east represents 27% of the variance. According to these figures the relative effect of continentality on glacier foreland species composition is greater than for the roadside data set (29% rather than 25%), the relative effect of altitude is lower (26% rather than 64%) while the variance shared by altitude and distance east is greater (27% compared with 11%). However, as the total variance within the data is so low, these two factors are both explaining only a small absolute amount of variation in species composition.

Table 6-13 Variance explained by altitude and distance east for the glacier foreland pioneer data set. TVE = total variance explained, A = altitude, E = distance east. All values are significant at $p = 0.002$.

Variable	VE (% TVE)
TVE	0.007 (1.00)
A	0.0045 (0.64)
E	0.0038 (0.54)
A∩E	0.0019 (0.27)
A|E	0.0026 (0.37)
E|A	0.0020 (0.29)

6.4.2 Geographical distribution of glacier foreland pioneer sub-communities

6.4.2.1 Distribution of two glacier foreland pioneer sub-communities

In Figure 6-21 the two glacier foreland sub-communities are superimposed on the NMS ordination diagram rotated for maximum correlation between axis 1 and altitude. The two groups are clearly divided along axis 1 and display a continuum of variation with altitude/distance east without any area of discontinuity. Group 2B appears to consist of sites at higher altitudes and distances further east than group 2A.

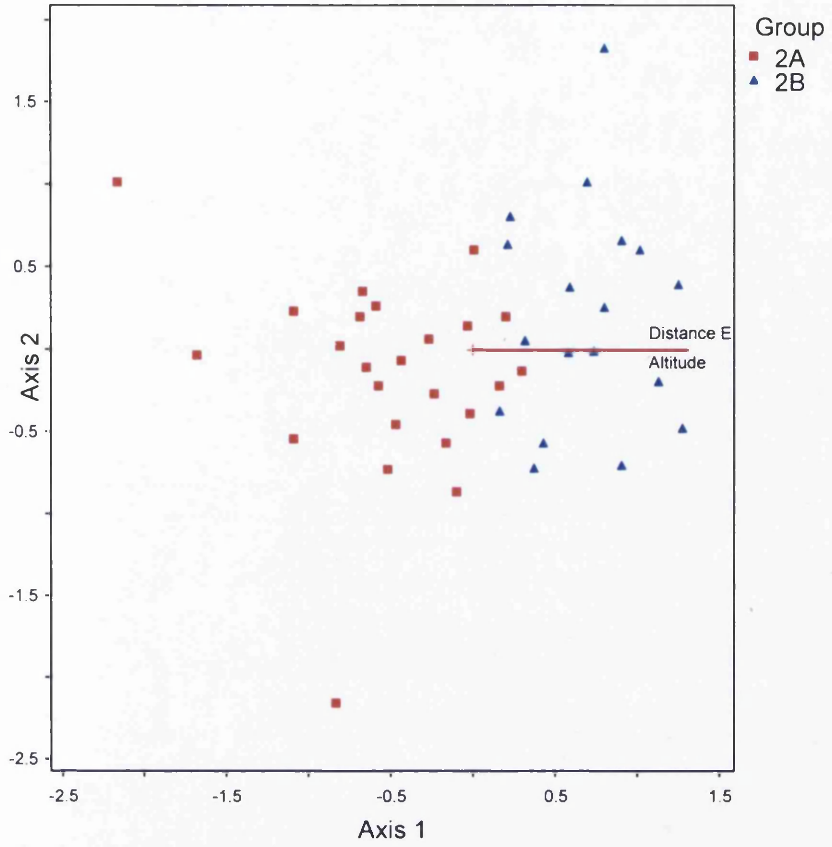


Figure 6-21. NMS ordination diagram rotated for maximum correlation between axis 1 and altitude showing two glacier foreland pioneer sub-communities.

When sites within the sub-communities are plotted according to their altitude and continentality (Figure 6-22) for comparison with their positions in ordination space, the resulting graph shows that 2A sites occur across the entire range of altitudes and distances east but that 2B sites only occur at altitudes of 1100 m and above and at a minimum distance east of 60 km. Although Table 6-14 and Figure 6-23 show that the two sub-communities have different mean altitudes and mean distances east (1162 m for 2A and 1575 m for 2B; 59 km for 2A and 90 km for 2B), Figure 6-22 indicates that, rather than being clearly separated in terms of altitude or region, 2B has a more restricted geographical distribution than 2A.

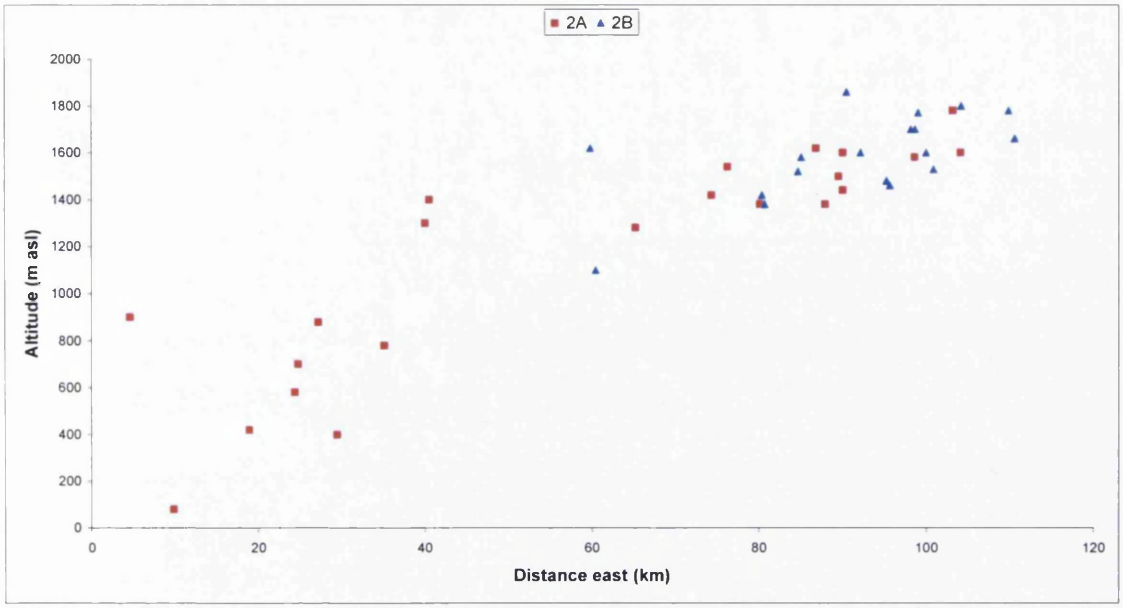


Figure 6-22. Altitude and distance east of two glacier foreland pioneer sub-communities.

Table 6-14. Mean altitude and distance east of the two glacier foreland pioneer sub-communities.

Sub-Community	**Mean ± 95% confidence interval** **Altitude (m a.s.l.)**	**Distance east (km)**
2A	1162 ± 206	59 ± 14
2B	1587 ± 87	92 ± 7

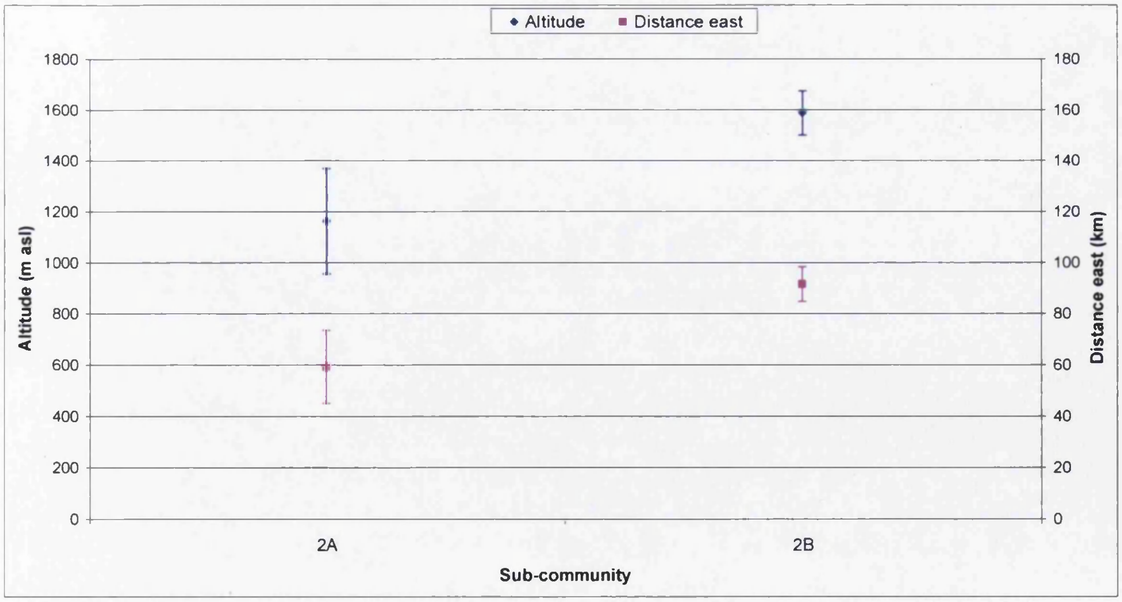


Figure 6-23. Mean altitude and distance east of the two glacier foreland pioneer sub-communities.

6.4.2.2 Distribution of four glacier foreland pioneer cluster analysis groups

Analysis of the four-group level in rotated ordination space (Figure 6-24) again shows groups primarily distributed along axis 1, with group 4C having the lowest scores and groups 4B and 4D having the highest scores on this axis.

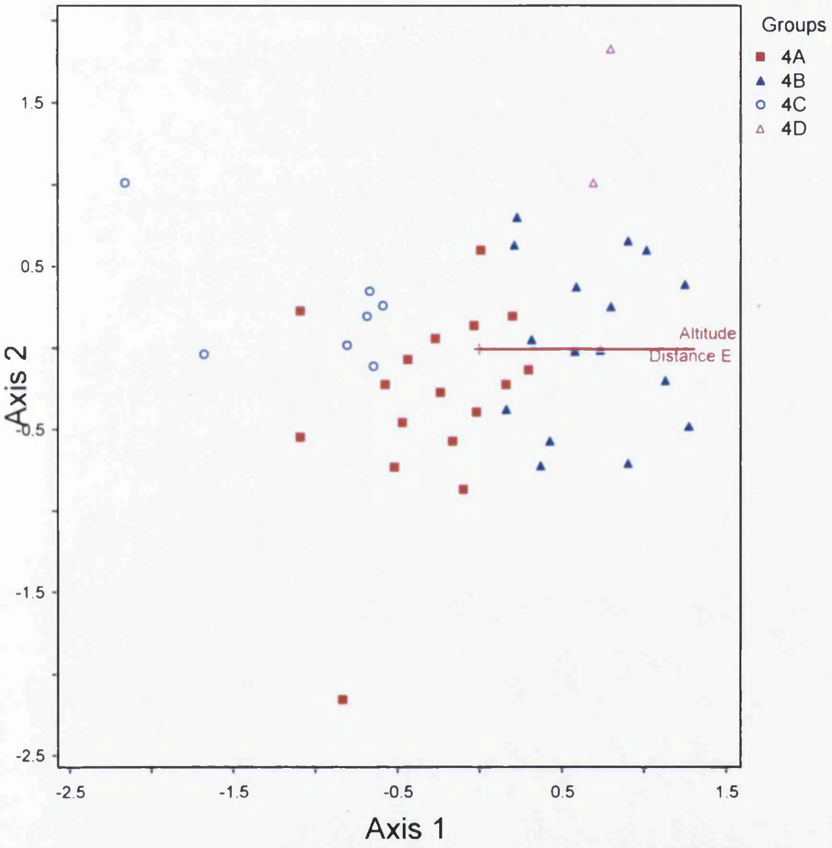


Figure 6-24. NMS ordination diagram rotated for maximum correlation between axis 1 and altitude showing four glacier foreland pioneer cluster analysis groups.

Direct gradient analysis of the four-group level (Figure 6-25) shows that group 4A consists of sites with a broad altitudinal and regional range, while group 4C is restricted to sites to the west of the region (a maximum of 40 km east) the majority of which are below 1000 m. Group 4D is not separated from groups 4A or 4B in terms of altitude or continentality. Examination of the mean altitude and distance east for each group (Table 6-15 and Figure 6-26) verifies these findings, with groups 4A, 4B and 4D having overlapping 95% confidence intervals for their mean altitudes and distances east and only group 4C having confidence intervals which do not overlap with those of the other three groups.

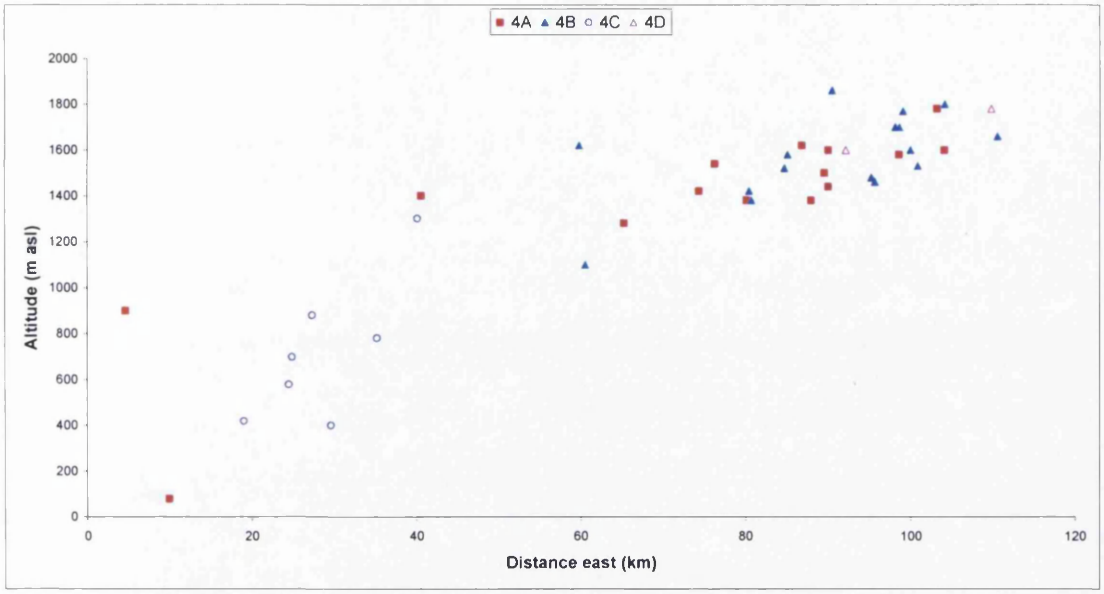


Figure 6-25. Altitude and distance east of the four glacier foreland pioneer groups.

Table 6-15. Mean altitude and distance east of the four glacier foreland pioneer groups.

Group	Mean ± 95% confidence interval Altitude (m a.s.l.)	Distance east (km)
4A	1367 ± 214	74 ± 16
4B	1549 ± 111	87 ± 11
4C	823 ± 241	33 ± 11
4D	1690 ± 176	101 ± 17

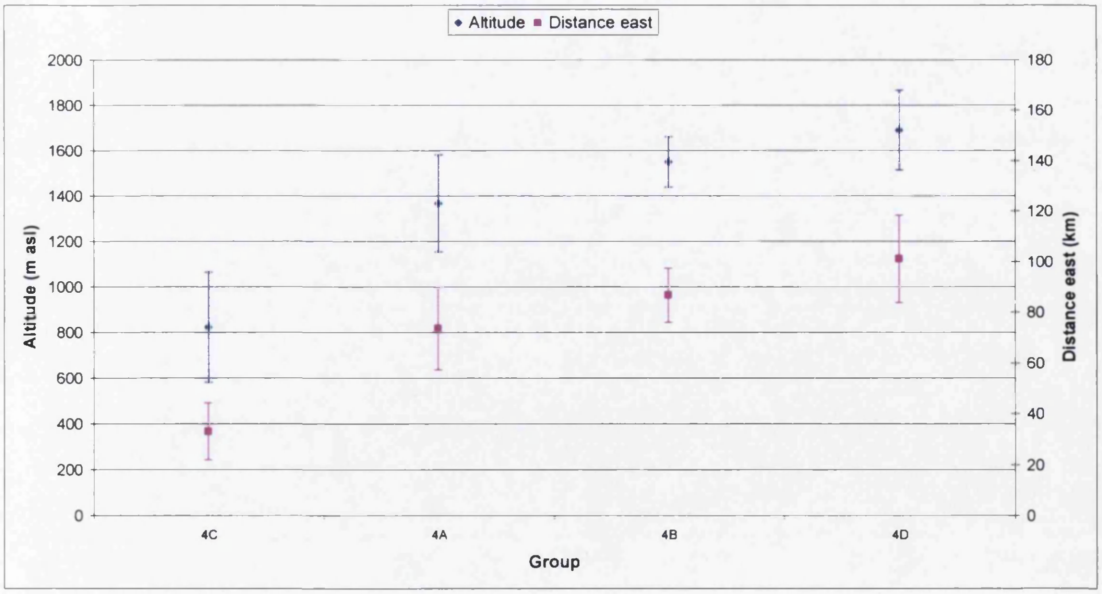


Figure 6-26. Mean altitude and distance east of four glacier foreland pioneer cluster analysis groups.

The findings indicate that, at the two sub-community stage, there is no clear geographical separation between the clusters and, at the four group stage, only group 4C has an altitudinal and regional distribution which is distinguishable from the other three groups. This provides further evidence in support of the proposition that the glacier foreland pioneer sites belong to one broad community with high level of continuity.

6.5 The use of Ellenberg indicator values to detect environmental differences between glacier foreland pioneer communities

Weighted mean EI values for light, moisture, pH and nitrogen were calculated for all glacier foreland pioneer sites to provide a measure of possible relationships in environmental variation, firstly across ordination space and secondly between cluster analysis groups.

6.5.1 The relationship between EI values of glacier foreland pioneer sites and NMS axes.

Figure 6-27 visualizes the relationships between weighted mean EI values and the position of glacier foreland pioneer sites on the NMS ordination diagram when it is rotated for maximum correlation between axis 1 and altitude. The correlation coefficients between the two ordination axes and the four indicators are listed in Table 6-16.

Table 6-16. Pearson's r coefficients for correlations between EI values and glacier foreland pioneer NMS axes ($p < 0.01$**, $p < 0.05$*).

	Axis 1	**Axis 2**
Light	n.s.	-0.384*
Moisture	-0.312*	n.s.
pH	+0.651**	n.s.
Nitrogen	-0.433**	+0.295*

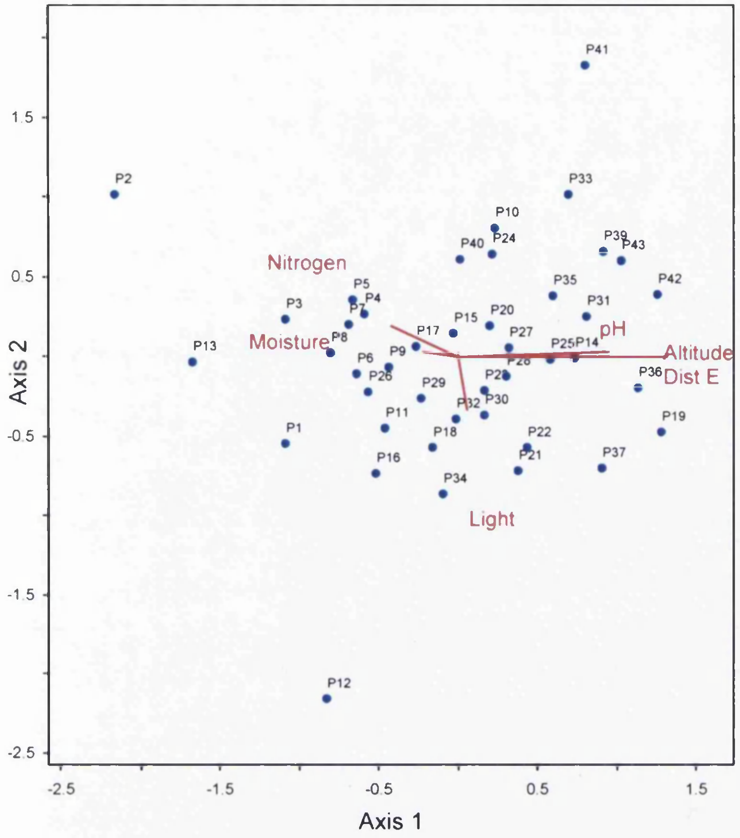


Figure 6-27. NMS ordination of glacier foreland pioneer sites rotated for maximum correlation between axis 1 and altitude showing vectors for mean weighted Ellenberg indicator values.

Figure 6-27 and Table 6-16 show that the strongest positive correlation is between axis 1 and mean weighted EI values for pH (r = +0.651). The values for nitrogen show a moderate negative correlation with axis 1 and a weak positive correlation with axis 2. The mean EI values for light have a weak negative correlation with axis 2 while those for moisture have a weak negative correlation with axis 1.

Correlations between all six variables are listed in Table 6-17. The correlation between altitude and pH is r = +0.371, while that for distance east and pH is slightly higher at r = +0.429. It is possible that this reflects the high base status yet low cation exchange capacity characteristic of glacier foreland pioneer sites and/or the effects of variation between the underlying geology of the Jotunheim and Jostedalsbreen sub-regions. This contrasts with the findings for the roadside sites, which showed a weak negative correlation between altitude and pH (r = -0.215) and no significant correlation between distance east and pH. It therefore seems likely that the high base status of the fresh glacial till is the major influence, rather than the underlying geology.

The EI value for light does not have a statistically significant correlation with altitude or distance east. This contrasts with the roadside pioneer results which show a positive correlation between light and altitude (r = +0.551), presumably due to the presence of trees and shrubs alongside roadsides at many lower altitude sites. On the Jostedalsbreen forelands, the trees are further from the pioneer zone; they are absent altogether from the Jotunheim forelands. The other correlations between EI values and altitude and continentality for glacier foreland pioneer sites are statistically significant but weak to moderate: nitrogen has negative correlations with altitude and distance east; moisture has a negative correlation with distance east but not with altitude. The latter may be reflecting an effect of continentality independent of altitude which was not detectable in the roadside data set.

The strongest correlation between EI values is a negative relationship between light and nitrogen (r = -0.615); the only other statistically significant correlation between EI values is between light and moisture (r = -0.330). If a relatively high EI value for light is a reflection of generally low vegetation cover, then this could be related to low nutrient and moisture levels due to the greater erosive and drying effects of glacial winds where cover is generally poor. For the roadside data set, EI values for light were negatively correlated with moisture but were not significantly correlated with nitrogen values.

Table 6-17. Pearson's r coefficients for correlations between glacier foreland pioneer site environmental variables ($p < 0.01$**, $p < 0.05$*).

	Altitude	**Distance East**	**pH**	**Light**	**Moisture**
Distance East	+0.889**				
pH	+0.371*	+0.429**			
Light	n.s.	n.s.	n.s.		
Moisture	n.s.	-0.371*	n.s.	-0.330*	
Nitrogen	-0.392*	-0.461**	n.s.	-0.615**	n.s.

The following four figures (Figures 6-28 to 6-31) illustrate the relationship between the mean site EI values and their position in ordination space. The figures showing variation in mean EI value for light and moisture (Figures 6-28 and 6-29) support the evidence for continuous variation across ordination space rather than clear discontinuities between sites in terms of these two variables.

Figures 6-30 and 6-31, which show the pattern of variation in mean pH and mean nitrogen EI values, again confirm the existence of a continuum of variation throughout the ordination space. However, these latter two sets of values do show distinct trends in relation to axis 1, with nitrogen also exhibiting a significant relationship with axis 2.

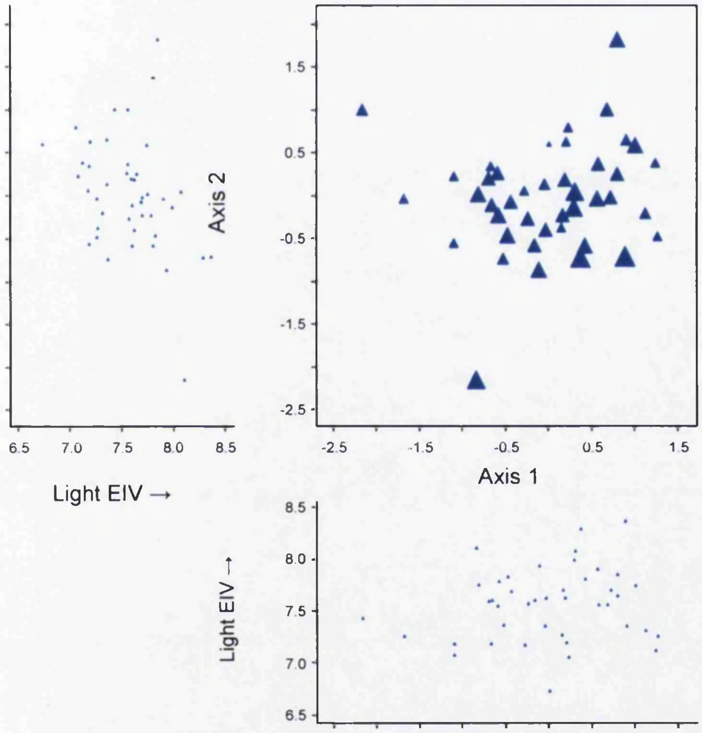


Figure 6-28. NMS ordination and scatter-plots showing mean weighted EI values for light on glacier foreland pioneer sites. The size of each site symbol in the ordination diagram is relative to its mean EI value.

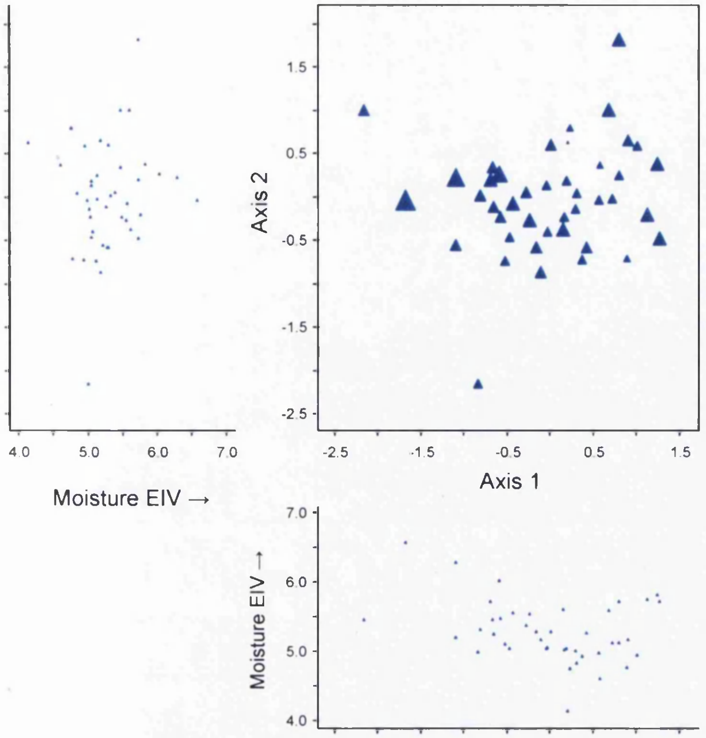


Figure 6-29. NMS ordination and scatter-plots showing mean weighted EI values for moisture on glacier foreland pioneer sites. The size of each site symbol in the ordination diagram is relative to its mean EI value.

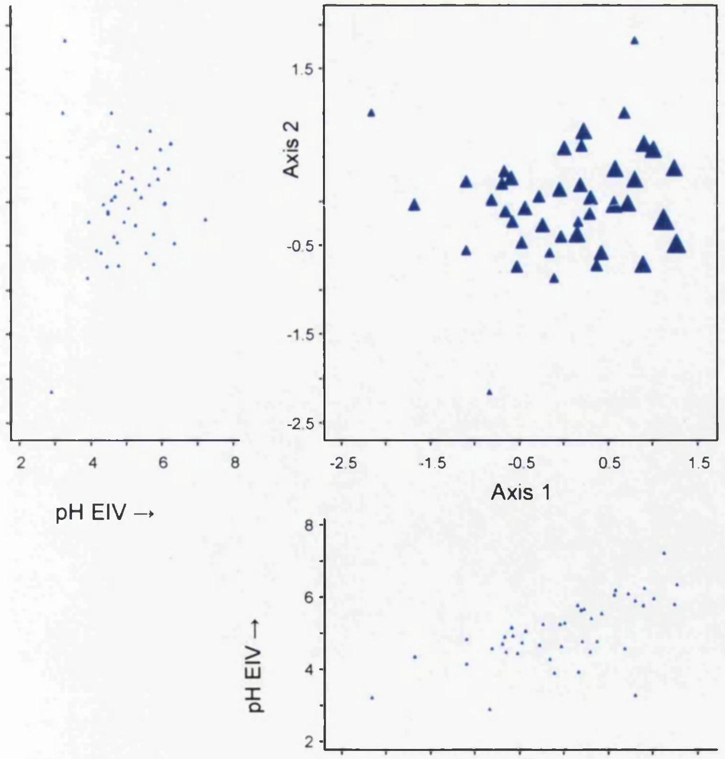


Figure 6-30. NMS ordination and scatter-plots showing mean weighted EI values for pH on glacier foreland pioneer sites. The size of each site symbol in the ordination diagram is relative to its mean EI value.

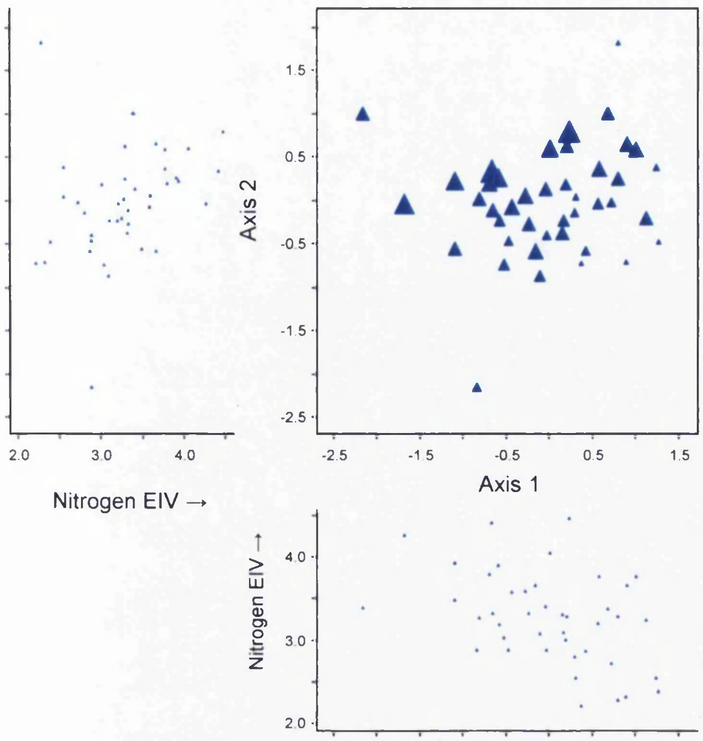


Figure 6-31. NMS ordination and scatter-plots showing mean weighted EI values for nitrogen on glacier foreland pioneer sites. The size of each site symbol in the ordination diagram is relative to its mean EI value.

When variance partitioning was carried out on the glacier foreland pioneer data set, the variance explained by each of the mean EI values was not statistically significant. Altitude and distance east are therefore the only two significant factors. It is not appropriate, therefore, to explore further the relative influences of other environmental factors through variance partitioning. Figure 6-32 summarizes the independent and non-independent variance explained by altitude and distance east when all measured environmental factors are taken into account.

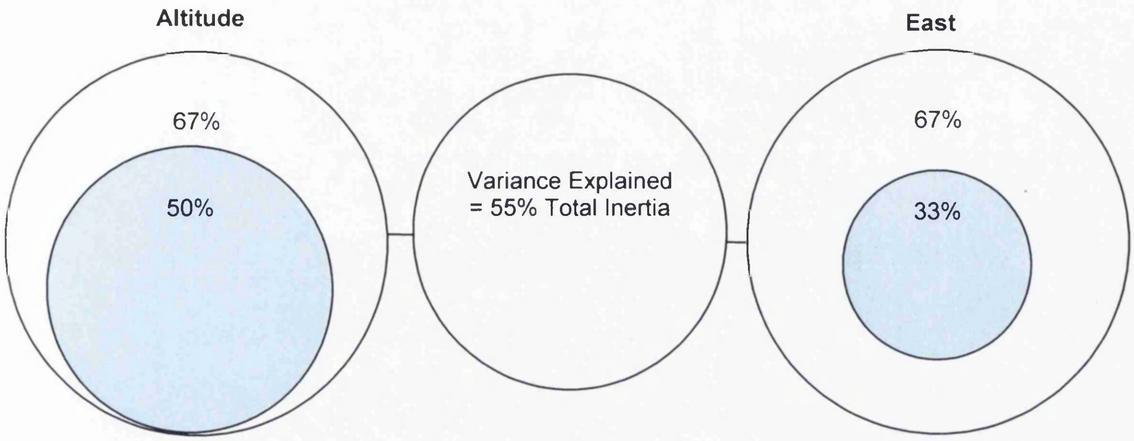


Figure 6-32. Variance explained by measured environmental factors for glacier foreland pioneer sites. Large circles represent % non-independent variance explained, smaller shaded circles represent % independent variance explained.

The evidence for a continuum of change between glacier foreland pioneer sites is investigated further in the next section, which analyses cluster analysis groups in terms of their mean EI values to look for evidence of environmental factors determining group membership. The two- and four-group levels of clustering are examined using means and 95% confidence intervals for all four EI values. However, in light of the results of variance partitioning, it is unlikely that a strong pattern of environmental differences between the groups will emerge.

6.5.2 EI values of glacier foreland pioneer sub-communities

6.5.2.1 EI values at the two-group level

At the two-group level of cluster analysis the mean EI values for light, moisture and nitrogen all have overlapping 95% confidence intervals (Table 6-18 and Figure 6-33) and a clear difference between the two groups can only be identified in terms of the mean EI value for pH which is lower in group 2A (4.7) than group 2B (5.6). The division of these two sub-communities along axis 1 of ordination space in terms of mean EI values is therefore primarily on the basis of variation in pH.

Table 6-18. Mean EI values for the two glacier foreland pioneer sub-communities.

Sub-Community	**Mean EIV ± 95% confidence interval**			
	Light	**Moisture**	**pH**	**Nitrogen**
2A	7.5 ± 0.13	5.4 ± 0.18	4.7 ± 0.19	3.5 ± 0.20
2B	7.6 ± 0.19	5.2 ± 0.22	5.6 ± 0.41	3.1 ± 0.30

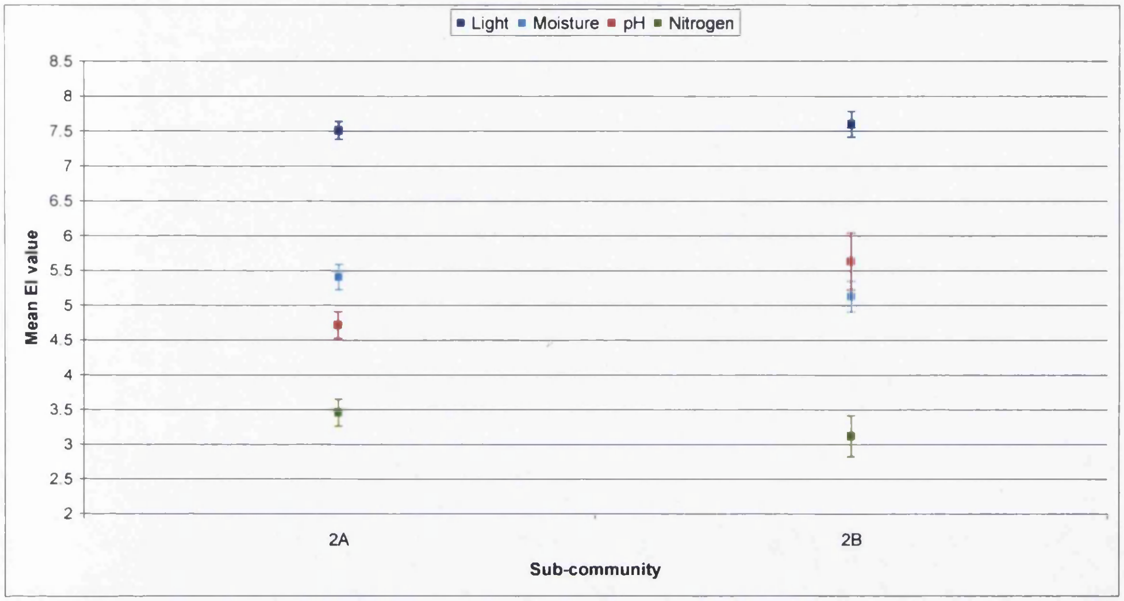


Figure 6-33. Mean EI values for the two glacier foreland pioneer sub-communities.

6.5.2.2 EI values at the four-group level

Analysis of the four-group level of cluster analysis of the glacier foreland pioneer sites (Table 6-19 and Figure 6-34) shows no difference between the four groups in terms of mean EI value for light. The mean EI values and 95% confidence intervals for moisture split the four groups into two with relatively low values (group 4A at 5.2 and group 4B at 5.1) and two with relatively high values (group 4C at 5.8 and group 4D at 5.7), whereas the mean EI values for pH show identical values for groups 4A and 4C (4.7) and higher values for groups 4B (5.7) and 4D (5.3). Group 4C, which was the only distinguishable group at this level of cluster analysis in terms of mean altitude and distance east (having the lowest mean altitude and lowest mean distance east), has a higher mean EI value for nitrogen than the other three groups (3.9 as opposed to 2.8 to 3.3) and the 95% intervals show a difference between this group and groups 4A and 4B which have similar values. As group 4D has only two members, its 95% confidence intervals (particularly for pH) are very wide and its values are not distinguishable with confidence from those of the other three groups.

Table 6-19. Mean EI values for the four glacier foreland pioneer groups.

Group	Mean EIV ± 95% confidence interval Light	Moisture	pH	Nitrogen
4A	7.5 ± 0.17	5.2 ± 0.10	4.7 ± 0.28	3.3 ± 0.19
4B	7.6 ± 0.23	5.1 ± 0.25	5.7 ± 0.31	3.1 ± 0.36
4C	7.4 ± 0.20	5.8 ± 0.41	4.7 ± 0.22	3.9 ± 0.34
4D	7.6 ± 0.54	5.7 ± 0.04	5.3 ± 3.88	2.8 ± 0.95

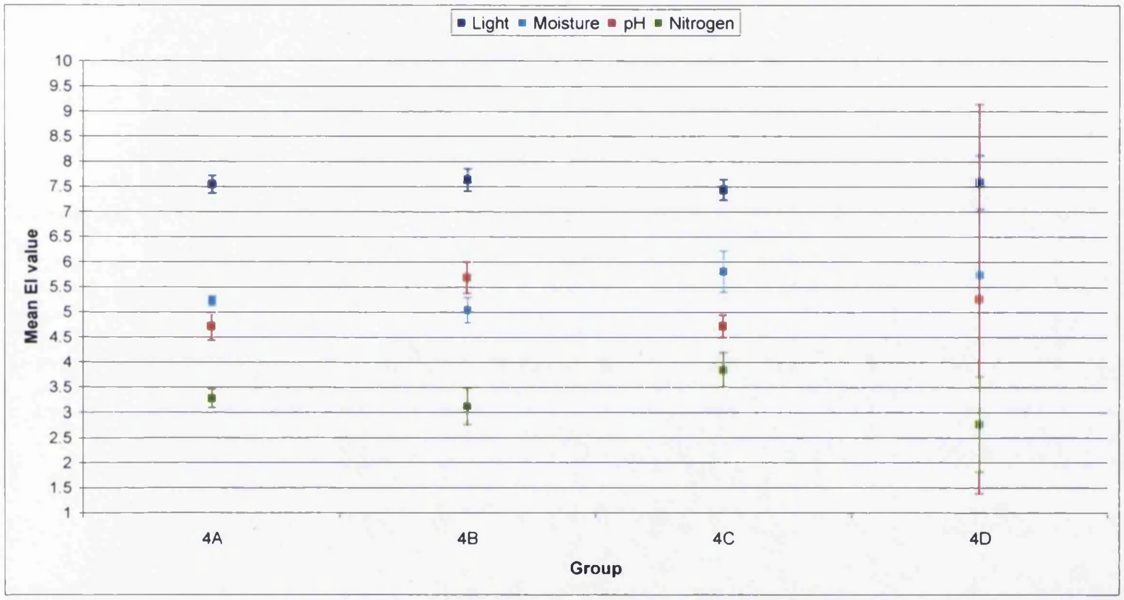


Figure 6-34. Mean EI values for the four glacier foreland pioneer groups.

This section has shown that at the two-group level, glacier foreland sites are only distinguishable in terms of their mean EI value for pH, suggesting that, in other respects, the sites tend to form a continuum of variation rather than a number of distinct groups in vegetation space. The pattern of variation in mean EI values and 95% confidence intervals between the four groups (Figure 6-34) more closely resembles a continuum of variation rather than a number of distinct groups. This is supported by the results of variance partitioning, which do not show that mean EI values provide a significant explanation of variation in species composition.

6.6 Geographical and environmental influences on pioneer vegetation across habitat types

The previous sections of this chapter have demonstrated a strong correlation between the species composition of roadside and glacier foreland pioneer sites and their altitudes and distances east. Patterns have also been identified regarding correlations between mean site EI values and ordination axis scores for these two data sets. This section uses the additional pioneer habitats data set and the combined data sets to examine such relationships across a broader range of habitat types.

6.6.1 Geographical distribution of the communities in additional pioneer habitats

In order to assess whether pioneer species colonization on a range of disturbed habitats follows altitudinal and regional patterns of distribution, the additional disturbed habitat sites are plotted according to their altitude and distance east and colour coded according to the four communities identified from the analysis of these sites in chapter 5 (Figure 6-35).

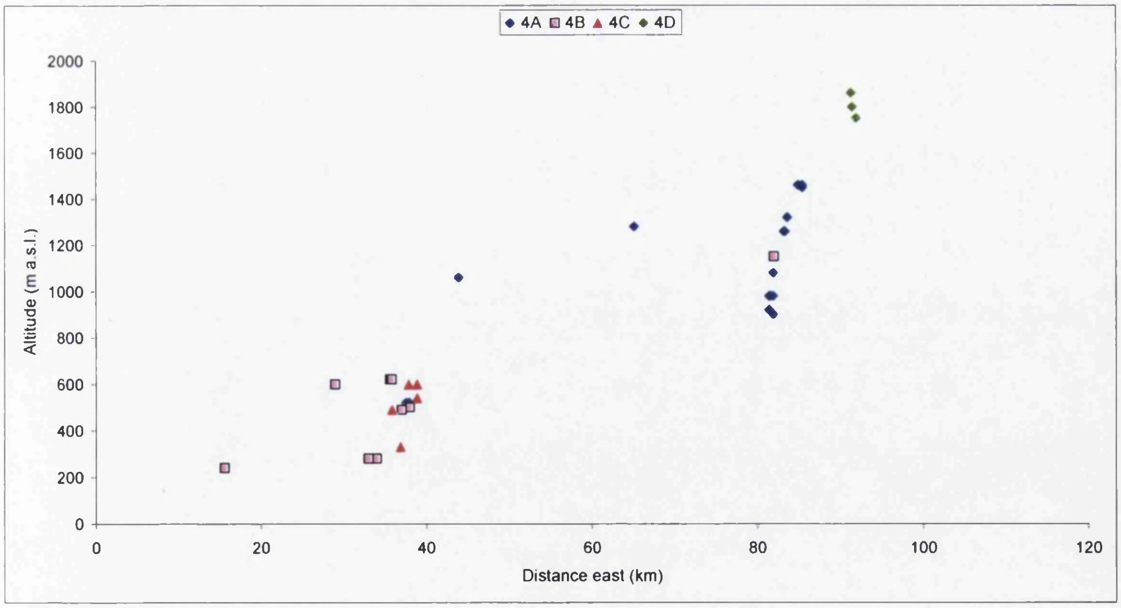


Figure 6-35. Altitude and distance east of the four communities in additional pioneer habitats.

Altitudinal zonation is evident, with the majority of sites in communities 4B and 4C occurring up to 620 m, 4A mainly consisting of sites between 900 and 1460 m, and 6D sites at 1750 m and above. Sites are primarily grouped according to altitude rather than habitat type. An exception to this is the formation of the two lower altitude communities, one of which (4C) contains all four river levée sites and one gravel pit, while the other (4B) consists of a mixture of habitat types. The data set does not extend further than 92 km east of the most western glacier foreland and no clear pattern can be seen which could reflect the effects of continentality rather than altitude. The two community 4A sites at 520 m are both avalanche tracks, the most easterly site in 4B at 1150 m is a river outwash. The highest altitude community (4D) consists of three patterned ground sites, while the lower altitude patterned ground site at 1280 m is included in 4A.

Variance partitioning (Table 6-20) shows that altitude independently explains 48% of the TVE, distance east 28%, and 25% is shared between these two variables. Continentality therefore has a stronger effect than that demonstrated for the roadside data set, and the shared variance between altitude and distance east is higher (25% rather than 11%). The portion of variance independently explained by altitude is lower than for the roadside pioneer sites (48% rather than 64%).

Table 6-20 Variance explained by altitude and distance east for the additional pioneer habitats data set. TVE = total variance explained, A = altitude, E = distance east. All values are significant at $p = 0.002$.

Variable	VE (% TVE)
TVE	0.81 (1.00)
A	0.59 (0.73)
E	0.42 (0.52)
A∩E	0.20 (0.25)
A|E	0.39 (0.48)
E|A	0.23 (0.28)

6.6.2 *Geographical distribution of pioneer communities from the combined data set*

The altitudinal and regional distribution of roadside, glacier foreland and additional pioneer habitat communities classified by a single cluster analysis are next examined for three- and six-group levels (see section 5.6.5 for a description of these groups). Figure 6-36 illustrates how the three communities are distributed and shows that the glacier forelands and additional pioneer habitats extend the lower altitudinal boundary and western regional boundary of 3B.

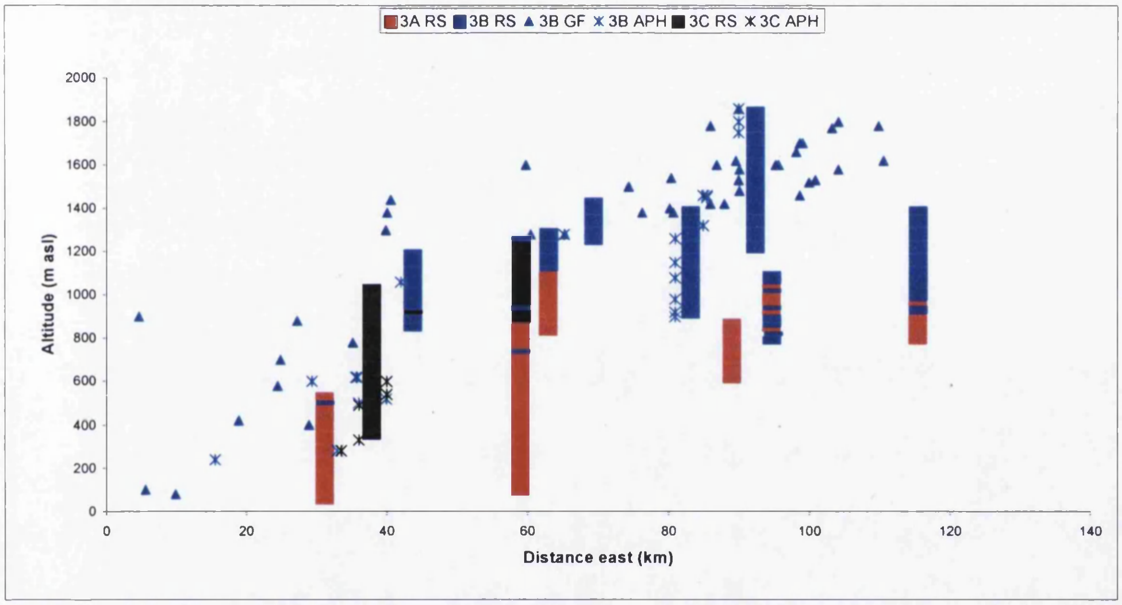


Figure 6-36. Altitude and distance east of three pioneer roadside (RS), glacier foreland (GF) and additional pioneer habitat (APH) combined analysis communities. Coloured vertical columns represent the altitudinal range of individual roads.

The roadside sites belonging to 3B are (with one exception at 500 m) at least 740 m, whereas seven sites in 3B from the additional pioneer habitats data set occur below this altitude, the lowest being at 240 m, and glacier forelands in this group extend down to 80 m. There is also a different regional distribution between the data sets, with additional pioneer habitat sites within community 3B occurring further west (seven sites are less than 40 km east) than roadside sites within this community which extend mainly to 44 km east. Glacier foreland sites in 3B extend to 5 km east (the most westerly point of the data set). The seven 3B sites at lower altitudes are a mixture of site types including three river sites, one avalanche track and three debris flows. The debris flows are those found on the Fåbergstølsbreen glacier foreland and the avalanche track is close to the Austerdalen glacier foreland. The lower altitudinal limit of 3C is very similar for both data sets (340 m for roadsides and 280 m for additional pioneer habitats), while the upper altitudinal limit of this community is much higher for roads at 1260 m as opposed to 600 m.

At the six-group level (Figure 6-37), the roadside sites follow the same altitudinal and regional zonation as when they were analysed separately (with group membership changes as described in section 5.6.5.2). All but four of the glacier forelands belong to the same sub-community as the highest altitude roadside sites (6E) and bring the lower altitudinal boundary of this group down to 80 m. The glacier forelands also extend its western distribution from 31 to 5 km east.

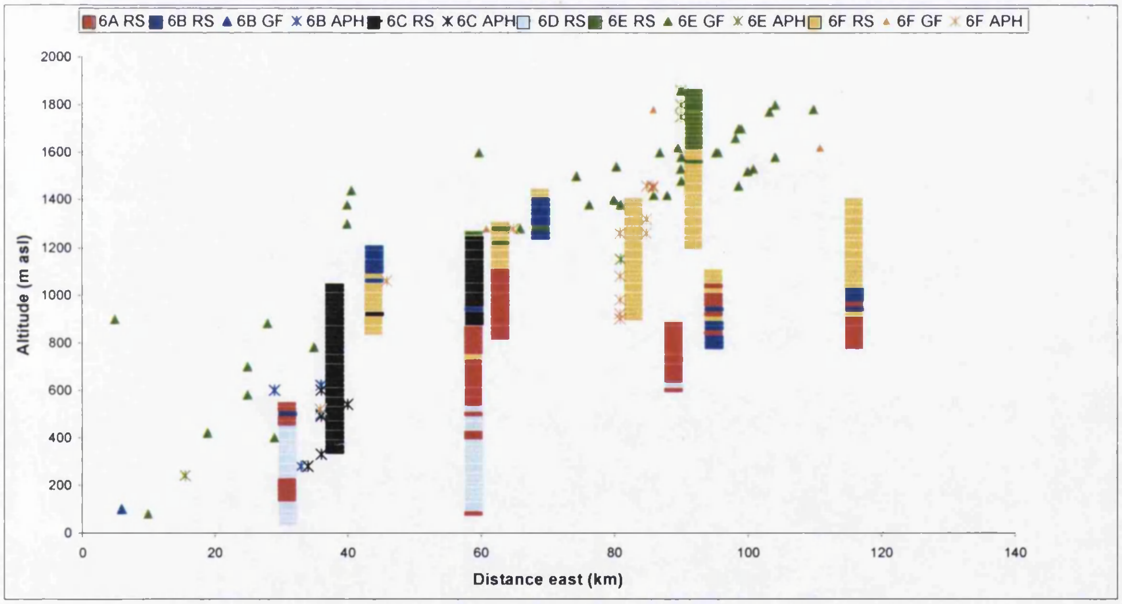


Figure 6-37. Altitude and distance east of six pioneer roadside (RS), glacier foreland (GF)and additional pioneer habitat (APH) combined cluster analysis groups. Coloured vertical columns represent the altitudinal range of individual roads.

The altitudinal zonation of the additional pioneer habitat sites belonging to sub-communities 6E and 6C has not changed. Sub-communities 6B and 6F occupy altitudes which are intermediate between 6A and 6E for roadsides but include sites at lower altitudes in additional pioneer habitats. The distribution of sites between 6B and 6F has changed, for example sites along Leirdalen road at 83 km east now all belong to 6F, whereas, when the glacier foreland sites were not included, two sub-communities (6B and 6F) occurred along this road. This points to the fact that these two sub-communities are not as clearly differentiated as the other four.

Table 6-21 presents the results of variance partitioning of the combined data set in terms of altitude and distance east. The partitioned variances explained by altitude and distance east are almost identical to those for the roadside data set (Table 6-2), with altitude independent of distance east accounting for 66%, distance east independent of altitude accounting for 25%, and 9% being shared (Table 6-21).

Table 6-21 Variance explained by altitude and distance east for the combined pioneer data set. TVE = total variance explained, A = altitude, E = distance east. All values are significant at *p* = 0.002.

Variable	VE (% TVE)
TVE	0.71 (1.00)
A	0.53 (0.75)
E	0.24 (0.33)
A∩E	0.06 (0.09)
A|E	0.47 (0.66)
E|A	0.18 (0.25)

6.6.3 The relationship between mean EI values of additional pioneer habitat sites and NMS axes

The correlations between NMS ordination axis scores and altitude and distance east were generally comparable for the roadside and glacier foreland data sets (see Table 6-24). However, there were considerable differences between the two data sets in terms of correlations between the ordination axes and mean weighted EI values. In order to explore these relationships for a broader selection of pioneer sites, correlations found within the additional pioneer habitats data set are presented in Figure 6-38 and Table 6-22 for comparison with the other two data sets. Correlations between the position of sites in ordination space and their mean EI value scores follow a similar pattern to that observed for the roadside data set (Figure 6-11), with axis 1 having a positive correlation with light and a negative correlation with moisture and axis 2 having a positive correlation with nitrogen and pH. The similarities between the three data sets in terms of correlation between environmental factors and ordination axes are explored further in the next sub-section.

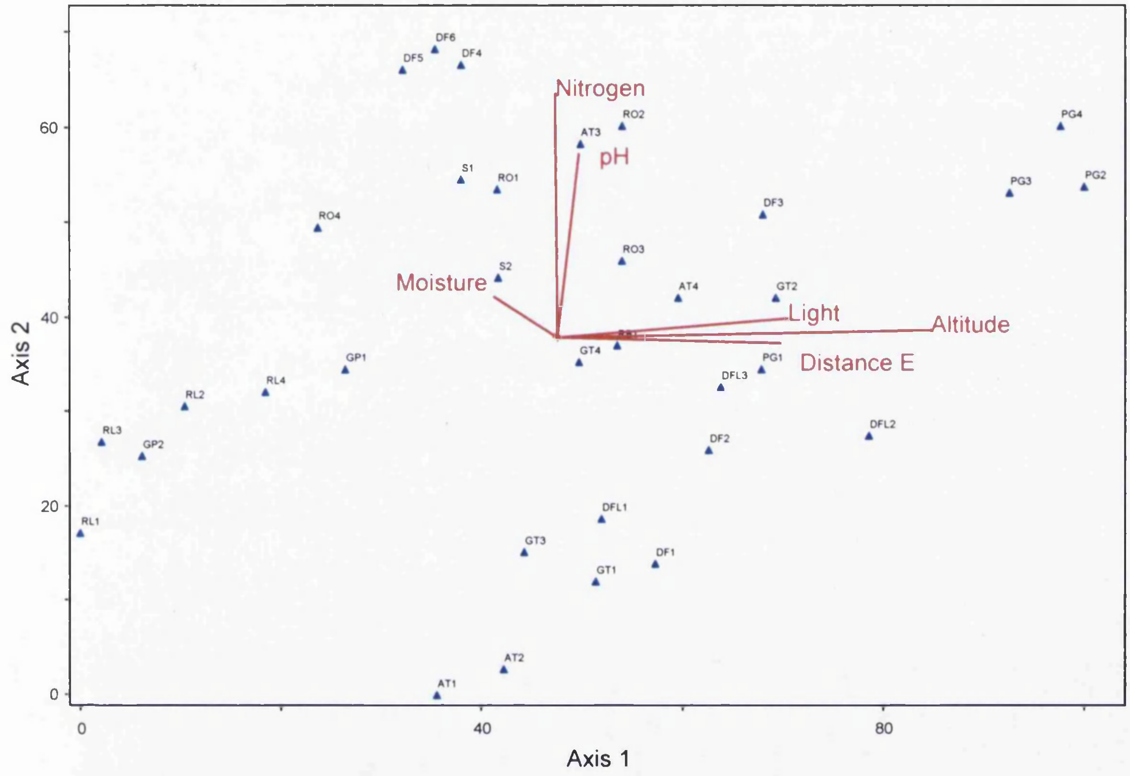


Figure 6-38. NMS ordination of additional pioneer habitat sites rotated for maximum correlation between axis 1 and altitude showing vectors for altitude, distance east and mean weighted EI values.

Table 6-22. Pearson's r coefficients for correlations between altitude, distance east, mean EI values and NMS axes for additional pioneer habitat sites (*p* < 0.01**, *p* < 0.05*).

Axis	1	2
Altitude	+0.862**	n.s.
Distance east	+0.667**	n.s.
Light	+0.676**	n.s.
Moisture	-0.354*	n.s.
pH	n.s.	+0.604**
Nitrogen	n.s.	+0.696**

Variance partitioning of altitude, distance east and mean EI values for the additional pioneer habitats data set (Table 6-23 and Figure 6-39) confirms the dominant effect of altitude on species composition, with this factor explaining

27% of the TVE and co-varying with light and distance east by 8%. In contrast to the roadside data set, altitude and moisture do not appear to co-vary and co-variance between moisture and distance east is also minimal. Eleven of the additional pioneer habitat sites are associated with rivers and this may explain the reduction in covariance of moisture levels with altitude or continentality. The independent contribution of the mean moisture EI values to TVE is also greater in this data set (20% compared with 11% for the roadside sites). The values show a much lower co-variance between pH and nitrogen than the roadside data set with a shared component of only 1%. This is probably related to the inclusion of riverine habitats, in which rapid leaching of nutrients occurs.

Table 6-23. Variance explained by altitude (A), distance east (E) and mean EI values for light (L), moisture (M), pH and nitrogen (N) for the additional pioneer habitats data set. TVE = total variance explained. VE| = variance explained with factor partitioned out. a) VE, b) VE expressed as percentages of TVE. All values are significant at *p* = 0.002.

a)

Variable	VE	VE|A	VE|E	VE|AE	VE|L	VE|M	VE|pH	VE|N
TVE	2.17	1.59	1.75	0.81	1.74	1.67	1.71	1.77
A	0.59	N/A	0.39	N/A	0.41	0.58	0.59	0.58
E	0.42	0.23	N/A	N/A	0.32	0.41	0.42	0.39
L	0.43	0.25	0.32	0.24	N/A	0.39	0.40	0.43
M	0.50	0.50	0.49	0.50	0.44	N/A	0.47	0.50
pH	0.47	0.47	0.47	0.45	0.43	0.43	N/A	0.45
N	0.41	0.40	0.38	0.32	0.41	0.41	0.39	N/A

b)

Variable	VE	VE|A	VE|E	VE|AE	VE|L	VE|M	VE|pH	VE|N
TVE	1.00	0.73	0.81	0.37	0.80	0.77	0.79	0.82
A	0.27	N/A	0.18	N/A	0.19	0.27	0.27	0.27
E	0.19	0.11	N/A	N/A	0.15	0.19	0.19	0.18
L	0.20	0.12	0.15	0.11	N/A	0.18	0.18	0.20
M	0.23	0.23	0.23	0.23	0.20	N/A	0.22	0.23
pH	0.22	0.22	0.22	0.21	0.20	0.20	N/A	0.21
N	0.19	0.18	0.18	0.15	0.19	0.19	0.18	N/A

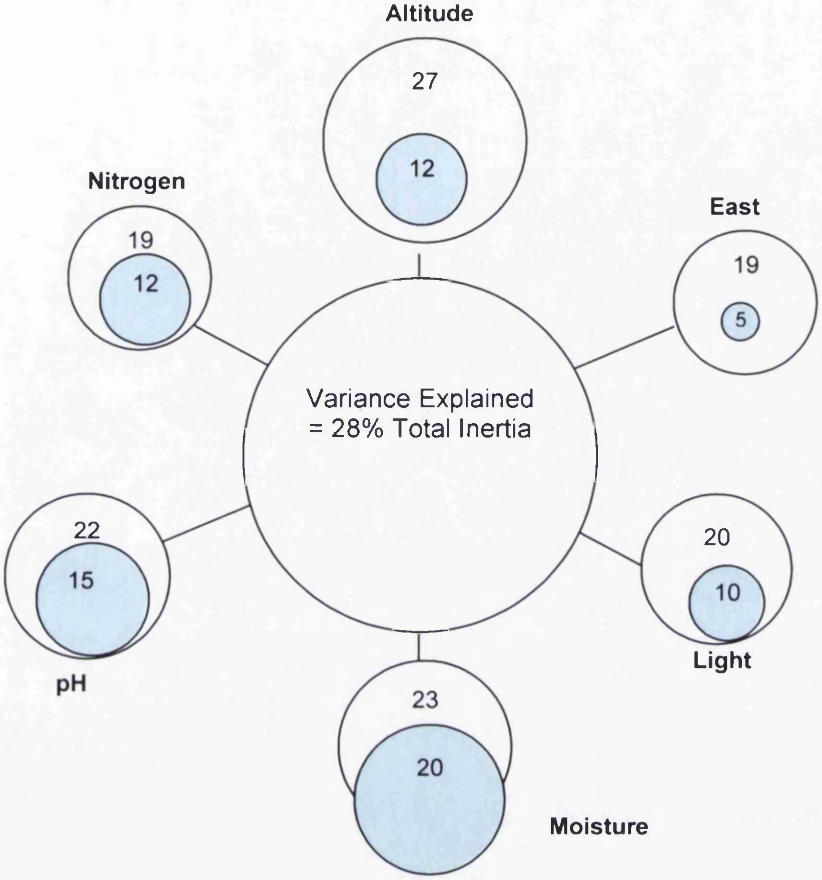


Figure 6-39. Variance explained by measured environmental factors for additional pioneer habitat sites. Large circles represent % non-independent variance explained, smaller shaded circles represent % independent variance explained.

6.6.4 Correlations between altitude, distance east, mean EI values and NMS axes for the three data sets

6.6.4.1 Comparisons between individual data sets

In order to compare the pattern of correlations for all the different types of pioneer sites, Table 6-24 gives r-values for all three data sets. (The results for the roadside and glacier foreland data sets are taken from Tables 6-1, 6-6, 6-12 and 6-16.) Strong correlations are shown between NMS ordination axis 1 and altitude for all three data sets after rotation of the ordination axes for maximum correlation between these two variables. It should be noted that the correlation for glacier foreland sites is weaker than for the other two data sets. Correlation between axis 1 and distance east is highest for glacier forelands and weakest for roadsides. A similar level of correlation between mean light EI value and axis 1 is seen for roadsides and other pioneer habitats, whereas for glacier forelands, the strongest r-value shows a negative relationship between light and axis 2, probably due to the lack of shade-creating trees near the glacier foreland pioneer sites.

Table 6-24. Pearson's r coefficients for correlations between altitude, distance east, EI values and NMS ordination axes for each data set ($p < 0.01$**, $p < 0.05$*).

Data Set	**Roadsides**		**Glacier forelands**		**Other pioneer habitats**	
Axis	1	2	1	2	1	2
Altitude	+0.897**	n.s.	+0.753**	n.s.	+0.862**	n.s.
Distance east	+0.446**	+0.221**	+0.764**	n.s.	+0.667**	n.s.
Light	+0.655**	+0.361**	n.s.	-0.384*	+0.676**	n.s.
Moisture	-0.556**	n.s.	-0.312*	n.s.	-0.354*	n.s.
pH	-0.272**	+0.794**	+0.651**	n.s.	n.s.	+0.604**
Nitrogen	-0.521**	+0.538**	-0.433**	+0.295*	n.s.	+0.696**

The negative correlations between mean moisture EI values and axis 1 reveal a similar trend for all three data sets with a stronger negative correlation for the roadside sites. Similar trends are also evident for the roadsides and other pioneer habitats in terms of correlations between axis 2 and both pH and nitrogen. For the glacier foreland pioneer sites, the strongest correlation for mean pH EI values is with axis 1 rather than axis 2. Mean nitrogen EI values show a negative correlation with axis 1 and a weak positive correlation with axis 2. It is interesting that the glacier forelands have a "unique" set of environmental relationships, probably related to their narrow habitat range and single community structure. As variance partitioning demonstrated, the relatively low variability in species composition on the glacier forelands is explained by altitude and distance east rather than the mean EI values.

The correlations between ordination axes and altitude, distance east and mean EI values therefore display a higher level of agreement between the roadsides and other pioneer habitats than between these two data sets and glacier forelands. However, all three data sets show similar underlying patterns but with different levels of correlation for altitude, distance east, moisture and nitrogen. The fact that the correlation between light and axis 2 is negative for glacier forelands but positive for roadsides and that the correlation between pH and axis 1 is positive for glacier forelands and negative for the other two data sets, demonstrates qualitative as well as quantitative differences in the environmental relationships between habitat types. In light of the fact that ordination and classification of the glacier foreland pioneer sites have shown weaker patterns of variation between sites, the likelihood is that the findings for glacier forelands are either a special case or an extreme example of pioneer vegetation.

6.6.4.2 Combined analysis

In order to assess the relationship between environmental variables and ordination axes when the glacier forelands are put into the framework of the roadside and additional pioneer habitat sites, Table 6-25 and Figure 6-40 show the environmental correlations for the combined data sets. Not surprisingly, the overall relationships reflect those of the larger roadside data set. However, the relationships between axis 1 and moisture, pH and nitrogen, and between axis 2 and distance east and light have been weakened due to the influence of the glacier forelands and additional pioneer habitats.

The overall relationship between EI values and NMS axes is consistent with the interpretation of axis 1 as primarily representing altitude and climate and axis 2 primarily representing nutrient factors.

Table 6-25. Pearson's r coefficients for correlations between altitude, distance east, EI values and NMS ordination axes for combined data set ($p < 0.01$).

Combined Data Set		
Axis	1	2
Altitude	+0.865	n.s.
Distance east	+0.425	n.s.
Light	+0.718	+0.210
Moisture	-0.395	+0.199
pH	n.s.	+0.744
Nitrogen	-0.373	+0.565

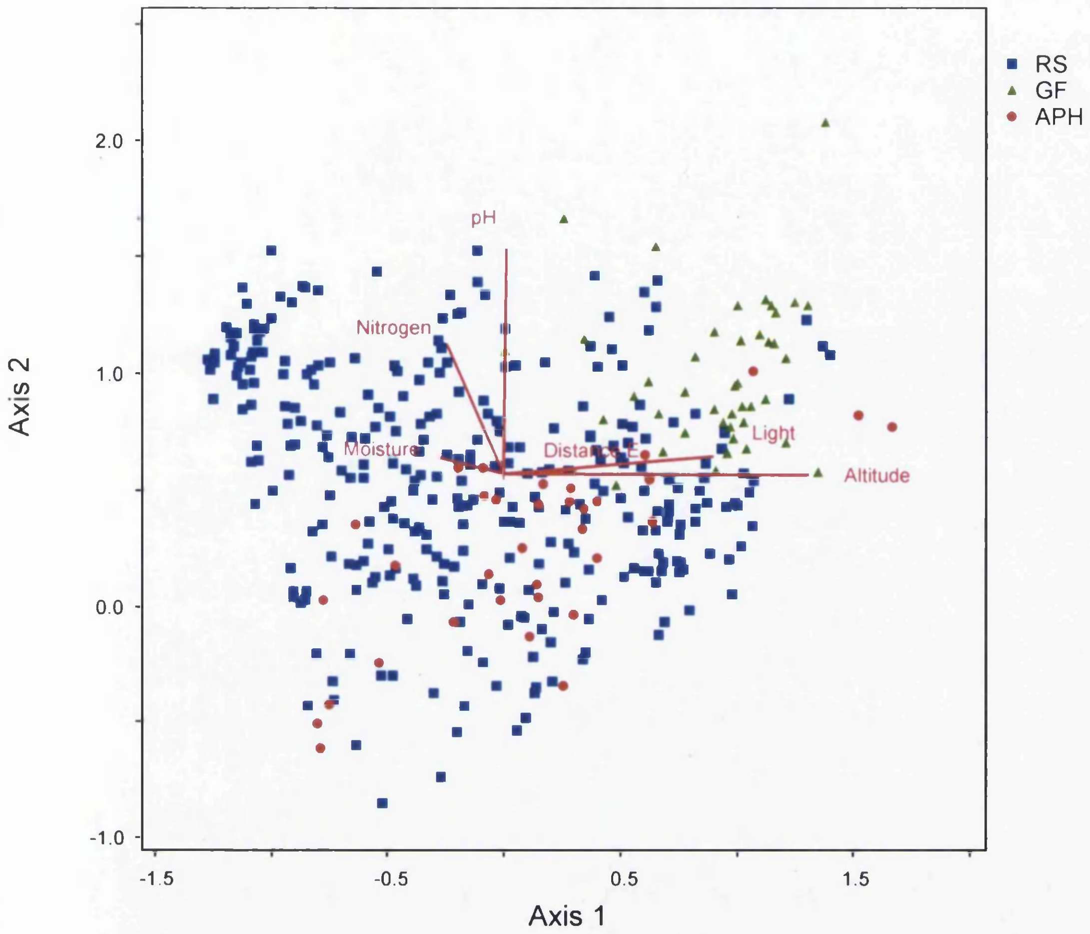


Figure 6-40. NMS ordination of combined data sets rotated for maximum correlation between axis 1 and altitude showing vectors for altitude, distance east and mean weighted El values. Different symbols are used to indicate glacier forelands (GF), roadsides (RS) and additional pioneer habitats (APH).

When all measured environmental factors are analyzed by variance partitioning (Table 6-26 and Figure 6-41), all factors have very similar values to those for the roadside data set but a slightly lower percentage of the total inertia is explained (24% rather than 28%), reflecting the lack of significant values for the Ellenberg indicators in the glacier foreland data set.

Table 6-26. Variance explained by altitude (A), distance east (E) and mean EI values for light (L), moisture (M), pH and nitrogen (N) for the combined data set. TVE = total variance explained. VE| = variance explained with factor partitioned out. . a) VE, b) VE expressed as percentages of TVE. All values are significant at p = 0.002.

a)

Variable	VE	VE|A	VE|E	VE|AE	VE|L	VE|M	VE|pH	VE|N
TVE	1.75	1.23	1.51	0.71	1.27	1.44	1.3	1.37
A	0.53	N/A	0.47	N/A	0.32	0.45	0.53	0.46
E	0.24	0.18	N/A	N/A	0.14	0.18	0.23	0.23
L	0.48	0.28	0.38	0.27	N/A	0.43	0.45	0.47
M	0.32	0.25	0.26	0.24	0.26	N/A	0.32	0.28
pH	0.45	0.45	0.44	0.43	0.43	0.45	N/A	0.41
N	0.39	0.32	0.38	0.31	0.37	0.35	0.34	N/A

b)

Variable	VE	VE|A	VE|E	VE|AE	VE|L	VE|M	VE|pH	VE|N
TVE	1.00	0.70	0.86	0.41	0.73	0.82	0.74	0.78
A	0.30	N/A	0.27	N/A	0.18	0.26	0.30	0.26
E	0.14	0.10	N/A	N/A	0.08	0.10	0.13	0.13
L	0.27	0.16	0.22	0.15	N/A	0.25	0.26	0.27
M	0.18	0.14	0.15	0.14	0.15	N/A	0.18	0.16
pH	0.26	0.26	0.25	0.25	0.25	0.26	N/A	0.23
N	0.22	0.18	0.22	0.18	0.21	0.20	0.19	N/A

For the pioneer community as a whole, altitude is therefore the dominant influence (30% TVE) and its main co-variant is the mean EI value for light (27% TVE), which is affected by the level of vegetation cover and the presence of a climax tree canopy or shrub layer. These two factors have the highest correlation with axis 1 of the NMS ordination. Mean EI values for moisture (18% TVE) are negatively correlated with axis 1 and reflect the drying effects of high altitude winds and frozen substrate rather than precipitation levels. Mean EI values for pH (26% TVE) and nitrogen (22% TVE) are also important influences, particularly on the roadside sites where their co-variance is greatest, and they are most strongly correlated with axis 2 of the ordination diagram. This axis is also thought to represent the disturbance regime of sites, with less disturbed sites having lower scores on axis 2. Distance east (14% TVE) co-varies with altitude but also has an independent effect, reflecting the increasing precipitation levels and lower tree-line towards the west of the study region and, to a lesser extent, the underlying geology.

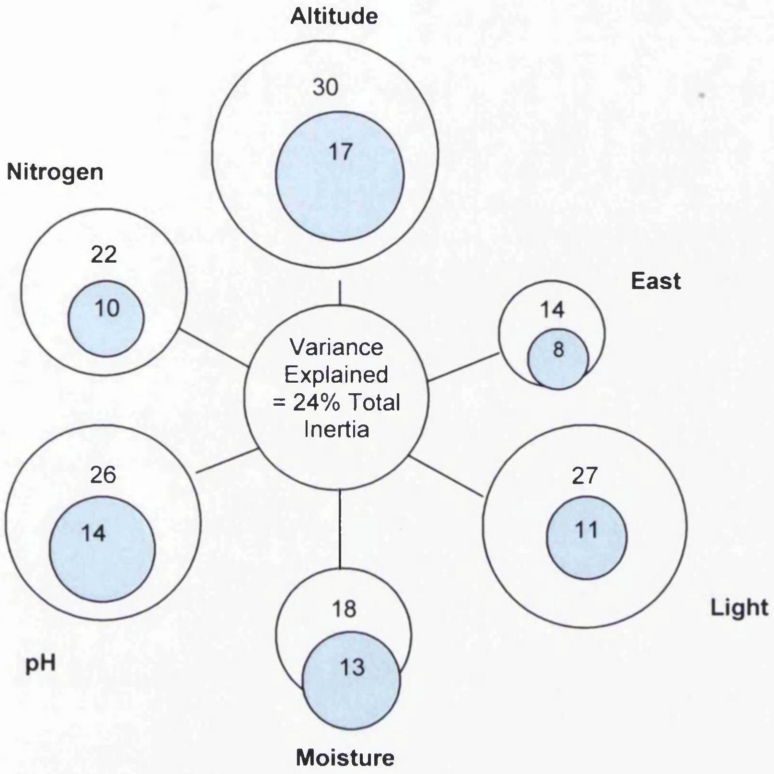


Figure 6-41. Variance explained by measured environmental factors for combined data set. Large circles represent % non-independent variance explained, smaller shaded circles represent % independent variance explained.

6.7 Summary of pioneer communities and sub-communities

To summarize the key findings relating to each pioneer communities and sub-community, Table 6-27 presents mean values for each data set and for the combined analysis of all three data sets. For completeness, mean altitude, distance east and EI values are included for the additional pioneer habitats and the combined data.

Table 6-27. Summary of pioneer communities and sub-communities.

Community/*Sub-community*	**Key species**	**DI**	**Mean**		**Mean EI Value**			
			Alt (m)	**E (km)**	**L**	**M**	**pH**	**N**
ROADSIDES								
3A Desces-Trirep	*Deschampsia cespitosa* *Trifolium repens* *Plantago major* *Agrostis capillaris* *Ranunculus acris*	1.3	597	64	6.8	5.6	4.6	4.1
6A Desces-Taragg	*Deschampsia cespitosa* *Taraxacum* aggregate *Stellaria graminea* *Euphrasia agg.* *Veronica officinalis*	1.2	740	72	6.8	5.6	4.4	3.8
6D Plamaj-Trirep	*Plantago major* *Trifolium repens* *Ranunculus acris* *Agrostis capillaris* *Fragaria vesca*	2.0	326	47	7.0	5.5	5.0	4.7
3B Fesovi-Luzspi	*Festuca ovina* *Luzula spicata* *Poa alpina* *Cerastium cerastoides* *Deschampsia alpina*	1.2	1247	83	7.4	4.8	3.9	3.2
6B Cercer-Desalp	*Cerastium cerastoides* *Deschampsia alpina* *Sagina saginoides* *Phleum alpinum* *Rumex acetosella*	1.2	1169	76	7.3	5.3	4.3	3.8
6E Luzarc-Rangla	*Luzula arcuata* *Ranunculus glacialis* *Saxifraga cespitosa* *Cerastium alpinum* *Saxifraga cernua*	1.8	1644	87	7.9	4.8	4.1	2.8
6F Fesovi-Antdio	*Festuca ovina* *Antennaria dioica* *Luzula spicata* *Polygonum viviparum* *Campanula rotundifolia*	1.5	1192	89	7.3	4.4	3.6	2.8

Community/*Sub-community*	Key species	DI	Mean		Mean El Value			
			Alt (m)	E (km)	L	M	pH	N
3C Desfle-Salgla	*Deschampsia flexuosa* *Salix glauca* *Betula pubescens* *Empetrum hermaphroditum* *Vaccinium myrtillus*	1.9	819	45	6.6	5.5	2.6	2.9
6C Desfle-Betpub	*Deschampsia flexuosa* *Betula pubescens* *Empetrum hermaphroditum* *Salix glauca* *Vaccinium myrtillus*	2.0	827	47	6.6	5.5	2.6	2.9
GLACIER FORELANDS								
Poaalp-Oxydig	*Poa alpina* *Oxyria digyna* *Deschampsia alpina* *Festuca ovina* *Cerastium alpinum*	N/A						
Desalp-Oxydig (2A)	*Deschampsia alpina* *Oxyria digyna* *Saxifraga stellaria* *Epilobium anagallidifolium* *Cerastium alpinum*	1.2	1162	59	7.5	5.4	4.7	3.5
Saxces-Trispi (2B)	*Saxifraga cespitosa* *Trisetum spicatum* *Poa alpina* *Arabis alpina* *Ranunculus glacialis*	1.1	1587	92	7.6	5.2	5.6	3.1
ADDITIONAL PIONEER HABITATS								
Fesovi-Antdio (4A)	*Festuca ovina* *Antennaria dioica* *Juncus trifidus*	1.3	1089	74	7.3	4.9	3.7	3.0
Phlalp-Stegra (4B)	*Phleum alpinum* *Stellaria graminea* *Deschampsia flexuosa* *Epilobium anagallidifolium* *Oxyria digyna*	1.3	540	38	7.1	5.5	4.1	3.8
Betpub-Gymdry (4C)	*Betula pubescens* *Gymnocarpium dryopteris* *Vaccinium uliginosum* *Vaccinium myrtillus* *Solidago virgaurea*	2.5	512	47	6.8	7.0	3.0	3.1
Saxces-Saxopp (4D)	*Saxifraga cespitosa* *Saxifraga oppositifolia* *Luzula arcuata* *Ranunculus glacialis* *Salix herbacea*	3.3	1803	92	7.7	6.1	3.5	3.1
COMBINED DATA								
Desces-Plamaj (3A)	*Deschampsia cespitosa*	1.3	585	65	6.8	5.6	4.6	4.1

Community/*Sub-community*	Key species	DI	Mean		Mean EI Value			
			Alt (m)	E (km)	L	M	pH	N
	Plantago major *Trifolium repens* *Agrostis capillaris* *Ranunculus acris*							
Desces-Taragg (6A)	*Deschampsia cespitosa* *Taraxacum aggregate* *Euphrasia spp.* *Veronica officinalis* *Cerastium fontanum*	1.2	735	72	6.7	5.6	4.4	3.8
Plamaj-Trirep (6D)	*Plantago major* *Trifolium repens* *Poa pratensis* *Agrostis capillaris* *Ranunculus acris*	2.0	285	49	7.0	5.5	5.1	4.7
Fesovi-Poaalp (3B)	*Festuca ovina* *Poa alpina* *Deschampsia alpina* *Cerastium alpinum* *Luzula spicata*	1.2	1215	78	7.4	5.0	4.2	3.2
Phlalp-Sagsag (6B)	*Phleum alpinum* *Sagina saginoides* *Epilobium anagallidifolium* *Omalotheca norvegica* *Veronica alpina*	1.1	942	63	7.1	5.5	4.4	4.2
Ceralp-Rangla (6E)	*Cerastium alpinum* *Ranunculus glacialis* *Saxifraga cespitosa* *Oxyria digyna* *Deschampsia alpina*	1.3	1422	76	7.7	5.2	4.7	3.1
Fesovi-Luzspi (6F)	*Festuca ovina* *Luzula spicata* *Antennaria dioica* *Cerastium cerastoides* *Rumex acetosella*	1.3	1186	84	7.4	4.7	3.8	3.0
Desfle-Salgla (3C)	*Deschampsia flexuosa* *Salix glauca* *Betula pubescens* *Empetrum hermaphroditum* *Vaccinium myrtillus*	1.7	783	45	6.6	5.6	2.7	2.9
Desfle-Betpub (6C)	*Deschampsia flexuosa* *Betula pubescens* *Salix glauca* *Empetrum hermaphroditum* *Vaccinium myrtillus*	1.7	783	45	6.6	5.6	2.7	2.9

6.8 Summary

6.8.1 Does pioneer vegetation exhibit altitudinal and/or regional patterns of distribution?

1. Roadside pioneer vegetation is strongly influenced by altitude with evidence of clear altitudinal zonation in species composition from both direct and indirect gradient analysis. There is a strong positive correlation (r = 0.90) between site scores on NMS ordination axis 1 and altitude. Axis 1 scores also show a moderate correlation with distance east of r = 0.47.

2. A discontinuity between upper and lower altitude sites (the *Deschampsia cespitosa-Trifolium repens* (3A) and *Festuca ovina-Luzula spicata* (3B) communities at the three-group level of cluster analysis) is evident on NMS ordination diagrams of the roadside pioneer sites. This is shown by direct gradient analysis to occur between 740 and 1100 m. The mean altitude of community 3A is 597 m (with a range of 80 to 1100 m), while that of 3B is 1247 m (with a range of 740 to 1860 m). The *D. flexuosa-Salix glauca* community (3C) consist of roads towards the west of the study area (44 to 59 km east). All three communities consist of predominantly contiguous sites on direct gradient analysis (Figure 6-3).

3. At the six-group level of cluster analysis, altitudinal zonation in geographical and ordination space still applies to most sub-communities but with more evidence of smaller-scale patterns within a continuum of variation (Figure 6-6). The *D. cespitosa-Taraxacum* (6A) and *D. flexuosa- Betula pubescens* (6C) sub-communities and the *Cerastium cerastoides-D. alpina* (6B) and *Festuca ovina-Antennaria dioica* (6F) sub-communities are not distinguishable by altitude. Sub-regional patterns in the upper and lower altitudinal limits of sub-communities are evident in some cases. The upper altitudinal limit of the *Plantago major-Trifolium repens* (6D) sub-community increases from 440 m at 31 km east to 620 m at 89 m east. Differences in mean distance east can be used to distinguish sub-communities 6A and 6C and 6B and 6F (6A and 6B being more oceanic in distribution).

4. Altitudinal zonation is still recognisable at the nine-group level of cluster analysis but with even more variations (Figure 6-9). A number of groups which do not have significantly different mean altitudes are also indistinguishable by mean distance east at this level.

5. Variance partitioning confirms that a significant proportion of the variation in species composition can be explained by the effects of altitude and continentality. When these two factors are assessed together, 64% of the variance explained is attributed to altitude independently, 25% to distance east independently and 11% is shared between them. Therefore, although altitude and distance east co-vary due to the regional topography, their independent effects are important.

6. Glacier foreland pioneer vegetation is influenced by altitude, with evidence of a continuum of variation in species composition with increasing altitude and a moderately strong positive correlation ($r = 0.75$) between the ordination score of a site on NMS axis 1 and altitude. Distance east is also highly correlated with altitude ($r = 0.89$). Variance partitioning shows that altitude independently accounts of 37% of the variance, distance east for 29%, with 27% shared by these two factors. Continentality therefore has a greater relative influence on glacier forelands than on roadside sites and the shared variance between these two factors is also greater.

7. The altitudinal distribution of cluster analysis groups within the glacier-foreland data set at the two- and four-group levels supports the existence of a continuum of variation rather than discrete pioneer communities. There are no obvious discontinuities in ordination space between groups. At the two-group level, sub-communities *Deschampsia alpina-Oxyria digyna* (2A) and *Saxifraga cespitosa-Trisetum spicatum* (2B) have significantly different mean altitudes and distances east. Direct gradient analysis shows that 2B has a more restricted geographical distribution than 2A (Figure 6-22). At the four-group level, only group 4C is significantly different from the other three groups in terms of mean altitude and distance east.

6.8.2 Does the use of Ellenberg indicator values to quantify environmental factors provide further explanation of spatial patterns?

1. Mean EI values for light in the roadside pioneer sites show a significant positive correlation with altitude and with NMS axis 1, while mean EI values for moisture, nitrogen and pH show a significant decrease with altitude and a negative correlation with axis 1. Mean EI values for light, pH and nitrogen show a significant positive correlation with site scores on axis 2 of the NMS ordination diagram (Table 6-6). It is suggested, therefore, that axis 1 is primarily an altitude-related climatic axis, whereas axis 2 is primarily a nutrient axis that is independent of altitude. Both are also influenced by relative levels of disturbance.

2. Roadside pioneer cluster analysis groups that were not distinguished by differences in altitude and/or region can, in some cases, be distinguished by differences in mean EI values. At the three-group level of cluster analysis, mean EI values for the three communities are all significantly different for light, moisture, pH and nitrogen with the exception of the mean moisture EI value for the *Deschampsia cespitosa-Trifolium repens* and the *D. flexuosa-Salix glauca* communities.

3. At the six-group level, the *Cerastium cerastoides-D. alpina* and *Festuca ovina-Antennaria dioica* sub-communities (6B and 6F), which were indistinguishable by altitude, have significantly different mean moisture, pH and nitrogen EI values. Sub-community 6F, which is further east, is drier and has a lower mean pH and nitrogen value. The *D. cespitosa-T. repens* and *D. flexuosa-S. glauca* sub-communities (6A and 6C), which have similar mean altitudes, have significantly different mean EI values for light, pH and nitrogen, 6A having higher values for all three variables. At the nine-group level, the existence of several scales of environmentally-determined pattern within a continuum of variation between sites is confirmed by analysis of mean EI values using 95% confidence intervals.

4. When the NMS ordination of glacier foreland pioneer sites is rotated for maximum correlation with altitude (Figure 6-27), site scores along axis 1 show a moderate positive correlation with mean EI values for pH and weak to moderate negative correlations with mean EI values for moisture and nitrogen. There is a low negative correlation between scores on axis 2 and mean EI values for light and a low positive correlation between scores on axis 2 and moisture. Unlike the roadside ordination data set, the glacier forelands are therefore characterized by correlations between altitude and mean nutrient and pH values along axis 1.

5. The two-group level of cluster analysis results in sub-communities which are significantly different in their mean EI values for pH, the *Deschampsia alpina-Oxyria digyna* (2A) sub-community having a lower mean EI value for pH than the *Saxifraga cespitosa-Trisetum spicatum sub-community (2B).* At the four-group level, group 4C has higher mean EI values for moisture and nitrogen than groups 4A and 4B. Group 4D consists of only two sites and therefore has very wide 95% confidence intervals. The evidence reinforces the predominance of continuity of variation in mean EI values between glacier foreland pioneer sites.

6. The roadside and additional pioneer habitat data sets show a level of agreement in terms of correlation coefficients between EI values and ordination axes. Notably, they have similar levels of correlation between NMS axis 1 (rotated for maximum correlation with altitude) and mean light EI value and both have significant correlations between NMS axis 2 scores and mean EI values for pH. In contrast, there is no significant correlation between mean light EI value and axis 1 for the glacier foreland sites and the mean EI value for pH is correlated with axis 1. This suggests that for the glacier foreland pioneer sites altitude is not a major influence on vegetation cover and pH is not independent of altitude.

7. All three data sets show similar trends in correlations between NMS axes and mean values for altitude, distance east, moisture and nitrogen (Table 6-

24), suggesting more consistent relationships between these four variables across habitat types.

8. Variance partitioning confirms that altitude and the mean EI value for pH are the dominant influences on the roadside pioneer sites and all mean EI values independently explain a significant portion of the variance within this data set (Figure 6-16). For the glacier forelands, however, the level of variance explained by mean EI values is not statistically significant and the low overall variance within this data set is confirmed. For the additional pioneer habitats, the variance explained is significant for all four mean EI values, with a higher proportion of the TVE explained by mean moisture EI values and a lower proportion by the other three values (Figure 6-39). This is explained by the inclusion of a number of fluvial habitats in this data set.

9. The use of EI values, in conjunction with variance partitioning, has therefore proved valuable in explaining variability within and between pioneer communities.

6.8.3 What are the relative influences of habitat type and altitude/ continentality on pioneer colonization?

1. Altitudinal zonation is evident in the communities found in additional pioneer habitats (Figure 6-35). At the four-group level, sites are clustered primarily according to altitude rather than habitat type. The exception to this is community 4C which consists primarily of sites from one habitat type. A regional pattern cannot be identified for this data set. Variance partitioning shows the independent proportion of the TVE explained by altitude to be 12% and by distance east to be 5%.

2. When correlations between NMS axis 1 (rotated for maximum correlation with altitude) and altitude are compared for individual ordinations of the three data sets (Table 6-24), all three show significant strong positive correlations between site ordination score and altitude. There is a stronger correlation

for the glacier foreland and additional pioneer habitat data sets between axis 1 and distance east.

3. For the combined data set at the three-group level, the glacier forelands extend the lower altitudinal limit of the *Festuca ovina-Poa alpina* community (3B) down to 80 m, with sites from the additional pioneer habitats data set extending down to 240 m. The roadside sites in this community are, with the exception of one site at 500 m, at 740 m or above. The glacier foreland data set also extends community 3B to 5 km east (the most westerly point sampled) and other pioneer habitats extend it to 16 km east, whereas the roadside sites are, with the exception of one site at 31 km east, at least 44 km east (Figure 6-36).

4. At the six-group level, the majority of glacier foreland pioneer sites are equivalent to the highest altitude roadside pioneer sub-community, thus extending its lower altitudinal boundary from 1560 m to 80 m (Figure 6-37). One site (an avalanche track) from the additional pioneer habitats data set falls within this group and is at 240 m.

5. Variance partitioning of the combined data set gives a value of 17% for the proportion of TVE explained independently by altitude and 8% for the proportion explained by distance east. These values are higher than those for the additional pioneer habitats (12% and 5% respectively) and roadside sites (16% and 6% respectively) and lower than for the glacier forelands (50% and 33% respectively).

6. Thus, although altitude has a dominant influence on pioneer colonization, continentality and habitat type are also important both within and between the pioneer communities and sub-communities that have been recognised. The highest percentage of variance explained by altitude and continentality is for the glacier forelands, the most uniform habitat type. The lowest percentage is for the data set of additional habitats, which is the most diverse.

7 PIONEER COMMUNITY CHANGE DURING PRIMARY SUCCESSION

7.1 Introduction

In this chapter the focus changes to a comparison of pioneer communities with those of later stages of succession; i.e. changes that occur to the pioneer stage during primary succession. Of particular interest is the extent to which pioneer communities converge or diverge along successional trajectories. A second theme is the extent to which such trajectories are related to altitude. Finally, Ellenberg indicator values (EI values) are explored as a means of providing further explanation of patterns of successional change.

The key questions addressed are: (1) is pioneer species composition more or less variable than that of later stages of succession?; (2) is there an altitudinal pattern in the relative variability of vegetation at pioneer and later stages of succession?; and (3) are there consistent changes in mean EI values which may help to explain successional processes? The relative abundances of species recorded in two successional stages of the roadside data set and four stages of the glacier foreland data set are used in turn to address these questions.

7.2 The relative variability of pioneer and climax roadside vegetation

The first question is investigated within the context of the roadside data set by calculating the mean within-stage Sørensen distance for the pioneer and climax stages of succession to provide a measure of the overall variability between sites within each stage. The results are used to assess whether variability increases, decreases or remains unchanged during succession i.e. whether the successional trajectory is divergent, convergent or parallel. A combined NMS ordination of pioneer and climax (mature) stages allows visual assessment and further analysis of the dissimilarity between sites within each stage in terms of their species composition. Cluster analysis of both stages is then used to compare the relative number of higher-level groups within each stage.

7.2.1 Within-stage variability of roadside pioneer and climax sites

The overall variability within each stage of roadside vegetation succession is measured using the mean Sørensen distance between sites within each stage. The mean within-stage distance for pioneer sites is 0.81 ± 0.004 (see Chapter 4, section 4.3), while that for the climax sites is 0.77 ± 0.007 (Figure 7-1). The mean distance between sites in the climax stage is therefore significantly lower than the mean distance between sites in the pioneer stage, indicating less variability in the climax stage, although the slightly broader confidence interval indicates that the mean variability cannot be defined as precisely for the climax stage.

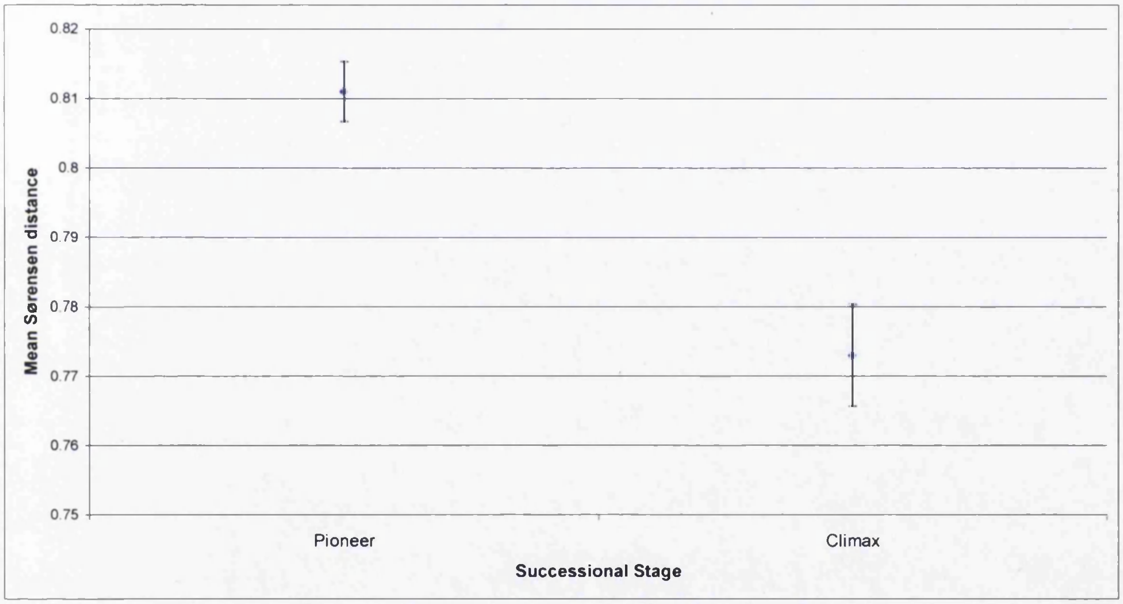


Figure 7-1. Mean Sørensen distance and 95% confidence intervals for pioneer and climax stages on roadsides.

When the frequency distribution of mean Sørensen distances for sites within each stage is examined (Figure 7-2), the mean distances within the pioneer stage are normally distributed (see Chapter 4, section 4.3). In contrast, the mean distances for the climax stage, as well as displaying a wider range of values (0.293 compared with 0.196 for the pioneer stage), have a positively skewed distribution with the means of the majority of sites occurring towards the lower end of the scale (skewness = 0.838). Considerable variability therefore occurs within the climax stage of succession on roadsides but the majority of sites are more similar to each other in terms of species composition than those of the pioneer stage. This may signify the formation of tight communities within the climax vegetation. A D'Agostino-Pearson test for normality confirmed that the climax site data are not normally distributed ($p < 0.001$).

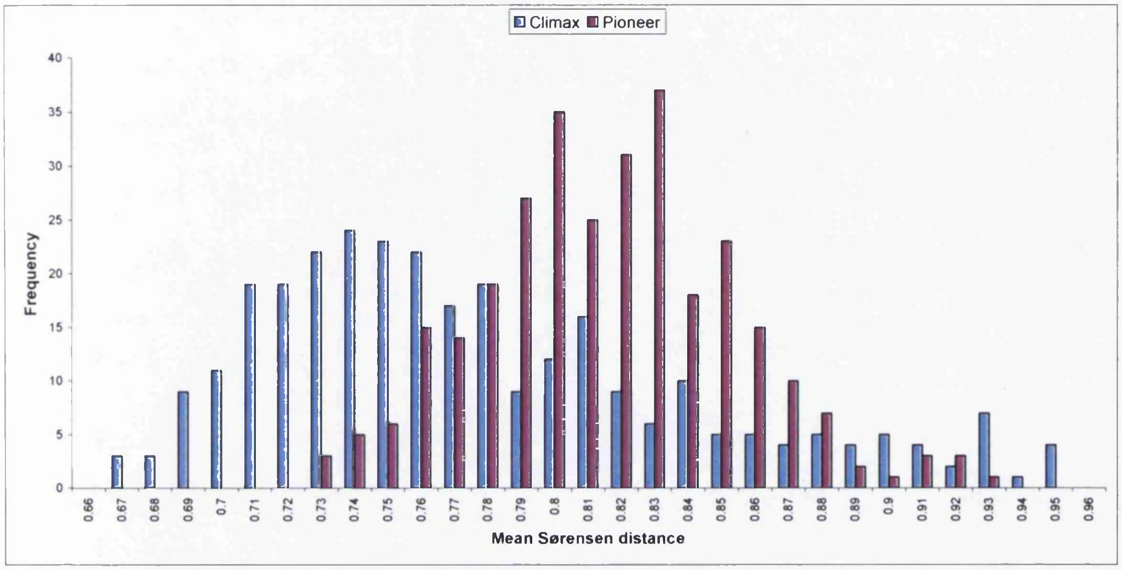


Figure 7-2. Frequency distribution of mean Sørensen distances for pioneer and climax stages on roadsides.

However, outlier analysis of the climax sites showed that there were no sites with mean distances more than 3 standard deviations from the grand mean. The extreme climax sites are at a maximum of 2.7 standard deviations from the mean and consist of sites at both low and high extremes of the altitudinal range, where high levels of disturbance occur due to human activity or permafrost respectively. At these sites, there is less difference between pioneer and climax stages in terms of species composition.

7.2.2 NMS ordination of within and between stage variability

NMS ordination of pioneer and climax roadside sites in a single analysis was carried out to show the within- and between stage-variability of sites in terms of their species composition. The stress level for the two-dimensional ordination is 22.2% ($p = 0.03$), with an acceptable instability of 10^{-4} after 90 iterations. Figure 7-3 shows the ordination diagram with axis 1 rotated for maximum correlation with successional stage ($r = 0.845$, $p < 0.01$). Examination of this diagram confirms the findings of the last sub-section, with pioneer sites appearing less tightly clustered than the majority of climax sites. In particular, the pioneer sites are less tightly grouped along axis 1 with 95% confidence interval of 0.045, compared with 0.038 for the climax sites. However, there are two areas of ordination space (towards the upper and lower limits of axis 2) in which climax sites show greater dissimilarity to the majority of other sites within this stage. These areas correspond to the tail of the climax site distribution in Figure 7.2.

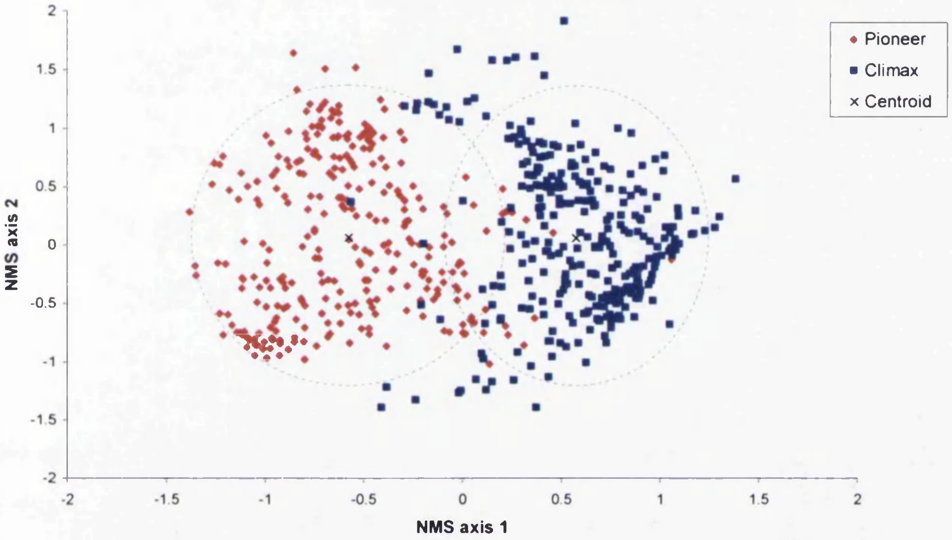


Figure 7-3. NMS ordination of roadside pioneer and climax sites rotated for maximum correlation between axis 1 and successional stage (r = 0.845). Dashed lines indicate centroid ± 2 standard deviations.

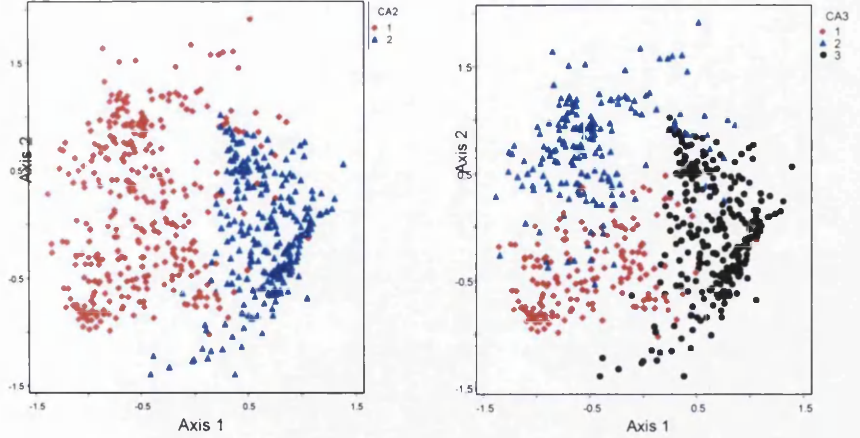
It is interesting to note that with the ordination rotated in this way, axis 2 has a strong positive correlation with altitude (r = 0.879, $p < 0.01$). The upper and lower limits of axis 2 therefore correspond to high and low altitude sites respectively and it appears that climax sites at the extremes of the altitudinal range are further from the centroid of the cluster. Additionally, there appears to be an unoccupied area of less tightly clustered climax sites with ordination scores between 0 and 0.5 on axis 2 suggesting a possible discontinuity in species composition. On the other hand, pioneer sites with relatively low scores on axis 2 appear to have a wider range of scores along axis 1 and this range has a tendency to decrease as scores on axis 2 increase, suggesting greater dissimilarity between pioneer sites at lower altitudes which is related to greater variability in the rate of succession. The relationship between altitude and variability will be explored further in section 7.3.

7.2.3 Cluster analysis of within- and between-stage variability

In order to explore further the differences between pioneer and climax vegetation in terms of variability, classification of both stages in a single analysis was carried out using cluster analysis. This is initially used to ascertain the extent to which the analysis clusters sites according to successional stage and then to measure variability in terms of the number of groups which are formed within each stage.

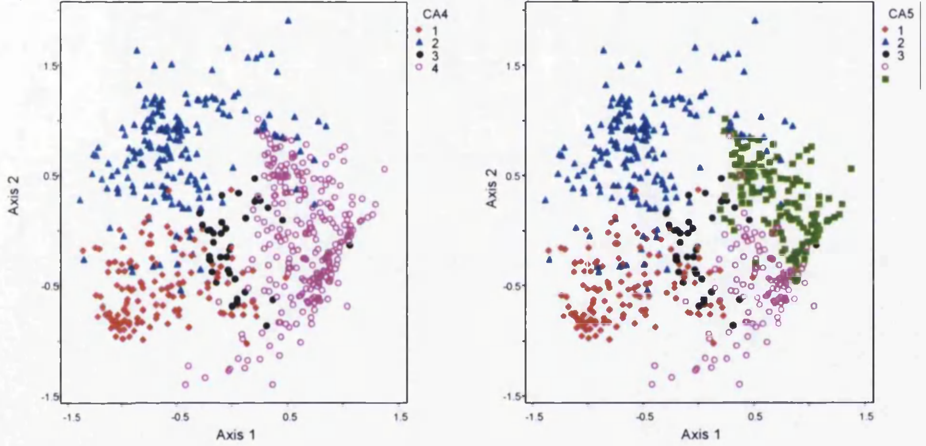
Figure 7-4 shows the results of selecting two to six cluster analysis groups. Comparison of Figure 7-4a with Figure 7-3 confirms that, at the two-group level, 93% of sites are grouped according to successional stage. All the pioneer sites are classified in group 1 and 36 climax sites towards the upper end of axis 2 (at altitudes between 1180 and 1860 m) are also classified within this group, suggesting that the species composition of these climax sites is more similar to pioneer sites than to other climax sites. Six climax sites at lower altitudes (360 to 980 m on Vetlestølsdalen road) are also clustered with the pioneer sites in group 1.

When the sites are classified at the three-group level (Figure 7-4b), the pioneer sites split into two groups along the centre of axis 2, confirming the major altitudinal division which was suspected at the two-group level and in agreement with the results obtained when pioneer sites were classified independently (see Figure 4-7). The pioneer vegetation therefore forms two relatively distinct high and low altitudinal groups, in contrast to the climax vegetation which appears to vary more gradually with altitude without such clear discontinuity.



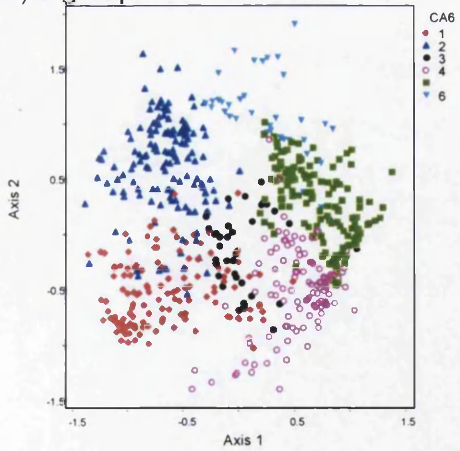
a) 2 groups

b) 3 groups



c) 4 groups

d) 5 groups



e) 6 groups

Figure 7-4. NMS ordination showing roadside pioneer and climax cluster analysis groups.

The four-group level of classification (Figure 7-4c) shows an additional pioneer group (group 3), again confirming the results described in Chapter 4 (Figure 4-7), when pioneer sites were classified independently. (Group 3 in Figure 7-4c is equivalent to group 3C in Figure 4-7.) This group includes pioneer sites along two roads (Vetlestølsdalen and Fortundalen) and a single climax site (CC1160). It has fewer sites than the corresponding group 3C in Figure 4-7 as, in contrast to the independent classification of pioneer sites, sites between 340 and 740 m a.s.l on the two roads. have been classified with group 1 rather than group 3. In Chapter 4 it was suggested that this group may consist of sites which are less frequently disturbed and have therefore reached a later stage of colonization than other pioneer sites. The position of group 3 sites on axis 1 (rotated for maximum correlation with successional stage) supports this hypothesis, showing these sites to be positioned towards the upper end of axis 1 in ordination space. However, the fact that this group only includes one climax site indicates that it can still be considered primarily a pioneer group.

At the five-group level (Figure 7-4d), the climax sites split into high and low altitude groups (groups 4 and 5) at approximately the same values on axis 2 as the division between pioneer groups 1 and 2. Although the boundary between these two climax groups shows less discontinuity than that between the pioneer groups, there appears to be a clear correspondence between groups 1 and 4 and between groups 2 and 5 in terms of the position of their respective boundaries along axis 2. Indicator species analysis reveals group 4 to be characterized by typical woodland species including *Sorbus aucuparia*, *Betula pubescens*, *Gymnocarpon dryopteris*, *Trientalis europaea* and *Melampyrum sylvaticum*, while group 5 is characterized by dwarf shrubs including *Empetrum hermaphroditum*, *Vaccinium vitis-idaea, V. myrtillus, V. uliginosum* and *Betula nana*. These indicator species suggest that the border between these two groups occurs at the tree-line, the precise altitude of which varies according to local conditions.

At the six-group level (Figure 7-4e), the higher altitude climax sites, which were previously classified with pioneers in group 2, now form a separate group (group 6). Again there is no sharp discontinuity between groups 5 and 6, although a number of group 6 sites appear to form a separate cluster. The main indicator species for this group are *Salix herbacea* and *Carex bigelowii*, both dominant species of high-altitude climax vegetation. Figure 7-5 reproduces Figure 7-4e with centroids ± 2 standard deviations showing the relative variability within each group.

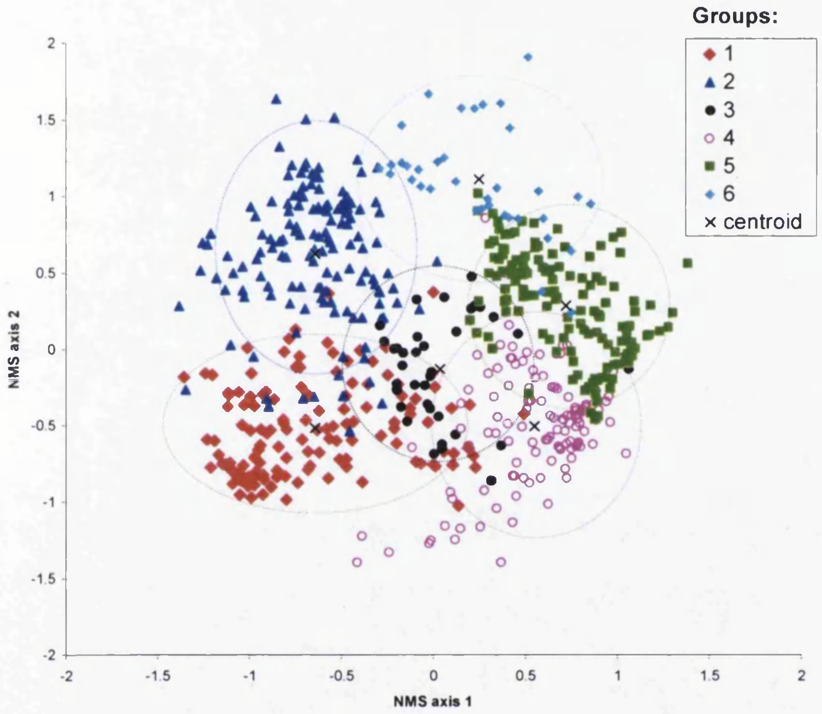


Figure 7-5. NMS ordination showing six roadside pioneer and climax cluster analysis groups. Dashed lines indicate centroid ± 2 standard deviations.

MRPP statistics for the six-group level of cluster analysis (Table 7-1) show that within-group agreement for the three groups which consist mainly of pioneer sites (groups 1 – 3), A = 0.156, is greater than for the three main climax groups (groups 4 – 6), A = 0.129, and that separation between groups is also greater at T = -128 for pioneers, compared to T = -107 for the three climax groups.

The evidence therefore points to a difference between the pioneer and climax stages in terms of their overall variability; pioneer vegetation being more variable but forming tighter and more discrete groups. However, when the individual within-group distances are considered, the lower overall dissimilarity within the pioneer groups appears to be dependent on group 3, the other two pioneer groups having higher within-group distances than the climax groups (Table 7-1). This is confirmed by examining the centroids ± 2 standard deviations superimposed on the NMS ordination in Figure 7-5.

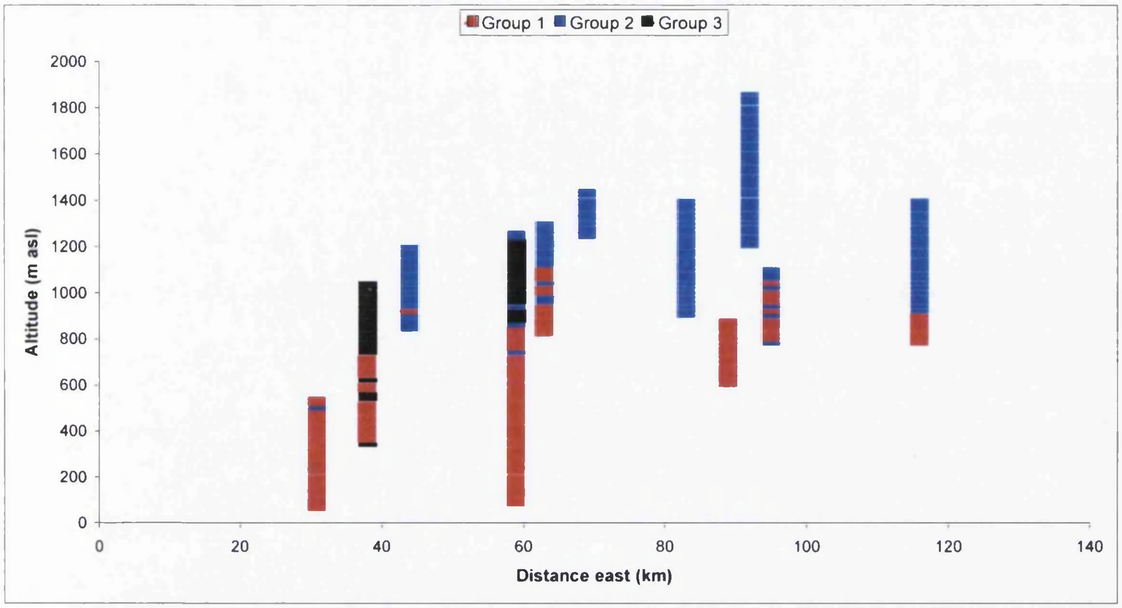
Table 7-1. MRPP statistics and mean within-group distances for the six-group level of pioneer and climax cluster analysis.

	A statistic	**T statistic**
3 pioneer groups	0.156	-128
3 climax groups	0.129	-107
Group	**Mean within-group distance (Sørensen)**	
1	0.713	
2	0.735	
3	0.410	
4	0.702	
5	0.656	
6	0.615	

Comparison of the direct gradient analysis of pioneer and climax sites at the six-group level of combined cluster analysis (Figure 7-6) shows the altitudinal zonation of groups within both stages and confirms the general correspondence between altitudinal boundaries for the two stages. While the pioneer sites are restricted to groups 1, 2 and 3, the climax sites, while predominantly classified in groups 4, 5 and 6, also appear in groups 1 and 3 towards the west of the study area. There are no climax sites in group 2.

The low altitude pioneer group (group 1/3A) occurs up to approximately 1100 m and is characterized by *Deschampsia cespitosa, Trifolium repens, Agrostis capillaris* and *Plantago major.* A small number of climax sites towards the west of the region are also characterized by this vegetation type. The high altitude pioneer group (group 2/3B) mainly occurs between 800 and 1860 m and is characterized by *Festuca ovina*, *Cerastium cerastoides, Luzula spicata* and *Poa alpina.* The third pioneer group (group 3/3C), which occurs on only two roads towards the west of the region, is characterized by *D. flexuosa* and *Salix glauca.* These correspond to the three pioneer communities identified in Chapter 4, Section 4.5.2.

a) Pioneer sites



b) Climax sites

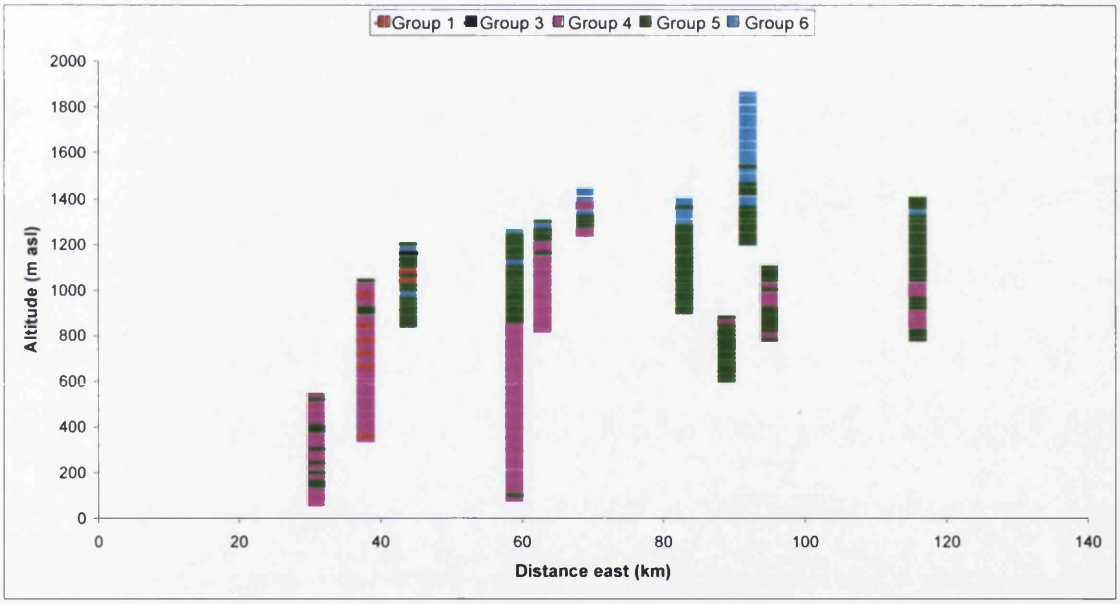


Figure 7-6. Direct gradient analysis of a) pioneer and b) climax sites at the six-group level of combined cluster analysis. The column at 59 km east has been displaced from 61 km to avoid overlap of columns.

The low altitude climax vegetation (group 4), most of which is found below approximately 1200 m, is characterized by *Gymnocarpium dryopteris, Deschampsia flexuosa, Sorbus aucuparia* and *Betula pubescens*. Group 5 forms the predominant climax vegetation between approximately 800 and 1500 m but it also occurs at low altitudes towards the west of the study area. This vegetation type is characterized by *Empetrum hermaphroditum, Betula nana* and *Vaccinium* spp. Group 6, characterized by *Salix herbacea* and *Carex bigelowii*, forms the climax vegetation up to 1860 m and most sites in this group are above 1200 m.

7.3 The relationship between the relative variability of roadside pioneer and climax sites and altitude

This section addresses the second key question of this chapter by analyzing the relationship between altitude and variability within the pioneer and climax stages of succession on roadsides. As noted in section 7.2.2, when the NMS ordination of pioneer and climax roadside sites is rotated to obtain maximum correlation between axis 1 and successional stage, axis 2 is highly correlated with altitude. These relationships are illustrated in Figure 7-7.

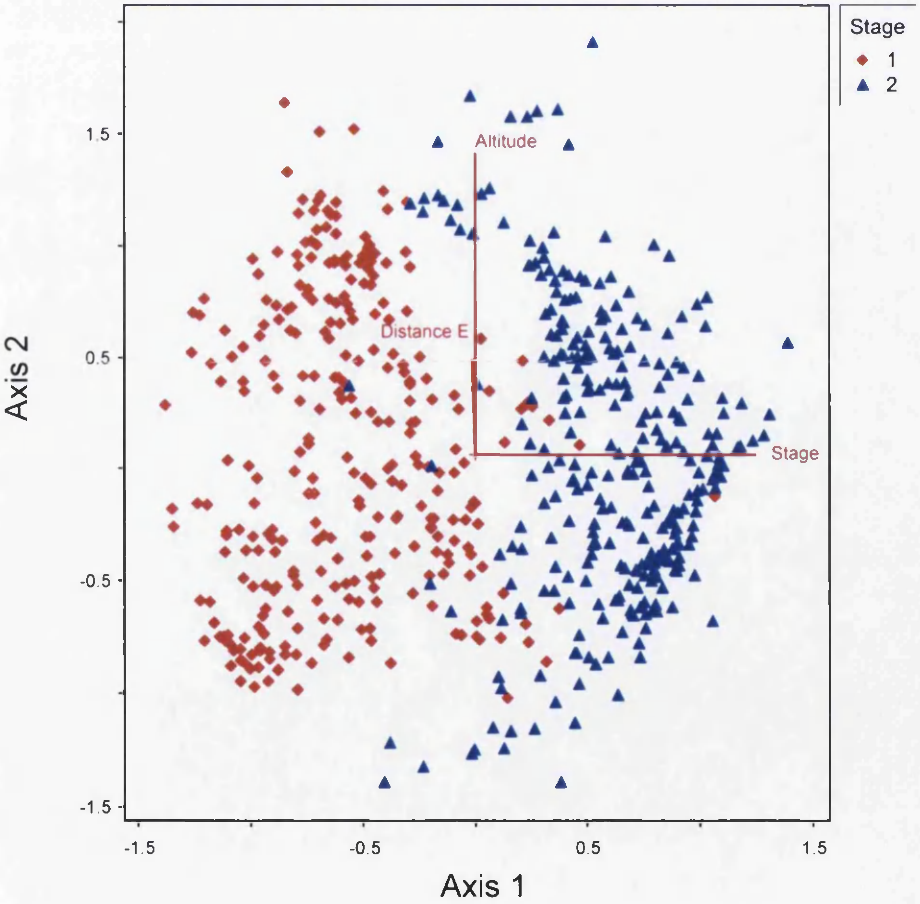


Figure 7-7. NMS ordination of roadside pioneer and climax sites showing correlations between axes, successional stage and altitude.

In order to examine the relationship between variability and altitude in more detail, the roadside data set was split into nine 200 m zones and the mean Sørensen distances between sites were calculated for each of the successional stages within these zones (Figure 7-8). In the two lowest zones, 0 – 200 m and 220 – 400 m, variability between sites is greater in the climax than the pioneer stage: the mean Sørensen distance increases from 0.51 to 0.73 between pioneer and climax stages in the 20 – 200 m zone and from 0.52 to 0.72 in the 220 – 400 m zone. In the next five altitudinal zones, ranging from 420 to 1400 m, the mean Sørensen distance is lower in the climax than the pioneer stages, indicating decreased variability with succession. However, the decrease in variability with succession tends to become less as altitude increases: in the 420 – 600 m zone, the mean Sørensen distance decreases from 0.71 to 0.58 between pioneer and climax sites, whereas in the 1220 – 1400 m zone it decreases from 0.70 to 0.66. For the two highest altitudinal zones, the 95% confidence intervals for the mean Sørensen distances for pioneer and climax stages indicate no significant change in variability with succession.

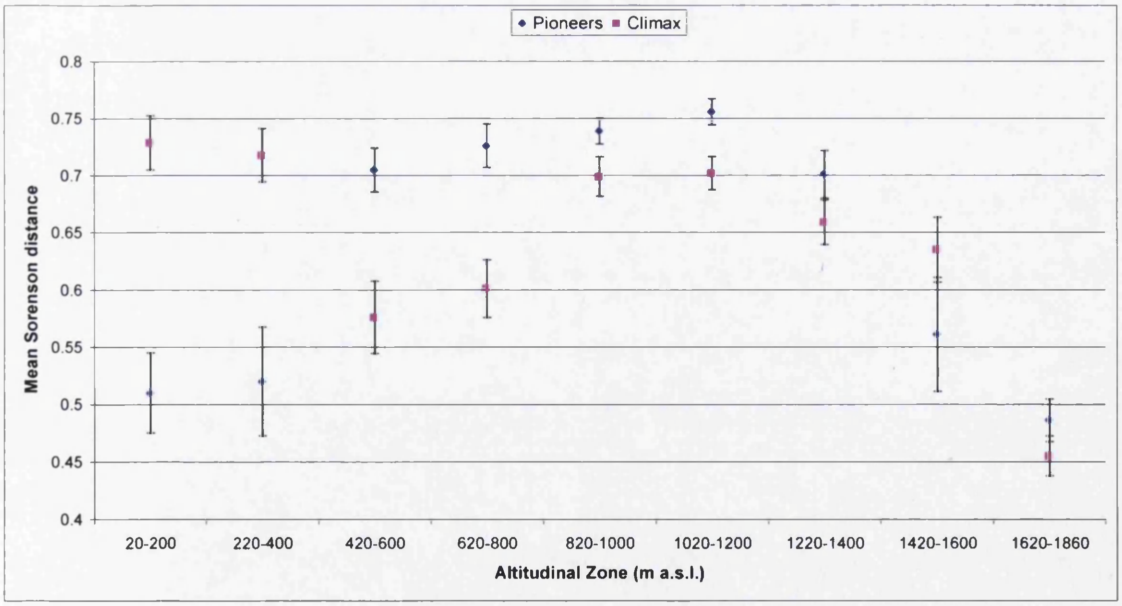
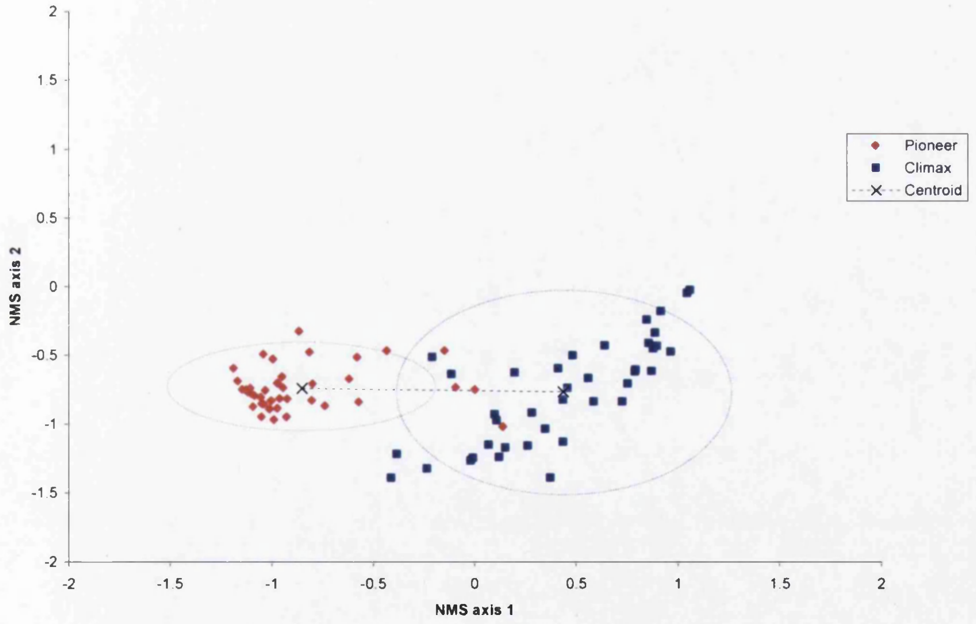


Figure 7-8. Mean Sørensen distances and 95% confidence intervals for pioneer and climax roadside sites within 200 m altitudinal zones.

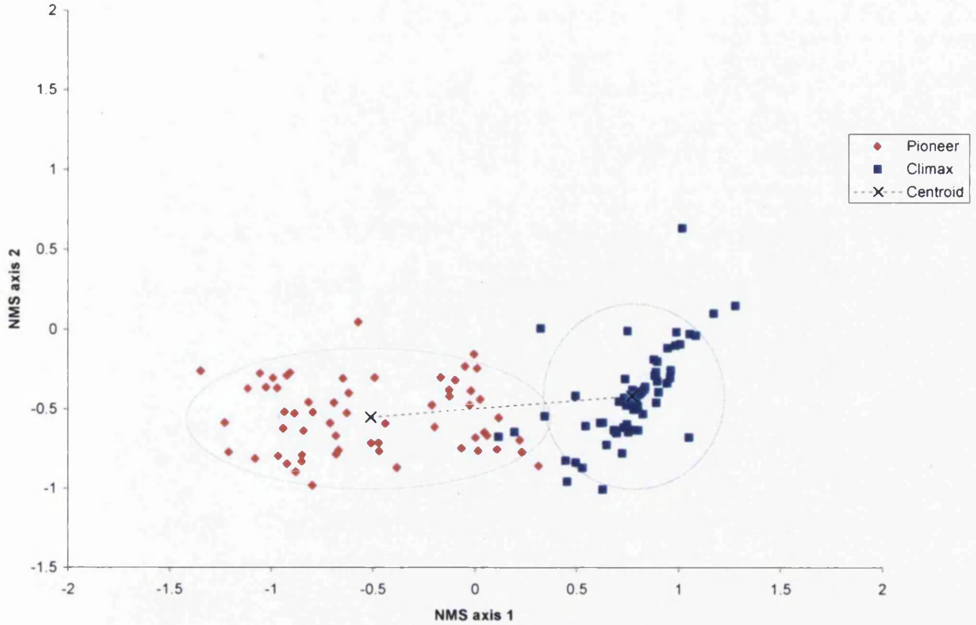
These results suggest that the pattern of succession on roadsides changes from one of strong divergence up to 400 m, strong convergence from 420 to

800, moderate convergence from 820 to 1200 m, weak convergence from 1220 to 1400 m and parallel succession from 1420 to 1860 m. This would be consistent with the existence of a mosaic of climax habitats at lower altitudes, partly due to the effects of human activity, a more uniform forest climax vegetation at intermediate altitudes and increasing similarities between pioneer and climax vegetation at higher altitudes. It is suggested that strong convergence indicates the influence of trees, moderate convergence the presence of shrubs (low alpine zone) and weak convergence the presence of snowbed and heath communities (mid alpine zone), with parallel trajectories or no succession occurring in areas of permafrost disturbance at the highest altitudes. These findings are explored further by plotting site NMS scores with their centroids ± 2 standard deviations for five altitudinal zones, 20 – 400 m, 420 – 800 m, 820 – 1200 m, 1220 – 1400 and 1420 – 1860 m (Figure 7-9).

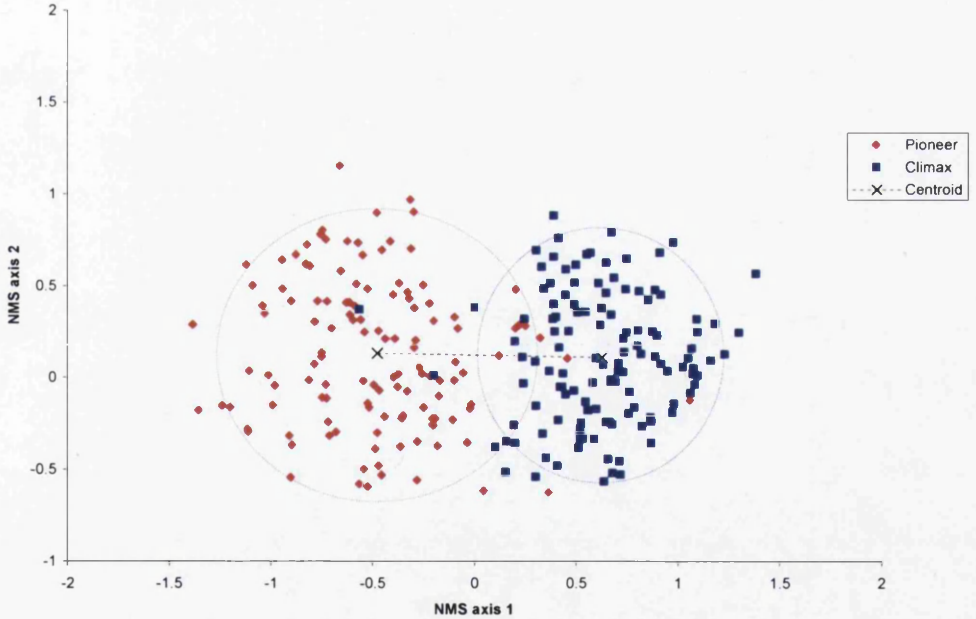
a) 20 – 400 m



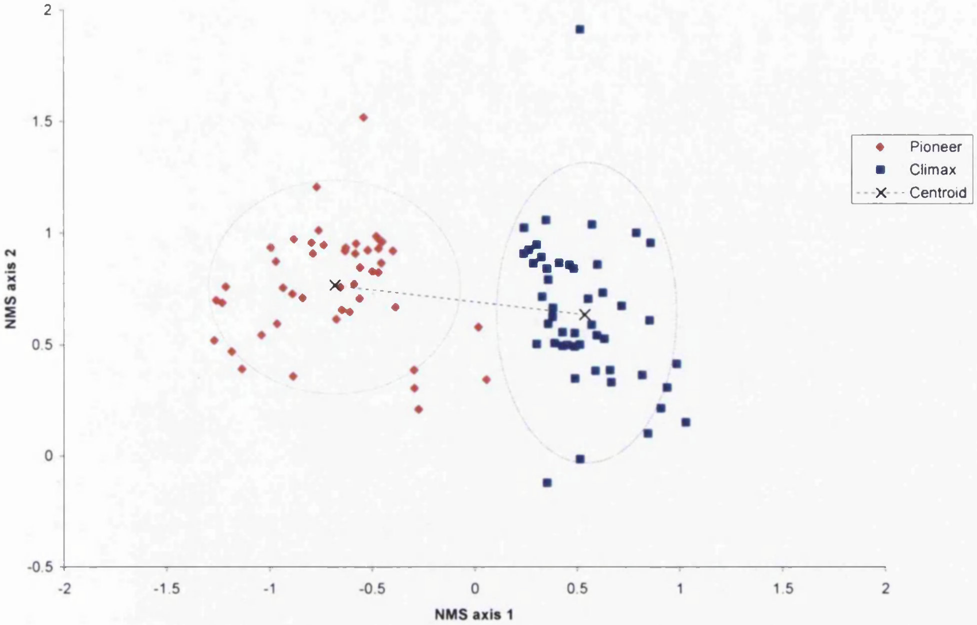
b) 420 – 800 m



c) 820 – 1200 m



d) 1220 – 1400 m



e) 1420 – 1860 m

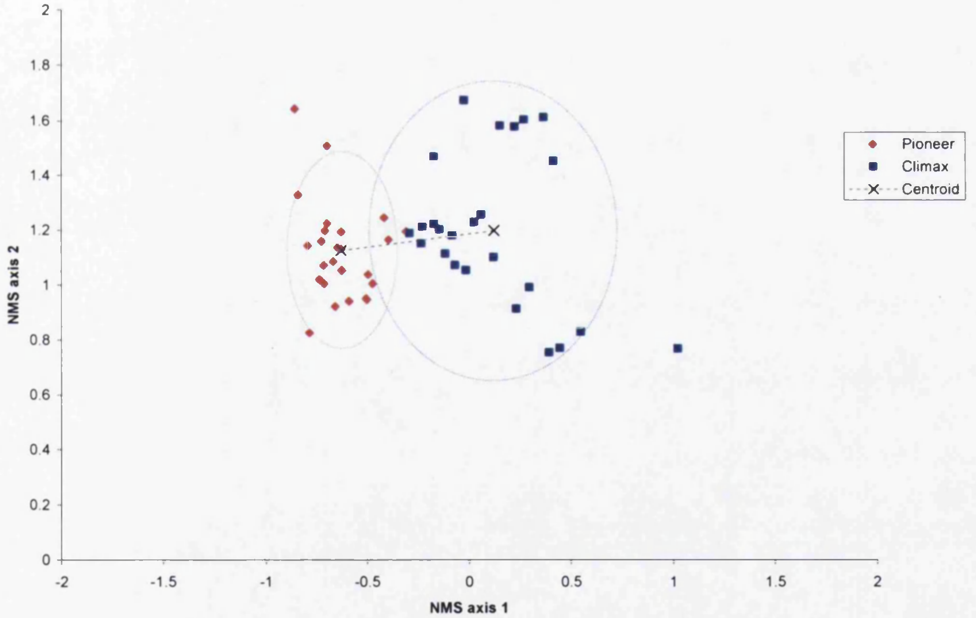


Figure 7-9. NMS ordination of roadside pioneer and climax sites plotted according to altitudinal zone a) 20 – 400 m, b) 420 – 800 m c) 820 – 1200 m, d) 1220 – 1400 m, e) 1420 – 1860 m. Ellipses indicate centroid ± 2 standard deviations. Dashed line joins centroids of each stage.

Figures 7-9a, b and c graphically show the successional trajectories identified in Figure 7-8, with divergence between the pioneer and climax stages from 20 to 400 m and decreasing convergence with altitude between 420 and 1200 m. However, the trajectories shown in Figures 7-9d and e are less clear, with the 1220 – 1400 m zone showing little change in the size of ellipses representing the pioneer and climax stages and the 1420 – 1860 m zone appearing to show successional divergence rather than a parallel trajectory. The 1220 – 1400 m zone therefore shows extremely weak convergence, with the 95% confidence intervals only just failing to overlap, and may therefore be better interpreted as a parallel trajectory. Although successional divergence appears to be identified at the highest altitude sites, the 95% confidence intervals within the 1420 – 1860 m zone do not show significant differences between the two stages, with the mean Sørensen distances of 0.57 ±. 0.06 for the pioneer stage and 0.60 ± 0.08 for the climax stage.

The figures in Table 7-2 show that the mean difference in NMS axis 1 scores between the pioneer and climax stages, interpreted as the total amount of change in species composition during succession, decreases with altitudinal zone, the lowest amount of change between pioneer and climax occurring in the 1420 to 1860 m zone.

Table 7-2. Mean change in NMS axis 1 score between roadside pioneer and climax stages.

Altitude (m a.s.l.)	Mean change in NMS axis 1 score between pioneer and climax
0 - 400	1.286
420 - 1400	1.173
1420 - 1860	0.748

7.4 The relationship between successional stage and EI values of roadside sites

This section addresses the third key question from the point of view of the roadside data set, i.e. are there consistent changes in mean EI values which may help to explain successional processes? The validity of using EI values to quantify environmental factors associated with pioneer vegetation is explored further by assessing these values within the context of the surrounding climax vegetation. Furthermore, analysis of the patterns of change in mean EI value with succession may enable assessment of the relative successional development of sites within each stage; for example, where pioneer sites display characteristics more indicative of later stages of succession. Relating differences between stages to patterns in mean EI values would also add to an understanding of the environmental changes which drive primary succession.

Overall trends in mean EI values in relation to successional change are obtained by comparing mean weighted site EI values between successional stages and calculating correlations between site EI values and their ordination scores when the ordination diagram is rotated for maximum correlation between axis 1 and succession. Examination of Table 7-3 confirms that there is a change in all four mean EI values between the pioneer and climax stages of succession on roadsides. Mean EI values for light, pH and nitrogen are all significantly lower for climax (6.37, 3.02 and 2.85, respectively) than for pioneer vegetation (7.04, 3.94 and 3.47, respectively), while the mean value for moisture is significantly higher for climax (5.59) than pioneer vegetation (5.22).

Table 7-3. Mean EI values and 95% confidence intervals for two successional stages on roadsides.

Stage	Mean EIV ± 95% confidence interval			
	Light	**Moisture**	**pH**	**Nitrogen**
Pioneer	7.04 ± 0.05	5.22 ± 0.08	3.94 ± 0.10	3.47 ± 0.11
Climax	6.37 ± 0.08	5.59 ± 0.05	3.02 ± 0.08	2.85 ± 0.08

These relative differences, which are all ecologically explicable, support the validity of using EI values to quantify environmental factors within the context of vegetation succession. The values reflect decreasing light levels as vegetation cover increases with succession, decreasing nitrogen as it is taken up by the established vegetation, and the soil acidifying effects of many climax trees and shrubs. The increasing soil depth and increased cover leads to greater retention of soil moisture.

Figure 7-10 and Table 7-4 confirm the existence of differences in mean EI values between successional stage, demonstrating that the relationship between mean site EI values and NMS ordination scores presented in Chapter 6 for pioneer sites (Figure 6-11) also applies when pioneer and climax stages are combined in a single data set. When the ordination diagram is rotated for maximum correlation between axis 1 and successional stage, axis 1 has a strong negative correlation with mean pH EIV (r = -0.745) , a moderate negative correlation with mean EI values for nitrogen (r = -0.548) and light (r = -0.537) and a weak positive correlation with mean EIV for moisture (r = 0.267). Axis 2, which has a strong positive correlation with altitude (r = 0.879), is also positively correlated with light (r = 0.651) and negatively correlated with moisture (r = -0.407) and nitrogen (r = -0.451) and pH (r = -0.219). These values are comparable with those obtained when pioneer vegetation was analysed independently in Chapter 5. (Direct correlations between EI values and successional stage are r = -0.493 for light, r = 0.308 for moisture, r = -0.493 for pH and r = -0.343 for nitrogen.)

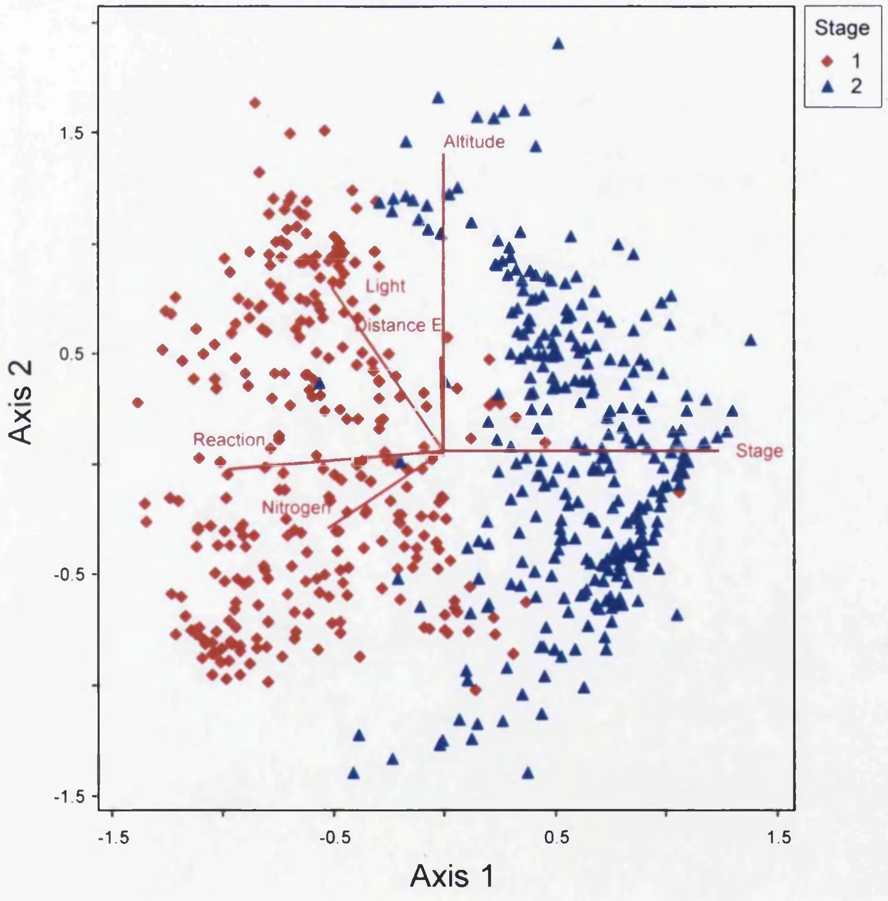


Figure 7-10. NMS ordination of roadside pioneer and climax sites rotated for maximum correlation between axis 1 and successional stage showing relationships to EI values.

Table 7-4. Pearson's r coefficients for correlations between roadside pioneer and climax NMS axes and successional stage, altitude, distance east and EI values ($p < 0.01$).

	Axis 1	Axis 2
Stage	0.845	n.s.
Altitude	n.s.	0.879
Distance east	n.s.	0.494
Light	-0.537	0.651
Moisture	0.267	-0.407
pH	-0.745	-0.209
Nitrogen	-0.548	-0.451

The findings in this section support the conclusions reached from analysis of EI values for pioneer vegetation in Chapter 6. Pioneer sites which have relatively high ordination scores on axis 1 (pioneer group 3C) are more similar to climax vegetation in terms of species composition and are therefore likely to be at a slightly later stage of colonization. The two NMS ordination axes therefore primarily represent changes in altitude and successional stage, respectively. The case for using mean EI values in analysis of primary succession has thus been further strengthened.

The roadside sites show a consistent trend in mean EI values between the pioneer and climax stages which may help to explain aspects of environmental change during primary succession. The mean EI values for light are positively correlated with altitude and negatively correlated with successional stage, reflecting the increasing UV levels with altitude, increasing shade with succession and the lower vegetation cover in the climax vegetation at higher altitudes. Mean pH EI values are strongly negatively correlated with successional stage, while mean nitrogen values are negatively correlated with altitude and successional stage reflecting the influence of climax vegetation on the soil and also human influence at lower altitudes.

7.5 The relative variability of pioneer, successional and climax stages of glacier foreland vegetation

The glacier foreland data set is investigated in a similar way to the roadside data for patterns in relative variability with successional stage. Four stages are used in this analysis: pioneer sites, two successional stages which were deglaciated approximately 70 years and 250 years ago, and climax vegetation (approximately 9000 years since deglaciation). The intermediate stages of succession available for the glacier foreland sites allow vegetation change to be analysed in terms of four successional stages instead of two and therefore give a more detailed picture of successional change, including the amount and rate of change in the early and later stages.

7.5.1 Mean within-stage dissimilarity of glacier foreland pioneer and later stage sites

Overall variability was calculated for each stage of succession on glacier forelands using the mean Sørensen distance between sites within each stage. The results reveal that pioneer sites have the lowest mean within-stage variability at 0.651 and that this tends to increase asymptotically with successional stage to 0.708 at 70 years, 0.746 at 250 years and 0.760 at 9000 years (Figure 7-11).

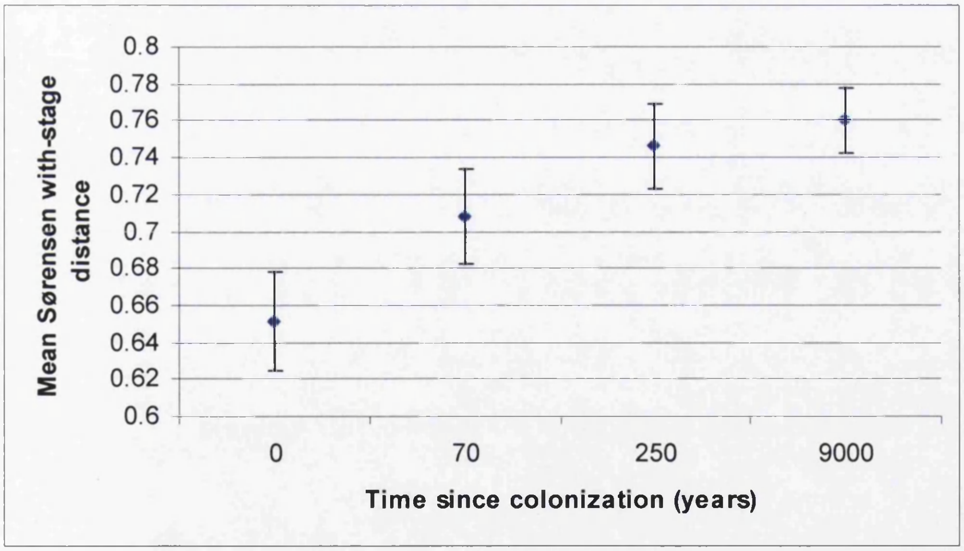
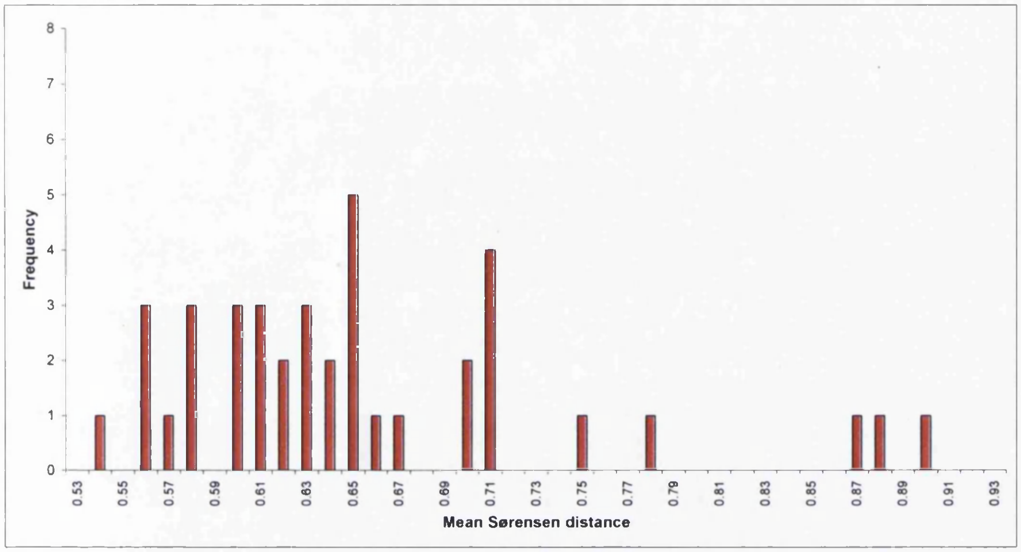


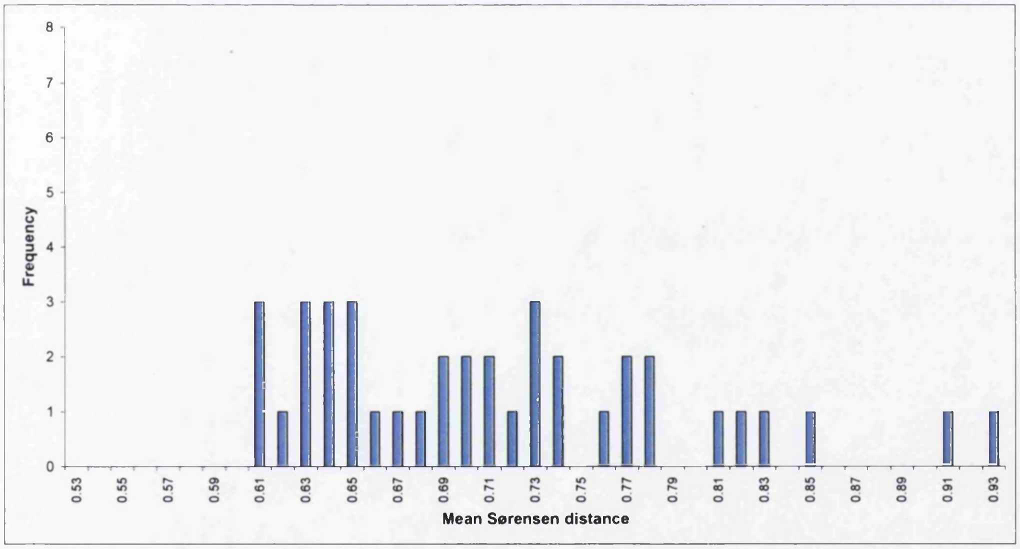
Figure 7-11. Mean Sørensen distance and 95% confidence intervals for successional stages on glacier forelands.

The differences in mean Sørensen distance between the pioneer stage and all later stages are statistically significant, as is that between 70 and 9000 years. However, differences in variability 70 and 250 years and between 250 and 9000 years since deglaciation are not significant. The most rapid change in variability therefore occurs between the initial pioneer colonization and the 70-year stage, with a comparable amount of change in variability occurring between 70 and 9000 years of colonization.

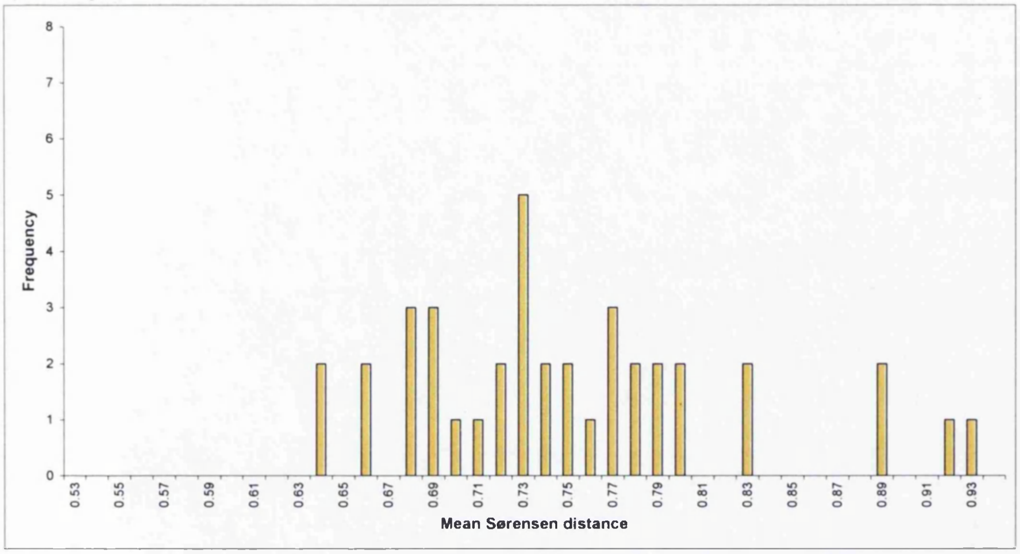
a) Pioneer



b) 70 years



c) 250 years



d) Climax

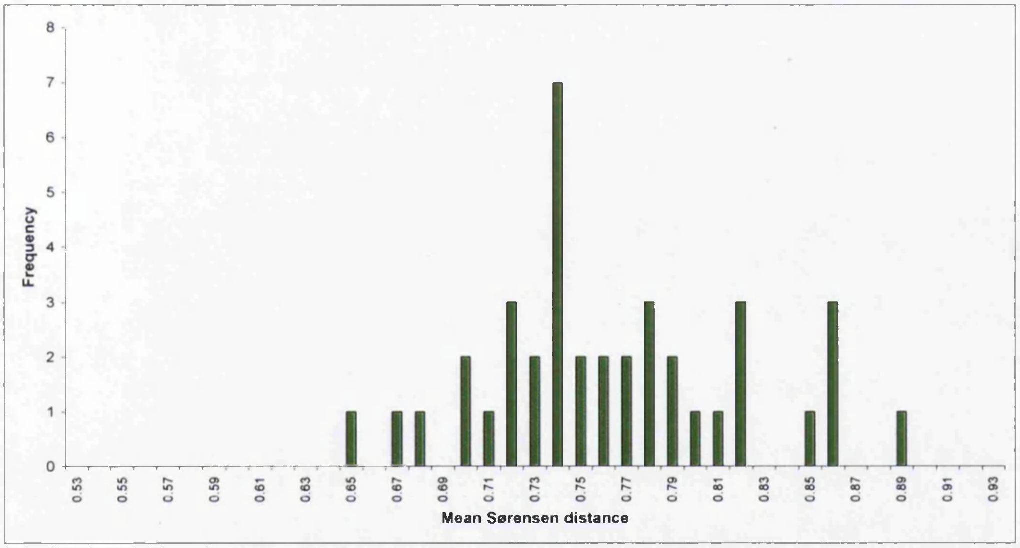


Figure 7-12. Frequency distribution of mean Sørensen distances for successional stages on glacier forelands, a) pioneer, b) 70 years, c) 250 years, d) climax.

The frequency distributions of mean Sørensen distances for sites within each successional stage are shown in Figure 7-12. All four stages have positively skewed distributions and the amount of skewness decreases with successional stage: skewness = 1.41 for the pioneer stage, 0.89 for the 70 year stage, 0.78 for the 250 year stage and 0.30 for the climax stage. Figure 7-12 confirms the trend of a general increase in within-stage variability with succession. Outlier analysis of sites within each stage identified no sites more than 3 standard deviations from the mean. Only the pioneer stage failed to show a normal distribution with a D'Agostino-Pearson test ($p < 0.001$).

7.5.2 NMS ordination of glacier foreland pioneer and later stage sites

A single ordination of all four stages of succession on glacier forelands was conducted to investigate within- and between-stage relationship between sites in terms of their species composition (Figure 7-13).

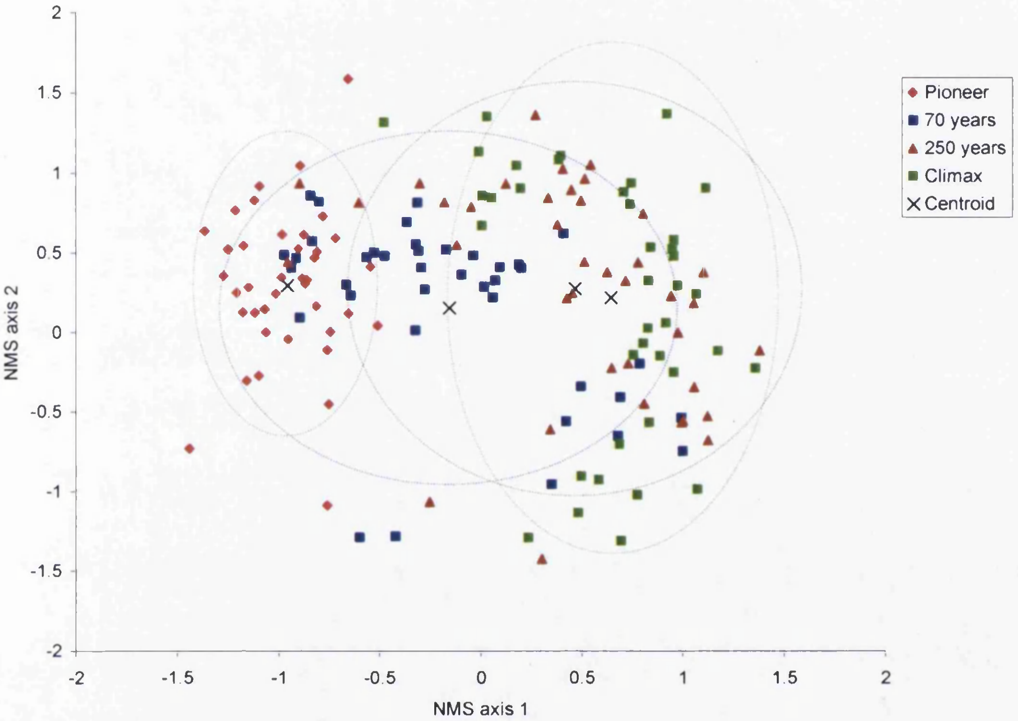


Figure 7-13. NMS ordination of four glacier foreland successional stages rotated for maximum correlation between axis 1 and successional stage. Dashed lines indicate centroid ± 2 standard deviations.

The stress for the two-dimensional NMS ordination is 20% (p = 0.03) with an instability of 10^{-4} after 75 iterations. The ordination has been rotated to obtain maximum correlation between axis 1 and successional stage (r = 0.792, p < 0.01) and the four stages are colour-coded. The pioneer sites appear more tightly clustered than subsequent stages, confirming the findings of section 7.5.1, and are more widely distributed along axis 2 than axis 1. The scores of 70-year sites on axis 1 are more variable than those for the pioneer sites. They appear to form two clusters within which a range of points on axis 1 is related to variable rates of succession in relation to habitat differences between sites. The two clusters primarily constitute a split between the lower altitude Jostedalen sites with lower scores on axis 2 and the higher altitude Jotunheimen sites with higher scores on axis 1. The 250-year and climax sites are the least tightly clustered on the ordination diagram, indicating successional divergence, and have a range of scores along both axes but have higher scores on axis 1 than the other two stages. These findings support those of the previous sub-section in that overall variability appears to increase with successional stage and that NMS axis 1 represents vegetation succession.

As was also noted for the roadside data set, when the glacier foreland site ordination is rotated for maximum correlation between axis 1 and successional stage, axis 2 has a positive correlation with altitude ($r = 0.785$, $p < 0.01$), the strength of which is only marginally less than the strength of the correlation between axis 1 and successional stage. The position of sites in ordination space therefore again suggests that variability within the pioneer stage is related as much to altitude as to successional stage. The glacier foreland results also indicate that the 70-year stage has the highest variation in scores along axis 1 and that this reflects relatively high variability in the rate of succession.

7.5.3 Cluster analysis of glacier foreland pioneer and later stage sites

Cluster analysis of all four stages of succession on glacier forelands was carried out in a single analysis to assess further the relationship between the species composition of sites and variability within each stage. The two-group level of cluster analysis (Figure 7-14) splits the data into a smaller group which includes all but one of the pioneer sites, seventeen 70-year sites and three 250-year sites, and a larger group which includes all the climax sites and the remainder of sites from the other stages. The fact that the majority of the pioneer sites constitute the basis of a group at this level of classification, while sites within the other three stages are grouped together, supports the existence of a relatively tight cluster of pioneer sites compared to later stages.

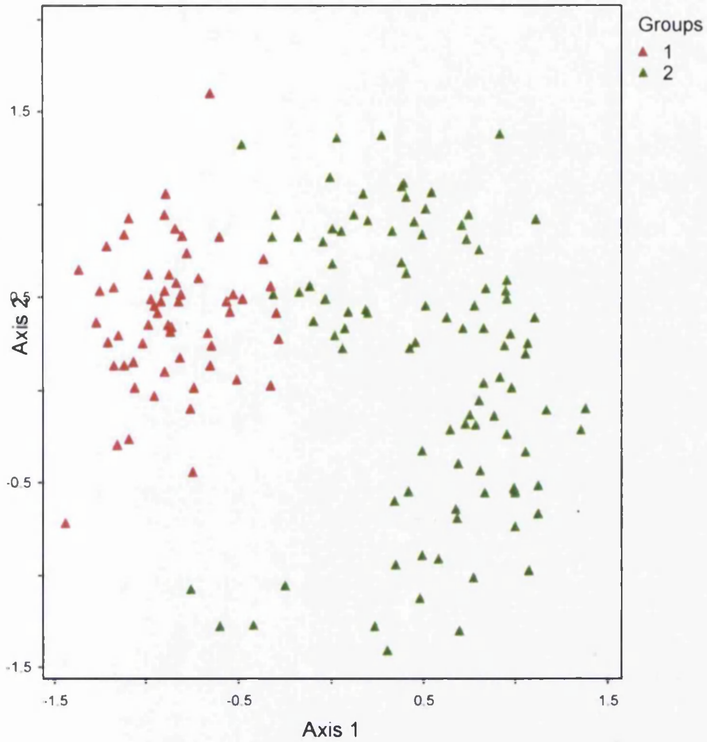
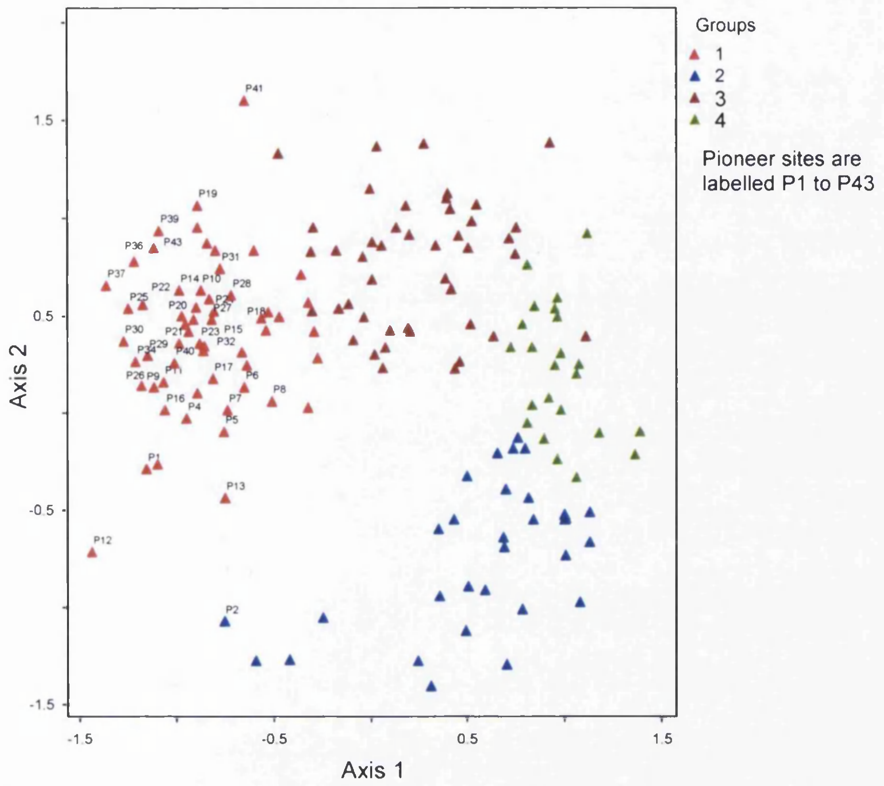


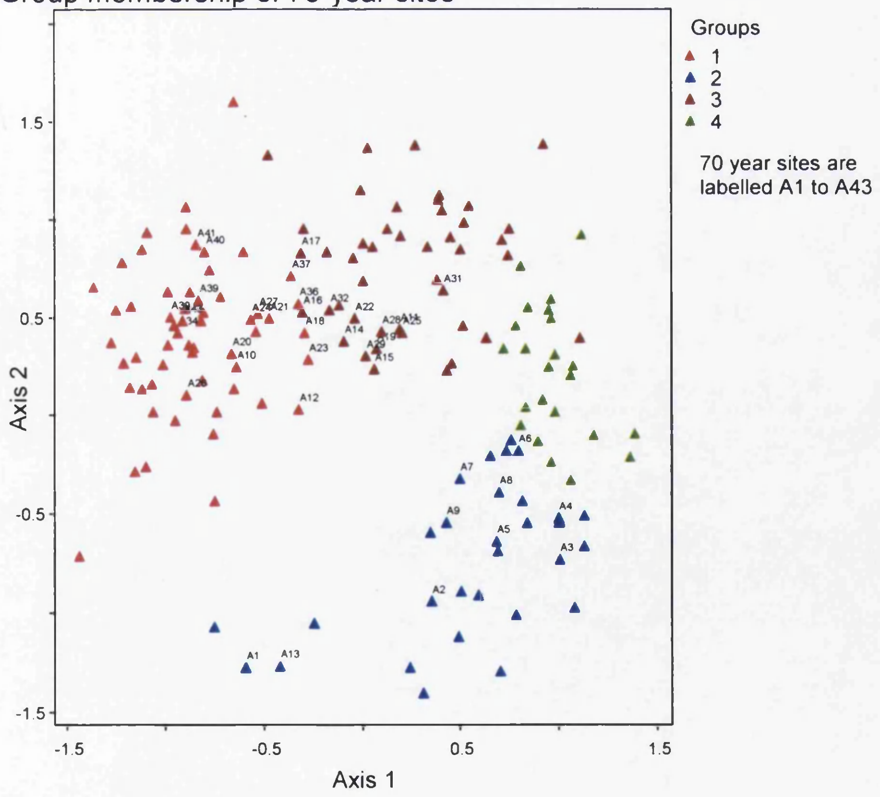
Figure 7-14. NMS ordination of glacier foreland sites showing two cluster analysis groups.

Assessment of the four-group level of cluster analysis (Figure 7-15) shows that the "pioneer" group from the two-group level is still a single group whereas the other group from the two-group level has split into three sub-groups. All but one of the pioneer stage sites therefore still belong to a single group (Figure 7-15a) at this level of classification, whereas the three later stages are distributed between at least three groups (Figure 7-15 b-d). In Figure 7-15b, sites from the 70-year stage of succession belong to groups 1, 2 and 3; sites from the 250-year stage are present in all four groups; and climax sites are present in all groups except group 1. This would seem to be evidence of an increase in between-group variability in vegetation composition with succession, with the greatest variability in terms of membership of cluster analysis groups occurring at the 250-year stage, again suggesting successional divergence.

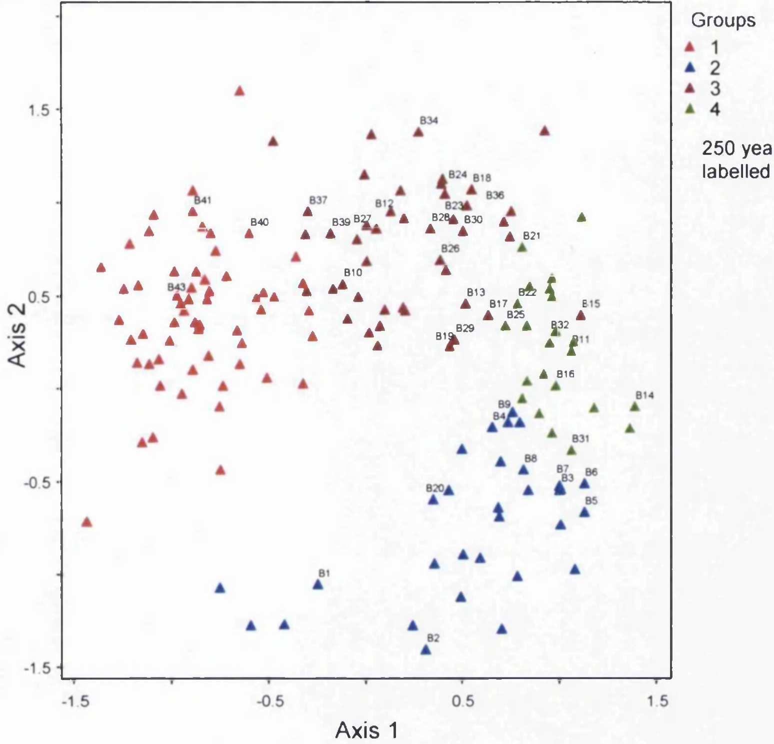
a) Group membership of pioneer sites



b) Group membership of 70-year sites

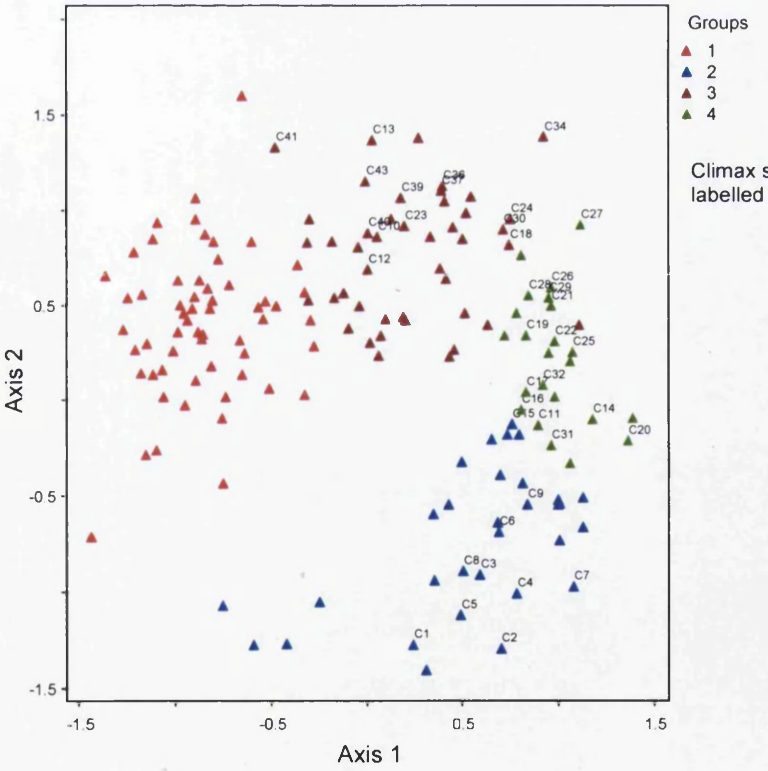


c) Group membership of 250-year sites



250 year sites are labelled B1 to B43

d) Group membership of climax sites

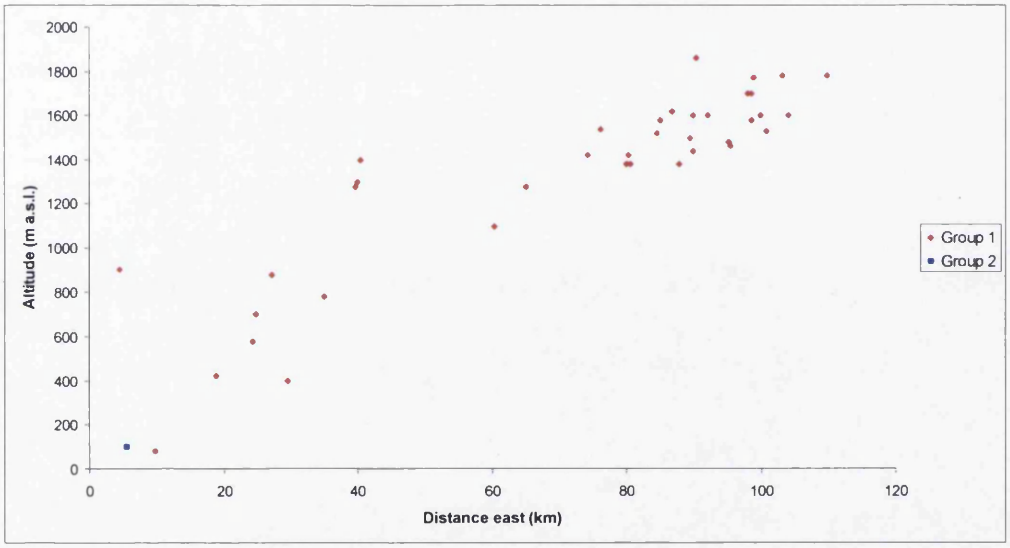


Climax sites are labelled C1 to C43

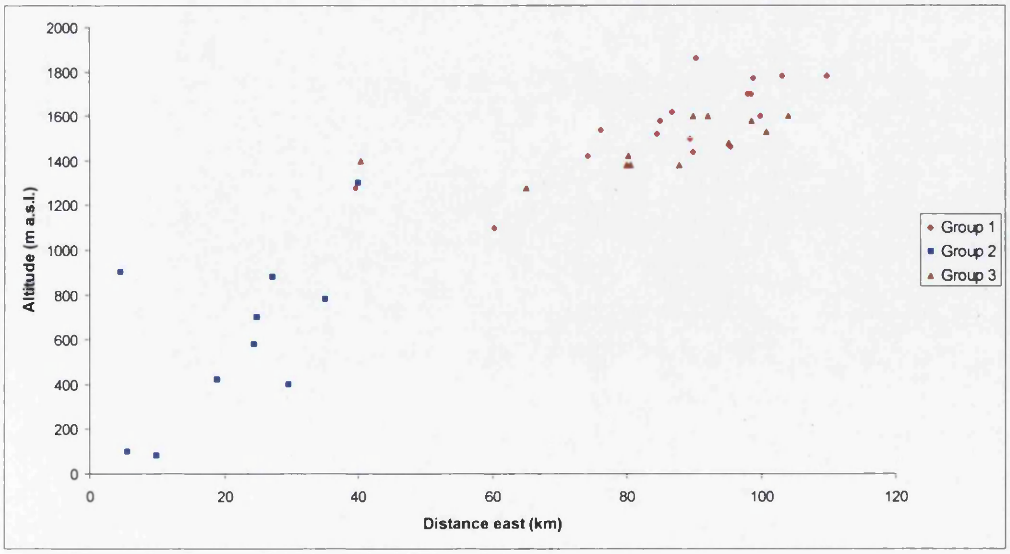
Figure 7-15. NMS ordination of glacier foreland sites showing cluster analysis group membership of a) pioneer sites, b) 70 year sites, c) 250 year sites, d) climax sites. Individual sites within each stage are labelled on the relevant diagram.

The main indicator species for the four groups are *Poa alpina, Oxyria digyna* and *Deschampsia alpina* for group 1, *Vaccinium myrtillus, Betula pubescens* and *Calluna vulgaris* for group 2, *Salix herbacea, Luzula arcuata* and *L spicata* for group 3, and *Juncus trifidus, Betula nana* and *Hieracium alpinum* for group 4. The latter three groups of indicators suggest the existence of altitudinal vegetation zones, in line with the strong correlation between axis 2 and altitude. In order to explore the altitudinal, regional and successional distribution of these groups further, the sites within each stage are plotted according to altitude and distance east.

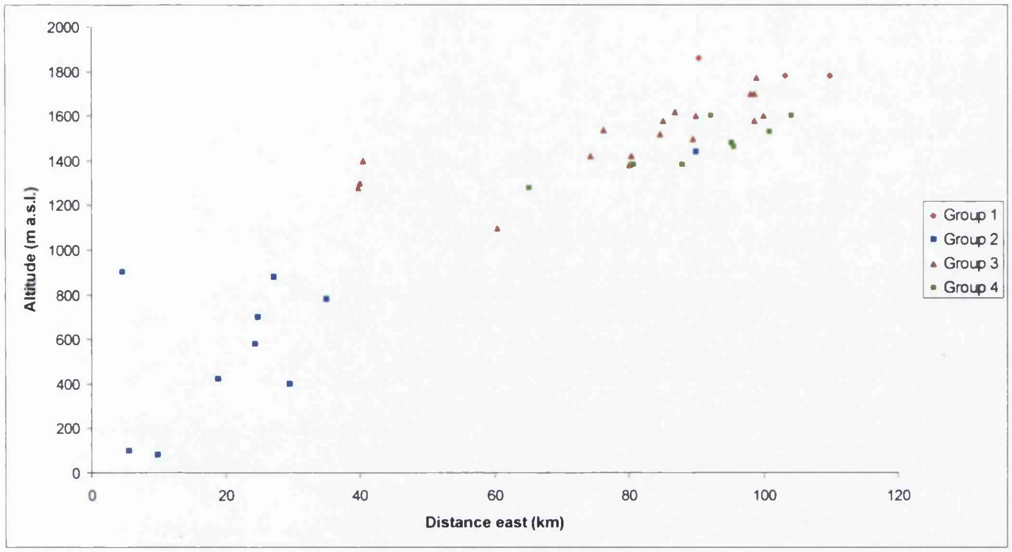
a) Pioneer sites



b) 70-year sites



c) 250-year sites



d) Climax sites

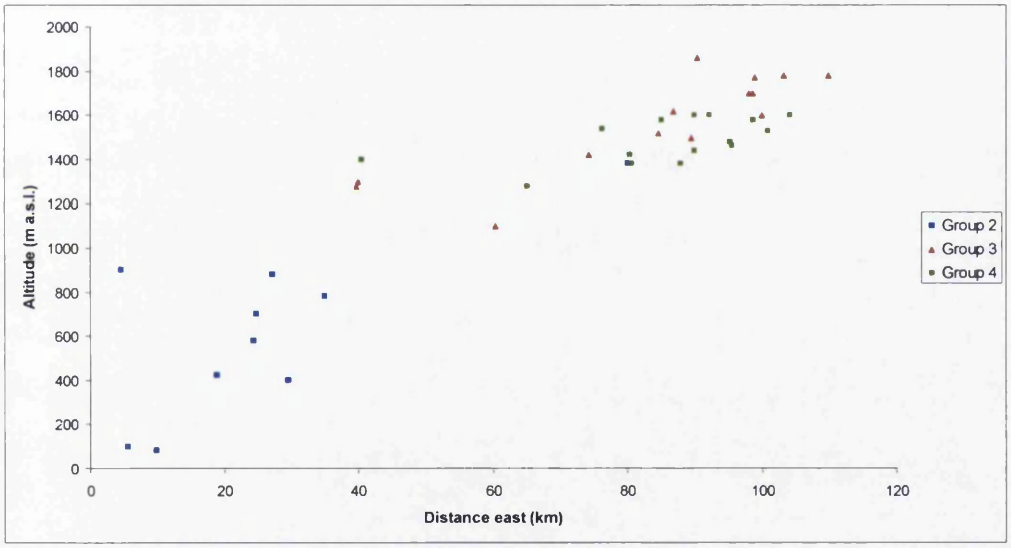


Figure 7-16. Altitude and distance east of sites within each cluster analysis group for a) pioneer, b) 70-year, c) 250-year, d) climax sites.

The four graphs in Figure 7-16 show the group membership of glacier foreland sites plotted according to altitude, distance east for each of the four successional stages, respectively. All the pioneer sites, as already stated, belong to group 1 with the exception of one low altitude site (Bøyabreen) belonging to group 2 (Figure 7-16a). Figures 7-16 b to d show that sites belonging to this group 1 which have reached later stages of succession occur only at high altitudes (seventeen 70-year sites and three 250-year-sites).

Climax sites are absent from this group. This shows that the 70-year stage of a number of high altitude forelands have similar vegetation to pioneer sites, whereas after 250 years of succession, only sites on the three highest altitude forelands still have similar species composition to the pioneer stage. Group 2 is virtually confined to the low altitude sites in the west of the study region, with only two exceptions (one higher altitude site further east at 70 years and one at 250 years) and there is no change in group membership of these low altitude sites from 70 years onwards. This is consistent with a more rapid succession at low altitudes. Twelve sites at the 70-year stage are classified within group 3, increasing to 18 sites at the 250-year stage and then decreasing to 14 at the climax stage, where it includes but is not confined to the highest altitude sites. Group 4 does not include any pioneer or 70-year sites and consists of 8 sites at the 250-year stage and 17 at the climax stage.

Analysis of these figures in conjunction with group indicator species reveals two clear trends with succession: (1) at lower altitudes vegetation develops from domination by *O. digyna* and *P. alpina*, to vegetation characterized by *V. myrtillus* and *B. pubescens*; (2) at higher altitudes development is from similar pioneer species composition to either *S. herbacea* and *L. arcuata* or *J. trifidus* and *B. nana*. *S. herbacea* and *L. arcuata* dominate at the very highest altitudes. Succession would therefore seem to follow an overall pattern of divergence on glacier forelands. However, there is also evidence to suggest that this may not be true for all altitudinal zones.

7.6 The relationship between the relative variability of glacier foreland successional stages and altitude

This section analyses the relationship between altitude and variability within all four successional stages on glacier forelands. Figure 7-17 shows the relationship between altitude, distance east and successional stage of glacier foreland sites and their positions in NMS ordination space. As already indicated, when the NMS ordination is rotated to obtain maximum correlation between axis 1 and successional stage, axis 2 is highly correlated with altitude.

The position of pioneer sites on this diagram would suggest that there is perhaps more variability within this stage at lower altitudes. The three post-pioneer stages appear to be more widely distributed along axis 1 suggesting considerable variability between sites in the rate of succession.

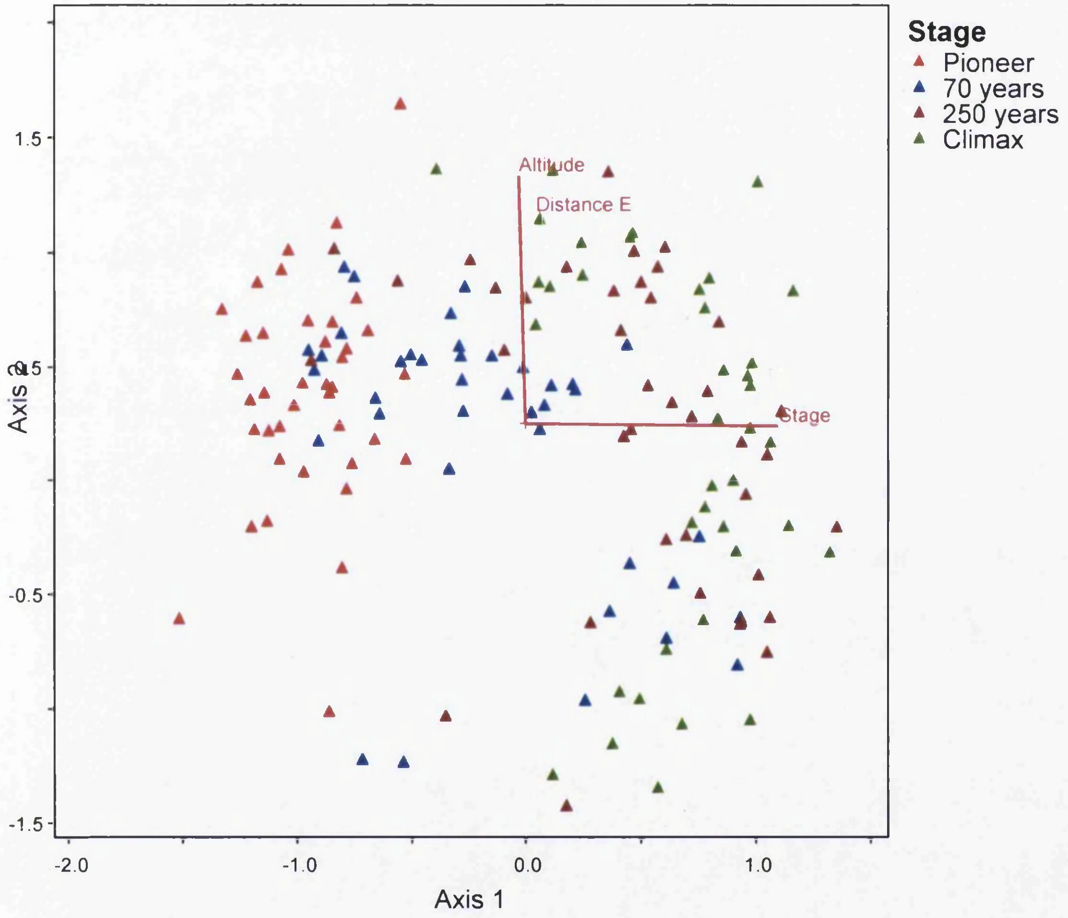


Figure 7-17. NMS ordination of glacier foreland sites showing correlations between axes, successional stage and altitude.

In order to assess the relative variability within each successional stage of glacier foreland vegetation at different altitudes, the sites are divided into four altitudinal zones. (In contrast to the roadside sites, the glacier foreland data set does not form a continuous range of altitudes and possibilities for division into zones are therefore more restricted.) The zones used consist of approximately equal numbers of forelands (9 to 11 sites within each zone). The overall change in mean Sørensen distance between pioneer and climax zones is first discussed for all four altitudinal zones, and then each zone is considered individually in more detail by including the two intermediate successional stages.

Figure 7-18 shows that for the three lower altitudinal zones the climax vegetation is more variable than the pioneer vegetation, but mean Sørensen distances for the 1000 – 1480 m zone do not show a significant difference in within-stage variability between pioneer and climax stages. In the highest altitudinal zone, the mean Sørensen distance for the climax stage is lower than for the pioneer stage but the two values are not significantly different. The general pattern suggests that divergent succession occurs on glacier forelands in all but the highest altitudinal zone, where there is no clear tendency to either converge or diverge. Within the highest altitude zone, a parallel trajectory may therefore be occurring. Within both of the stages, variability at different altitudes is fairly constant within the lower three altitudinal zones, but pioneer stage variability is greater in the highest altitude zone than at 1000 to 1600 m, possibly linked to the effects of disturbance associated with permafrost.

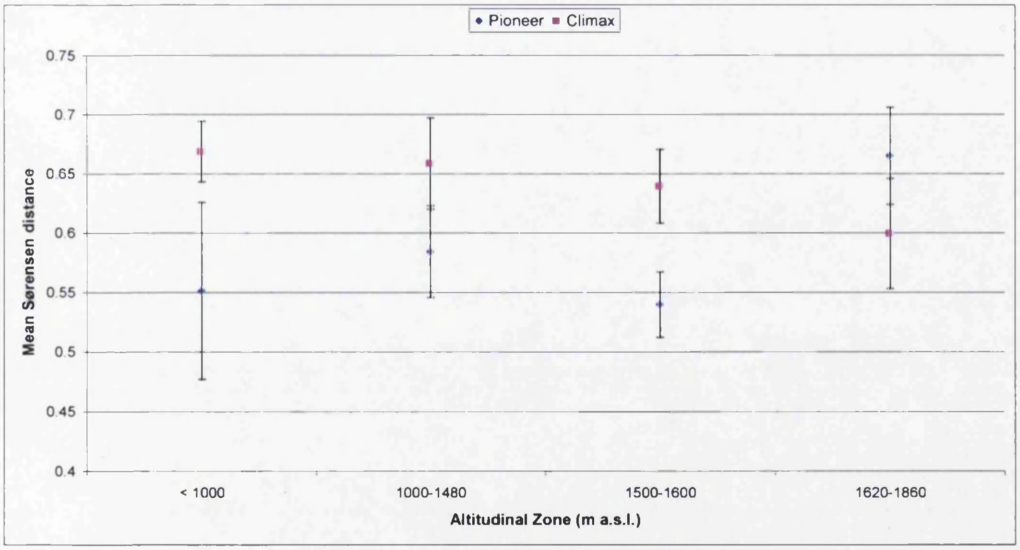
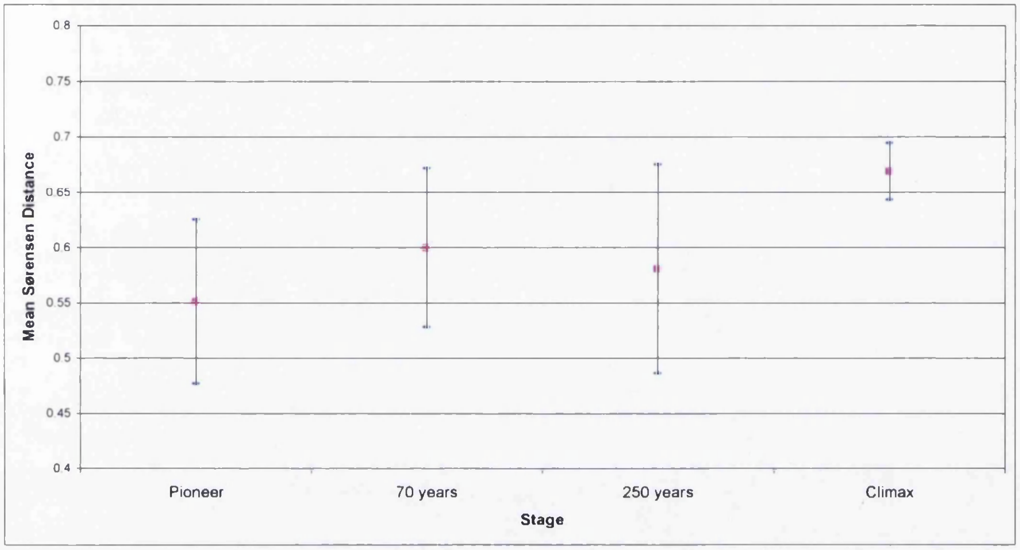


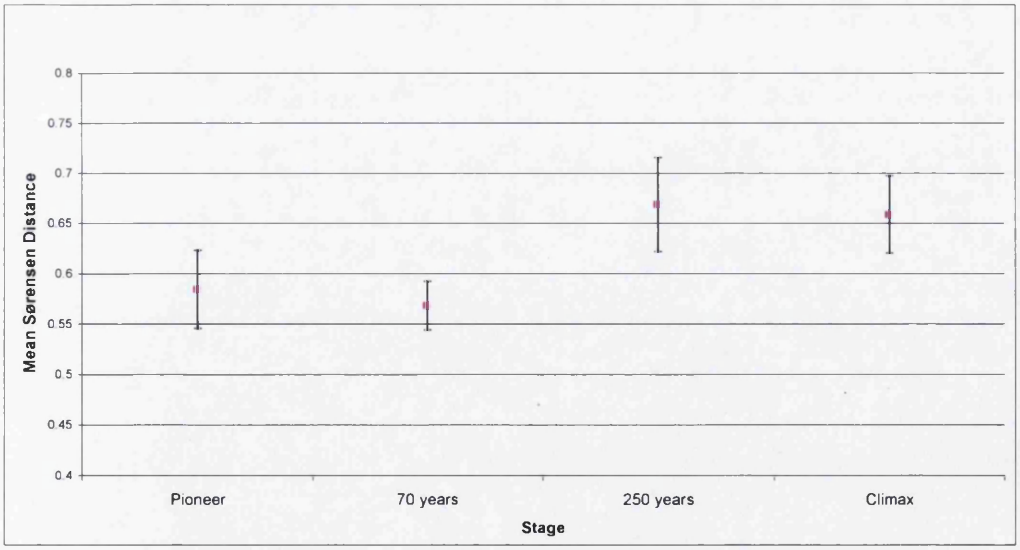
Figure 7-18. Mean Sørensen distances and 95% confidence intervals for pioneer and climax glacier foreland sites within four altitudinal zones.

The graphs in Figure 7-19 show the differences in mean Sørensen distance between all four successional stages within each altitudinal zone. The lowest altitudinal zone shows no change in variability within the first three stages, the only significant difference in mean Sørensen distance being between pioneer and climax stages (Figure 7-19a). This suggests that divergence does not occur until relatively late in the successional process. However, the broad confidence intervals within this altitudinal zone make it difficult to detect differences between stages and high within-stage variability in the early stages may be indicative of some sites diverging rapidly at lower altitudes.

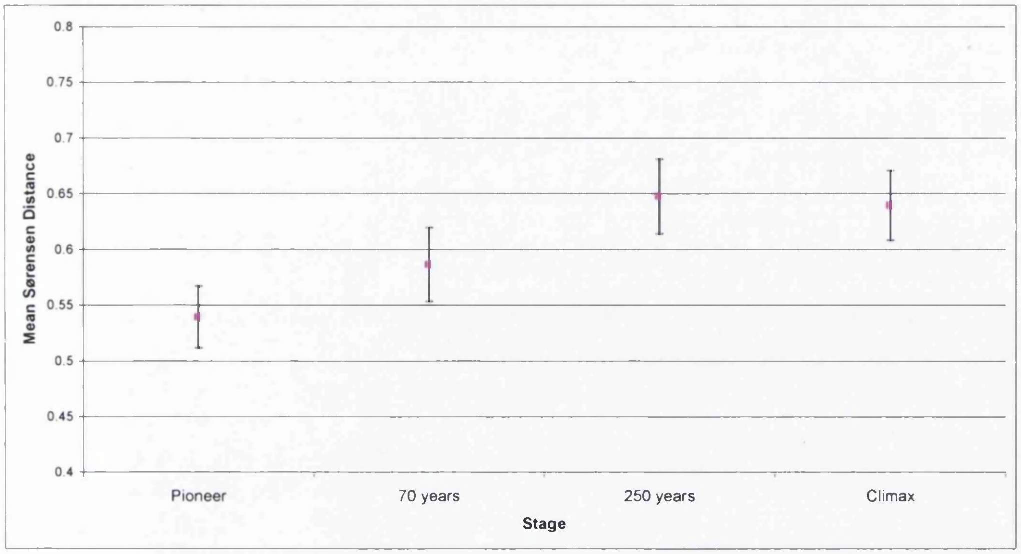
a) Below 1000 m



b) 1000 to 1480 m



c) 1500 – 1600 m



d) 1620 – 1860 m

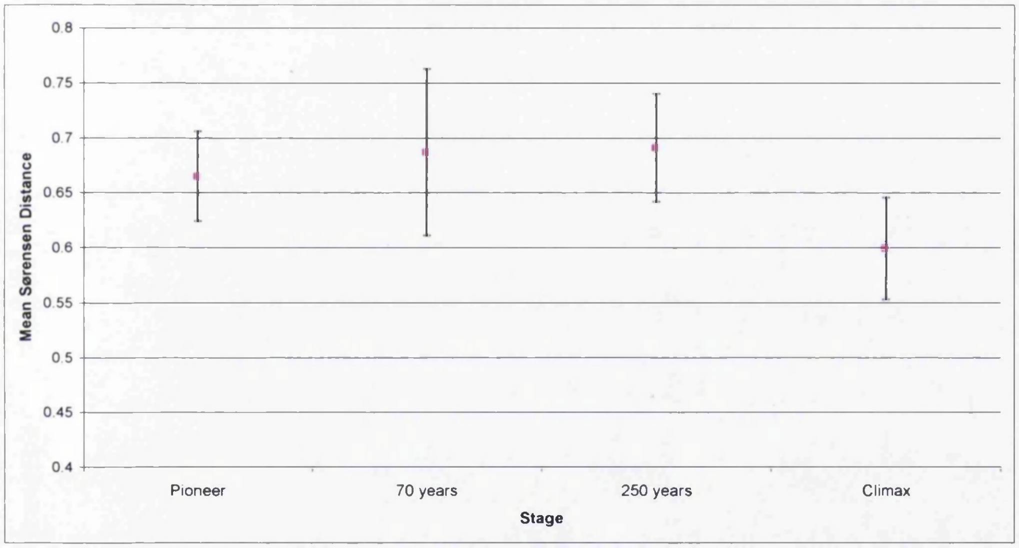
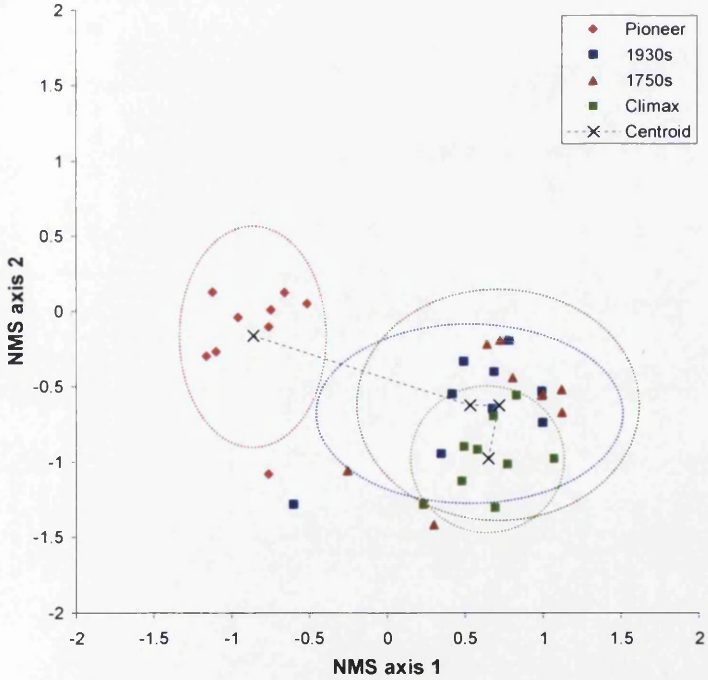


Figure 7-19. Mean Sørensen distances and 95% confidence intervals for four stages of succession on glacier foreland sites within four altitudinal zones.

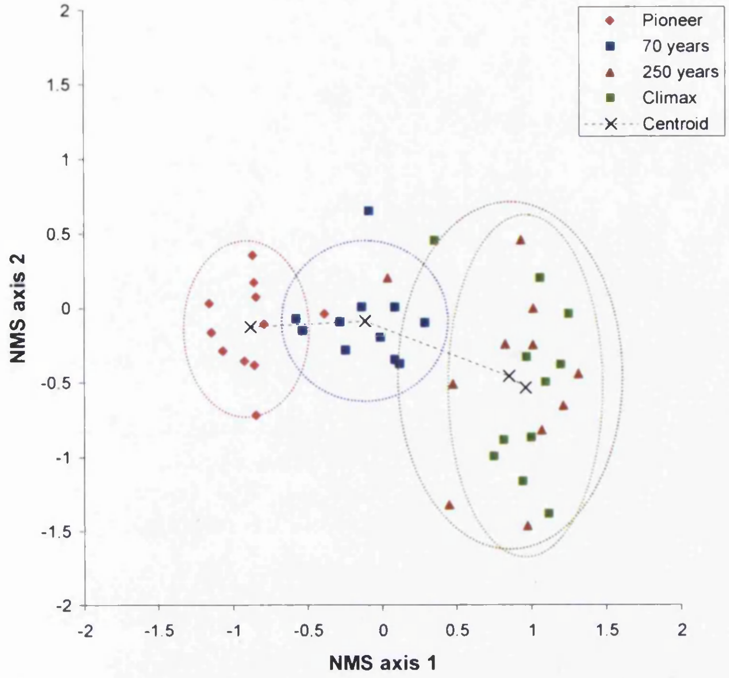
The 1000 – 1480 m zone (Figure 7-19b) shows little change in variability between pioneer and 70 years but change between 70 and 250 years followed by no further change. Divergence therefore appears to be occurring at an earlier stage at these altitudes. In the 1500 – 1600 m zone (Figure 7-19c), change in variability occurs between the pioneer and 250-year stages, suggesting that it takes longer for divergence to occur at this altitude. For the highest altitudinal zone, there is no consistent change in variability between stages (Figure 7-19d).

The evidence indicates that successional divergence occurs on glacier forelands at all altitudes, except within the highest altitudinal zone, where parallel succession occurs. In the three altitudinal zones where divergence occurs, it possibly occurs at a later stage in the lowest zone than in the two intermediate zones. Below 1000 m, divergence can only be detected between the pioneer and climax stages, whereas in the 1000 – 1480 m and 1500 – 1600 m zones it can be detected between the pioneer and 250-year stages. In the 1000 – 1480 m zone, most of the change in variability occurs between 70 and 250 years, whereas in the 1500 – 1600 m zone a more gradual change occurs between the pioneer and 250 year stages. These observations are explored further by plotting the NMS scores for sites according to their altitudinal zones (Figure 7-22).

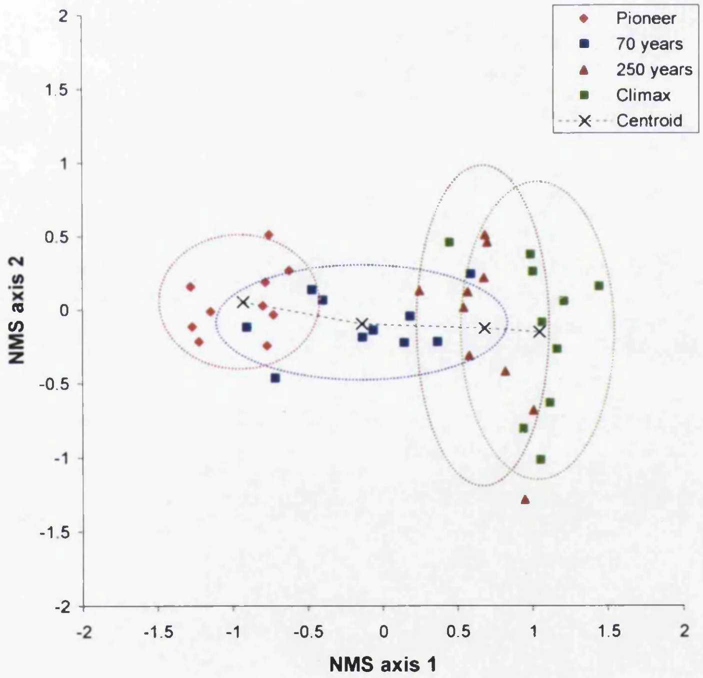
a) Sites below 1000 m



b) Sites from 1000 – 1480 m



c) Sites from 1500 – 1600 m



d) Sites from 1620 – 1860 m

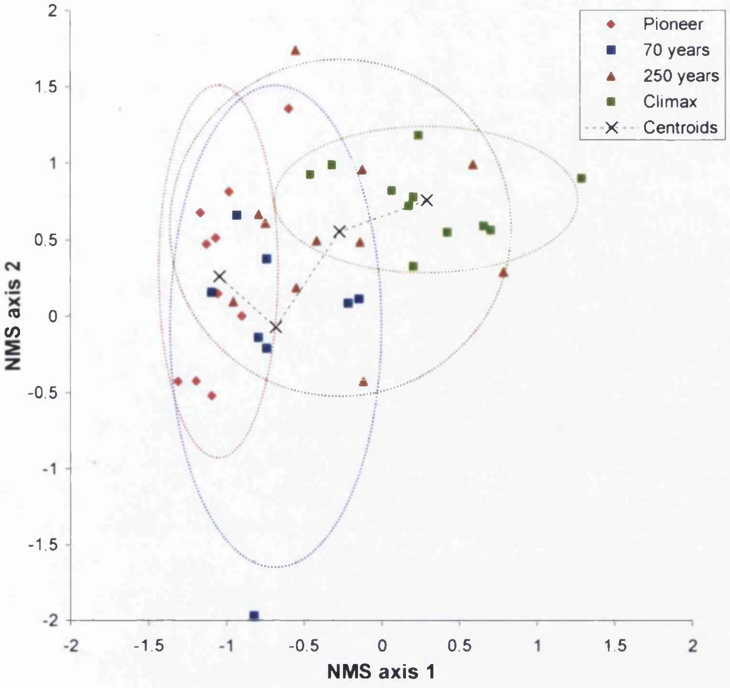


Figure 7-20. Glacier foreland sites plotted according to altitudinal zone. Ellipses indicate centroids ± 2 standard deviations. Dashed lines join centroids of each stage.

Figure 7-20 further elucidates the differences in successional trajectory according to altitudinal zone. Figure 7-20a is particularly interesting as it shows that the greatest successional change (movement along axis 1) below 1000 m occurs early in succession, between the pioneer and 70-year stage and that there is very little subsequent movement along this axis. The values in Table 7-5 confirm that this constitutes the greatest mean movement along axis 1 between successional stages. This could not be determined by analysis of the mean within-stage distances alone. The figure also appears to show early divergence followed by late convergence, which was not detectable from mean within-stage distances due to the large confidence intervals in Figure 7-19a.

Figure 7-20b and Table 7-5 show that, for the 1000 to 1480 m, zone the greatest movement along axis 1 occurs between the 70- and 250-year stages and that it is also between these two stages that divergence occurs. This is consistent with Figure 7-19b. In the 1500 to 1600 m zone, mean movement along axis 1 is again greatest between the 70- and 250-year stages but movement between the 250-year and climax stages is also greater than in the two lower zones. Divergence appears to occur in mid-succession at these intermediate altitudes. Figure 7-20d supports the interpretation of Figure 7-19d in showing a parallel trajectory, and shows less movement along axis 1 early in succession than later in succession, a pattern which is confirmed by the figures in Table 7-5. .

Table 7-5. Mean change in NMS axis 1 score between successional stages on glacier forelands.

Altitude (m a.s.l.)	**Mean change in NMS axis 1 score**			
	Pioneer to 1930s	**1930s to 1750s**	**1750s to climax**	**Pioneer to climax**
0-980	1.354	0.185	-0.097	1.442
1000-1480	0.694	0.914	0.060	1.668
1500-1600	0.698	0.797	0.322	1.817
1620-1860	0.368	0.429	0.521	1.318

The mean distance between centroids along NMS axis one is highly correlated (r = 0.92, $p < 0.01$) with the mean Sørensen distances between stages (Figure 7-21), confirming that the former is a reliable measure of changes in relative species composition.

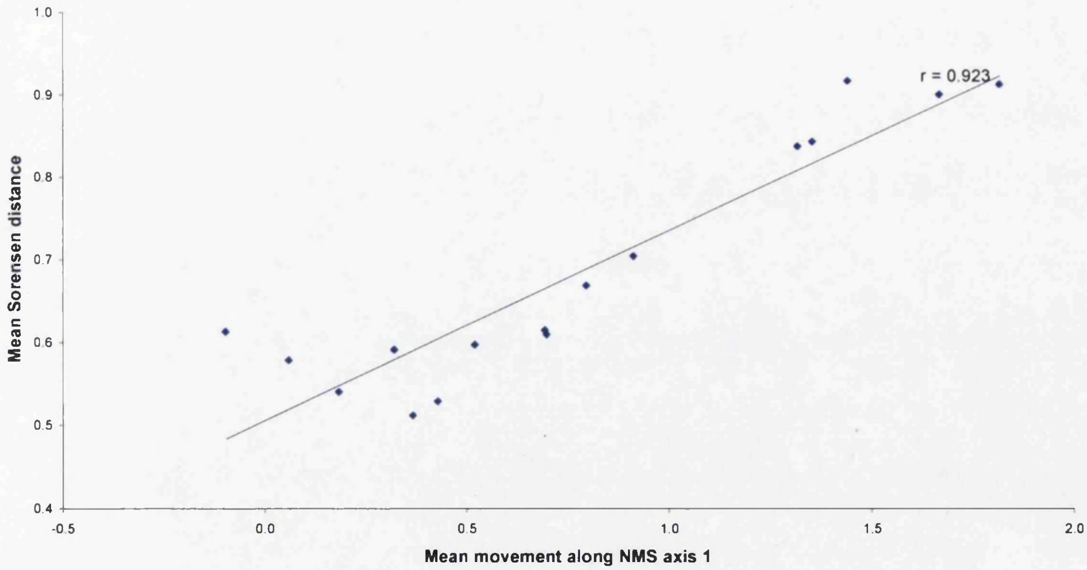


Figure 7-21. Correlation between mean movement of stage centroids along NMS axis 1 and mean between-stage Sørensen distance.

7.7 The relationship between successional stage and EI values of glacier foreland sites

Mean EI values for the four stages of succession recorded on glacier forelands are used in this section to assess whether there is a change in EI values with successional stage and, if so, whether there is a consistent trend over the four stages. Correlations are calculated between site EI values and NMS ordination scores to provide further evidence of overall trends with succession and for comparison with the roadside data set.

Table 7-6 gives the mean EI values for four stages of succession on glacier forelands. The mean values for light, moisture and nitrogen show no significant change between the pioneer and 70-year stages but the mean EIV for pH decreases significantly from 5.01 at the pioneer stage to 4.27 after 70 years of succession. This reflects the rapid leaching of bases from the fresh till. Similarly, between the 70 and 250-year stages and between the 250-year and climax stages there is no significant difference in mean EI values for light, moisture or nitrogen, but the mean EIV for pH shows a significant decrease from 4.27 at 70 years to 3.67 at 250 years and 3.07 at the climax stage. The mean EIV for light shows a significant decrease between the pioneer (7.57) and 250 year (7.25) stages, between pioneer and climax stages (7.02) and between 70 years (7.45) and climax stages. These values reflect the high light levels on glacier forelands, with a significant but small decrease compared that for the roadside sites where the mean value decreases from 7.04 in the pioneer stage to 6.37 in the climax stage. A dense tree canopy rarely develops on the forelands, even below the tree-line. The mean EIV for nitrogen shows a significant decrease between pioneer (3.29) and 250 years (2.58) and between pioneer and climax (2.58 at the climax stage) but not between 70 years or 250 years and the climax stage. Nitrogen levels are generally low but what little there is tends to be used up rapidly by pioneers and later colonizers. Mean moisture EI values show no significant changes between successional stages. The water supply on forelands is generally good, due to the presence of glacial meltwater but the substrate is generally well-drained and the open terrain is under the influence of glacier winds.

The trends in mean EI values for light, nitrogen and pH with successional stage are consistent with those identified for the roadside data set in section 7.4. However, the roadside sites showed a significant increase in the mean EIV for moisture in the climax roadside sites compared to the pioneer sites.

Table 7-6. Mean EI values and 95% confidence intervals for four stages of succession on glacier forelands.

	Mean EIV ± 95% confidence intervals			
Stage	**Light**	**Moisture**	**pH**	**Nitrogen**
Pioneer	7.57 ± 0.12	5.31 ± 0.14	5.01 ± 0.27	3.29 ± 0.17
70 years	7.45 ± 0.16	5.24 ± 0.14	4.27 ± 0.23	2.93 ± 0.23
250 years	7.25 ± 0.18	5.29 ± 0.11	3.67 ± 0.23	2.58 ± 0.19
Climax	7.02 ± 0.17	5.31 ± 0.16	3.07 ± 0.16	2.58 ± 0.13

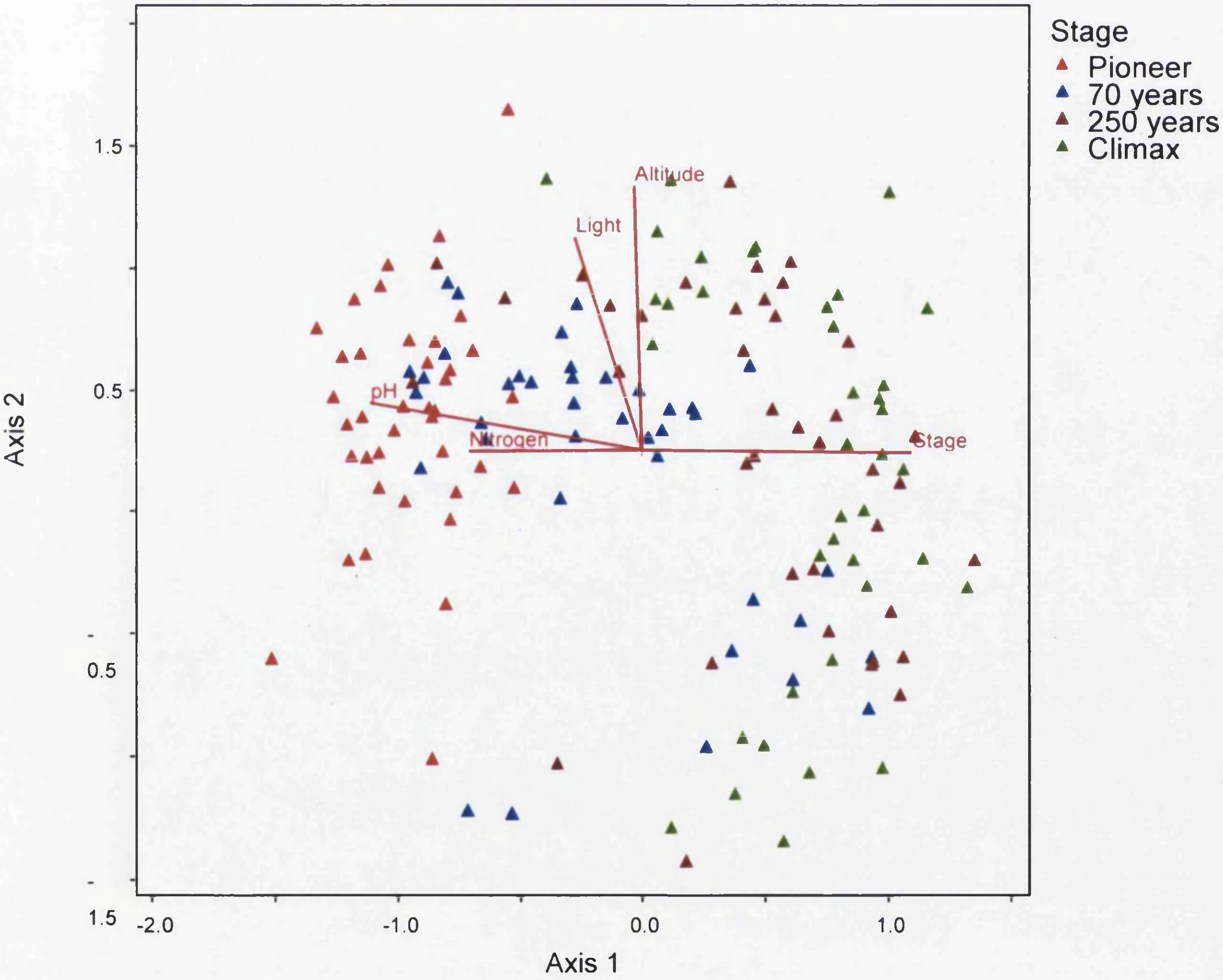


Figure 7-22. NMS ordination of glacier foreland sites rotated for maximum correlation between axis 1 and successional stage showing relationships to EI values.

Figure 7.22 shows these trends in relation to succession by correlating site mean EI values with NMS ordination scores when the ordination diagram is rotated for maximum correlation between axis 1 and successional stage. Axis 1 has a strong negative correlation with pH (r = -0.802) and a moderate negative correlation with nitrogen (r = -0.621) and light (r = -0.431). Axis 2 also has a strong positive correlation with light (r = 0.682) and a weak positive correlation with pH (r = 0.262). These are similar to the relationships between mean EI values and ordination axes for the roadside data set (Figure 7-10). (Direct correlations between EI values and successional stage are r = -0.380 for light, r = -0.712 for pH and r = -0.433 for nitrogen. There is no significant correlation between successional stage and moisture EI value.)

Table 7-7. Pearson's r coefficients for correlations between roadside pioneer and climax NMS axes and successional stage, altitude, distance east and EI values ($p < 0.01$).

	Axis 1	**Axis 2**
Stage	0.785	n.s.
Altitude	n.s.	0.787
Distance east	n.s.	0.721
Light	-0.431	0.682
Moisture	n.s.	-0.307
pH	-0.802	0.262
Nitrogen	-0.621	n.s.

The evidence presented in this section strongly supports and extends the findings described for the roadside data set, by the use of intermediate stages of succession from the glacier forelands. Results confirm that there are consistent successional trends in mean EI values for light, pH and nitrogen. Failure to confirm the increasing mean EIV for moisture with succession found for the roadside data set is explained by the specific habitat conditions occurring on glacier forelands. The relationship between ordination axes, succession, altitude and EI values (other than moisture) has also been shown to be remarkably consistent between the two data sets (see Table 7.4).

7.8 Summary

7.8.1 Is pioneer species composition more or less variable than that of later stages of succession?

Roadsides

1. Mean Sørensen distances indicate greater overall variability within the pioneer communities on roadsides (81%) than within the adjacent climax communities (77%). The climax stage shows a greater range of mean Sørensen distances (range = 0.293) than the pioneer stage (range = 0.196). Despite this, 24% of the climax sites have a lower mean distance from other climax sites than the lowest mean pioneer distance of 0.724. This also indicates lower variability in the climax than the pioneer stage. .

2. NMS ordination of pioneer and climax sites together (Figure 7-3) shows that pioneer sites are less tightly grouped than climax sites, especially along axis 1. Both pioneer and climax sites show an area of discontinuity or more sparsely distributed points approximately parallel to axis 1 which may correspond to an altitudinal change in vegetation type.

3. Cluster analysis at the two-group level results in one group which consists of all the pioneer sites plus 42 climax sites, and a second group consisting of climax sites only. The climax sites which are classified in the "pioneer group" are mainly at extremes of altitude. The three- and four-group levels of cluster analysis show pioneer sites forming two or three groups respectively, whereas the majority of climax sites still form a single group, again indicating the existence of greater compositional variability within the pioneer than the climax stage of succession (Figure 7-4b and c).

4. At the six-group level of cluster analysis, sites are grouped into three predominantly pioneer groups and three climax groups (Figure 7-4e). There appears to be a corresponding altitudinal zonation within the pioneer and climax vegetation. The higher altitude climax sites which were classified with the pioneer sites now form a separate group. MRPP (A and T) statistics

confirm that agreement within groups and separation between groups is greater for the pioneer groups than for the climax groups.

5. Independent analyses of the pioneer and climax stages confirm that the pioneer stage shows both greater dissimilarity between and agreement within groups at the three- and six-group level of cluster analysis. In spite of its greater variability, the pioneer vegetation therefore consists of relatively discrete groups compared with the climax vegetation.

Glacier forelands

1. In contrast to the roadside data set, glacier foreland pioneer sites show lower variability than later stages: mean Sørensen dissimilarity is 65% for pioneers, 71% after 70 years, 75% after 250 years and 76% at the climax stage. However, mean within-stage Sørensen distances for the climax stages of roadsides and glacier forelands are comparable. NMS ordination of the four stages of glacier foreland succession (Figure 7-13) confirms that the pioneer stage is more tightly clustered than any of the later stages.

2. Statistically significant differences in within-stage variability can be detected between pioneer and all later stages and between the 70-year and climax stages, confirming the overall pattern of successional divergence on glacier forelands. The increase in within-stage variability between the pioneer and the 70-year stages and between the 70-year and climax stages is comparable, indicating considerable change at an early stage of succession.

3. Cluster analysis at the four-group level showed that all but one of the pioneer sites belong to a single group, whereas sites from three later stages are split between three or four groups, again confirming that the lowest compositional variability is in the pioneer stage. The three groups composed of later stage sites appear to show altitudinal zonation and indicator species analysis confirms that two successional trends can be identified.
    a) *Oxyria digyna* and *Poa alpina* pioneer vegetation develops into *Betula pubescens* and *Vaccinium myrtillus* woodland on forelands below 1000 m.

b) *O. digyna* and *P. alpina* pioneer vegetation develops into either *Juncus trifidus-Betula nana* or *Salix herbacea-Luzula arcuata* vegetation on forelands above 1000 m.

7.8.2 Is there an altitudinal pattern in the relative variability of vegetation at pioneer and later stages of succession?

Roadsides

Within-stage variability of roadside sites analyzed according to altitudinal zone (Figure 7-8) indicates the following.

- Greater variability within the climax than the pioneer stage at lower altitudes (20 – 400 m) signifies successional divergence.

- Greater variability within the pioneer than the climax stage at intermediate altitudes (420 – 1400 m) indicates successional convergence. This can be further sub-divided into zones of strong, moderate and weak convergence, the strongest divergence occurring between 420 and 800 m and the weakest divergence occurring between 1220 and 1400 m.

- No difference in the amount of variability within the two stages is characteristic at the highest altitudes (1420 – 1860 m), indicating a parallel successional trajectory or little successional change. The mean change in NMS axis 1 score between stages is lowest within this zone, which is consistent with the latter explanation.

Glacier forelands

Analysis of within-stage variability of the glacier forelands according to altitudinal zone (Figure 7-19) indicates the following.

- Below 1600 m, there is significantly greater variability in the climax than at the pioneer stage, indicating divergence. However, within this zone, the difference in variability between pioneer and climax stages in the 1000 – 1480 m zone is not statistically significant. Below 1000 m, the earliest evidence of divergence and the greatest variation in species composition occurs between the pioneer and 70-year stages. The strongest divergence also occurs within this altitudinal zone;

- A significant increase in within-stage variability occurs between the 70- and 250-year stages in the 1000 – 1480 m zone and between the pioneer and 250-year stages in the 1500 – 1600 m zone. This implies that a longer time-span is required for divergence to occur as altitude increases;

- No significant difference in variability between stages in the 1620 – 1860 m zone, indicating a parallel trajectory or little successional change. The degree of successional change between the pioneer and climax stages at this altitude is comparable with that which occurs between the pioneer and 1930s stages below 1000 m, indicating slow successional development.

7.8.3 Are there consistent changes in mean EI values which may help to explain successional processes?

Roadsides

1. The mean EI values for light, pH and nitrogen are significantly lower for climax than for pioneer sites, while the mean EI value for moisture is significantly higher for climax than for pioneer sites (Table 7-3). This is consistent with decreasing light levels as vegetation cover increases with succession, decreasing nitrogen as nutrients are taken up by the established vegetation, and the acidifying effects of many climax species, especially the trees and shrubs. Increasing soil depth and increased cover leads to greater retention of soil moisture.

2. The environmental patterns identified from correlations between mean EI values and NMS ordination scores for the two-stage succession on

roadsides (Figure 7-10) are largely consistent with the patterns identified when the pioneer stage was ordinated independently (Figure 6-11). This consistency therefore supports the use of EI values within the context of pioneer vegetation.

Glacier forelands

1. The mean EI values for light, pH and nitrogen show a significant decrease between the pioneer and climax stages, whereas the mean value for moisture shows no significant change (Table 7-6). EI values for light are consistent with the generally high light levels on forelands compared with roadsides and the slight decrease with succession as a dense tree canopy rarely develops. The rapid leaching of bases from the fresh till possibly combined with the early utilization of nutrients by colonizing vegetation seems to explain the decrease in values for pH and nitrogen. The water supply on forelands is generally good, due to the presence of glacial meltwater but moisture retention tends to be poor and may vary little due to generally well-drained substrates and drying winds.

2. The correlations between mean site EI values and NMS ordination scores (Table 7-7) are similar to those obtained for the roadside data set (Table 7-4). This consistency supports the use of mean site EI values to assess aspects of successional change. Successional trends in both habitats are characterized by decreasing light, pH and nitrogen levels and, in the case of the roadsides, by increasing moisture levels.

3. The results are consistent with the decline in pioneers occurring in conjunction with a decrease in the availability of minerals due to leaching and acidification and an increase in vegetation cover, suggesting the onset of biotic interactions.

8 DISCUSSION

8.1 Introduction

The main objectives of this thesis are: (1) to describe the pioneer vegetation of roadside verges, glacier forelands and additional pioneer habitats within the Jotunheim and Jostedalsbreen regions of south-central Norway; (2) to assess the extent of variability of initial plant colonizers within these habitats; (3) to relate these findings to altitudinal gradients and regional influences; (4) to assess environmental influences on pioneer vegetation using Ellenberg's indicator values; and (5) to investigate the influence of altitude on successional trajectories. Variability of pioneer vegetation has been taken to include the extent to which it forms predictable plant communities and the extent to which pioneer taxa are habitat-specific. The term community is used here, as defined in Chapter 1 (section 1.2).

The first and second objectives are the focus of sections 8.2 to 8.6, in which the key characteristics of the pioneer vegetation, the existence or not of a number of relatively discrete communities, and the nature of these communities in terms of their key indicator species are discussed. Objectives three and four are addressed in sections 8.3 to 8.8, where the focus becomes geographical patterns and environmental influences. In section 8.9, discussion of the relative variability of the pioneer and later stages of succession on roadsides and glacier forelands, particularly in relation to the altitudinal patterns and Ellenberg indicator values, addresses the fifth objective. Finally, in sections 8.10 and 8.11, further theoretical and methodological implications are discussed and critically assessed.

8.2 Species level characteristics of pioneer vegetation

This section discusses characteristics of the most frequent pioneer colonizers and the extent of variability in pioneer vegetation within each of the three data sets. This leads to a consideration of the extent to which pioneer colonization follows a random or predictable pattern.

8.2.1 Growth forms and adaptations

All three data sets are characterized primarily by grasses and forbs. The most frequently recorded species within each data set (present on ≥ 20% sites) are herbaceous perennials and the majority of these are adapted for wind dispersal, (with small, light seeds or the presence of a pappus) and are also able to reproduce vegetatively. Many of the most frequent pioneer species on glacier forelands and in additional pioneer habitats are also adapted for water dispersal, particularly species such as *Poa alpina* and *Deschampsia alpina,* which can produce viviparous seeds. However, two of the most common species on roadsides (*Agrostis capillaris* and *Rumex acetosella*) do not have specific dispersal adaptations but may be spread by grazing animals (Pakeman et al. 1998).

The fact that the pioneer vegetation in primary succession is dominated by perennial grasses and forbs is consistent with the findings of Chapin (1993) and Matthews (1992). Perennial plants are known to predominate in alpine tundra, where the low summer temperatures are not sufficient for annuals to reach maturity and set seed in a single season (Bliss 1971). However, within the context of the study area, this thesis has demonstrated that perennials dominate the pioneer vegetation across a wide range of altitudes. Dispersal mechanisms have been addressed in a number of studies, and wind-dispersal has been cited as a major mode of pioneer immigration onto glacier forelands (Ryvarden 1971, Stocklin and Baumler 1996). Glacial meltwater streams and rivers as important dispersal routes for species with or without adaptive structures have also been considered (Stocklin and Baumler 1996). The high incidence of capacity to reproduce vegetatively in pioneer species is also consistent with the findings of Matthews (1992) and (Whittaker 1993) on glacier forelands and Fuller (1999) on roadsides. However, although many pioneer species are capable of vegetative propagation, this may dominate only on relatively undisturbed sites (Whittaker 1993). Vegetation on pumice at Mount St Helens was also found to be initially dominated by species with good dispersal (del Moral and Jones 2002). The possibility of dispersal by human transport or grazing animals must not be discounted, particularly on the roadside sites.

However, the prevalence of wind and water-dispersed seeds emphasizes the strong influence of environmental factors on seed distribution in the pioneer stage (Jumpponen et al. 1999).

Whether seed dispersal is a limiting factor in pioneer colonization appears to be an unresolved question. Ryvarden (1975) concluded that, as the pioneer zone of glacier forelands are well supplied with seeds, differential arrival was not a major factor in determining species establishment. However, other researchers such as Whittaker (1993) found that propagule supply is limiting on the youngest terrain of glacier forelands due to the fact that propagules do not disperse long distances from parent plants. A high production of small wind-dispersed seeds is therefore vital for early pioneers. Del Moral *et al.* (2005) found that rates of succession were strongly influenced by distance to sources of propagules but that the effects of adjacent mature vegetation as a seed source were limited to a distance of approximately 20 m. The fact that pioneer communities in this thesis are found to be primarily influenced by altitude rather than habitat-type implies that the degree of isolation of a site is not a major factor and therefore dispersal distance is not limiting. However, site conditions may be a limiting factor as certain pioneer species are absent from roadsides but present on glacier forelands and fluvial sites within the same altitudinal zone. Furthermore, two pioneer sub-communities are limited to roadside sites.

Substrate type and texture and moisture supply on glacier forelands are favourable for seed trapping and germination, although glacier winds, moisture retention and substrate instability may inhibit the establishment of many species. The trapping of seeds in safe-sites such as depressions and the shelter of large rocks has been well-documented in a variety of pioneer habitats (e.g. Jumponnen *et al.* (1999), Stocklin and Baumler (1996) and Walker *et al.* (2006)). Roadside sites have a relatively uniform substrate size and texture compared to glacier forelands, but the loose gravel on frequently disturbed areas provides suitable sites for trapping seeds and some protection from frost action at high altitudes due to relatively good drainage. The other habitats studied provide a range of suitable safe-sites, the main differences between them being substrate texture, moisture availability and disturbance frequency.

Colonization by pioneer species with either nitrogen-fixing symbioses or mycorrhizae is not typical of this study, *Trifolium repens* being the most common roadside pioneer with this capacity. A number of other Fabaceae with nitrogen-fixing associations, including *T. pratense*, and *Lotus comiculatus,* were recorded at low frequencies on roadsides and the latter species also occurs on one glacier foreland site and on nine additional pioneer habitat sites. This is consistent with Grubb (1986) who considers plants with nitrogen-fixing symbionts to be subject to strong dispersal limitations on pioneer sites, due to the relatively large size of their seeds. This would explain why they are virtually absent from glacier forelands, the most isolated group of sites, but are more common on roadsides and in additional pioneer habitats, such as river outwash plains and river levées, where dispersal distances are potentially lower. Raffle et al. (2006) found that most of the early dominants (i.e. plants colonizing immediately after the initial pioneers) on Rotmoosferner glacier foreland, Austria, were species capable of nitrogen fixation, but they do not become widespread until 40 years post-deglaciation.

8.2.2 Variability of pioneer vegetation at the species level

8.2.2.1 Roadside verges

Although a large number of species (152) were recorded on roadside verges (Section 4.2) indicating that many species are capable of colonizing disturbed roadsides, the majority of species were shown to have limited distributions. Only four species were recorded on more than 50% of the roadside sites and 105 species occurred on less than 5%, suggesting a high degree of variability within the roadside pioneer vegetation as a whole. This is confirmed by a mean Sørensen dissimilarity of 81% which is slightly higher than the mean dissimilarity of 77% for the adjacent climax vegetation. The mean Sørensen dissimilarity is comparable with values of 80 - 89% found for roadside verges in West Virginia, USA, (Rentch et al. 2005), the only study identified in the literature which analyzes roadside vegetation in this way.

Even the most widespread and abundant species (*Festuca ovina*) was recorded on only 72% of sites, and the low number of species attaining high frequencies strongly suggests that pioneer species on roadsides do not form a single community. This is not surprising, considering the wide altitudinal range of the sites sampled (40 to 1860 m). Few species have the physiological adaptations necessary for survival at such a wide range of altitudes which corresponds, for example, with a difference in mean annual temperature of over 12 degrees centigrade. The most dissimilar sites, identified as extremes of the normal range rather than outliers, are six high altitude sites with high relative abundances of a small number of species and two lower altitude sites with relatively high abundances of shrubs and tree seedlings. Most surprising, perhaps, is the fact that the level of variability in the pioneer roadside vegetation is so similar to that of the climax vegetation. The initial conclusion, therefore, based on the roadside data set is that the pioneer vegetation is not a random assortment of species but is not sufficiently uniform to be considered a single community.

8.2.2.2 Glacier forelands

Fewer species were recorded in the pioneer zones of the glacier forelands sampled (71), with seven species recorded on at least 50% of sites and 33 on less than 5% of sites (Section 5.2). This suggests that glacier foreland pioneer vegetation is less variable in terms of species composition than roadside pioneer vegetation and this is confirmed by the lower mean Sørensen dissimilarity of 65%. The climax vegetation outside the forelands has a mean Sørensen dissimilarity of 76% which is very similar to that for roadside climax vegetation (77%) and supports the hypothesis that glacier foreland pioneer vegetation has a relatively low variability. Importantly, this also shows that the different methodologies (particularly quadrat size) used for data collection on roadsides and glacier forelands has not had an appreciable effect on mean Sørensen distance within the climax vegetation and justifies further comparison of the different data sets. The percentage dissimilarity is comparable with the value of 70% for sites deglaciated for up to 23 years on Coleman Glacier foreland, Washington (Jones and del Moral 2005b).

Five of the most widespread pioneer species on glacier forelands occur on a higher percentage of sites than the most frequently recorded roadside pioneer species, four species attaining a percentage frequency of over 80%. This can be viewed as evidence to support the existence of a single community of pioneer species on glacier forelands, the most frequently recorded species (*Poa alpina*) being absent from only one foreland. Although this is a much smaller data set than that of roadside pioneer sites and perhaps represents a more uniform habitat, it still incorporates a wide altitudinal range (80 – 1860 m). A highly varied species composition would therefore not be surprising. As for the roadside data set, no glacier foreland pioneer sites are considered to be outliers.

The most frequent pioneer species in the glacier foreland data set are consistent with those identified by Matthews (1978a) on Storbreen glacier foreland. Matthews found a core group of pioneer species consisting of *Saxifraga stellaris, Deschampsia alpina* and *Cerastium* spp, with *S. cespitosa* and *Arabis alpina* also being confined to the youngest terrain. *Oxyria digyna, Cardamine bellidifolia, Luzula arcuata, L. spicata* and *Ranunculus glacialis* were found in conjunction with the core pioneers and *Poa alpina* and *Trisetum spicatum* were commonly found in the pioneer zone. Eight of these species were recorded on at least 45% of the 41 glacier forelands in this study, with *S. stellaris*, *L. spicata* and *L. arcuata* recorded on 38%, 26% and 17% respectively. The one exception is *C. bellidifolia*, which was only recorded on one foreland (Tjukningsbreen). Only two frequent pioneer species (*Festuca ovina* and *Salix glauca*) were not included in Matthews' pioneer group. (The *Cerastium* genus is identified to the species level in this thesis and *C. alpina* is found to be the most frequent species of this genera on glacier forelands at 76%, *C. cerastoides* being recorded on only one foreland.) The pioneer species identified by Matthews at Storbreen are therefore confirmed as being highly representative of glacier foreland pioneer sites within the study area.

Seven of the ten most frequently recorded pioneer species in this study were also found by Stork (1963) in northern Sweden on ground deglaciated for less than 20 to 30 years (*Saxifraga cespitosa, Festuca ovina, Oxyria digyna, Arabis* *alpina, Cerastium alpinum, Poa alpina* and *Trisetum spicatum*). These findings were also substantiated by Elven (1978a) who identified a similar group of pioneer species in front of Hardangerjokulen, southern Norway. Slightly further afield, two *Saxifraga* species and *Poa alpina* were among the five most constant pioneer species identified on Rotmoosferner glacier foreland in the Austrian Alps (Raffl et al. 2006).

8.2.2.3 Additional pioneer habitats

Ninety-four species were recorded on the 34 sites sampled in additional types of pioneer habitat (Section 5.6.1), which range from low altitude river levées to high altitude patterned ground. Eleven of these were recorded on at least 50% of sites and 19 occurred on less than 5% of sites. The mean Sørensen distance for this data set is 77%, which is comparable with the value for the climax vegetation adjacent to glacier forelands and roadsides, and no sites were considered to be outliers. The fact that this is slightly lower than the overall level of dissimilarity within the roadside data set (81%) suggests that, even though a wide range of habitats were sampled, the composition of pioneer vegetation is relatively consistent. The two sites with the greatest mean Sørensen distances from other sites within this data set are two of the high-altitude patterned ground sites, which have high relative abundances of *Luzula arcuata*.

8.2.3 General species-level conclusions

Although the three data sets have important differences in species composition, they also have many species in common. The ten most frequent species on glacier forelands were also recorded on roadside sites, three of them being included in the ten most frequent roadside species (*Poa alpina*, *Festuca ovina* and *Salix glauca*). Only one of the ten most frequent roadside pioneers (*Deschampsia flexuosa*) was not recorded on glacier foreland sites. The majority of the eleven most frequently recorded species in the additional pioneer habitats data set also attain high percentage frequencies on roadsides and a smaller number are also frequent on glacier foreland pioneer sites. The relative proportions of frequently occurring grasses, forbs and shrubs are similar for all data sets and the preponderance of wind-dispersed perennials, many of which can also reproduce by vegetative means are also consistent factors.

The evidence therefore points to a degree of predictability in the pioneer vegetation, at least in terms of the most frequently recorded species and their general characteristics. This is especially true for the glacier foreland pioneer sites and less so for the other two data sets. The fact that the varied habitats sampled in the additional pioneer habitats data set have frequent species in common with the roadside data set provides further support for the pioneer vegetation being more predictable than haphazard. Consideration of all three data sets therefore supports the hypothesis that the pioneer vegetation is not a random collection of species but it is also not a single community.

8.3 Roadside pioneer communities and sub-communities

8.3.1 Roadside pioneer communities

Ordination of the roadside pioneer sites (Figure 4-3) suggests the existence of three major clusters of sites (with complementary areas of lower site density) within an otherwise fairly even distribution of sites in ordination space. The overall pattern therefore supports the existence of communities within a continuum of variation in species composition. Cluster analysis and MRPP of the data showed that the greatest separation between and agreement within groups is found at the three-group level and plotting these groups onto the ordination diagram (summarized in Figure 8-1) confirmed that objective quantitative analysis produces similar conclusions to subjective visual examination.

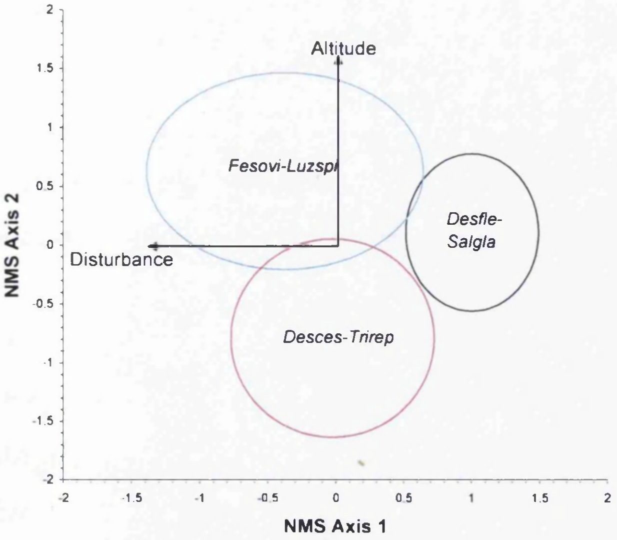


Figure 8-1 NMS ordination of roadside pioneer sites with the three communities represented by ellipses (indicating ±2 standard deviations from each group centroid).

8.3.1.1 Indicator species analysis

Indicator species analysis of the three communities revealed that species with the highest indicator values were those most frequently recorded within the pioneer roadside data set as a whole. The case for classification of the roadside sites into three groups is therefore strengthened by the fact that it is not dependent on the distribution of infrequent species. Furthermore, the majority of indicator species are faithful to a particular community, having low values in or being absent from other communities, adding further support to their validity as distinct communities (Table 4-6).

More detailed consideration of indicator species revealed that the distribution of the *Deschampsia cespitosa-Trifolium repens* (*Desces-Trirep*) community (3A) and the *Festuca ovina-Luzula spicata* (*Fesovi-Luzspi*) community (3B) can be broadly explained in terms of their altitudinal ranges. The higher altitude *F. ovina-L. spicata* community is also characterized by species such as *Deschampsia alpina* and *Cerastium alpinum,* which tend to be found on disturbed ground above the tree-line. The majority of indicator species for this community are also present on glacier foreland pioneer sites, whereas the main indicators for the *D. cespitosa-T. repens* community are either completely absent from or present on a very small percentage of glacier foreland pioneer sites. Indicator species within the *D. cespitosa-T. repens* community, however, are clearly representative of more than one habitat-type, suggesting that further sub-division is justified on ecological grounds. For example, species such as *Plantago major* and *Poa pratensis,* suggest agricultural influence, while *Fragaria vesca* and *Pinus sylvestris* seedlings are characteristic of woodland edges.

The *Deschampsia flexuosa-Salix glauca* (*Desfle-Salgla*) community (3C) is characterized by a number of shrubs which are usually associated with later stages of succession and with acid, relatively infertile soils. An example is *Empetrum hermaphroditum,* which was found by Whittaker (1993) to be present on Storbreen foreland only after 20 years of deglaciation and was thought to be limited by seed dispersal. *E. hermaphroditum* and *S. glauca* were also found by Matthews (1978b) to be relatively late colonizers on Storbreen, increasing at a slower rate than the more typical pioneers. *E. hermaphroditum* is not a frequent roadside pioneer, being recorded on only 12% of sites, but the fact that it is more frequently recorded here than on glacier foreland pioneer sites (5%) would support the hypothesis that it is subject to dispersal limitations on the glacier forelands where the distance between pioneer and climax vegetation is greater. However, *E. hermaphroditum* was not recorded on all pioneer roadside sites, where it is was present in the adjacent climax vegetation so other factors must also be affecting its success as a pioneer species. According to Bliss (1971), it is restricted to sites of winter snow protection, probably due to low drought resistance. The main indicator for this community, *D. flexuosa*, as previously stated, is a widespread species on roadside sites but is completely absent from glacier forelands. It is present on 82% of the additional pioneer habitat sites, where it is only completely absent from the four patterned ground sites. Its frequency is said to be negatively correlated with pH (Scurfield 1954), which may explain its absence from glacier forelands, where substrate pH is comparatively high. Ordination and classification of the pioneer and climax stages of succession on roadsides in a single analysis (Figure 7-3) showed that, although the *D. flexuosa-S. glauca* community may represent a slightly later stage of succession than the other two pioneer roadside communities, it is not sufficiently similar to the climax vegetation to be classified with it.

The existence of these three communities rather than a single pioneer community on roadsides provides an explanation for the low overall frequency of most pioneer species, only four species occurring on more than 50% of the roadside sites. Of great importance is the fact that species are not distributed randomly throughout the roadside sites, but occur in higher abundances and with greater frequency in conjunction with other indicator species. Indicator values are based on the fidelity of a species to a particular community and its abundance within that community relative to its abundance in other communities (Dufrene and Legendre 1997). For the majority of the widespread species, it has been shown that where a species occurs in more than one community, its relative abundance, as well as its relative frequency, varies considerably between communities. For example, although *Festuca ovina* was recorded on 72% of roadside sites, its relative abundance (Figure 4-19) in the *F. ovina- L. spicata* community is 75%, compared with only 8% in the *D. cespitosa-T. repens* community and 16% in the *D. flexuosa-S. glauca* community.

8.3.1.2 The influence of altitude and continentality

Analysis of the three communities in terms of their mean altitude and distance east adds further evidence to support their validity, with significant separation between the three communities in terms of these two factors. Direct gradient analysis also confirms that there is an altitudinal boundary between the *Deschampsia cespitosa-Trifolium repens* and *Festuca ovina-Luzula spicata* communities, which lies between 740 and 1100 m (Figure 6-3). On the roads along which this boundary occurs, it appears to have a decreasing altitude as distance east increases, suggesting that it is not coincidental with the altitudinal treeline. Of particular importance is the fact that sites within all three communities form a predominantly contiguous series along the roads sampled, thus forming geographically clustered groups of sites.

8.3.1.3 Interpretation of EI values

It is important to note that, although the variation in EI values between the three communities is not necessarily wide, there are significant differences in their mean EI values for moisture, light, pH and nitrogen with the exception of the mean moisture values for the *Deschampsia cespitosa-Trifolium repens* and *D. flexuosa-Salix glauca* communities (Table 6-9). The respective EI values can be explained in terms of altitudinal and temporal differences. For example, the higher altitude community (*Festuca ovina-Luzula spicata*) has a higher mean light EI value than the lower altitude community (*D. cespitosa-T. repens*) which in turn has a higher mean light value than the less disturbed community (*D. flexuosa-S. glauca*).

In terms of moisture, the lower altitude and more established communities have higher mean EI values than the upper altitude community. This is thought to be a reflection of water availability to plants, rather than precipitation levels, as, although precipitation tends to increases with altitude, at high altitudes the groundwater is frozen for a large part of the year and therefore unavailable to plants. As seasonal frost or permafrost thaws, this leads to saturated soils near the ground surface in the spring and early summer. Later in the summer, these soils may experience drought. Above the altitudinal limit of permafrost, the seasonal differences in soil drainage and available moisture may be even more pronounced. There is also greater variation in mean moisture EI values at higher than at lower altitudes, perhaps due to variation in snow depth and time of snowmelt, which influence both the supply of meltwater and the degree of protection from winds. The drying effect of strong winds at higher altitudes through their influence on evapotranspiration is an important factor (Bliss 1971). EI values for moisture at high altitude are therefore ambiguous. However, the findings are consistent with Ertsen et al. (1998), who concluded that the EI value for moisture most accurately reflects ground water levels.

Mean EI values for pH and nitrogen are comparatively low in the high altitude community and the less disturbed community. At high altitudes, the cold alpine tundra soils are generally deficient in nutrients, particularly nitrogen, although the permafrost layer may limit leaching (Bliss 1971). It is difficult to distinguish cause and effect in the *D. flexuosa-S. glauca* community, as the shrubs present would tend to have an acidifying effect on the substrate, as well as being more tolerant of acidic soils, which restrict nutrient availability to plants. Furthermore, the effects of human activity may increase nitrogen levels at lower altitudes, whereas needle fall from *Pinus sylvestris* would also have an acidifying affect below the treeline. A further piece of evidence is that the *D. flexuosa-S. glauca* community has *Betula pubescens* seedlings as an indicator species; Grubb (1986) considers tree species to be pioneers of sites with insufficient mineral nutrients for herbs.

8.3.1.4 Interpretation of ordination axes

Within each community, the ordination diagram suggests a continuum of variation in species composition, with variation along one ordination axis reflecting an altitudinal gradient and variation along the second axis reflecting disturbance or successional change (Figure 8-1). The latter is obviously affected by factors such as frequency of disturbance and time since last disturbance. The roads along which the *D. flexuosa-S. glauca* community occurs are used mainly for access to dams for maintenance work rather than providing routes to tourist attractions or summer farms and their verges are therefore likely to be disturbed less frequently than other roads in the data set. This is supported by two further pieces of evidence: 1) the river levées which are included in this community when additional pioneer habitats are included in the analysis, are known to have been constructed in response to the 1979 floods in Jostedalen and can therefore be considered to represent vegetation after approximately 35 years of succession i.e. the late pioneer stage; 2) when pioneer and climax sites are ordinated and classified in one analysis, these sites occur adjacent to the climax sites. The evidence discussed in section 8.3.1.3 indicates that this axis reflects the interaction between the level of disturbance, substrate pH and nutrient availability.

This interpretation is consistent with Whittaker's (1987) two ordination axes which represent a 'terrain-age factor complex' based on measures of soil development and soil disturbance, and an 'exposure-moisture regime-snowmelt factor complex'. The latter refers to the exposure effects of wind, the effects of site drainage on moisture and the duration of snow lie, all of which could correspond to the influence of altitude. Although Whittaker included altitude in the former rather than latter complex, his data was based on sites that were controlled for altitude and therefore had a very limited altitudinal range and where altitude decreases with successional stage on a single foreland.

8.3.2 Roadside pioneer sub-communities

8.3.2.1 Six roadside pioneer sub-communities

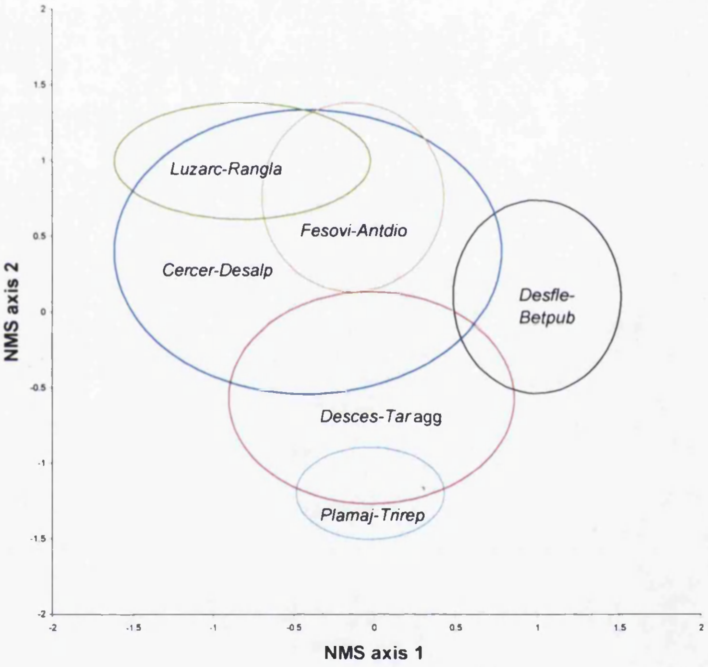


Figure 8-2. NMS ordination of roadside pioneer sites with the six sub-communities represented by ellipses (indicating ±2 standard deviations from each group centroid).

The six-group level of cluster analysis produced less well-separated groups on the ordination diagram (Figure 8-2) and these are considered to represent sub-communities. Examination of these six groups in terms of their indicator species (Table 4-6 and Figures 4-34 to 4-39) shows that they form a *Deschampsia cespitosa-Taraxacum* agg. (*Desces-Tar*agg) sub-community (6A) of species likely to be found in disturbed woodland, a *Plantago major-Trifolium repens* (*Plamaj-Trirep*) sub-community (6D) of species associated with grassland and agriculture, a *Deschampsia flexuosa-Betula pubescens* (*Desfle-Betpub*) sub-community (6C) (synonymous with the *D. flexuosa-Salix glauca* community) of less disturbed/later successional sites, a *Cerastium cerastoides-Deschampsia alpina* (*Cercer-Desalp*) sub-community (6B) of relatively wet sites at higher altitudes; a *Festuca ovina-Antennaria dioica* (*Fesovi-Antdio*) sub-community (6F) of relatively dry sites at higher altitudes and a *Luzula arcuata-Ranunculus glacialis* (*Luzarc-Rangla*) sub-community (6E) with species indicative of more extreme alpine conditions.

Analysis of these six sub-communities in terms of their altitude and distance east by direct gradient analysis (Figure 6-6) shows clear altitudinal zonation and significant differences between mean altitudes for all sub-communities with the exception of *C. cerastoides-D. alpina* and *F. ovina-A. dioica.* However, a significant regional difference was found between these two sub-communities; the *former* is characterized by more moisture-loving species and has a lower mean distance east, which is consistent with the expected influences of continentality.

The mean EI values for these six sub-communities (Table 6-10) reflect the altitudinal gradients already described for the three communities and also provide additional information. The two sub-communities which are not distinguished altitudinally (*C. cerastoides-D. alpina* and *F. ovina-A. dioica*) have the same mean EI values for light, but significantly different mean values for moisture, pH and nitrogen. The values for pH and nitrogen tend to co-vary, as would be expected, especially if the nitrogen value is considered to be a reflection of overall nutrient levels (Hill and Carey 1997, Ertsen et al. 1998). In this case, the drier sub-community (*F. ovina-A. dioica*) has significantly lower mean EI values for pH and nitrogen than the wetter sub-community (*C. cerastoides-D. alpina*). The values for the former are, in fact, closest to the values for the highest altitude sub-community (*L. arcuata-R. glacialis*), where it is argued that drying winds and a shorter growing season limit moisture and the accumulation of organic matter respectively. Variation in mean nitrogen EI values is consistent with Messer's (1988) identification of more rapid rates of soil CEC increase (i.e. ability to retain nutrients) in Jostedalsbreen (to the west of the study region) than in Jotunheimen, which she attributed to the wetter and milder climate of the former.

The lowest mean values for light were those in the less disturbed *D. flexuosa-B. pubescens* sub-community (mean EI value = 6.6 indicating semi-shade to well-lit conditions). This compares with a mean value of 7.9 (indicating light-loving species) for the highest altitude *L. arcuata-R. glacialis* sub-community and 7.0 for the lowest altitude *P. major-T. repens* sub-community. It is possible that this value is a reflection of the higher ground cover levels within the pioneer vegetation in the *D. flexuosa-B. pubescens* sub-community, rather than the influence of adjacent climax species.

Mean moisture EI values have a negative correlation with altitude, with a low mean EI values of 4.4 for the *F. ovina-A. dioica* sub-community (mean altitude 1192 m) and 4.8 for the *L. arcuata-R. glacialis* sub-community (mean altitude 1644 m). For the other four sub-communities, the mean moisture EI value varies between 5.3 and 5.6, indicating little difference in their moisture levels. Mean nitrogen and pH EI values show the greatest variation between sub-communities, the highest mean values for both factors being in the *P. major-T. repens* sub-community, presumably under the influence of local agricultural practices.

These six groups therefore form interpretable sub-communities of the three major roadside communities, perhaps the least convincing being the *C. cerastoides-D. alpina* and *F. ovina- A. dioica* sub-communities, which are particularly poorly separated on the ordination diagram. When the roadside classification is compared with a combined cluster analysis of all three data sets, the greatest change in group membership occurs between these two sub-communities. Furthermore, this change in group membership is accompanied by a transfer of indicator species between the two groups. These two sub-communities therefore display considerable evidence of a continuum of change along a moisture gradient, rather than a discontinuity in species composition.

8.3.2.2 Nine roadside pioneer sub-communities

The nine-group level of clustering produces a mixed picture, with some fairly well-differentiated groups and some which were poorly defined and/or not interpretable (Figure 4-41). The division of the *D. cespitosa-Taraxacum* sub-community into groups 9A and 9G is particularly unsatisfactory and is mainly based on comparatively uncommon species such as *Veronica officinalis* and *Viola biflora*. Furthermore, the mean altitudes and 95% confidence intervals of groups at this level of clustering show much more of a continuum of variation rather than discrete zonation, with the exception of the lowest and highest altitude groups (9D and 9E respectively). Similarly, mean distance east shows a continuum of variation (with the exception of group 9I, which has the lowest mean distance east) and direct gradient analysis confirms that there is a less clear geographical zonation of sites into groups.

However, even at this level of clustering, there is evidence that pioneer colonization is not haphazard. The usefulness of mean EI values is still evident and groups which cannot be distinguished in terms of mean altitude or distance east can be distinguished in terms of mean EI values (Table 6-11) These follow the same pattern in relation to altitude as at the six-group stage but display even more of a continuum of variation. Indicator values have decreased to lower levels than those found at the six sub-community level, suggesting that they are now defined by less consistent species distribution and abundance. This level of classification can therefore be summarized as dissecting a continuum of variation rather than recognizing natural communities.

8.4 The glacier foreland pioneer community and sub-communities

8.4.1 The glacier foreland pioneer community

The lower overall variability of the glacier foreland pioneer sites compared to the roadside sites suggests that this data set possibly consists of a single *Poa alpina-Oxyria digyna* community, which should not be artificially subdivided. The distribution of sites on the ordination diagram (Figure 5-3) indicates that there are no obvious clusters of sites or zones in which sub-division of the data set would be suggested. Variance partitioning (Section 6.4.1) also confirms the low overall variance within this data set. There therefore appears to be a single community of glacier foreland pioneer sites within which a continuum of variation in species composition occurs. The necessity of including rare species in order to reach a stable NMS ordination also points to a relatively weak structure in the data (McCune and Grace 2002). Furthermore, MRPP of the cluster analysis groups showed no sharp improvements in within-group agreement or between-group separation as additional groups were formed.

8.4.2 Glacier foreland pioneer sub-communities

Evidence for the possible existence of sub-communities on glacier forelands was sought, however, and the two-group level of cluster analysis was examined in some detail. This level of classification showed fairly good separation of indicator species (Table 5-7) but their patterns of abundance revealed gradual variations in abundance across the data set, strengthening the argument for a continuum of variation rather than the existence of two natural groups. The groups are therefore considered to be two sub-communities: a lower-altitude, more westerly, *Deschampsia alpina-Oxyria digyna* (*Desalp-Oxydig*) sub-community (2A) and a higher altitude, more easterly, *Saxifraga cespitosa-Trisetum spicatum* (*Saxces-Trispi*) sub-community (2B). The two sub-communities were found to have significantly different mean altitudes and distances east, but direct gradient analysis revealed that the *D. alpina-O. digyna* sub-community occurs at a wide range of altitudes (80 to 1800 m) whereas the *S. cespitosa-T. spicata* sub-community is confined to forelands above 1000 m (Figure 6-21). There is, therefore, no clear geographical separation between the two sub-communities, although the latter has a considerably more restricted distribution.

Calculation of mean EI values, produced a significant difference in pH only, the *S. cespitosa-T. spicata* sub-community having a higher mean pH. The majority of Messer's (1988) recorded pH values for the pioneer zone of 18 glacier forelands ranged from 5.3 to 8.5, while the mean EI pH values for the pioneer stage within this study range from 3.3 to 7.2, a slightly wider but comparable range of values. However, variance partitioning did not show mean site pH EI value to explain a significant proportion of the total variance in this data set.

It is interesting to note that the relative positions of pioneer species in Matthews (1978b) principal components analysis of species recorded at Storbreen show considerable congruence with the division of indicator species between these two sub-communities (Figure 5-7). Two indicator species within the *S. cespitosa-T. spicata* sub-community, *S. cespitosa* and *Arabis alpina*, were identified by Matthews (1978b) as indicating the youngest terrain at Storbreen and were also found by Whittaker (1993) to be characteristic of the youngest ground. This would suggest that a number of forelands at higher altitudes are characterized by species that tend to colonize at a slightly earlier stage of succession and that there is a degree of zonation within the pioneer stage as a whole. Messer (1988) found that pH of the fresh till declines rapidly during the first 20 years following deglaciation and this is consistent with the differences in EI values identified for these two sub-communities. However, the accompanying reduction in nutrients with succession identified by Messer is not reflected in significant differences in mean EI values for nitrogen between the two pioneer sub-communities. Whittaker (1993) found *T. spicatum* on Storbreen foreland to be characteristic of relatively exposed sites affected by summer drought but again this is not reflected in the mean EI values for moisture of these two sub-communities.

O. digyna (sub-community 2B) was found by Matthews (1978b) to be a late pioneer on Storbreen and was identified as common after 40 years by Whittaker (1993), who considered the possible control of its distribution by microsite variations in moisture availability. *D. alpina* was also found by Whittaker to have a 40-49 year peak on Storbreen foreland and to colonize older sites supplied with fresh glacial silt from meltwater. Other indicator species within sub-community 2B include *Omalotheca supina* and *O. norvegica,* which are included in Matthews' (1978b) snowbed group and *Phleum alpinum,* which he considered to be a transitional species between the pioneer and the snow bed group. The *D. alpina-O. digyna* sub-community may therefore be characteristic of wetter sites, with later-lying snow. This is supported by Whittaker's (1991) identification of a shift in species composition over 12 years on Storbreen foreland from *D. alpina* and *O. digyna* characteristic of wetter conditions to species characteristic of drier conditions (including *T. spicatum*).

8.5 Pioneer communities across habitat types

8.5.1 Evidence from additional pioneer habitats

The additional pioneer habitats data set was used primarily to provide a wider range of habitats in which to look for evidence of single or multiple pioneer communities and to assess further the predictability of pioneer colonization. Within this data set is a wide range of types of pioneer site ranging from wet, and unstable sandar (river outwash plains) to relatively dry and stable river levées and gravel tips, and from the fine substrates found on sandar to the larger boulders of river levées and avalanche tracks. The overall similarity between these sites in terms of their species composition is therefore a good measure of the degree to which pioneer colonization is determined by factors other than habitat type.

The mean Sørensen distance between sites within this data set is 77%, greater than that for the glacier foreland sites (65%) but lower than for the relatively uniform habitat present at the roadside sites (81%). Cluster analysis of the additional pioneer habitat sites (Figure 5-16) was found to be optimum at the four-group level according to MRPP statistics and resulted in all except one of the groups (the high altitude patterned ground sites) containing sites from a mixture of habitat types. The largest group consists of sites from avalanche tracks, gravel tips, debris flows, debris flow levées, a river outwash site, a river bar site and a frost-patterned ground site. The species composition of a site is not therefore primarily dependent on habitat type. The four groups are considered to show evidence of being well-differentiated communities, with unambiguous indicator species and relatively high discreteness indices (Tables 5-14 and 5-15).

Direct gradient analysis of sites within the four communities (Figure 6-33) provided evidence of altitudinal zonation within this data set, with sites predominantly clustered according to altitude rather than habitat type. For example, the three high-altitude patterned ground sites are grouped together while the lower-altitude patterned ground site is classified with sites from other habitats within the same altitudinal range. Sites at the lowest altitudes, however, are divided into two groups, one consisting of a mixture of habitats and the other consisting of all four river levée sites plus one gravel pit. This may be indicative of habitat type having a stronger influence on species composition at lower altitudes. As already described in section 8.3.1.4, the river levées are sites which were constructed in response to the 1979 Jostedalen floods and are likely to have been subject to comparatively little disturbance since this event. This supports the findings for the roadside data set, in which the level of disturbance has an important influence on pioneer species composition.

8.5.2 Evidence from combined analysis of all three data sets

In a combined cluster analysis of all three data sets, at the three-group level, the roadside sites fall into their three original communities, the additional pioneer habitats into two communities and the glacier forelands into a single community (Figure 8-3). Indicator species analysis at the three-group level identified a *Deschampsia cespitosa-Plantago major* (*Desces-Plamaj*) community on roadside sites only, a *Festuca ovina-Poa alpina* (*Fesovi-Poaalp*) community on sites from all three data sets and a *Deschampsia flexuosa-Salix glauca* (*Desfle-Salgla*) community on roadside sites and the group of additional pioneer habitats identified in the previous sub-section as occurring predominantly on river levées. This level of analysis therefore supports the existence of a single glacier foreland community, three roadside communities and two communities in the additional pioneer habitats.

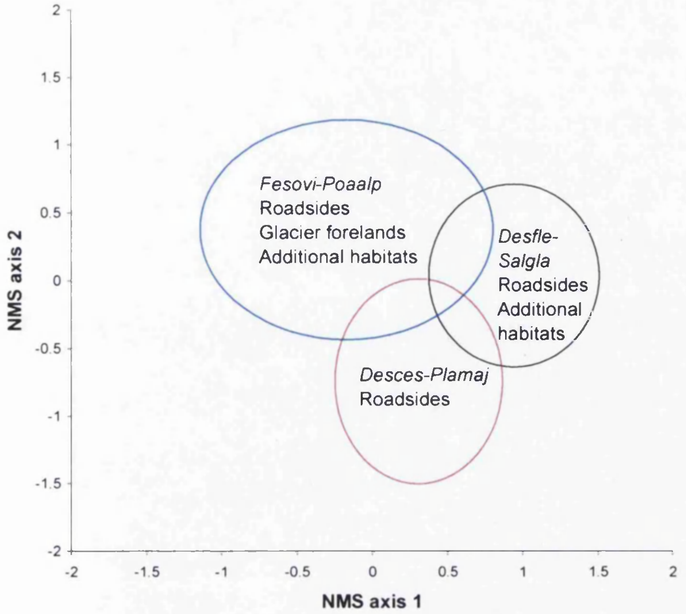


Figure 8-3. NMS ordination of pioneer sites with the three communities represented by ellipses (indicating ±2 standard deviations from each group centroid).

Cluster analysis of the combined data set at the six-group level, generally recreated the sub-communities obtained from individual data set analyses, with roadside sites occurring in six groups and additional pioneer habitat sites in four groups (Figure 8-4). However, the majority of glacier foreland sites were classified in a single group rather than the two sub-communities identified in section 5.5.2. This again supports the conclusions reached from independent analysis of the glacier foreland sites i.e. of a continuum of variation rather than a number of distinct communities. The overall similarity between the classification results for the combined and independent data set cluster analyses indicates that the more extensive roadside data set is not unduly influencing the combined analysis.

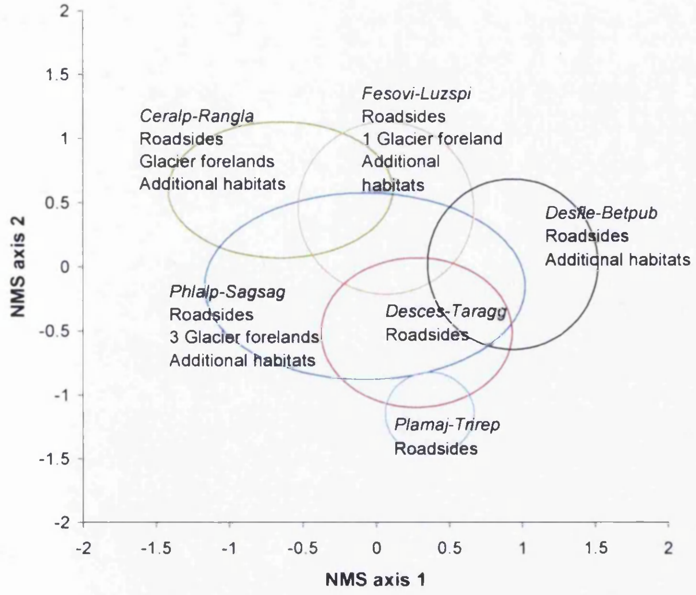


Figure 8-4. NMS ordination of pioneer sites with the six sub- communities represented by ellipses (indicating ±2 standard deviations from each group centroid).

It is therefore possible, based on cluster analysis of the combined data set and subsequent indicator species analysis, to classify the pioneer vegetation as a whole into the following six sub-communities: *Deschampsia cespitosa-Taraxacum* agg. (*Desces-Tar*agg, 6A) sub-community on roadsides only, *Plantago major-Trifolium repens* (*Plamaj-Trirep*, 6D) sub-community on roadsides only, *Deschampsia flexuosa-Betula pubescens* (*Desfle-Betpub*,6C) sub-community/community on roadsides, river levées and one gravel pit, *Cerastium alpinum-Ranunculus glacialis* (*Ceralp-Rangla*, 6E) sub-community on roadsides, the majority of glacier forelands, sorted circles, one avalanche track and one river outwash, and *Festuca ovina-Luzula spicata* (*Fesovi-Luzspi*, 6F) sub-community on roadsides, one glacier foreland, three debris flows, two sandurs, one river outwash and one gravel pit. The final sub-community, *Phleum alpinum- Sagina saginoides* (*Phlalp-Sagsag*, 6B), found on roadsides, three glacier forelands and sites on debris flows and debris flow levées, avalanche tracks, a river bar, a river outwash plain, gravel tips, and sorted circle, is more problematic as it has involved considerable differences in group membership for the roadside sites. For example, all sites on Leirdalen Road are now classified in the *F. ovina-L. spicata* sub-community whereas when roadsides were classified independently these sites were distributed between sub-communities *C. cerastoides-D. alpina* and *F. ovina-A. dioica.* Furthermore, the two main indicators for the *C. cerastoides-D. alpina* roadside data set sub-community are indicators for two different combined data set sub-communities. The poor differentiation between these two sub-communities has therefore been emphasized.

8.6 General conclusions regarding pioneer communities

The evidence discussed in section 8.3 lends weight to the argument that pioneer vegetation on roadsides has a compositional and geographical pattern of distribution which is not random. This implies that the pioneer stage of colonization on roadsides is not controlled by chance events to the extent that researchers have previously supposed. For example, Walker and del Moral's survey of research into primary succession (Walker and del Moral 2003) concludes that strong stochastic influences result in highly variable pioneer vegetation. Of particular relevance is a study of pioneer communities along roadsides in West Virginia (Rentch et al. 2005), which found that different roads were characterized by distinct assemblages. Although the authors found evidence of non-random colonization, communities were thought to be strongly influenced by sequences of species colonization and the introduction of non-native species.

On the basis of the evidence discussed in section 8.4, it seems valid to consider the glacier foreland sites as representing a continuum of variation within a single community. This continuum can be dissected in a way that reflects the influence of environmental factors and possibly successional zonation within the pioneer stage. If this continuum were to be subdivided, however, the two-group level provides a meaningful level at which to do so. The findings are in agreement with previous studies which have found consistent groups of species on glacier forelands, including Caccianiga et al. (2001), Caccianiga and Andreis (2004) and Haugland and Beatty (2005).

As discussed in section 8.5, pioneer species colonization does not appear to be primarily dependent on habitat type: altitude and disturbance regime have an apparently greater influence. However, these findings are not consistent with van der Valk (1992) who found pioneer vegetation to be highly site-specific and variable due to its dependence on dispersal from local vegetation and local conditions. However, variation in species composition according to habitat is reflected in differences in species indicator values according to whether the data sets are analysed separately or together. The altitudinal and regional distribution of communities are also influenced by habitat type. The effects of altitude and continentality are discussed further in the next section. Table 8-1 summarizes the characteristics of the pioneer communities and sub-communities identified.

Table 8-1. Summary of pioneer communities and sub-communities.

			Mean		Mean EI Value			
Community	**Sub-community**	**DI**	**Alt (m)**	**East (km)**	**Light**	**Moisture**	**pH**	**Nitrogen**
Roadsides								
Desces-Trirep (3A)		1.3	597	64	6.8	5.6	4.6	4.1
	Desces-Taragg (6A)	1.2	740	72	6.8	5.6	4.4	3.8
	Plamaj-Trirep (6D)	2.0	326	47	7.0	5.5	5.0	4.7
Fesovi-Luzspi (3B)		1.2	1247	83	7.4	4.8	3.9	3.2
	Cercer-Desalp (6B)	1.2	1169	76	7.3	5.3	4.3	3.8
	Luzarc-Rangla (6E)	1.8	1644	87	7.9	4.8	4.1	2.8
	Fesovi-Antdio (6F)	1.5	1192	89	7.3	4.4	3.6	2.8
Desfle-Salgla (3C)		1.9	819	45	6.6	5.5	2.6	2.9
	Desfle-Betpub (6C)	2.0	827	47	6.6	5.5	2.6	2.9
Glacier Forelands								
Poaalp-Oxydig		N/A						
	Desalp-Oxydig (2A)	1.2	1162	59	7.5	5.4	4.7	3.5
	Saxces-Trispi (2B)	1.1	1587	92	7.6	5.2	5.6	3.1
Additional Pioneer Habitats								
Fesovi-Antdio (4A)		1.3	1089	74	7.3	4.9	3.7	3.0
Phlalp-Stegra (4B)		1.3	540	38	7.1	5.5	4.1	3.8
Betpub-Gymdry (4C)		2.5	512	47	6.8	7.0	3.0	3.1
Saxces-Saxopp (4D)		3.3	1803	92	7.7	6.1	3.5	3.1
Combined Data								
Desces-Plamaj (3A)		1.3	585	65	6.8	5.6	4.6	4.1
	Desces-Taragg (6A)	1.2	735	72	6.7	5.6	4.4	3.8
	Plamaj-Trirep (6D)	2.0	285	49	7.0	5.5	5.1	4.7
Fesovi-Poaalp (3B)		1.2	1215	78	7.4	5.0	4.2	3.2
	Phlalp-Sagsag (6B)	1.1	942	63	7.1	5.5	4.4	4.2
	Ceralp-Rangla (6E)	1.3	1422	76	7.7	5.2	4.7	3.1
	Fesovi-Luzspi (6F)	1.3	1186	84	7.4	4.7	3.8	3.0
Desfle-Salgla (3C)		1.7	783	45	6.6	5.6	2.7	2.9
	Desfle-Betpub (6C)	1.7	783	45	6.6	5.6	2.7	2.9

8.7 The effects of altitude and continentality on pioneer communities

As discussed in section 8.3.1.2, altitudinal zonation is evident for the roadside data set with significant differences in mean altitude between all three communities, but with evidence of more of a continuum at the sub-community level and with no significant difference in mean altitude between *F. ovina-A. dioica* and *C. cerastoides-D. alpina* sub-communities. However, these sub-communities were distinguished by significantly different values for mean distance east, suggesting that continentality is important in explaining the differences between them, and significantly different mean moisture EI values for these groups substantiate this theory. Furthermore, the *D. flexuosa-S. glauca* community (and *D. flexuosa-B. pubescens* sub-community) only occurs towards the west of the study area, possibly reflecting the more oceanic climate, more acidic underlying geology and/or the lower level of disturbance at these sites. Variance partitioning confirmed that a significant proportion of the explained variation in species composition on roadsides can be attributed to the effects of altitude and continentality. When only these two factors are included in the analysis, 64% of the variance is explained by altitude, 25% by distance east and 11% of the explained variance is shared between them. Therefore, although altitude and distance east co-vary due to the regional topography, continentality has a significant independent influence.

Although the effect of altitude on glacier foreland pioneer colonization is also evident, with a correlation of r = 0.75 between the ordination score of a foreland on axis 1 and its altitude, the low overall variance within this data set indicates that this correlation is not related to a high level of variation in species composition. The two glacier foreland sub-communities had significantly different mean altitudes and distances east, but there were no obvious discontinuities in ordination space, and direct gradient analysis shows a more restricted geographical (altitudinal and regional) distribution for sub-community *S. cespitosa-T. spicata* than *D. alpina-O. digyna*. Variance partitioning confirms that, of the variation in species composition on glacier forelands explained by altitude and distance east, altitude independently accounts for 37% of the variance, distance east for 29% and 27% is shared by these two factors. The inter-correlation between altitude and distance east was also high for the glacier foreland sites at r = 0.89. Continentality therefore has a greater relative influence on glacier forelands than on roadside sites and the shared variance between these two factors is also greater.

Direct gradient analysis produced a clear pattern of altitudinal and regional distribution of pioneer communities particularly the altitudinal distribution of roadside communities, which are composed of sites distributed at regular intervals along an altitudinal gradient. When all three data sets are combined, however, there are interesting habitat-related differences in the altitudinal ranges of the pioneer communities (Figure 6-36). The *F. ovina-P. alpina* community extends to lower altitudes on glacier forelands than on roadsides. The direct effects of glacier ice on the proximal foreland, including cooling effects of katabatic winds and disturbance due to freeze-thaw cycles (Ballantyne and Matthews 1982), would therefore appear to be creating conditions which facilitate colonization by species restricted to higher altitudes on roadside sites. A number of sites within the additional pioneer habitats data (three river sites, one avalanche track and three debris flows) which have a direct connection with one or more glacier forelands also extend the lower altitudinal range of this community. It is possible that seeds migrate from the glacier foreland pioneer zone to these sites via wind or water dispersal. Although altitude has the dominant influence, habitat type is therefore also an important factor in the altitudinal and continental distribution of pioneer communities.

The highest percentage of variance explained by altitude and continentality is for the glacier forelands (50% and 33% respectively), the most uniform habitat type, while the lowest percentage is for the additional habitats data set (12% and 5% respectively) which is the most diverse. Altitude and continentality therefore have the greatest relative influence when there is little overall variability in the data set. Greater overall variability occurs when the data set is subject to the significant influence of other factors. Variance partitioning of the combined data set gives a value of 17% for the proportion of TVE explained independently by altitude and 8% for the proportion explained by distance east.

8.8 Ellenberg's indicator (EI) values and pioneer communities

The use of EI values added considerably to interpretation of the patterns of pioneer colonization across the study region and to detecting significant differences between communities and sub-communities which were not separated in terms of mean altitude or distance east. The Ellenberg indicators used did not have a very wide range of values within the data collected but this is consistent with the environmental parameters of the study area. It is possible that mean EI values in the pioneer stage are reflecting the conditions of safe sites for plant establishment, rather than general environmental conditions. However, the relationships between mean EI values and between these values and mean altitudes and distance east can be explained in ecological terms and make sense as a reflection of overall conditions.

On the glacier forelands, the fresh till has a relatively high pH, high base saturation, and a low level of nitrogen. These conditions therefore favour pioneer species with low N requirements and would tend to inhibit those which are dependent on mycorrhizal associations. Frost disturbance also provides fresh supplies of parent material, with less frost-active ground having a lower pH due to more intense leaching. Mean roadside EI values for pH are generally lower than on the forelands and nitrogen values are more varied, particularly reflecting the effects of human influence at lower altitudes. Moisture values are also more variable than on the forelands primarily due to the effects of altitude and continentality on groundwater levels in the absence of a consistent source of moisture. Pioneer communities in additional habitats, on more varied substrates, also have lower mean pH EI values and more variable moisture values than the glacier forelands. The values for light are generally high in all pioneer communities, but slightly lower where the nature of the vegetation suggests that the pioneer vegetation is no longer in its earliest stage.

Variance partitioning confirmed that altitude and substrate pH are the dominant influences on the roadside pioneer vegetation and that all mean EI values explain a significant portion of the variance within this data set. For the glacier forelands, however, the level of variance explained by mean EI values was not statistically significant and the low overall variance within this data set was also confirmed. The variance explained within the additional pioneer habitats data set is significant for all four mean EI values, with a higher proportion of the TVE attributed to mean moisture EI values and a lower proportion to the other three values than for the roadside sites. This is consistent with the inclusion of a number of fluvial habitats in this data set.

8.9 Pioneer communities within the context of primary succession

In this section, pioneer communities are discussed in relation to later stages of primary succession. The relative variability of pioneer species composition and abundance is compared with that of later stages of succession for both the roadside and glacier foreland data sets and the results are used to test hypotheses regarding the nature of successional trajectories. In particular, the relationship between successional trajectories and altitudinal zones is discussed. The use of EI values in quantifying changes in environmental factors between successional stages is considered in terms of its possible contribution to the testing of successional models and investigation of primary successional processes.

8.9.1 Relative variability during succession

The case for overall successional convergence at roadside sites is evident from the decrease in mean Sørensen distance of 4% between the pioneer and climax stages. Although this is a small decrease, evidence for convergence is also provided by cluster analysis of both stages together. This is reflected in the majority of climax sites forming a single group at a level of clustering where pioneer sites form three separate groups, confirming the existence of greater compositional variability in the pioneer stage (Figure 8-5). The overall pattern is therefore consistent with Clements' theory and other `climax models' (Clements 1916) of an initially heterogeneous vegetation becoming more homogeneous, which has subsequently been substantiated in many studies of, for example forest succession (Christensen and Peet 1984) and salt marsh succession (Wilson and Whittaker 1995).

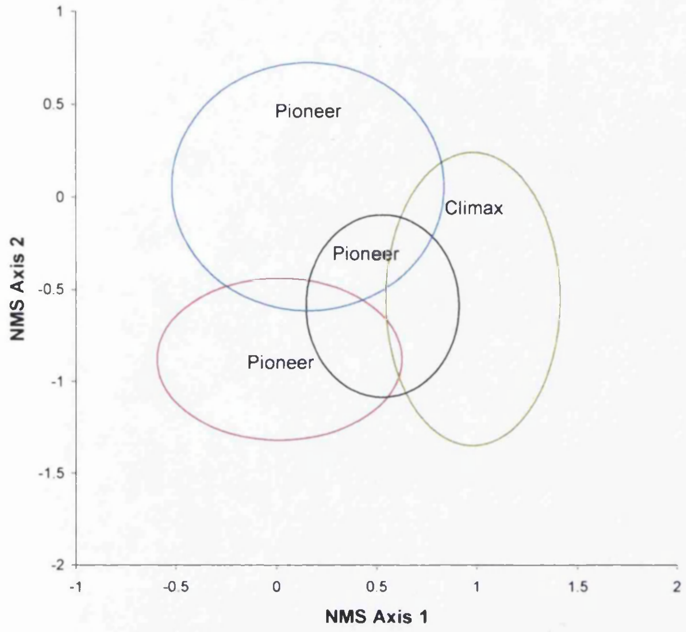


Figure 8-5. Roadside pioneer and climax cluster analysis groups (ellipses indicate centroid ± 2 standard deviations).

The glacier foreland data set presents a contrasting picture, with an increase in mean Sørensen distance with successional stage, from 65% in the pioneer stage to 76% in the climax stage. The pioneer stage on glacier forelands has much lower variability than this stage in other habitat types, although variability within the climax stage is similar to that for roadsides. Figure 8-6 summarizes the average successional trajectories identified on glacier forelands and roadsides.

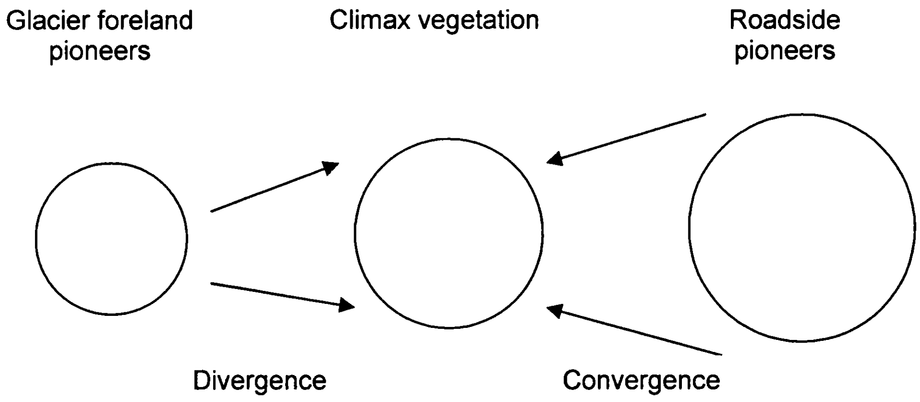


Figure 8-6. Diagrammatic representation of average successional trajectories on glacier forelands and roadsides.

All three later stages on glacier forelands show significantly greater mean within-stage distance than the pioneer stage (Figure 8-7) and a considerable change in the amount of variability occurs at a relatively early stage of succession, the increase in variability between the pioneer and 70-year stage being comparable with that between the 70-year stage and the climax stage. This is supported by cluster analysis which, at the four-group level, shows all but one of the pioneer sites belonging to a single cluster, while sites from the other three successional stages are each distributed between at least three clusters (Figure 7-15). The results are therefore not consistent with the theory that pioneer communities are less well-defined than climax communities (Friedel 1938, Solomina 1989). However, the pattern is consistent with the association of divergent pathways with the relatively harsh environments of glacier forelands and convergence where stronger biotic controls occur due to the proximity of the climax vegetation on roadsides (Matthews 1979b, a, Matthews 1992).

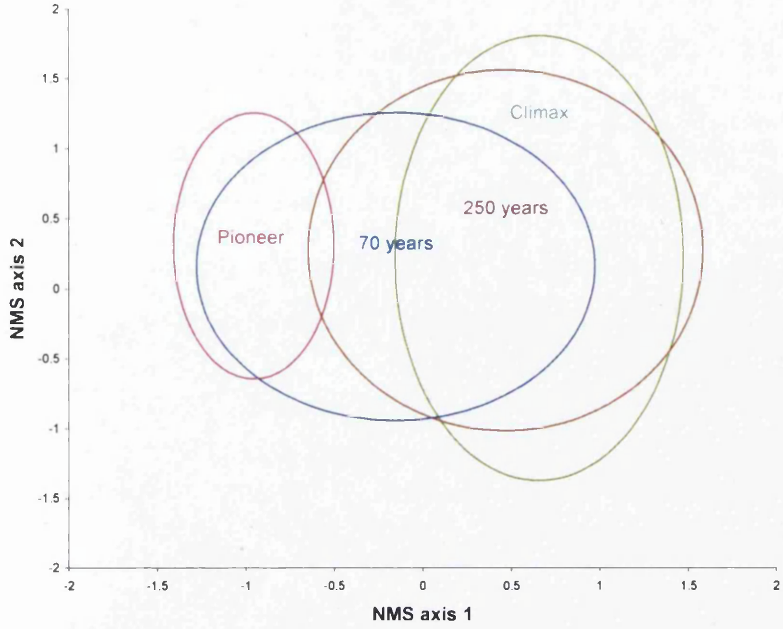


Figure 8-7. NMS ordination of four stages of glacier foreland succession. Ellipses represent stage centroid ± 2 standard deviations.

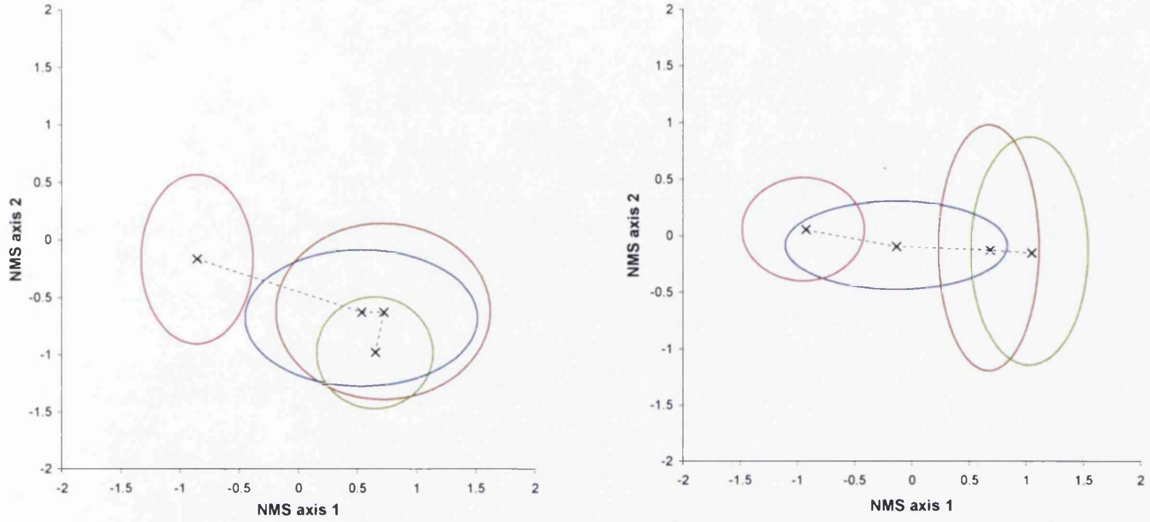
8.9.2 The influence of altitude on successional change

8.4.2.1 Glacier forelands

Cluster analysis of the four stages of succession on glacier forelands suggests a higher degree of altitudinal zonation in the three later stages than in the pioneer stage (Figure 7-17). Indicator species analysis confirms that below 1000 m *Poa alpina-Oxyria digyna* pioneer vegetation develops into a single climax vegetation type dominated by *Betula pubescens* and *Vaccinium myrtillus*, whereas above this level, it develops into one of two types characterized by either *Juncus trifidus* and *B. nana* or *Salix herbacea* and *Luzula arcuata*. All climax sites above approximately 1600 m develop into the latter, whereas those between 1000 and 1600 m follow either trajectory. These findings are broadly consistent with the traditional climax vegetational zones and belts described by Moen (1987), as the boundary between low- and mid-alpine belts occurs within this altitudinal range. Mean Sørensen distances confirm that the pattern is one of divergence between pioneer and climax within this altitudinal zone.

In the lower altitudinal zone (sub-alpine birch belt) (< 1000 m), significant differences between mean Sørensen distances within the first three successional stages could not be identified due to large confidence intervals. However, the climax vegetation is significantly more variable than the pioneer stage, suggesting successional divergence (Figure 7-19a). All sites developed *Vaccinium myrtillus-Betula pubescens* vegetation by the 70-year stage, and NMS ordination (Figure 8-8a) is consistent with comparatively early successional development within this altitudinal zone with little subsequent change. Therefore, although succession on glacier forelands below 1000 m proceeds to a single vegetation type, a divergent trajectory appears to be occurring within this altitudinal zone. Successional convergence between the 1930 and 1750 moraines was identified by Vetaas (1994) on Bødalsbreen foreland (700 m), attributed to the presence of *B. pubescens* as a community dominant. This constitutes a different pattern from the one detected from comparison of mean Sørensen within-stage distances in this study, perhaps due to the large confidence intervals. If variability is measured in terms of standard deviations of the mean, however, divergence can be demonstrated between the pioneer and the 70-year stages and convergence between the 250- year and climax stages (Figure 8-8a), which is more consistent with the findings of Vetaas. This is also supported by the comprehensive review of research into glacier foreland succession (Matthews 1992), which concluded that divergence generally occurs early in succession and in relatively severe environments. A divergent pathway, due to the presence of woody species, which can establish early and gain dominance, is also consistent with the interpretation of successional processes at Glacier Bay, Alaska (Fastie 1995). However, convergence has also been identified on sub-alpine glacier forelands (Faegri 1933). The picture within this altitudinal zone is therefore somewhat ambiguous. Divergence clearly occurs within the chronosequence but evidence for the exact stage at which it occurs is not consistent.

a) Below 1000 m c) 1500 – 1600 m



b) 1000 – 1480 m d) 1620 - 1860 m

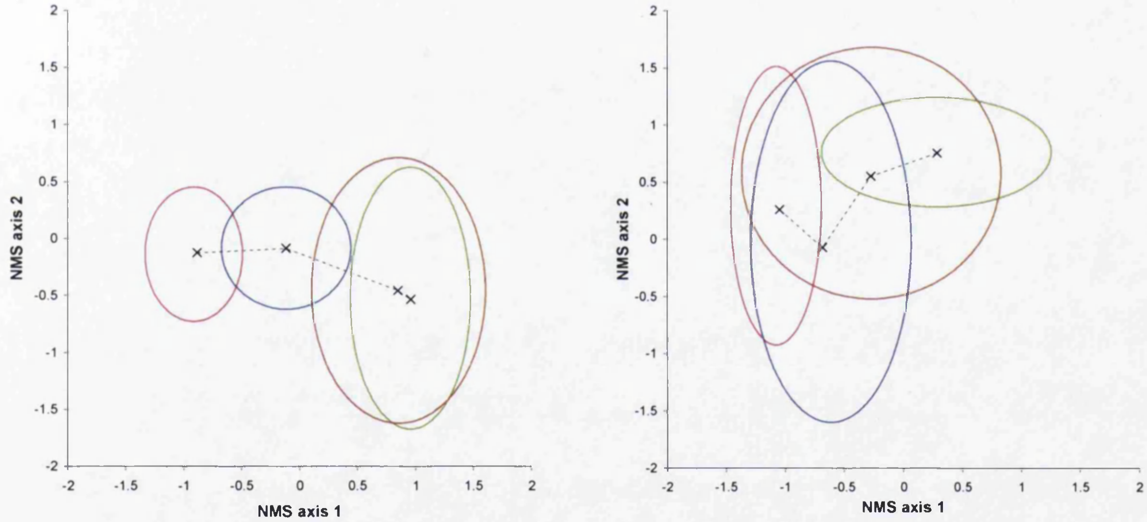


Figure 8-8. Glacier foreland sites plotted onto NMS ordination according to altitudinal zone. Ellipses indicate centroids ± 2 standard deviations. Dashed lines join centroids of each stage. Red = pioneer, blue = 70-year, brown = 250-year, green = climax stage.

In the 1000 to 1480 m zone and 1500 to 1600 m zones, both analytical methods (Sørensen distance and standard deviation) show a significant increase in variability between the pioneer and the 250-year stages which does not subsequently increase further (Figures 7-19b and c and 8-8b and c). Divergence therefore appears to occur at a later stage than in the lower altitudinal zone, suggesting slower successional development. Examination of the distances between successional stage centroids on the NMS diagram confirms that the greatest change in centroid score along axis 1 (interpreted as successional change) occurs between the 70- and 250-year stages (Table 7-5). Matthews' (1979b) use of multiple discriminant analysis to assess the relationship between within-group and between-group variability on Storbreen foreland (1380 m) also found evidence of successional divergence within this altitudinal zone.

In the highest altitudinal zone (1620 – 1860 m), mean within-stage Sørensen distances show no significant change with succession (Figure 7-19d), indicating a parallel trajectory or little successional change. The mean distance between successional stage centroids along NMS axis 1 is lower between the pioneer and 70-year stages and between the 70- and 250-year stages, but greater between the 250-year and climax stages, suggesting that successional change is delayed even further at this altitude (Figure 8-8d, Table 7-5). Previous research has found that the effect of adverse environmental factors at high altitudes can result in vegetation failing to progress beyond the pioneer stage (Svoboda and Henry 1987). In harsh conditions, environmental resistances oppose the biological forces which drive succession and the relatively low species richness weakens competitive interactions, so that stress tolerance becomes the major factor influencing survival. A study of mature arctic tundra vegetation (Griggs 1934) concluded that it most closely resembles that of the pioneer stage in temperate zones, the extreme climate with its associated physical disturbances preventing the vegetation from reaching a stable equilibrium or climax. The `problem of Arctic vegetation' that Griggs refers to in his paper is whether the concept of succession is applicable at all, especially in the High Arctic, which is equivalent to the high-alpine belt. .

Successional patterns on lahars on Mount St Helens (del Moral and Ellis 2004) displayed increasing within-plot variability with elevation and with distance from propagule source, and del Moral (1998) concluded that stochastic effects due to dispersal limitations may be preventing convergence. The correlation of the two ordination axes with age and altitude is consistent with the findings of Aplet and

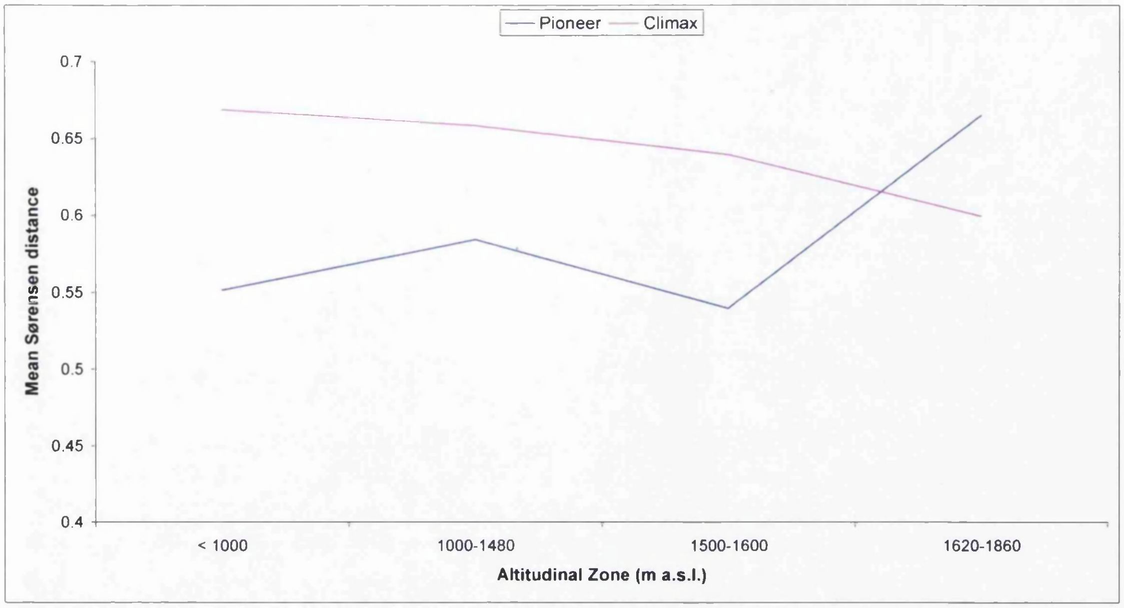
Vitousek (1994) who used CCA to analyze Hawaiian rainforest succession. They also found that primary succession is delayed at higher altitudes and that a different successional pathway is followed at each altitude due to climatic variation.

8.4.2.2 Roadsides

Variations in mean Sørensen distance with succession were calculated for the two roadside verge successional stages in 200 m altitudinal zones. The two zones between 20 and 400 m showed evidence of successional divergence, the five zones between 420 and 1400 m showed varying degrees of successional convergence, while the two highest altitude zones between 1420 and 1860 m showed no significant change in variability with succession (Figure 8-9b). There are therefore important differences between these altitudinal patterns and those shown by glacier forelands (Figure 8-9a) except at the highest altitudes (1620 to 1860 m), where both habitat types show no change in mean dissimilarity between stages.

It is suggested that, in the lowest two altitudinal zones on roadsides, human influence is resulting in more diverse climax vegetation than would occur naturally (i.e. a mosaic of agricultural land and forest). Furthermore, the glacier foreland pioneer stage has been shown to consist of a single community at all altitudes, with lower mean within-stage Sørensen distance than the roadside pioneer stage. Vegetation succession on glacier forelands therefore represents one community which diverges, whereas on roadsides the pioneer vegetation is extremely varied and tends to converge to a more homogeneous climax. A greater frequency and magnitude of disturbances on glacier forelands compared with roadsides is a possible explanation for successional divergence in the former habitat type (Matthews and Whittaker 1987).

a) Glacier forelands



b) Roadsides

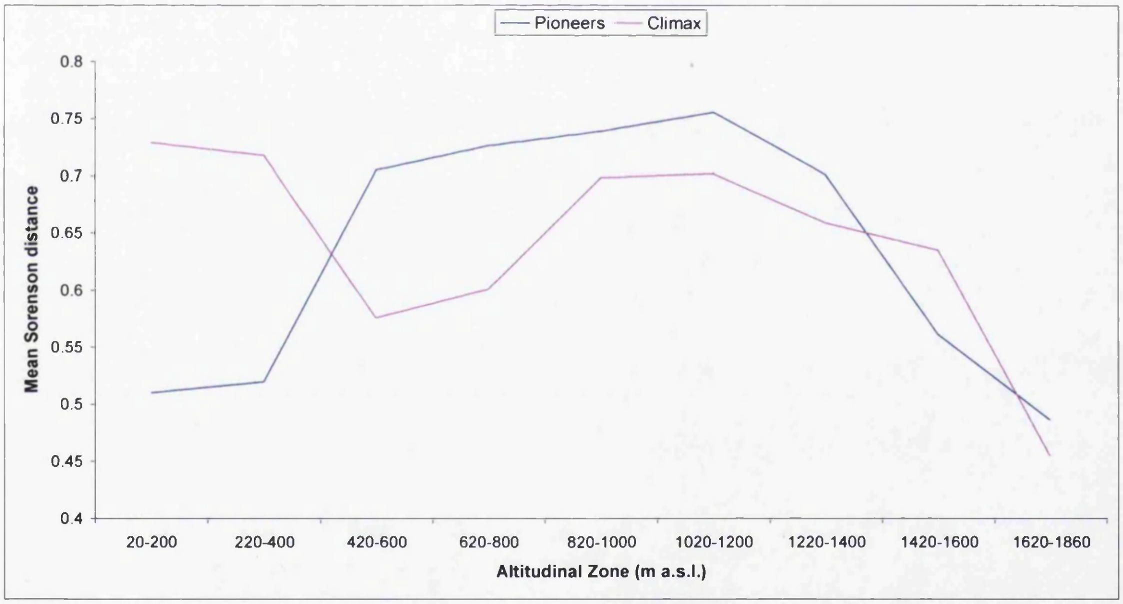
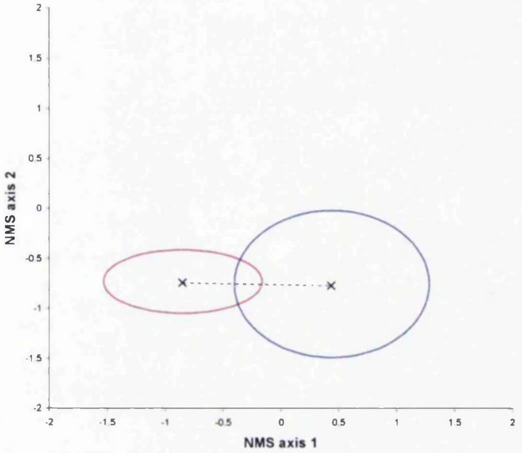


Figure 8-9. Mean Sørensen distances and 95% confidence intervals for pioneer and climax stages of a) glacier forelands and b) roadsides.

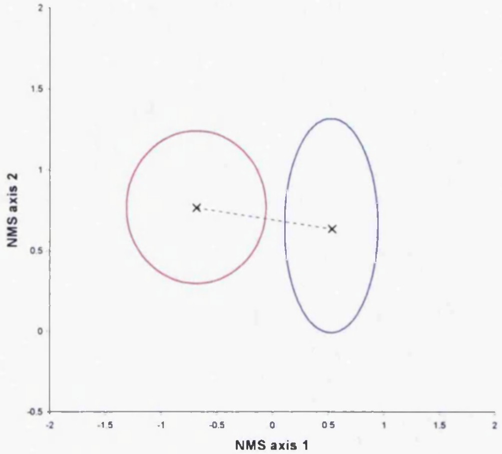
In the literature there are two conflicting views regarding the effects of altitudinal influences on successional pathways. For example, Walker and del Moral (2003) found that convergence is likely where there are few dispersal limitations and homogeneous initial conditions. Convergence will therefore tend to occur below the tree-line, supported by the effects of canopy development and competitive dominance by trees and shrubs. Recent research (Anthelme et al.

2007) supports this view, identifying a convergent trajectory in sub-alpine vegetation due to the effects of a single dominant species. However, Matthews (1979b) hypothesizes that divergence could occur at lower altitudes due to lower environmental stress, which is partially consistent with the findings of this study.

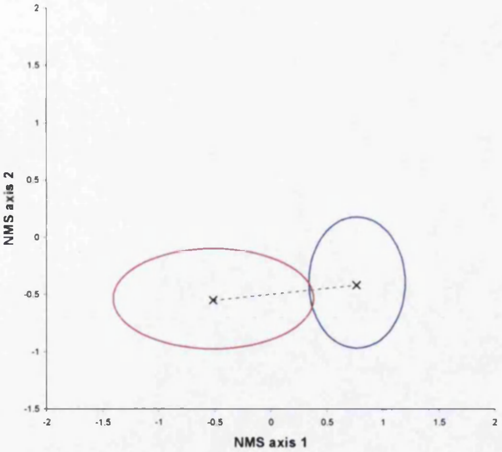
a) 20 – 400 m



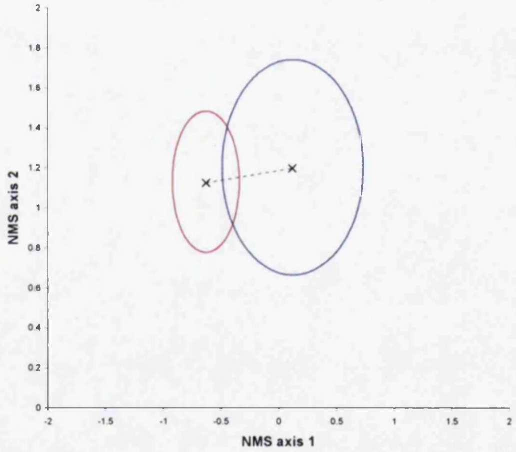
d) 1220 – 1400 m



b) 420 – 800 m



e) 1420 – 1860 m



c) 820 – 1200 m

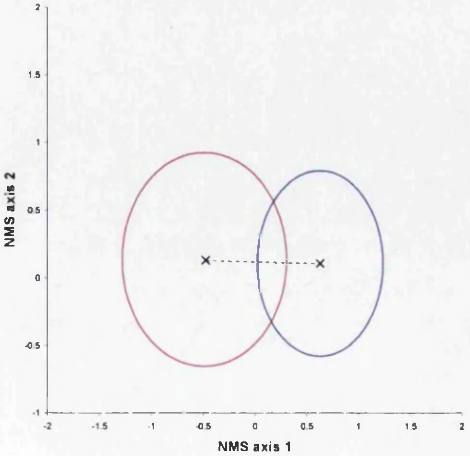


Figure 8-10. Roadside sites plotted onto NMS ordination according to altitudinal zone. Ellipses indicate centroids ± 2 standard deviations. Dashed lines join centroids of each stage.

Figure 8-10b shows relatively strong convergence within the 420 – 800 m zone on roadsides, where the adjacent climax is dominated by forest, and weaker convergence in the 820 – 1400 m zone (Figures 8-10c and d), where forest is gradually replaced by dwarf shrub climax communities. Figure 8-10e appears to show successional divergence in the 1420 – 1860 m zone, although the highest zone is characterized by little successional change.

Whether successional pathways ultimately follow a convergent or divergent trajectory depends on a combination of allo- and autogenic processes. On the glacier forelands, the more uniform pioneer community diverges, as environmental stress decreases with distance from the glacier and conditions become more variable. On the roadsides, strong biotic control in the boreal and sub-alpine zones and increasing environmental control in the low-alpine zone both lead to convergence. In the mid-alpine zone, succession is slower and tends to follow a parallel or divergent trajectory.

The overall findings are consistent with Walker and del Moral's conclusions from a review of the literature (2003), in that convergence is more likely where there are few limitations to dispersal and more homogeneous initial conditions, which more accurately describe the roadside sites than the generally greater isolation and substrate variability of the glacier forelands. The findings do not therefore support Rydin and Borgegard's (1988) hypothesis that convergence is more common where there are barriers to dispersal or Hatton and West's (1987) assertion that it is more likely to occur in stressful environments.

8.9.3 Ellenberg's indicator values and successional change

8.9.3.1 Glacier forelands

On the glacier forelands, mean EI values for light, pH and nitrogen all show significant decreases between the pioneer and climax stages whereas the mean EIV for moisture shows no significant change (Table 7-6). The only significant difference in mean EI values between consecutive successional stages is a decrease in the value for pH. This trend in mean pH values is consistent with the findings of Messer (1988) and Grimm (2000). Messer found the rate of decrease in pH and increase in CEC to be related to initial conditions rather than climate; with the underlying more acidic geology of the Jostedalsbreen region being reflected in a more rapid change in pH than the less acidic Jotunheim region. Whittaker (1993) also found a rapid decline in pH in the first 20 years post-deglaciation on Storbreen foreland and an accompanying reduction in nutrients. He considers the decline of pioneer species at Storbreen to have an allogenic basis but attributes their later disappearance to competitive interactions.

Chapin et al. (1994) also stress the importance of initial site conditions at Glacier Bay, where decreasing pH, but increasing moisture and total nitrogen, were found to be typical of succession following deglaciation. A decrease in pH and increase in organic matter was also found by Jones and del Moral (2005) on Coleman glacier foreland. CCA ordination of vegetation data from successional stages in the central Austrian Alps (Raffl et al. 2006) produced a first axis which was strongly correlated with terrain age and soil pH. However, water supply was considered to be the key limiting factor to pioneers, with freeze-thaw action influencing both moisture supply and grain size. The pioneer zone was characterized by high light and low nutrients levels and subsequent stabilization was considered to be due to increasing competition. Low nutrient levels were also found to be a characteristic of pioneer zone substrate in the high Arctic (Hodkinson et al. 2001) but processes such as nitrogen-fixation by soil bacteria and inputs from wind-borne insects are considered possible sources of nitrogen and phosphorus. Nitrogen levels would perhaps be expected to accumulate with succession, as the amount of organic matter in substrate increases. However, the young substrate is rich in minerals, with subsequent leaching by precipitation and meltwater and, to a lesser extent, absorption by plants removing them, as vegetation builds up and increasing the acidity of the till (Stork 1963). The pH trends found in this study are therefore consistent with those of other researchers.

The decreasing mean EI values for light associated with later stages of succession would be expected as vegetation cover increases. The lack of a trend in mean moisture EI values may be explained by the fact that data collection on the glacier forelands in this study was designed to record species on sites with similar moisture regimes. Furthermore, changes in moisture regime on forelands tend to be localized rather than general (Whittaker 1991). The decrease in mean nitrogen EI values (considered to reflect total nutrient levels) is most consistent with rapid leaching of minerals from fresh till and subsequent acidification of the substrate which makes nutrients less available. It is of course possible that mean EI values in the pioneer stage are reflecting microsite conditions rather than general site conditions.

8.9.3.2 Roadsides

Successional trends on the roadside sites follow a similar pattern to the glacier forelands in terms of the mean EI values for light, pH and nitrogen, but the mean EI value for moisture is significantly higher in the climax stage (Table 7-3). The latter is likely to reflect the relatively well-drained substrate of the roadside verges, compared with the adjacent ground. The decrease in mean nitrogen EI value in the climax stage is consistent with the findings of Truscott et al. (2005), who found that nitrogen values decrease with distance from the road due to traffic effects.

The correlations between mean site EI values and NMS ordination scores for the pioneer and climax sites combined (Figure 7-10) are similar to those obtained for the ordination of pioneer sites independently. This level of consistency lends additional support to the results obtained for the pioneer stage and therefore the use of EI values within the context of pioneer communities.

8.10 Further theoretical implications

8.10.1 Models of primary succession:

In a geoecological model, successional processes are considered an integral part of the developing landscape and depend on close interaction between biological and physical processes (Matthews 1992). For example, Whittaker

(1991) stresses the importance of physical driving forces, such as disturbance regimes, hydrological systems and climatic change within geoecological processes operating on glacier forelands. Colonization by pioneer species within the first ten years of landscape development post-deglaciation is evidence of early biotic input to the geoecological system, although successional processes at this stage are primarily under abiotic control. Pioneer plant distribution on glacier forelands has been attributed to the abiotic characteristics which influence seed-trapping, germination and establishment (Jumpponen et al. 1999). The biotic component of the model, although present at an early stage, may not be influencing such processes until vegetation cover has developed to a sufficient degree that interactions occur. For example, geoecological processes on patterned ground within glacier forelands may not be initiated until approximately 70 years after deglaciation, when biotic and abiotic processes begin to interact, due to declining frost action, increasing vegetation cover and soil development (Haugland 2006).

Evidence presented in this thesis generally supports the geoecological model of Matthews and Whittaker (1987): early colonizers of glacier forelands require a pool of uncontested resources including low vegetation cover, high moisture, high pH and undepleted nutrients. These are all supported by the mean EI values calculated for pioneer sites, although for the roadside pioneer communities there is more variation in mean EI values. The relative importance of physical and biological influences varies with environmental severity and therefore with factors related to altitude and continentality. In more favourable (high resource, low stress) environments biological factors become important earlier in succession, whereas, in severe environments, allogenic processes are more important for longer. As differences in environmental stress are closely related to climate, this model can be applied to gradients of altitude and continentality within the study region. For example, earlier biotic influences would be expected at low altitudes and in the west of the region. This is also consistent with Svoboda and Henry's (1987) emphasis on the importance of environmental resistance to succession.

Two of Grime's (2001) three plant strategies, adaptation to stress (stress-tolerators) and to disturbance (ruderals) can be applied to pioneer vegetation, but competition is not considered an important factor at this stage. The term 'stress' incorporates a range of factors, which may include low air and soil temperatures, extremes of temperature, a short growing season, high wind strength, frequent flooding, prolonged snow lie, nutrient deficiencies, cryoturbation and permafrost, many of which increase in severity from the sub-alpine to high-alpine belts and from west to east. The response of pioneer vegetation to many of these factors can be deduced from the clear division between low and high altitude roadside communities. The extension of the high altitude community to lower altitudes on glacier forelands is a reflection of the relatively harsh environment created by the presence of a glacier. The pioneer communities recorded are all present on frequently disturbed substrate, different habitats providing a variety of disturbance types. In the periglacial zone and on sorted circles, frost action is the major source of disturbance, decreasing with increasing distance from the glacier. Near the ice margin, disturbance is also related to increased soil moisture and freeze-thaw action, while permafrost is a unique aspect of the high altitude zone in all habitat types. The roadside sites, however, are generally better drained than the forelands and frost action is therefore reduced. In the roadside data set, disturbance by vehicles is the major factor and variation in the frequency of traffic means that lower levels of disturbance on some roads may lead to earlier biotic interactions and soil acidification. A higher vegetation cover results in greater stability, which, in turn, encourages more vegetation establishment. Grazing by sheep, goats and cattle is also an aspect of the disturbance pattern at low altitudes. Of great importance is the fact that disturbed sites show evidence of community assembly, even without species interactions. Use of the term "disturbance-tolerators" (Ecke and Rydin 2000) to characterize species able to tolerate and recover from relatively high levels of disturbance, is perhaps appropriate.

Other models which are consistent with the findings of this study are Noble and Slatyer's (1980) three vital attributes (particularly the importance of method of seed arrival as biotic influence is low), aspects of Walker and Chapin's (1987) process model, and Tilman's (1985) resource-ratio model, in which succession is driven by changing resource levels. However, mycorrhizae and stochastic events (Walker and Chapin III 1987) have not been identified as important factors within the context of this thesis. The mathematical models of van Hulst (1992) and Peet (1992) are not supported in that they emphasise importance of random events, the latter proposing the existence of an initially random collection of pioneers succeeding to predictable community. However, van Hulst proposes a degree of predictability in terms of dispersal and safe-site limitations, which is consistent with the pioneer communities identified.

8.10.2 Replacement by later colonizers

On the glacier forelands, leaching of cations and acidification, climatic and hydrological changes occur with increasing distance from the glacier snout; processes which may all be involved in the replacement of pioneers by later colonizing species. Specific mechanisms that may be involved in the decline of pioneers include nutrient depletion, changes in nutrient balance, and toxicity associated with pH change. The earliest decline of pioneers is generally considered to be due to abiotic factors but later replacement involves competitive interactions as biotic factors become more important (Whittaker 1993). In this thesis, mean EI values for pH and nutrients both decline along the chronosequence on glacier forelands. It is therefore possible that pioneers decline, either in response to nutrient shortages, or to changes in nutrient availability, as pH falls (Matthews and Whittaker 1987). The decrease in mean EI values for light as succession proceeds is also consistent with biotic interference as vegetation cover increases. Although a change in moisture regime with distance from the glacier is also cited as a possible factor, no evidence for this has been found in this study. The availability of safe sites may also become more limited as vegetation cover increases and species tolerant of more acidic soil conditions start to dominate.

The majority of these conclusions are also applicable to the roadside pioneer vegetation. Additionally, many roadside pioneer species (e.g. *Achillea millefolium, Agrostis capillaris, Plantago major*), particularly at lower altitudes, are known to be poor competitors and are therefore absent from the adjacent climax vegetation. From analysis of the *Deschampsia flexuosa-Salix glauca* roadside community which includes a number of species more usually associated with the climax stage, it seems likely that lack of disturbance is also a key factor leading to displacement of roadside pioneers. The proximity of pioneer and climax vegetation on roadsides, compared to glacier forelands also makes it possible for later colonizers to replace pioneers at an earlier stage due to shorter dispersal distances.

8.10.3 Homogeneous communities versus continuum

The findings support neither Clements' prediction that increasingly homogeneous, integrated and predictable communities are formed due to increasing interactions as succession proceeds (Clements 1916), nor Gleason's view of the pioneer stage as merely a "fortuitous juxtaposition of plant individuals" (Matthews 1996, p 200). Rather, results reflect the tendency for the pioneer stage to be relatively *predictable*, largely due to *abiotic* pressures.

The pioneer vegetation has been shown to form a number of distinct communities within which species composition varies along a continuum of change, in keeping with the ideas of Goodall (1963) and McIntosh (1958, 1967). This study has also demonstrated that the concept of the plant community need not be restricted to undisturbed stands of climax vegetation, supporting the view of Cottam (1966) that a meaningful study cannot exclude areas of disturbed ground. In the sense that the communities and sub-communities proposed have been shown to have clear contiguous geographical distributions, particularly in relation to altitude, but to vary continuously within those distributions, it may be accurate to describe them as meaningful abstract units in geographical space (Austin 2005).

8.11 Further methodological considerations

The combination of analytical techniques used in this research project has produced a broad picture of the nature and variability of the pioneer vegetation within the chosen study area. The overall strategy has been to approach the key research questions using complementary methods, each of which measures a different aspect of variability. In addition, the specific methods chosen for ordination and classification of the data have been compared with more widely used methods (Kent 2006), in order to provide an objective assessment of their efficacy and to ensure that the conclusions are not solely based on the results of a single method.

Non-metric multidimensional scaling (NMS) using the Sørensen distance coefficient was found to out-perform detrended correspondence analysis (DCA) consistently in terms of providing a two-dimensional site ordination, having a consistently stronger correspondence to the original distance matrix (Tables 4-2 and 5-2). This is consistent with the findings of Kenkel and Orloci (1986) and supports its selection on theoretical grounds (Minchin 1987, Austin 2005). The selection of a two- rather than three-dimensional NMS solution on grounds of interpretability generally resulted in higher stress levels. However, these levels were within the recommended parameters (Clarke 1993) and did not constitute a large increase in stress between the two solutions. Cluster analysis also compared well with TWINSPAN, achieving consistently more favourable multiresponse permutation procedure (MRPP) statistics as a measure of the degree of separation between and agreement within the resulting groups (sections 4.5.6 and 5.5.6). This is in agreement with the findings of McCune and Grace (2002) and Austin (2005). However, the level of similarity between the two sets of ordination and classification methods supports the overall conclusions of the study.

The combination of classification and ordination methods used has enabled objective appraisal of any apparent discontinuities or concentrated areas of sites within the ordination diagram, rather than relying on visual assessment alone. MRPP in conjunction with indicator species analysis (ISA) has provided a useful method of assessing the most appropriate level of clustering at which to examine individual groups i.e. the level at which the greatest mean between-group dissimilarity and least within-group dissimilarity occurred. This combination of methods was not, however, appropriate for indicating when a data set constituted a single community (in the case of the glacier forelands) and did not give entirely unambiguous results regarding the optimum level of classification. The use of the discreteness index (DI) to produce a measure of the combined tightness and separateness of each group, allowed a comparison of groups within each level of clustering. However, allowance had to be made for the fact that an increase in DI values would be expected as more groups are created. The use of centroids ± 2 standard deviations superimposed onto ordination diagrams is a methodological improvement for visually assessing the communities and sub-communities.

ISA proved valuable for describing and interpreting groups and, on the whole, identified indicator species which provided a clear distinction between groups. The ecological parameters of each group were assessed in terms of the known habitat preferences of indicator species and also the use of mean Ellenberg indicator (EI) values for sites within that group. The use of EI values to assess environmental influences on pioneer vegetation produced meaningful results and these were supported by examining mean EI values within the context of successional change. Interpretation of EI values is consistent with the findings of Hill and Carey (1997), Ertsen et al. (1998) and Grimm (2000). The results have shown that EI values can be a useful research tool within the context of pioneer vegetation and primary succession. Their use was to some extent limited by the lack of available values for a number of species but only one frequently recorded pioneer species (*Salix glauca*) was excluded from the calculation of mean values. Furthermore, the results are ecologically meaningful.

Direct gradient analysis of sites according to altitude and distance east provided an effective method of assessing the geographical distribution of individual pioneer sites and communities and of testing the conclusions reached by indirect gradient analysis (ordination). The combination of methods used to assess the relative influence of altitude and distance east, and of moisture, light, pH and nitrogen levels to species composition produced convincing evidence of the most important factors. However, other potentially important environmental variables were not included in the analysis. Of particular value was the use of variance partitioning to assess the relative influence of each variable. Without this method, it would not have been possible to determine the significance of each variable to the total explained variance, although this is based on canonical correspondence analysis which is considered by many authors to produce a misleading ordination. This method also highlights the need to assess correlations between environmental factors and ordination axis scores based on the total variance explained. Regression of ordination scores onto environmental variables (McCune and Mefford 1999a) was valuable in analyzing compositional gradients in relation to those variables but it did not quantify the amount of variance explained. The combination of EI values and variance partitioning showed that for the glacier forelands, although there were significant correlations between mean EI values and ordination axes, they were not explaining a significant amount of underlying variation in species composition.

Use of a different quadrat size for the glacier foreland data set was an initial cause for concern, as the literature states that direct comparisons between results using different quadrat sizes are not possible, e.g. McCune and Grace (2002). However, the results of the experiment outlined in section 3.2.4 showed that, for the glacier foreland vegetation, the difference in species *relative frequency* obtained from the two quadrat sizes is unlikely to be a problem and suggests relative frequency may be a generally appropriate method for comparing data sets based on different quadrat sizes. As this thesis aims to quantify vegetation rather than floristics, the omission of relatively rare species does not constitute a major problem. Furthermore, in order to avoid misleading interpretations, the data sets were first analyzed independently before being combined in a single analysis.

8.12 Summary

1. The characteristics of the most frequent pioneers are consistent with those identified by previous research, i.e. perennial species with small, wind-dispersed seeds. However, on the glacier forelands and in additional habitats, adaptation for water-dispersal was also notable. Site conditions, rather than dispersal distance, are therefore likely to be limiting factors for

most pioneer species, with the exception of nitrogen-fixers, which were absent from the most isolated sites.

2. A number of distinct pioneer communities and sub-communities, with predominantly contiguous geographical distributions, have been identified within the study region, indicating that the early stages of colonization are more predictable than previous research suggests. Within- and between-community variability (at the regional scale) are influenced by two main environmental axes: an altitude-continentality-moisture axis, and a pH-nutrient-disturbance axis, within a continuum of variation.

3. Analysis based on Ellenberg's indicator values proved important in understanding key differences between pioneer communities, and in interpreting ordination axes and successional change at regional- and habitat-scales. The trends identified were consistent with previous research and support a geoecological model of successional change.

4. Overall successional trajectories were divergent on glacier forelands and convergent on roadsides, consistent with the association of divergence with relatively harsh environments and convergence with stronger biotic influence. Analysis according to altitude revealed divergence below 400 m on roadsides due to human influence, strong convergence from 420 to 800 m, and decreasing convergence with increasing altitude above 800 m due to the lessening of biotic influence and increasing environmental severity with altitude. In both habitats, there was little successional change at the highest altitudes (above 1600 m). The results therefore indicate that successional trajectories vary according to habitat and altitude, both of which have considerable implications for any generalizations based on analysis of more limited data sets.

5. The overall approach has enabled a thorough and original investigation of the research questions using a wide range of advanced, numerical analytical methods. This confers a degree of confidence in the results which would not be possible from a narrower approach. Comparisons between more than

one method of classification and ordination have also given greater confidence in the reliability of the results. Original contributions have included the application of relatively new techniques, such as multiresponse permutation procedure and variance partitioning, to the investigation of plant communities and successional trajectories. In particular, the use of a combination of complementary techniques has gone a considerable way towards producing an objective rather than arbitrary definition of pioneer communities within the study region. The research strategy, based on the inclusion of sites across regional and altitudinal gradients, has allowed analysis of variation at regional and local scales, while the use of Ellenberg's indicator values has enabled further analysis of habitat-scale variability.

9 CONCLUSIONS

9.1 Introduction

This chapter summarizes the main conclusions of the thesis and its most important contributions to the field. As well as summarizing the main substantive findings, it includes the methodological contribution, the strengths and limitations of the project, and a number of suggestions for extending the work.

Previous research has not focused primarily on the pioneer stage of primary succession, but has tended to consider it within the context of longer term successional change. Furthermore, comparisons between primary successional sites have tended to be a secondary consideration in previous studies (Matthews 1992, Walker and del Moral 2003). Walker's (1999) book on disturbed ecosystems (natural and anthropogenic) and much `restoration ecology' research have given greater weight to the pioneer stage but even here the pioneer stage is usually given less attention than later stages. By making the pioneer stage the main focus for this study and by including a large number of sites from different habitats, this thesis has aimed to provide a thorough and comprehensive approach to the fundamentals of early successional vegetation.

The main aim of this thesis was to investigate the nature of pioneer vegetation on disturbed sites in the Jotunheim and Jostedalsbreen regions of southern Norway and, in particular to describe the overall characteristics of the pioneer vegetation and the extent of its variability (see summaries to chapters 4 and 5). In conjunction with this were the objectives of investigating the response of the pioneer vegetation to altitudinal and regional gradients within the study area and identifying additional environmental influences using Ellenberg's indicator values (see chapter 6 summary). Finally, data from the pioneer and later stages of succession were used to address the objective of describing the influence of altitude on successional trajectories (see chapter 7 summary). The main conclusions in relation to these aims and objectives are outlined below.

9.2 Variability of the pioneer vegetation

Although considerable variability in pioneer species composition is a characteristic of all three data sets (with a mean Sørensen dissimilarity ranging from 65% for glacier forelands to 81% for roadsides), there is a degree of predictability in the key characteristics of the pioneer species, which is not dependent on habitat-type, most species being perennial, wind-dispersed or vegetatively-propagated grasses and forbs plus a small number of shrubs and trees. However, pioneer species on glacier forelands and in additional habitats often have water-dispersed propagules.

There is also convincing evidence of the existence of a small number of pioneer communities and sub-communities with a clear altitudinal and, to a lesser extent, regional distribution. The three main pioneer communities were identified as *Deschampsia cespitosa-Plantago major,* which was restricted to roadsides, *Deschampsia flexuosa-Salix glauca,* which was present on roadsides and in additional habitats and *Festuca ovina-Poa alpina,* which was found in all three data sets and which was present on virtually all glacier forelands. The *D. cespitosa-P. major* roadside pioneer community is therefore the only one that is habitat-specific. At the level of six sub-communities, this community is split into two sub-communities which are exclusive to roadsides (*Plantago major-Trifolium repens* and *Deschampsia cespitosa-Taraxacum* aggregate). The higher altitude *F. ovina-P. alpina* community can be divided into three sub-communities (*Cerastium alpinum-Ranunculus glacialis, Festuca ovina-Luzula spicata* and *Phleum alpinum-Sagina saginoides*), although the latter two sub-communities are less clearly demarcated and are considered to represent a continuum of change along a moisture gradient. The *D. flexuosa-S. glauca* community is not sub-divided further but becomes the D. flexuosa-Betula pubescens “sub-community” at this level of classification.

It is therefore possible to state that three distinct communities exist within the pioneer vegetation of the study area and that within these communities, six sub-communities can be detected, which constitute sub-division along a continuum of variation. Two major environmental gradients have been shown to influence pioneer species composition: an altitudinal-continental-moisture gradient and a pH-nutrient-disturbance gradient. These are largely in keeping with the gradients identified within successional vegetation on Storbreen glacier foreland by Matthews and Whittaker (1987).

Although a degree of consistency in the pioneer species recorded on glacier forelands has been reported in previous research (Caccianiga et al. 2001, Caccianiga and Andreis 2004, Haugland and Beatty 2005), this project has both reinforced these findings and extended their applicability to other habitats. Conversely, the results show that the high degree of stochasticity in pioneer vegetation has been overestimated by other researchers (Walker and del Moral 2003).

9.3 Variation on altitudinal and continentality gradients

Geographical variation and the influence of altitude and continentality on the distribution of pioneer vegetation has previously been somewhat neglected. Whereas the climax vegetation is known to vary along these gradients in a largely predictable way, the response of the pioneer stage is poorly understood by comparison. The study of successional seres along environmental gradients such as elevation also provides an untapped resource for research into successional processes and trajectories (Walker and del Moral 2003). Data collected in connection with this research project provide a record of vegetation across a long altitudinal and continental gradient, allowing assessment of the effects of these two factors on pioneer colonization and subsequent successional trajectories.

Clear altitudinal patterns of distribution were identified for the majority of pioneer communities and sub-communities along the comprehensive altitudinal gradient provided by the roadside verge data set. Variance partitioning confirmed the extent to which altitude is the most important factor, independently explaining a significant proportion of the variance in pioneer species composition within all three data sets (50% for glacier forelands, 16% for roadsides, 12% for additional habitats), while continentality also explained a significant proportion of the variance, particularly on the glacier forelands (33% for glacier forelands, 6% for roadsides, 5% for additional habitats). The altitudinal distribution of the three pioneer communities was modified by the inclusion of glacier foreland and additional habitat sites, which extended the lower altitudinal limit of the high altitude *Festuca ovina-Poa alpina* community from 740 to 80 m. Therefore, although the primary influence on pioneer colonization appears to be related to two main environmental gradients, the presence of glaciers creates habitat-specific conditions which may have an over-riding effect. This finding also has important implications for the effects of current climate change on pioneer distribution: it suggests that, following further deglacierization, many pioneer species may be restricted to higher altitudes, as appropriate conditions for low altitude colonization disappear.

9.4 EI values and assessment of environmental influences

The value of using Ellenberg's indicator (EI) values to provide further evidence of environmental influences on the pioneer stage of succession has not previously been tested and their application has therefore been successfully extended by this thesis. Variation in mean weighted EI values added considerably to the understanding of community distribution patterns, enabling the altitudinal-continental axis to be related to mean moisture levels and the disturbance/successional change axis to be related to mean values for pH and nitrogen. Variance partitioning showed that mean EI values independently explain a significant proportion of the variability in species composition of sites on roadsides (pH 13%, light 11%, moisture 11% ,nitrogen 10%) and in the additional pioneer habitats (moisture 20%, pH 15%, nitrogen 12%, light 10%) but not on the glacier forelands where overall variance was also comparatively low. The latter finding was also valuable in supporting the evidence for a single pioneer community on the glacier forelands. Ecological explanation of mean EI values for moisture and nitrogen was consistent with previous interpretations (Hill and Carey 1997, Ertsen et al. 1998, Southall et al. 2003).

9.5 Pioneer vegetation within the context of successional change

A comparison of the relative variability of the pioneer and later stages of succession provided an additional perspective on the pioneer vegetation and enabled analysis of the nature of successional trajectories within the study area, particularly in relation to altitude. The key finding was that successional trajectories are influenced by altitude-related factors and vary according to habitat type.

On the glacier forelands, succession follows a divergent pattern (with mean dissimilarity increasing from 65% to 76%) from a single pioneer community to a more variable climax vegetation except at the highest altitudes (above 1620 m), where neither divergence nor convergence occurs and succession is relatively slow with little change in species composition between stages.

On the disturbed roadsides sites, the situation was more complicated, with overall convergence between pioneer and climax stages (with mean dissimilarity decreasing from 81% to 77%) but with considerable variation in successional trajectory according to altitude. Within the lowest altitudinal zone (20 – 400 m), a divergent pattern was observed, probably due to the influence of human activity on the climax vegetation, which created a mosaic of habitats including grazing pastures and arable farmland, in addition to the natural forested climax. At intermediate altitudes (420 – 1400 m), succession followed a convergent pattern in which the degree of convergence decreased with increasing altitude. This is assumed to be reflecting dominance by trees and shrubs, which decreases as abiotic environmental factors become more important with increasing altitude. Vegetation within the highest altitudinal zone (1420 – 1860 m), as on the glacier forelands, follows neither pattern and, again, there is considerable similarity between pioneer and climax stages suggesting a slow rate of succession. The results for the roadside data set are not consistent with the theory that pioneer communities are generally less well-defined than climax communities (Friedel 1938, Solomina 1989). However, the overall pattern supports the theory that divergent pathways are associated with the relatively harsh environments found on glacier forelands, while convergence occurs in conjunction with the stronger biotic controls exerted by the adjacent climax vegetation on roadsides (Matthews 1992).

Successional change on roadsides and glacier forelands is accompanied by a decrease in mean EI values for pH (3.9-3.0 on roadsides, 5.0-3.1 on forelands), light (7.0-6.4 on roadsides, 7.8-7.0 on forelands) and nitrogen (3.5-2.9 on roadsides, 3.3-2.6 on forelands), while the mean EI value for moisture increases with succession on roadsides (5.2-5.6) but not on glacier forelands. The latter is thought to be mainly due to the fact that they are generally well supplied with meltwater, whereas the pioneer zone on the roadsides is designed to facilitate drainage away from the roads. These results are consistent with the successional decline in pioneers being due to a combination of factors, including decreasing disturbance and an associated decrease in the availability of minerals due to leaching and acidification. The decrease in the mean EI value for light with succession is consistent with an increase in vegetation cover and the onset of biotic interactions such as competition. The use of mean EI values therefore proved useful in interpreting successional processes and extending the results of other researchers (Messer 1988, Whittaker 1993, Grimm 2000).

9.6 The methodological contribution

The combination of analytical techniques used has provided a comprehensive approach to assessing and describing variability within the pioneer stage of succession. Non-metric multidimensional scaling (NMS) was shown to perform better than detrended correspondence analysis (DCA) on the basis of its representation of distances in the original matrix. (The coefficients of determination for the roadside data set are 67% for two-dimensional NMS and 53% for three-dimensional DCA; and for forelands the corresponding coefficients are 76% for two-dimensional NMS and 60% for three-dimensional DCA.)

Inherent in any classification method is the limitation of not knowing the number or discreteness of the communities that have been defined or, indeed, whether they are merely subjective divisions along a continuum of variation in species composition. In an attempt to avoid unduly influencing the results by arbitrary decision-making (Kent 2006), a number of methods were used in this thesis to address this difficulty. Cluster analysis groups at each level of classification were assessed using multiple response permutation procedure (MRPP) and indicator species analysis (ISA). These enable identification of the level at which groups were characterized by the greatest within-group agreement and between-group separation and the greatest number of significant indicator species. MRPP results also demonstrated that the groups produced by cluster analysis were more clearly separated than those produced by TWINSPAN. The use of group centroids (± 2 standard deviations for each axis of the ordination diagrams) constitutes a methodological improvement for visually assessing groups and sub-groups. Additionally, the use of the discreteness index provides a quantitative measure of the relative separation between and agreement within groups. ISA was a valuable method on which to base description and ecological interpretation of groups in terms of their most important species.

The use of relative frequency as a measure of vegetation composition has its limitations (McCune and Grace 2002). It was chosen as a rapid method, allowing a large data set to be compiled, but it restricts the comparability of the results with other research. However, this has been addressed within the thesis and the limitations are perhaps not as great as would be expected. Indeed, there are certain advantages in playing down both the absolute abundance of dominant species and the presence of rarities in vegetation study. The problem of comparing and combining data collected using different quadrat sizes was to a large extent overcome by the methods used; i.e. individual assessment of each data set before performing a combined analysis. Furthermore, differences in the relative frequency of species using different quadrat sizes were found, in the context of the research questions addressed in this thesis, to be within acceptable limits.

9.7 The potential applied contribution

The implications of this research for vegetation restoration are potentially important, as understanding of pioneer vegetation and successional theory has been advanced in several respects. The findings show that pioneer communities and sub-communities are more strongly influenced by altitude-related factors than by habitat type and exhibit a well-developed altitudinal zonation. As this zonation is primarily determined by climate, global warming would be expected to change the altitudinal limits of component species and thus affect these communities. This thesis has also shown that the effects of climate change in decreasing the number and extent of glaciers in the region (Nesje et al. 2006) would further influence the altitudinal limits of those species that have a distribution at lower altitudes, which is restricted to the periglacial pioneer zone.

The increasing effects of tourism on mountainous regions, in particular, would make this information of use in conservation management protocols. A number of common pioneer plants within the study region are rare in other European countries such as the United Kingdom, where they may persist as populations of relict arctic-alpine species in postglacial refugia (Jones and Richards 1956, Anon 2001). It is therefore important that the habitat requirements of these species are investigated thoroughly.

9.8 Strengths and limitations of the thesis

The strengths of this thesis lie in (1) the combined use of a number of analytical methods to approach each research question, enabling the aims to be addressed from more than one perspective; and (2) the use of relatively new numerical techniques at the research frontier of vegetation analysis. Combined with (3) the large data set, (4) the use of data from a number of different habitats, and (5) the research design, this approach has yielded generalizations about the characteristics of pioneer vegetation and subsequent successional trajectories within the study area, and has made a contribution to ecological and biogeographical theory.

There are perhaps two main limitations to this study: one relating to the vegetation recording, the other to the environmental variables. The fact that lower plants were omitted from the data collection also limits the description and interpretation of the pioneer communities. However, bryophytes and lichens, do not form a major component of the pioneer vegetation on the majority of sites sampled (they become more important in later successional stages). This is particularly true of the roadside sites, where they were usually absent. Although it would have been interesting to assess the relative importance of these cryptogams in different habitats, this was not possible in the time available.

Limitations are also inherent in the restricted number of variables considered when analyzing possible environmental influences on pioneer vegetation and successional trajectories. This was again mainly due to time constraints which did not allow direct measurement of environmental parameters and partly due to the absence of data on EI values for temperature and continentality for the majority of pioneer species. Altitude and continentality are nevertheless surrogates for important environmental complexes at the regional scale.

9.9 Suggestions for further work

The research conducted for this thesis could be usefully extended in a number of ways. Although the combined data set is large, the number of sites sampled in additional pioneer habitats could be increased, so that each individual habitat would have a larger number of representative sites. This would enable the influence of altitude to be assessed in a wider range of habitats. Furthermore, sampling of climax vegetation adjacent to the additional pioneer habitats would extend the conclusions regarding successional trajectories. Variation in the rate of succession according to altitude and habitat could also be investigated using this data set.

Analysis of the data set could be extended with the aim of investigating further the nature of boundaries between pioneer communities and sub-communities in geographical, vegetational and environmental spaces. For example, analysis of variation in the frequency of indicator species at the geographical boundaries between groups would be possible for the roadside data set. The influence of spatial autocorrelation (Legendre 1993), particularly in relation to within-community variation along roadside verges would also be useful. In addition, the importance of roads and rivers as dispersal corridors between altitudinal zones could be investigated further. In particular, the value of roadside verges as a network of habitats of conservation value is being increasingly appreciated (Truscott et al. 2005).

If the results of this study were to be considered universally applicable, they would need to be tested in a number of different geographical regions and primary successional chronosequences. A logical extension of this thesis would therefore be to carry out investigations using similar methods in, for example other alpine regions and in other primary successional habitats such as volcanic deposits. The use of EI values in characterizing pioneer vegetation and subsequent successional processes also has further potential, which needs to be assessed in other regions. An interesting extension of the use of indicators would be to develop a set of "successional" indicator values based on the mean position of a species within a chronosequence.

9.10 Final word

This thesis has made at least four fundamental contributions to theory in the field of vegetation science. First, it has been shown that the pioneer stage of primary succession is less variable and more predictable than previously assumed. Second, at the regional scale, a number of pioneer communities and sub-communities have been recognized, which are explicable in terms of the dominant influence of altitude and the secondary influence of continentality. Third, these patterns in pioneer colonization have been convincingly linked to successional trajectories and climax communities. Fourth, at the habitat scale, a number of environmental influences related in particular to climatic and nutrient relations have been elucidated. In addition, a number of methodological contributions have been made, including the successful use of Ellenberg's indicator values within the context of succession, and the use of a combination of state-of-the-art numerical methods to approach the research questions from multiple perspectives.

BIBLIOGRAPHY

Abella, S. R., and W. W. Covington. 2004. Monitoring an Arizona Ponderosa Pine restoration: sampling efficiency and multivariate analysis of understory vegetation. Restoration Ecology **12**:359-367.

Aikio, S., H. Vare, and R. Strommer. 2000. Soil microbial activity and biomass in the primary succession of a dry heath forest. Soil Biology & Biochemistry **32**:1091-1100.

Anon. 2001. Natural Heritage Trends Scotland 2001. Scottish Natural Heritage, Perth.

Anon. 2005. Handbok i Plantekultur. Norgesfor.

Anthelme, F., J. C. Villaret, and J. J. Brun. 2007. Shrub encroachment in the Alps gives rise to the convergence of sub-alpine communities on a regional scale. Journal of Vegetation Science **18**:355-362.

Aplet, G. H., and P. M. Vitousek. 1994. An age-altitude matrix analysis of Hawaiian rain-forest succession. Journal of Ecology **82**:137-147.

Archer, A. C. 1973. Plant succession in relation to a sequence of hydromorphic soils formed on glacio-fluvial sediments in the alpine zone of the Ben Ohau Range, New Zealand. New Zealand Journal of Botany **11**:221-348.

Arevalo, J. R., J. D. Delgado, R. Otto, A. Naranjo, M. Salas, and J. M. Fernandes-Palacios. 2005. Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspectives in Plant Ecology Evolution and Systematics **7**:185-202.

Auerbach, M., and A. Shmida. 1993. Vegetation change along an altitudinal gradient on Mt. Hermon, Israel - no evidence for discrete communities. Journal of Ecology **81**:25-33.

Aune, B. 1993. Temperatur normaler, normalperiode 1961-1990, Rapport 02/93. Den Norske Meteorologiske Instituut, Oslo.

Austin, M. P. 2005. Vegetation and environment: discontinuities and continuities. Pages 52-84 *in* E. van der Maarel, editor. Vegetation Ecology. Blackwell Publishing, Oxford.

Austrheim, G. 2002. Plant diversity patterns in semi-natural grasslands along an elevational gradient in southern Norway. Plant Ecology **161**:193-205.

Austrheim, G., M. Evju, and A. Mysterud. 2005. Herb abundance and life-history traits in two contrasting alpine habitats in southern Norway. Plant Ecology **179**:217-229.

Ballantyne, C. K., and J. A. Matthews. 1982. The Development of Sorted Circles on Recently Deglaciated Terrain, Jotunheimen, Norway. Arctic and Alpine Research **14**:341-354.

Beals, E. W. 1969. Vegetational change along altitudinal gradients. Science **165**:981-985.

Bickerton, R. H., and J. A. Matthews. 1992. On the accuracy of lichenometric dates: an assessment based on the 'Little Ice Age' moraine sequence of Nigardsbreen, southern Norway. The Holocene **2**:227-237.

Bickerton, R. H., and J. A. Matthews. 1993. 'Little Ice Age' variations in outlet glaciers from the Jostedalsbreen ice-cap, southern Norway: a regional lichenometric-dating study of ice-marginal moraine sequences and their climatic significance. Journal of Quaternary Science **8**:45-66.

Birks, H. J. B. 1980. The present flora and vegetation of the moraines of the Klutlan Glacier, Yukon Territory, Canada. Quaternary Research **14**:60-86.

Bliss, L. C. 1971. Arctic and Alpine Plant Life Cycles. Annual Review of Ecology and Systematics **2**:405-438.

Bossuyt, B., O. Honnay, and M. Hermy. 2003. An island biogeographical view of the successional pathway in wet dune slacks. Journal of Vegetation Science **14**:781-788.

Brown, R. T., and J. T. Curtis. 1952. The upland conifer-hardwood forests of northern Wisconsin. Ecological Monographs **27**:217-234.

Bruun, H. H., J. Moen, R. Virtanen, J. A. Grytnes, L. Oksanen, and A. Angerbjorn. 2006. Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. Journal of Vegetation Science **17**:37-46.

Bullock, J. 1996. Plants. Pages 111-138 *in* W. J. Sutherland, editor. Ecological Census Techniques. Cambridge University Press, Cambridge.

Burrows, C. J. 1990. Processes of Vegetation Change. Unwin, London.

Caccianiga, M., and C. Andreis. 2004. Pioneer herbaceous vegetation on glacier forelands in the Italian Alps. Phytocoenologia **34**:55-89.

Caccianiga, M., C. Andreis, and B. Cerabolini. 2001. Vegetation and environmental factors during primary succession on glacier forelands: some outlines from the Italian Alps. Plant Biosystems **135**:295-310.

Caccianiga, M., A. Luzzaro, S. Pierce, M. Ceriani, and B. Cerabolini. 2006. The functional basis of a primary succession resolved by CSR classification. Oikos **112**:10-20.

Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature **417**:844-848.

Cazares, E., J. M. Trappe, and A. Jumpponen. 2005. Mycorrhiza-plant colonization patterns on a subalpine glacier forefront as a model system of primary succession. Mycorrhiza **15**:405-416.

Chapin III, F. S. 1993. Physiological controls over plant establishment in primary succession. Pages 161-178 *in* J. Miles and D. W. H. Walton, editors. Primary Succession on Land. Blackwell, Oxford.

Chapin III, F. S., L. R. Walker, C. L. Fastie, and L. C. Sharman. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs **64**:149-175.

Christensen, N. L., and R. K. Peet. 1984. Convergence during secondary forest succession. Journal of Ecology **72**:25-26.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117-143.

Clements, F. E. 1916. Plant Succession: An Analysis of the Development of Vegetation. 242, Carnegie Institute of Washington, Washington DC.

Clements, F. E. 1936. Nature and structure of the climax. Journal of Ecology **24**:252-284.

Collins, S. L., S. M. Glenn, and D. W. Roberts. 1993. The hierarchical continuum concept. Journal of Vegetation Science **4**:149-156.

Cottam, G. 1966. Vegetational continuum. Science **152**:546-547.

Curtis, J. T. 1955. A prairie continuum in Wisconsin. Ecology **36**:558-566.

Curtis, J. T., and R. P. McIntosh. 1951. An upland continuum in the prairie-forest border region of Wisconsin. Ecology **32**:476-496.

Daubenmire, R. 1966. Vegetation: Identification of typal communities. Science **151**:291-298.

del Moral, R. 1998. Early succession on lahars spawned by Mount St. Helens. American Journal of Botany **85**:820-828.

del Moral, R., and L. C. Bliss. 1993. Mechanisms of primary succession: Insights resulting from the eruption of Mount St. Helens. Pages 1-66 *in* Advances in Ecological Research.

del Moral, R., and A. J. Eckert. 2005. Colonization of volcanic deserts from productive patches. American Journal of Botany **92**:27-36.

del Moral, R., and E. E. Ellis. 2004. Gradients in compositional variation on lahars, Mount St. Helens, Washington, USA. Plant Ecology **175**:273-286.

del Moral, R., and C. Jones. 2002. Vegetation development on pumice at Mount St. Helens, USA. Plant Ecology **162**:9-22.

del Moral, R., and I. L. Lacher. 2005. Vegetation patterns 25 years after the eruption of Mount St. Helens, Washington. American Journal of Botany **92**:1948-1956.

del Moral, R., D. M. Wood, and J. H. Titus. 2005. Proximity, microsites, and biotic interactions during early succession. Pages 93-109 *in* V. H. Dale, F. J. Swanson, and C. M. Crisafulli, editors. Ecological Responses to the 1980 Eruption of Mount St. Helens. Springer.

Dlugosch, K., and R. del Moral. 1999. Vegetational heterogeneity along elevational gradients. Northwest Science **73**:12-18.

Duffey, E. 2004. Definition of ecological community. Bulletin of the British Ecological Society **35**:21.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **61**:345-366.

Ecke, F., and H. Rydin. 2000. Succession on a land uplift coast in relation to plant strategy theory. Ann. Bot. Fennici **37**:163-171.

Egler, F. E. 1954. Vegetation schience concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio **4**:412-417.

Ellenberg, H. 1974. Zeigerwerte von Gefasspflanzen Mitteleuropas. Scripta Geobotanica **9**:97-219.

Ellenberg, H., H. E. Weber, R. Dull, V. Wirth, W. Werner, and D. Paulissen. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica **18**:1-166.

Elven, R. 1978a. Association analysis of moraine vegetation at the glacier Hardangerjokulen, Finse, South Norway. Norwegian Journal of Botany **25**:171-191.

Elven, R. 1978b. Vegetasjonen ved Flatisen og Osterdalsisen, Rana, Nordland, med vegetationskart over Vesterdalen i 1: 5,000. Norske Videnskabers Selskab.

Enright, N. J., B. P. Miller, and R. Akhter. 2005. Desert vegetation and vegetation-environment relationships in Kirthar National Park, Sindh, Pakistan. Journal of Arid Environments **61**:397-418.

Erschbamer, B., and V. Retter. 2004. How long can glacier foreland species live? Flora **199**:500-504.

Ertsen, A. C. D., J. R. M. Alkemade, and M. J. Wassen. 1998. Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in the Netherlands. Plant Ecology **135**:113-124.

Ewald, J. 2003. The sensitivity of Ellenberg indicator values to the completeness of vegetation releves. Basic and Applied Ecology **4**:507-513.

Faegri, K. 1933. Uber die Langenvariationen einiger Gletscher des Jostedalsbre und die dadurch bedingten Pflanzensukzessionen. Bergens Museums Arbok 1933, Naturvidenskapelig rekke:1-255.

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio **69**:57-68.

Fastie, C. L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology **76**:1899-1916.

Fitter, R., A. Fitter, and M. Blamey. 1978. The Wild Flowers of Britain and Northern Europe. Collins, London.

Fitter, R., A. Fitter, and A. Farrer. 1984. Grasses, Sedges, Rushes and Ferns of Britain and Northern Europe. Harper Collins, London.

Førland, E. J. 1993. Nedbornnormaler normalperiode 1961-90, Rapport 39/93. Den Norske Meteorologiske Institutt, Oslo.

Foster, B. L., and D. Tilman. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. Plant Ecology **146**:1-10.

Frenot, Y., J. C. Gloaguen, M. Cannavacciuolo, and A. Bellido. 1998. Primary succession on glacier forelands in the subantarctic Kerguelen Islands. Journal of Vegetation Science **9**:75-84.

Friedel, H. 1938. Die Pflanzenbesiedlung im Vorfeld des Hintereisferners. Zeitschrift fur Gletscherkunde **26**:73-86.

Fuller, R. N. 1999. The role of refugia in primary succession on Mount St. Helens, Washington. M.S. Thesis. University of Washington, Seattle.

Gillman, M. 1996. Community composition, structure and function. Pages 109-159 *in* G. Bearman, S. Dunleavy, G. Riley, B. Sharma, and M. Swithenby, editors. S328 Ecology. Open University, Milton Keynes.

Gjaerevoll, O., and R. Jorgensen. 2002. Mountain Flowers of Scandinavia, English edition. Gyldendal, Trondheim.

Gleason, H. A. 1917. The structure and development of the plant association. Bulletin of the Torrey Botanical Club **44**:463-481.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club **53**:7-26.

Gleason, H. A. 1927. Further views on the succession concept. Ecology **8**:299-236.

Gleason, H. A. 1939. The individualistic concept of the plant association. American Midland Naturalist **21**:92-110.

Goodall, D. W. 1963. The continuum and the individualistic association. Vegetatio **7**:297-316.

Grabherr, G., M. Gottfried, and H. Pauli. 1994. Climate effects on mountain plants. Nature **369**:488.

Griggs, R. F. 1934. The problem of arctic vegetation. Journal of the Washington Academy of Sciences **24**:153-175.

Grime, P. J. 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties., 2nd edition. John Wiley & Sons, Chichester.

Grimm, G. A. 2000. Vegetation Succession on Glacier Forelands in the Jostedalsbreen Region and Jotunheimen, South-Central Norway. Unpublished DPhil thesis. University of Oxford.

Grubb, P. J. 1986. The ecology of establishment. Pages 83-97 *in* A. D. Bradshaw, D. A. Goode, and E. H. P. Thorp, editors. Ecology and design in landscape. Blackwell, Oxford.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos **38**:210-221.

Harper, J. L., J. N. Clatworthy, I. H. McNaughton, and G. S. Sagar. 1961. The evolution of closely related species living in the same area. Evolution **15**:209-227.

Hatton, T. J., and N. E. West. 1987. Early seral trends in plant community diversity on a recontoured surface mine. Vegetatio **73**:21-29.

Haugland, J. E. 2006. Short-term periglacial processes, vegetation succession and soil development within sorted patterned ground: Jotunheimen, Norway. Arctic, Antarctic and Alpine Research **38**:82-89.

Haugland, J. E., and S. W. Beatty. 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. Journal of Biogeography **32**:145-153.

Hayward, J. 1995. A New Key to Wild Flowers. Cambridge University Press, Cambridge.

Heer, C., and C. Korner. 2002. High elevation pioneer plants are sensitive to mineral nutrient addition. Basic and Applied Ecology **3**:39-47.

Hill, M. O., R. G. H. Bunce, and M. W. Shaw. 1975. Indicator species analysis, a divisive polythetic method for classification, and its application to a survey of native pinewoods in Scotland. Journal of Ecology **63**:597-613.

Hill, M. O., and P. D. Carey. 1997. Prediction of yield in the Rothamsted Park Grass Experiment by Ellenberg indicator values. Journal of Vegetation Science **8**:579-586.

Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio **42**:47-58.

Hodkinson, I. D., S. J. Coulson, J. Harrison, and N. R. Webb. 2001. What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic - some counter-intuitive ideas on community assembly. Oikos **95**:349-352.

Hodkinson, I. D., S. J. Coulson, and N. R. Webb. 2003. Community assembly along proglacial chronosequences in the high Arctic: vegetation and soil development in north-west Svalbard. Journal of Ecology **91**:651-663.

Hovd, H., and A. Skogen. 2005. Plant species in arable field margins and road verges of central Norway. Agriculture, Ecosystems and Environment **110**:257-265.

Isaksen, K., Hauck, C., Gudevang, E., Odegard, R.S. and Sollid, J.L. 2002. Mountain permafrost distribution in Dovrefjell and Jotunheimen, southern Norway, based on BTS and DC resistivity tomography data. Norsk Geografisk Tidsskrift **56**:122-136.

Johnston, F. M., and S. W. Johnston. 2004. Impacts of road disturbance on soil properties and on exotic plant occurrence in subalpine areas of the Australian Alps. Arctic, Antarctic and Alpine Research **36**:201-207.

Jones, C. C., and R. del Moral. 2005a. Effects of microsite conditions on seedling establishment on the foreland of Coleman Glacier, Washington. Journal of Vegetation Science **16**:293-300.

Jones, C. C., and R. del Moral. 2005b. Patterns of primary succession on the foreland of Coleman Glacier, Washington, USA. Plant Ecology **180**:105-116.

Jones, G. A., and G. H. R. Henry. 2003. Primary plant succession on recently deglaciated terrain in the Canadian High Arctic. Journal of Biogeography **30**:277-296.

Jones, V., and P. W. Richards. 1956. *Saxifraga oppositifolia* L. Journal of Ecology **44**:300-316.

Jumpponen, A., H. Vare, K. G. Mattson, R. Ohtonen, and J. M. Trappe. 1999. Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain. Journal of Ecology **87**:98-105.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science **3**:157-164.

Kenkel, N. C., and L. Orloci. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology **67**:919-928.

Kent, M. 2006. Numerical classification and ordination methods in biogeography. Progress in Physical Geography **30**:399-408.

Kent, M., and P. Coker. 1992. Vegetation Description and Analysis: a Practical Approach. Belhaven Press, London.

Kessler, M. 2000. Altitudinal zonation of Andean cryptogam communities. Journal of Biogeography **27**:275-282.

Klanderud, K., and H. J. B. Birks. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. The Holocene **13**:1-6.

Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. Ecology **70**:36-47.

Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling. Sage Publications, Beverley Hills.

Lance, G. N., and W. T. Williams. 1967. A general theory of classification sorting strategies. I. Hierarchical systems. Computer Journal **9**:373-380.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology **74**:1659-1673.

Legendre, P., and L. Legendre. 1998. Numerical Ecology, 2nd edition. Elsevier, Amsterdam.

Leps, J., J. Michalek, O. Rauch, and P. Uhlik. 2000. Early succession on plots with the upper soil horizon removed. Journal of Vegetation Science **11**:259-264.

Leps, J., and P. Smilauer. 2003. Multivariate Analysis of Ecological Data using CANOCO. Cambridge University Press, Cambridge.

Leyer, I. 2006. Dispersal, diversity and distribution patterns in pioneer vegetation: The role of river-floodplain connectivity. Journal of Vegetation Science **17**:407-416.

Lid, J., and D. T. Lid. 1994. Norsk Flora. Det Norske Samlaget, Oslo.

Loffler, J., and O.-D. Finch. 2005. Spatio-temporal gradients between high mountain ecosystems in central Norway. Arctic, Antarctic and Alpine Research **37**:499-513.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. J Wiley, London.

Matthews, J. A. 1978a. An application of non-metric multidimensional scaling to the construction of an improved species plexus. Journal of Ecology **66**:157-173.

Matthews, J. A. 1978b. Plant colonization patterns on a gletschervorfeld, southern Norway: a meso-scale geographical approach to vegetation change and phytometric dating. Boreas **7**:155-178.

Matthews, J. A. 1979a. Refutation of Convergence in a Vegetation Succession. Naturwissenschaften **66**:47-49.

Matthews, J. A. 1979b. A study of the variability of some successional and climax plant assemblage-types using multiple discriminant analysis. Journal of Ecology **67**:255-271.

Matthews, J. A. 1992. The Ecology of Recently-Deglaciated Terrain. CUP, Cambridge.

Matthews, J. A. 1996. Classics in physical geography revisited. Gleason,HA 1939: The individualistic concept of the plant association. The American Midland Naturalist 21, 92-110. Progress in Physical Geography **20**:193-203.

Matthews, J. A. 1999. Disturbance regimes and ecosystem response on recently-deglaciated substrates. Pages 17-37 *in* L. R. Walker, editor. Ecosystems of Disturbed Ground. Elsevier, Amsterdam.

Matthews, J. A. 2005. 'Little Ice Age' glacier variations in Jotunheimen, southern Norway: a study in regionally controlled lichenometric dating of recessional moraines with implications for climate and lichen growth rates. Holocene **15**:1-19.

Matthews, J. A., and R. J. Whittaker. 1987. Vegetation Succession on the Storbreen Glacier Foreland, Jotunheimen, Norway - a Review. Arctic and Alpine Research **19**:385-395.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and M. J. Mefford. 1999a. PC-ORD Version 4: Multivariate Analysis of Ecological Data. User's Guide. MjM Software, Gleneden Beach, Oregon.

McCune, B., and M. J. Mefford. 1999b. PC-ORD. Multivariate Analysis of Ecological Data. Version 4.33. *in*. MjM Software, Oregon.

McGeoch, M. A., and S. L. Chown. 1998. Scaling up the value of bioindicators. Trends in Ecology & Evolution **13**:46-47.

McIntosh, R. P. 1958. Plant communities. Science **128**:115-120.

McIntosh, R. P. 1967. The continuum concept of vegetation. Botanical Review **33**:99-187.

Messer, A. c. 1988. Regional variations in the rates of pedogenesis and the influence of climatic factors on moraine chronosequences, southern Norway. Arctic and Alpine Research **20**:31-39.

Mielke, P. W. J., and K. J. Berry. 2001. Permutation Methods: A Distance Function Approach. Springer, New York.

Miles, J. 1979. Vegetation Dynamics. Chapman and Hall, London.

Miles, J., and D. W. H. Walton. 1993. Preface. Pages vii-viii *in* J. Miles and D. W. H. Walton, editors. Primary Succession on Land. Blackwell Scientific Publications, Oxford.

Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio **69**:89-107.

Moen, A. 1987. The regional vegetation of Norway; that of Central Norway in particular. Norsk Geografisk Tidsskrift **41**:179-225.

Nesje, A., J. Bakke, O. Lie, and S. O. Dahl. 2006. Dramatic future for Norwegian glaciers. Cicerone **1/2006**.

Nip-van der Voort, J., R. Hengeveld, and J. Haeck. 1979. Immigration rates of plant species in three Dutch polders. Journal of Biogeography **6**:301-308.

Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio **28**:795-800.

Økland, R. H. 1999. On variation explained by ordination and constrained ordination axes. Journal of Vegetation Science **10**:131-136.

Økland, R. H., and O. Eilertsen. 1994. Canonical Correspondence Analysis with variation partitioning: some comments and an application. Journal of Vegetation Science **5**:117-126.

Olsson, E. G. A., G. Austrheim, and S. N. Grenne. 2000. Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960-1993. Landscape Ecology **15**:155-170.

Olsson, E. G. A., S. K. Hanssen, and K. Ronningen. 2004. Different conservation values of biological diversity? A case study from the Jotunheimen mountain range, Norway. Norsk Geografisk Tidsskrift **58**:204-212.

Pakeman, R. J., J. P. Attwood, and J. Engelen. 1998. Sources of plants colonizing experimentally disturbed patches in an acidic grassland, in eastern England. Journal of Ecology **86**:1032-1041.

Pardoe, H. 1996. The influence of terrain age on the species composition of alpine "climax" heath communities in southern Norway. Oecologia Montana **5**:61-70.

Peat, H., and A. Fitter. 2007. Ecological Flora of the British Isles. www.york.ac.uk/res/ecoflora/cfm/ecofl/.

Peet, R. K. 1992. Community structure and ecosystem function. Pages 103-151 *in* S. D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant Succession: Theory and Prediction. Chapman & Hall, London.

Persson, A. 1964. The vegetation at the margin of the receding glacier Skaftafellsjokull, southeastern Iceland. Botaniska Notiser **117**:323-354.

Persson, S. 1981. Ecological indicator values as an aid in the interpretation of ordination diagrams. Journal of Ecology **69**:71-84.

Poore, M. E. D. 1964. Integration in the plant community. Journal of Ecology **52**:213-226.

Post, W. M., and J. D. Sheperd. 1974. Hierarchical Agglomeration. Unpublished typescript University of Wisconsin, Madison.

Raffl, C., M. Mallaun, R. Mayer, and B. Erschbamer. 2006. Vegetation succession pattern and diversity changes in a glacier valley, Central Alps, Austria. Arctic, Antarctic and Alpine Research **38**:421-428.

Rentch, J. S., R. H. Fortney, S. L. Stephenson, H. S. Adams, W. N. Grafton, and J. T. Anderson. 2005. Vegetation-site relationships of roadside plant communities in West Virginia, USA. Journal of Applied Ecology **42**:129-138.

Roberts, D. W. 1986. Ordination on the basis of fuzzy set theory. Vegetatio **66**:123-131.

Rose, F. 1981. The Wild Flower Key. Warne, London.

Rydin, H., and S. O. Borgegard. 1988. Primary succession over sixty years on hundred-year old islkets in Lake Hjalmaren, Sweden. Vegetatio **77**:159-168.

Ryvarden, L. 1971. Studies of seed dispersal I. Trapping of diaspores in the alpine zone at Finse, Norway. Norwegian Journal of Botany **18**:215-226.

Ryvarden, L. 1975. Studies in seed dispersal II. Winter-dispersed species at Finse, Norway. Norwegian Journal of Botany **22**:21-24.

Schauer, T. 1982. Cappelens Flora, Norwegian edition. J W Cappelens Forlag.

Schlag, R. N., and B. Erschbamer. 2000. Germination and establishment of seedlings on a glacier foreland in the central Alps, Austria. Arctic Antarctic and Alpine Research **32**:270-277.

Schmidtlein, S., and J. Ewald. 2003. Landscape patterns of indicator plants for soil acidity in the Bavarian Alps. Journal of Biogeography **30**:1493-1503.

Schubiger-Bossard, C. M. 1988. Die Vegetation des Rhonegletshervorfeldes, Ihre Sukzession und Naturraumliche Gliederung. Beitrage zur Geobotanischen Landesaufnahme der Schweiz **64**:1-228.

Scurfield, G. 1954. Biological flora of the British Isles: Deschampsia flexuosa (L.) Trin. Journal of Ecology **42**:225-233.

Shipley, B., and P. A. Keddy. 1987. The individualistic and community-unit concepts as falsifiable hypotheses. Vegetatio **69**:47-55.

Soininen, J., R. Paavola, and T. Muotka. 2004. Benthic diatom communities in boreal streams: community structure in relation to environmental and spatial gradients. Ecography **27**:330-342.

Solomina, O. N. 1989. Phytocoenic method. Pages 139-146 *in* L. R. Serebryanny, A. V. Orlov, and O. n. Solomina, editors. Moraines as a Source of Glaciological Information. Nauka, Moscow.

Southall, E. J., M. P. Dale, and M. Kent. 2003. Spatial and temporal analysis of vegetation mosaics for conservation: poor fen communities in a Cornish valley mire. Journal of Biogeography **30**:1427-1443.

Spence, J. R. 1989. Plant succession on glacial deposits of Mount Kenya, East Africa. Pages 279-290 *in* W. C. Mahaney, editor. Quaternary and Environmental Research on East African Mountains. Balkema, Rotterdam.

Stace, C. 1999. Field Flora of the British Isles. Cambridge University Press, Cambridge.

Stocklin, J., and E. Baumler. 1996. Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. Journal of Vegetation Science **7**:45-56.

Stork, A. 1963. Plant immigration in front of retreating glaciers, with examples from the Kebnekajse area, northern Sweden. Geografiska Annaler **45**:1-22.

Svoboda, J., and G. H. R. Henry. 1987. Succession in Marginal Arctic Environments. Arctic and Alpine Research **19**:373-384.

Tabachnik, B. G., and L. S. Fidell. 1989. Using Multivariate Statistics, 2nd edition. Harper & Row, New York.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology **69**:1167-1179.

ter Braak, C. J. F., and P. Smilauer. 2006. Canoco for Windows version 4.54. *in*. Biometris - Plant Research International, Wageningen.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. The American Naturalist **125**:827-852.

Truscott, A. M., S. C. F. Palmer, G. M. McGowan, J. N. Cape, and S. Smart. 2005. Vegetation composition of roadside verges in Scotland: the effects of nitrogen deposition, disturbance and management. Environmental Pollution **136**:109-118.

Ullmann, I., P. Bannister, and J. B. Wilson. 1995. The vegetation of roadside verges with respect to environmental gradients in southern New Zealand. Journal of Vegetation Science **6**:131-142.

van der Maarel, E., and M. T. Sykes. 1993. Smale scale plant species turnover in a limestone grassland - the carousel method and some comments on the niche concept. Journal of Vegetation Science **4**:199-208.

van der Valk, A. G. 1992. Establishment, colonization and persistence. Pages 61-102 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant succession: theory and prediction. Chapman & Hall, London.

van Hulst, R. 1992. From population dynamics to community dynamics: Modelling succession as a species replacement process. Pages 188-214 *in* S. D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant Succession: Theory and Prediction. Chapman & Hall, London.

Vetaas, O. R. 1994. Primary succession of plant assemblages on a glacier foreland - Bødalsbreen, southern Norway. Journal of Biogeography **21**:297-308.

Vevle, O. 1985. Okologiske faktortal for Norske karplanter. Telemark Distriktschogskole.

Walker, L. R., editor. 1999. Ecosystems of Disturbed Ground. Elsevier, Amsterdam.

Walker, L. R., P. J. Bellingham, and D. A. Peltzer. 2006. Plant characteristics ar poor predictors of microsite colonization during the first two years of primary succession. Journal of Vegetation Science **17**:397-406.

Walker, L. R., and F. S. Chapin III. 1987. Interactions among processes controlling successional change. Oikos **50**:131-155.

Walker, L. R., and R. del Moral. 2003. Primary Succession and Ecosystem Rehabilitation. CUP, Cambridge.

Ward, J. H. 1963. Hierarchical groupings to optimize an objective function. Americal Statistical Association Journal **58**:236-244.

Wardle, P. 1980. Primary succession in Westland National Park and its vicinity. New Zealand Journal of Botany **18**:221-232.

Weiher, E., and P. A. Keddy. 1995. Assembly rules, null models, and trait dispersion - new questions from old patterns. Oikos **74**:159-164.

Whittaker, R. H. 1951. A criticism of the plant association and climatic climax concepts. Northwest Science **25**:7-31.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Review **49**:207-264.

Whittaker, R. J. 1987. An application of detrended correspondence analysis and non-metric multidimensional scaling to the identification and analysis of environmental factor complexes and vegetation structures. Journal of Ecology **75**:363-376.

Whittaker, R. J. 1991. The Vegetation of the Storbreen Gletschervorfeld, Jotunheimen, Norway. IV. Short-Term Vegetation Change. Journal of Biogeography **18**:41-52.

Whittaker, R. J. 1993. Plant population patterns in a glacier foreland succession: pioneer herbs and later-colonizing shrubs. Ecography **16**:117-136.

Wiegleb, G. 1986. Grenzen und Moglichkeiten der Datenanalyse in der Pflanzenokologie. Tuexenia **6**:365-378.

Williams, W. T., J. M. Lambert, and G. N. Lance. 1966. Multivariate methods in plant ecology. V. Similarity analysis and information analysis. Journal of Ecology **54**:427-445.

Wilson, J. B., and R. J. Whittaker. 1995. Assembly rules demonstrated in a saltmarsh community. Journal of Ecology **83**:801-807.

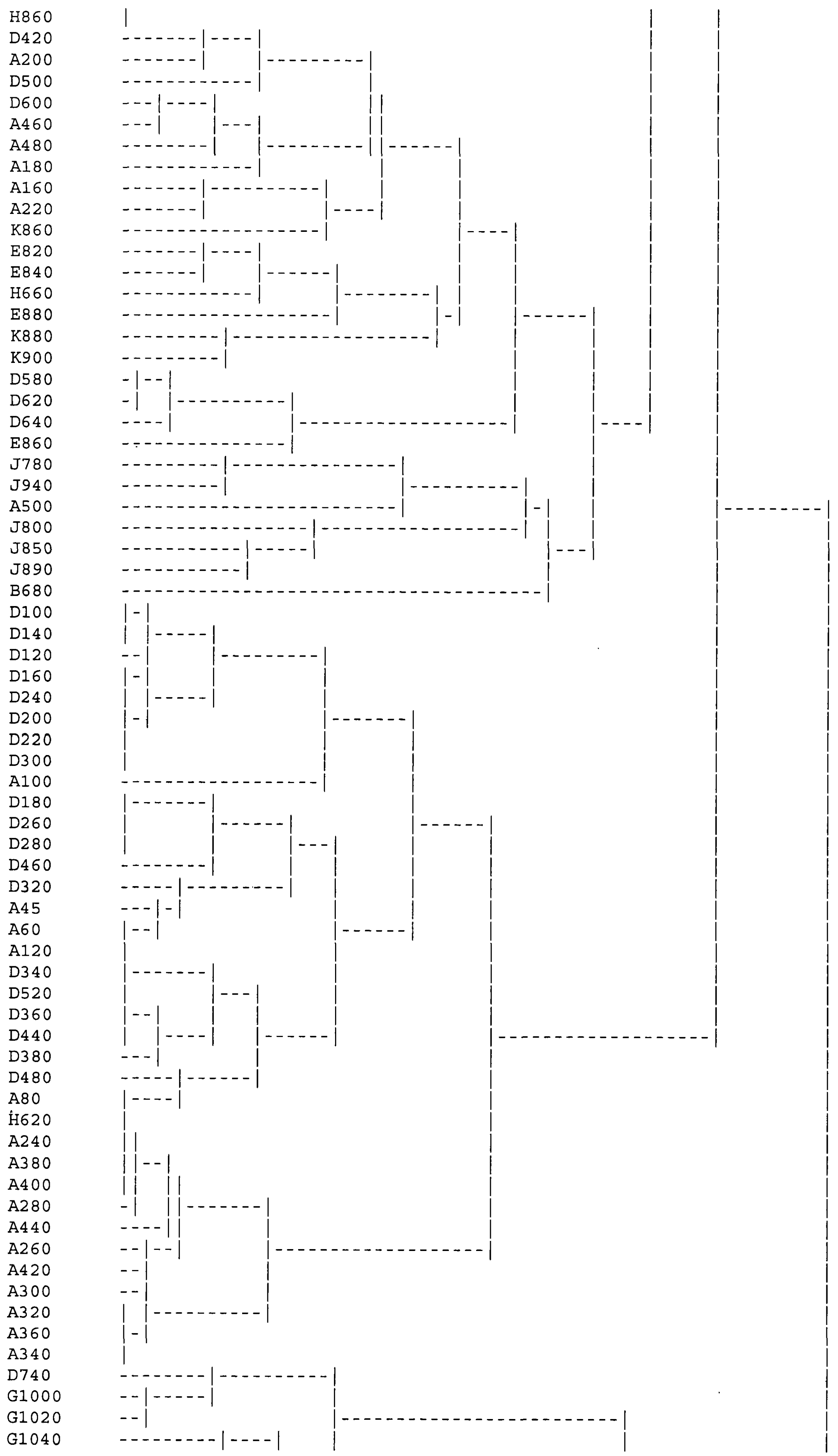
Wischmann, F. 2000. Norsk fargeflora, Norwegian edition. NKS-Forlaget, Oslo.

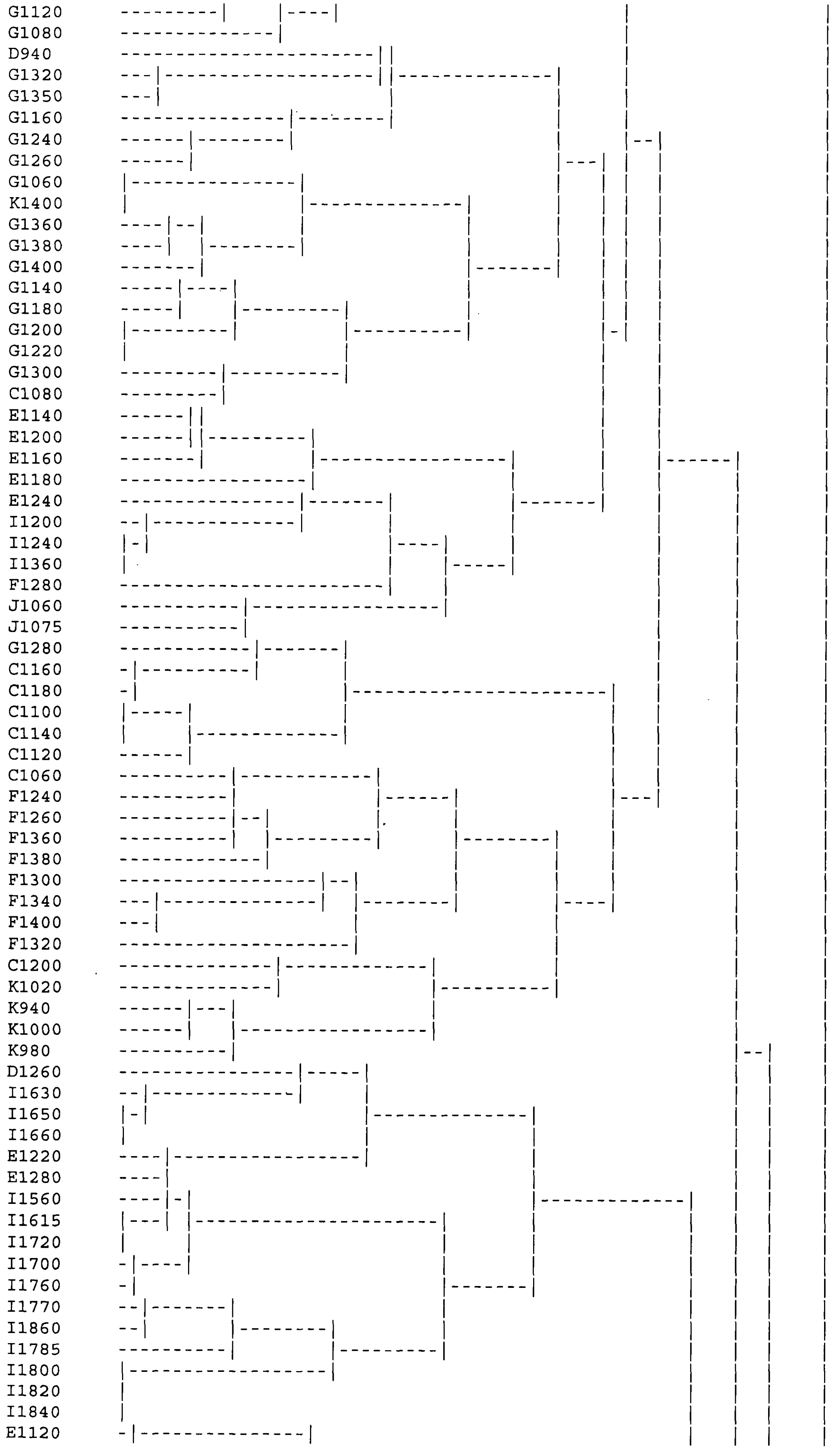
Wishart, D. 1969. An algorithm or hierarchical classifications. Biometrics **25**:165-170.

APPENDIX I Cluster analysis of roadside pioneer sites

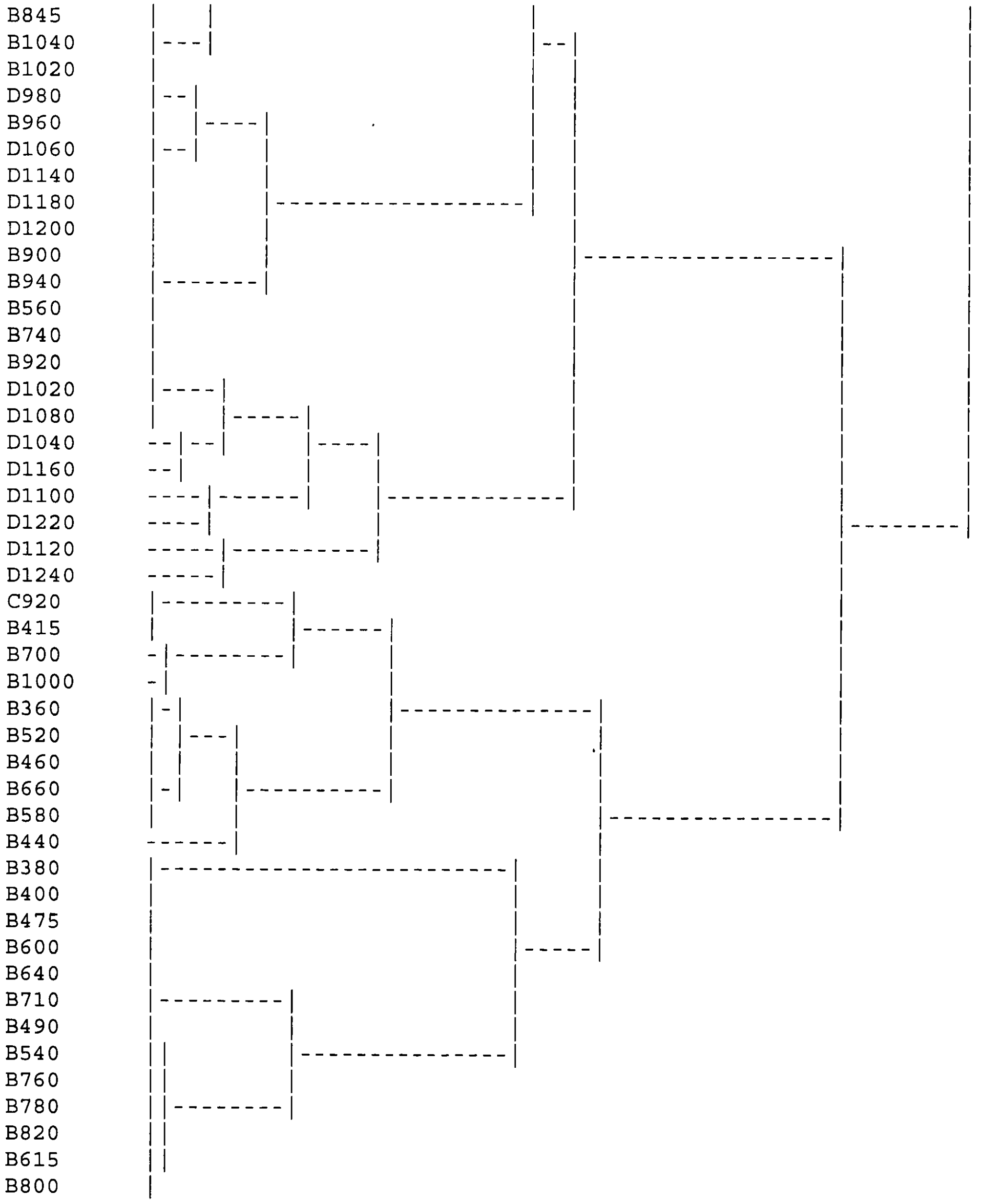
Linkage method: Flexible beta
Distance measure: Relative Sørensen
Flexible beta value selected is -0.250
Percent chaining = 0.50

```
                         Distance (Objective Function)
         0.003          12.305          24.606          36.908          49.209
          |-------+-------+-------+-------+-------+-------+-------+-------+
                         Information remaining (%)
     100.000          75.000          50.000          25.000           0.000
          |-------+-------+-------+-------+-------+-------+-------+-------+
D80       ------|--------|
D780      ------|        |----------|
D540      ----|---------||          |
D680      --|-|         ||          |
D720      --|           |           |----|
D800      --------------|           |    |
D400      |-|                       |    |
D760      | |-----------------------|    |
D660      --|                            |
E900      ---|-----|                     |---------|
A140      ---|     |--|                  |         |
E1000     |--------|  ||                 |         |
E1020     |           ||                 |         |
E920      --|---------||-------|         |         |
E940      --|          |       |---------|         |
E1080     -------------|       |                   |
E960      --------|------------|                   |
E980      --------|                                |
D560      ------------------|------|               |----|
H600      ------------------|      |------|        |    |
K800      -------|-|               |      |        |    |
K840      -------| |---------------|      |        |    |
K820      ---------|                      |        |    |
D700      |---------|                     |-|      |    |
D840      |         |---|                 | |      |    |
K780      ----------|   |------|          | |      |    |
E1060     ----|---------|      |--|       | |      |    |
E1100     ----|                |  |-------| |------|    |
E1040     ---------------------|  |         |           |
D820      --------------|---------|         |           |
D860      ------|-------|                   |           ||
K960      ------|                           |           ||
A520      ----|-----------------------------|           ||
A540      ----|                                         ||
J840      -----------|---------|                        ||
J920      -----------|         |---|                    ||
H720      |----|               |   |                    ||
H760      |    |---------------|   |                    ||
H740      |----|                   |-------|            ||
H780      |                        |       |            ||
J960      -----|---|               |       |            ||
J1040     -----|   |--------|      |       |            ||
J1000     ---------|        |------|       |------------||
J980      -------------|----|              |             |
H700      -------------|                   |             |
H640      -----|--------|                  |             |
H880      -----|        |------------------|             |
H680      -------|------|                                |
H800      -|-----|                                       |
H820      ||                                             |
H840      |                                              |-----|
```


H860
D420
A200
D500
D600
A460
A480
A180
A160
A220
K860
E820
E840
H660
E880
K880
K900
D580
D620
D640
E860
J780
J940
A500
J800
J850
J890
B680
D100
D140
D120
D160
D240
D200
D220
D300
A100
D180
D260
D280
D460
D320
A45
A60
A120
D340
D520
D360
D440
D380
D480
A80
H620
A240
A380
A400
A280
A440
A260
A420
A300
A320
A360
A340
D740
G1000
G1020
G1040


G1120
G1080
D940
G1320
G1350
G1160
G1240
G1260
G1060
K1400
G1360
G1380
G1400
G1140
G1180
G1200
G1220
G1300
C1080
E1140
E1200
E1160
E1180
E1240
I1200
I1240
I1360
F1280
J1060
J1075
G1280
C1160
C1180
C1100
C1140
C1120
C1060
F1240
F1260
F1360
F1380
F1300
F1340
F1400
F1320
C1200
K1020
K940
K1000
K980
D1260
I1630
I1650
I1660
E1220
E1280
I1560
I1615
I1720
I1700
I1760
I1770
I1860
I1785
I1800
I1820
I1840
E1120

```
K1060     -|                |-----|                            |   |  |    |
K1040     ------------------|     |---|                        |   |  |    |
J1020     ----------|---------|   |   |                        |   |  |    |
K1140     ----------|         |---|   |                        |   |  |    |
K1080     ---|--------|       |       |------|                 |   |  |    |
K1300     ---|        |-------|       |      |                 |   |  |    |
K1240     ---------|--|               |      |                 |   |  |    |
K1280     ---------|                  |      |--|              |   |  |    |
F1440     ------------|---------------|      |  |              |   |  |    |
K1160     ------------|                      |  |              |   |  |    |
I1580     |---------------|                  |  |              |---|  |    |
I1600     |               |------------------|  |              |      |    |
K1200     -|-|            |                     |              |      |    |
K1220     -| |------------|                     |              |      |    |
K1260     ---|                                  |              |      |    |
E1260     -----|--------|                       |              |      |    |
E1300     -----|        |                       |              |      |    |
I1220     -|-|          |------|                |--|           |      |    |
I1300     || |--------| |      |                |  |           |      |    |
I1315     |  |        | |      |                |  |           |      |    |
I1260     ---|        |-|      |                |  |           |      |    |
I1280     ||          |        |                |  |           |      |    |
I1420     ||----------|        |------|         |  |           |      |    |
I1460     -|                   |      |         |  |           |      |    |
I1340     ||                   |      |         |  |           |      |    |
I1440     ||----|              |      |         |  |           |      |    |
I1480     ||    |-------|      |      |         |  |           |      |    |
I1380     -|    |       |      |      |         |  |           |      |    |
I1400     ------|       |------|      |---------|  |           |      |    |
I1500     -|-----|      |             |            |           |      |    |
I1520     -|     |------|             |            |           |      |    |
I1540     -------|                    |            |           |      |    |
F1420     --|--------------------|    |            |           |      |    |
K1340     -||                    |    |            |-----------|      |    |
K1380     -|                     |----|            |                  |----|
K1100     |-----|                |                 |                  |
K1320     |     |----------------|                 |                  |
K1360     ------|                                  |                  |
G900      |---|                                    |                  |
G960      |   |-----------|                        |                  |
K1120     -|--|           |                        |                  |
K1180     -|              |------------|           |                  |
J900      |--|            |            |           |                  |
J1100     |  |------------|            |           |                  |
K920      ---|                         |-------|   |                  |
G940      --|--|                       |       |   |                  |
C840      |-|  |-----------|           |       |   |                  |
C900      |    |           |           |       |   |                  |
C940      -----|           |-----------|       |   |                  |
C850      -------------|   |                   |   |                  |
C880      |------|     |---|                   |---|                  |
C1000     |      |-----|                       |                      |
C960      ||     |                             |                      |
C980      ||-----|                             |                      |
C1020     ||                                   |                      |
C1040     |                                    |                      |
G920      ---------------------|---------------|                      |
G980      ---|-----------------|                                      |
G1100     ---|                                                        |
D880      --------|                                                   |
D900      ---||   |---------|                                         |
D920      ---||---|         |                                         |
D960      |---|             |                                         |
D1000     |                 |---------|                               |
B340      ||                |         |                               |
B860      ||--|             |         |                               |
B880      ||  |             |         |                               |
B980      -|  |-------------|         |                               |
```


B845
B1040
B1020
D980
B960
D1060
D1140
D1180
D1200
B900
B940
B560
B740
B920
D1020
D1080
D1040
D1160
D1100
D1220
D1120
D1240
C920
B415
B700
B1000
B360
B520
B460
B660
B580
B440
B380
B400
B475
B600
B640
B710
B490
B540
B760
B780
B820
B615
B800

APPENDIX II TWINSPAN of roadside pioneer sites

```
ORDER OF SPECIES INCLUDING RARER ONES
   8  Araalp  |  60  Luzarc  |  88  Rangla  | 100  Saxcer  | 101  Saxces
 102  Saxopp  | 103  Saxriv  |  18  Carbel  |  21  Ceralp  |  99  Saualp
 106  Silaca  |  23  Cercer  | 107  Sildio  |   6  Antdio  |  30  Desalp
  97  Sallan  | 114  Tofpus  | 118  Trispi  |  34  Epiana  |  73  Oxydig
 104  Saxste  | 123  Veralp  |  13  Betnan  |  63  Luzspi  | 105  Sibpro
  96  Salher  |  47  Harhyp  |  53  Juntrf  |  57  Loipro  |  76  Phycae
   9  Arapet  |  81  Poaalp  |  84  Polviv  | 129  Visalp  |  59  Luzcon
  19  Carbig  |  40  Fesovi  |  70  Omasup  |  90  Rumace  |  48  Hiealp
  29  Crycri  |  33  Empher  | 121  Vaculi  |   7  Antodo  |  12  Athdis
  22  Cerarv  |  35  Equsci  |  17  Camrot  |  75  Phlalp  |  91  Rumlla
   3  Alcalp  |  32  Desfle  |  68  Narstr  | 120  Vacmyr  |  55  Leoaut
  67  Minbif  |  69  Omanor  |  93  Sagsag  |  16  Calvul  |  58  Lotcor
  95  Salgla  | 108  Solvir  |  10  Astalp  |  52  Junfil  |  77  Pinvul
 113  Taragg  |  45  Gersyl  |  82  Poapra  |   1  Achmil  |   4  Alcglo
   5  Alninc  |  15  Calpur  |  20  Carova  |  24  Cerfon  |  25  Chaang
  26  Chasua  |  27  Crecap  |  28  Cretec  |  41  Filuli  |  42  Fraves
  43  Galtet  |  44  Gerrob  |  50  Hypmac  |  51  Junbuf  |  62  Luzmul
  65  Maibif  |  72  Oxaace  |  79  Plamaj  |  83  Polavi  |  86  Pruvul
  87  Ranacr  |  89  Rubida  |  92  Sagpro  | 112  Stenem  | 116  Tripra
 117  Trirep  | 119  Urtdio  | 124  Veroff  | 125  Verser  | 127  Viopal
 128  Vioriv  |  11  Astnor  |  36  Equsp   |  37  Equsyl  |  38  Eriace
  39  Eupagg  |  49  Hieumb  |  56  Linbor  |  64  Luzsyl  |  74  Parpal
  80  Plamed  |  85  Potcra  | 110  Stegra  | 111  Stemed  | 115  Trieur
 126  Viobif  |   2  Agrcap  |  31  Desces  |  66  Melsyl  |  14  Betpub
  61  Luzcam  |  71  Ortsec  | 109  Sorauc  |  54  Juntrg  |  78  Pinsyl
  98  Salmyr  | 122  Vacvit  |  46  Gymdry  |  94  Salcap  |

 ORDER OF SAMPLES
 116 I1800    | 117 I1820    | 118 I1840    |  60 D1260    | 109 I1650
 110 I1660    | 107 I1615    | 111 I1700    | 112 I1720    | 113 I1760
 114 I1770    | 115 I1785    | 119 I1860    | 285 K1100    | 103 I1540
 105 I1580    | 106 I1600    | 108 I1630    | 101 I1500    | 102 I1520
 104 I1560    |  86 I1200    |  88 I1240    |  89 I1260    |  90 I1280
  91 I1300    | 127 G1040    | 132 G1140    | 133 G1160    | 135 G1200
 136 G1220    | 144 G1380    | 157 J1020    | 159 J1060    | 160 J1075
 284 K1080    | 287 K1140    | 288 K1160    | 289 K1180    | 290 K1200
 291 K1220    | 293 K1260    |  95 I1380    |  96 I1400    |  97 I1420
 140 G1300    | 143 G1360    | 261 F1300    | 267 F1420    | 268 F1440
 292 K1240    | 294 K1280    | 295 K1300    | 297 K1340    | 298 K1360
 299 K1380    | 300 K1400    |  87 I1220    |  92 I1315    |  93 I1340
  94 I1360    |  98 I1440    |  99 I1460    | 100 I1480    | 296 K1320
  78 E1160    |  79 E1180    |  80 E1200    |  81 E1220    |  82 E1240
  83 E1260    |  84 E1280    |  85 E1300    | 145 G1400    | 173 C1060
 174 C1080    | 175 C1100    | 176 C1120    | 177 C1140    | 179 C1180
 180 C1200    | 260 F1280    | 262 F1320    | 263 F1340    | 266 F1400
 258 F1240    | 259 F1260    | 264 F1360    | 265 F1380    | 120 G900
 121 G920     | 123 G960     | 137 G1240    | 286 K1120    | 122 G940
 139 G1280    | 169 C980     | 178 C1160    | 211 B940     | 215 B1020
 138 G1260    | 141 G1320    | 142 G1350    | 124 G980     | 125 G1000
 126 G1020    | 128 G1060    | 129 G1080    | 130 G1100    | 131 G1120
 134 G1180    | 161 J1100    | 171 C1020    | 172 C1040    | 163 C850
 164 C880     | 165 C900     | 167 C940     | 168 C960     | 170 C1000
 206 B845     | 209 B900     |  41 D880     |  42 D900     |  44 D940
  45 D960     |  47 D1000    |  67 E940     |  70 E1000    |  71 E1020
  73 E1060    |  74 E1080    |  75 E1100    |  72 E1040    |  76 E1120
  77 E1140    | 283 K1060    |  43 D920     |  46 D980     |  49 D1040
  50 D1060    |  55 D1160    |  48 D1020    |  51 D1080    |  58 D1220
  54 D1140    |  56 D1180    |  57 D1200    |  52 D1100    |  53 D1120
  59 D1240    | 241 A520     | 242 A540     | 198 B680     | 182 B360
 183 B380     | 184 B400     | 185 B415     | 186 B440     | 187 B460
 188 B475     | 189 B490     | 190 B520     | 193 B580     | 194 B600
 195 B615     | 196 B640     | 197 B660     | 199 B700     | 200 B710
 201 B740     | 202 B760     | 203 B780     | 162 C840     | 166 C920
 181 B340     | 204 B800     | 207 B860     | 208 B880     | 210 B920
 212 B960     | 213 B980     | 214 B1000    | 216 B1040    |  32 D700
  39 D840     | 191 B540     | 192 B560     | 205 B820     | 239 A480
 240 A500     | 282 K1040    |  38 D820     |  40 D860     |  62 E840
 151 J900     | 222 A140     | 276 K920     | 278 K960     |  65 E900
  66 E920     |  68 E960     |  69 E980     | 273 K860     | 279 K980
 280 K1000    |  63 E860     | 149 J850     | 150 J890     |  64 E880
 146 J780     | 147 J800     | 148 J840     | 152 J920     | 153 J940
 154 J960     | 155 J980     | 156 J1000    | 158 J1040    |  30 D660
```

```
 251 H760    |  269 K780    |  270 K800    |  271 K820    |  272 K840
  28 D620    |  277 K940    |  281 K1020   |   61 E820    |  245 H640
 246 H660    |  247 H680    |  248 H700    |  249 H720    |  250 H740
 252 H780    |  253 H800    |  254 H820    |  255 H840    |  256 H860
 257 H880    |   25 D560    |  243 H600    |  275 K900    |   26 D580
  27 D600    |   29 D640    |   33 D720    |   35 D760    |   31 D680
  34 D740    |   36 D780    |   37 D800    |   17 D400    |   24 D540
 233 A360    |  218 A60     |  223 A160    |  224 A180    |  225 A200
 226 A220    |  227 A240    |  228 A260    |  229 A280    |  230 A300
 231 A320    |  232 A340    |  234 A380    |  235 A400    |  236 A420
 237 A440    |  238 A460    |  219 A80     |  220 A100    |  221 A120
  13 D320    |   14 D340    |   15 D360    |   16 D380    |   18 D420
  20 D460    |   21 D480    |   22 D500    |   23 D520    |  274 K880
   6 D180    |    7 D200    |    8 D220    |    9 D240    |   10 D260
  11 D280    |   12 D300    |   19 D440    |  217 A45     |  244 H620
   1 D80     |    2 D100    |    3 D120    |    4 D140    |    5 D160
```

```
TWO-WAY ORDERED TABLE

               111 11111111121111111     1111111112222222   112222222223      12        111111112222222211112111122
               1116010111111800000008889923333455688889999994466699999908999990977888888477777786666556622238236711
               6780907123459535681246890172356479047890135670317824578907234890689012345534567900236894501376299815

   8  Araalp   -12---------------------------------------------------------------------------------1---------------   000000
  60  Luzarc   5445554454443-3355334------------------1---22-1-----2--------122211-5235-52-3-1-1-------------------   000000
  88  Rangla   555---1333334-------1-----------------------------2-----------------------------1-------------------   000000
 100  Saxcer   443----3--131--11-----------------------------------------------------------------------------------   000000
 101  Saxces   -1---2232322--31-2--1-------------------------------------------------------------------------------   000000
 102  Saxopp   --1---------1----21--------------------------------------------1------------------------------------   000000
 103  Saxriv   ------------2--22---1-------------------------------------------------------------------------------   000000
  18  Carbel   1122-12--2--3-----------------------------------2-----52--------------------------------------------   000001
  21  Ceralp   454-3-55555-55432-335-2222-2---2-2332-----332-3---523-32-1-322-2------------------------------------   000001
  99  Saualp   --2-----------1-1-------1---------------1------------1-----1----------------------------------------   000001
 106  Silaca   --1---1-1-----2224443---------------------231--------12-2--21213-1--32-2----------------------------   000001
  23  Cercer   -1---122-2343-23224-3554552222--15411--1--5452-4---33----5545554-244255-3--2-4-2445442413-----------   000010
 107  Sildio   --------------------------------------------------------------------------2----------322------------   000010
   6  Antdio   --------------2----------2----------1-2----2----212323121-12-1----------------------------11-2------   000011
  30  Desalp   ---1--2---242--2232--1-212---2-1-----322-2--1354452-21------112--5-3231121-------2354244----1--3-3--   000011
  97  Sallan   ---------------------1-----------------------------2------------------------------------------------   000011
 114  Tofpus   ----------------------------------1---------------1-------------------------------------------------   000011
 118  Trispi   2--1--2-21-23--2-123---1---3-2-2----1-----3522--43-4-4142-2-1221----22-----------51432-23-----------   000011
  34  Epiana   -----------------------------------------------1--------------1-----------33--4-4----2223-----------   000100
  73  Oxydig   ------------------------------1--11-----2---142---2-11-4-------1----321---221----23-13232------11--1   000100
 104  Saxste   -----------------------------------------------41--------3-----1-13221--2-22-1--1-3--2-2--------1---   000100
 123  Veralp   ----------------------------------------------------------------------------------1122222-----------   000100
  13  Betnan   -----------------------1-------------1-----------------------------------------------------2--------   000101
  63  Luzspi   ----------21-533--14---23345355541-53222-3443554333354445-3434445423444345-3------1---11-43444-31---   000101
 105  Sibpro   ----------------------1-1---2-------1-----21---112---3-22------------------------2--2-122-----------   000101
  96  Salher   -324-2-34-231-2331---1-------2---------------1112--2-1--1112---2--22222222--122---22--4-2---1--22---   000110
  47  Harhyp   ----------------------------------------------------------------------------------------------------   000111
  53  Juntrf   ---1---------------------------3---1-1--1----12------1--2--------425212333-------------------2-1----   000111
  57  Loipro   ----------------------------------------------------------------------------------------------------   000111
  76  Phycae   ----------------------------------------------------------------------------------------------------   000111
   9  Arapet   ---------------------------------32-----------------------------------------------------------------   00100
  81  Poaalp   44554431235541431322-55334-334413322222434322533-4323----31252-11222141534555555541243334---31-515-3   00100
  84  Polviv   ------23------355-1111--112--11---1-212555--2--43223-2-122-3-3221---11-----------------1-2322--1----   00100
 129  Visalp   --------------------------------2---2-3-11---------2221------1----------2------------------1--------   00100
  59  Luzcon   ----1--------3-------122-----12-2-4--2---2-1------1--1---2----1--24-----------------11--------------   00101
  19  Carbig   --1----2--1---21-------112----------21-2-1---1-----2-----1232212-23333431-1---------1---------------   0011
  40  Fesovi   2---5555544345555555544555352333444545555555522-55555555555545555534435552243233-31112--155535535344   0011
  70  Omasup   ---1-1------------------1-113242----2323--12221213111-1-1-11-2---112--2122-3-----15232333---1---3--1   0011
```

```
 90  Rumace   -----------------------1--------1--2------------11---------------354222-2-4-------43432-----1-------  0011
 48  Hiealp   -------------------------------------2--1----111232313-21----------1-11-2----1-------2-2-11---1-2---  0100
 29  Crycri   ----------------------------------------------------------------------------------------------------  01010
 33  Empher   ----------------------------------------------------------------2----------------------------2------  01010
121  Vaculi   ----------------------------------------------------------------------------------------------------  01010
  7  Antodo   -------------------------------------------------------------12---------1-2--------1--1-----2-224---  01011
 12  Athdis   ----------------------------------------------------------------------------------------------------  01011
 22  Cerarv   ---------------------1232-------1-------------------------------------------------------------------  01100
 35  Equsci   ------------------1-------4-4-----5------2--------------------2-------------------------------------  01100
 17  Camrot   -----------------------11--1-------1232--11-------2-1112---1---------------------------------133----  01101
 75  Phlalp   --------------------2------3-2---------------1-------2-----------1--3-----333-332123-2343--1--1-23-1  01101
 91  Rumlla   --------------------------455544454342533----34---3-------------------1----2-2---------444-455424--3  01101
  3  Alcalp   ------------------------------1----------------------------------111--------------------------------  01110
 32  Desfle   ---------------------3------2------------------------------------------------315---------4434-55-555  01110
 68  Narstr   --------------------------2--1----------------------------------------------------------------------  01110
120  Vacmyr   -----------------------------------------------------------------------------1----------------------  01110
 55  Leoaut   -----------------------------------1-----1---2----1--1--1----1--------1----1--------------3-2-12----  01111
 67  Minbif   -------------------22-12-1-----------------1----1---------1--1------------1--2----2---------3-------  100
 69  Omanor   -----------------------------------------------------------------111---1--42-33-12---4213-------2---  100
 93  Sagsag   ------------------3-2-1---3-5---4--2-----4221--4-3----3---1--12-----------41-2235-3443332---2-------  100
 16  Calvul   ----------------------------------------------------------------------------------------------------  101
 58  Lotcor   ------------------------------------------------------------------------------------------5---------  101
 95  Salgla   ---------------1---1-4222221-11-3222333342---2--1-333112232----1213113221--21-2-11---13--32234243-13  101
108  Solvir   --------------------------------2--122---2---------2-------------1---1----------------------------1-  101
 10  Astalp   ------------------------------------------1---------------------------------------------------------  1100
 52  Junfil   -------------------------------------2--------------------------------------------------------------  1100
 77  Pinvul   ----------------------------------------------------------------------------------------------------  1100
113  Taragg   --------------------1211----1---2--13413--21----24---3-1-2221-21-----------------11-12324211---1----  1100
 45  Gersyl   ----------------------------------------------------------------------------------------------------  11010
 82  Poapra   --------------------------53-------------------------------------------------------------1----------  11010
  1  Achmil   ----------------------------------------------------------------------------------------------------  110110
  4  Alcglo   ----------------------------------------------------------------------------------------------------  110110
  5  Alninc   ----------------------------------------------------------------------------------------------------  110110
 15  Calpur   ----------------------------------------------------------------------------------------------------  110110
 20  Carova   ----------------------------------------------------------------------------------------------------  110110
 24  Cerfon   ----------------------------------------------------------------------------------------------------  110110
 25  Chaang   -------------------------------------------------------------------------------------3--------------  110110
 26  Chasua   ----------------------------------------------------------------------------------------------------  110110
 27  Crecap   ----------------------------------------------------------------------------------------------------  110110
 28  Cretec   ----------------------------------------------------------------------------------------------------  110110
 41  Filuli   ----------------------------------------------------------------------------------------------------  110110
 42  Fraves   ----------------------------------------------------------------------------------------------------  110110
 43  Galtet   ----------------------------------------------------------------------------------------------------  110110
 44  Gerrob   ----------------------------------------------------------------------------------------------------  110110
 50  Hypmac   ----------------------------------------------------------------------------------------------------  110110
 51  Junbuf   ----------------------------------------------------------------------------------------------------  110110
```

```
  62  Luzmul    ----------------------------------------------------------------------------------------------------  110110
  65  Maibif    ----------------------------------------------------------------------------------------------------  110110
  72  Oxaace    ----------------------------------------------------------------------------------------------------  110110
  79  Plamaj    ----------------------1-----------------------------------------------------------------------------  110110
  83  Polavi    ----------------------------------------------------------------------------------------------------  110110
  86  Pruvul    ----------------------------------------------------------------------------------------------------  110110
  87  Ranacr    ---------------------------------------------------------------------------------------1------------  110110
  89  Rubida    ----------------------------------------------------------------------------------------------------  110110
  92  Sagpro    ----------------------------------------------------------------------------------------------------  110110
 112  Stenem    ----------------------------------------------------------------------------------------------------  110110
 116  Tripra    ----------------------------------------------------------------------------------------------------  110110
 117  Trirep    -----------------------------------------------------------------------------------------133--------  110110
 119  Urtdio    ----------------------------------------------------------------------------------------------------  110110
 124  Veroff    ----------------------------------------------------------------------------------------------------  110110
 125  Verser    ----------------------------------------------------------------------------------------------------  110110
 127  Viopal    -------------------------------------------------------------------------------------1--------------  110110
 128  Vioriv    ----------------------------------------------------------------------------------------------------  110110
  11  Astnor    ----------------------------------------------------------------------------------------------------  110111
  36  Equsp     ----------------------------------------------------------------------------------------------------  110111
  37  Equsyl    ----------------------------------------------------------------------------------------------------  110111
  38  Eriace    ----------------------------------------------------------------------------------------------------  110111
  39  Eupagg    ---------------------------------------------------------------------1--------------------2---------  110111
  49  Hieumb    ----------------------------------------------------------------------------------------------------  110111
  56  Linbor    ----------------------------------------------------------------------------------------------------  110111
  64  Luzsyl    ----------------------------------------------------------------------------------------------------  110111
  74  Parpal    ----------------------------------------------------------------------------------------------------  110111
  80  Plamed    ----------------------------------------------------------------------------------------------------  110111
  85  Potcra    ---------------------------------------------------------------2------------------------------------  110111
 110  Stegra    ----------------------------------------------------------------------------------------------------  110111
 111  Stemed    ----------------------------------------------------------------------------------------------------  110111
 115  Trieur    ----------------------------------------------------------------------------------------------------  110111
 126  Viobif    ----------------------------------------------------------------------------------------------------  110111
   2  Agrcap    ---------------------122-----------24---2------4--333-------------------------------------------45-3  1110
  31  Desces    --------------------------------22-424------------------------------2------22---2-------2------2----  1110
  66  Melsyl    ------------------------------------------------------------------------------------------2---1-----  1110
  14  Betpub    --------------------------------4-1-------------------------------------1---11-------------1--------  11110
  61  Luzcam    ----------------------------------------------------------------------------------------------------  11110
  71  Ortsec    ----------------------------------------------------------------------------------------------------  11110
 109  Sorauc    ----------------------------------------------------------------------------------------------------  11110
  54  Juntrg    ----------------------------------------------------------------------------------------------------  111110
  78  Pinsyl    ----------------------------------------------------------------------------------------------------  111110
  98  Salmyr    ----------------------------------------------------------------------------------------------------  111110
 122  Vacvit    ---------------------------------------------------1------------------------------------------------  111110
  46  Gymdry    ----------------------------------------------------------------------------------------------------  111111
  94  Salcap    ----------------------------------------------------------------------------------------------------  111111
```

```
               0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
               0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000011111111111
               0000000000000000000001111111111111111111111111111111111111111111111111111111111111111111100000000000
               0000000000000111111110000000000000000000000000000000000000000000000000000011111111111111100000000000
               0001111111111011111110000000000000000000000000000000000001111111111111111100000001111111100000000000
                  0001111111 000011100000000000000000000011111111111111100000001111111111000111100001111000001111111

TWO-WAY ORDERED TABLE

               1111111111111111111122              2              2211111111111111112222111222222222  112222   1222
               3442222233367766666700444446777777778444554555555554498888888889999990000668000111113399034834652776
               8124568901411234578069124577013452673369058184672391282345678903456790123261478023462912590280212685

   8 Araalp    ----------------------------------------------------------------------------------------------------  000000
  60 Luzarc    -2---------1---------------243-----------------1154--2--------------1--21----------------2---------2  000000
  88 Rangla    ------------------------------------------1---------------------------------------------------------  000000
 100 Saxcer    ----------------------------------------------------------------------------------------------------  000000
 101 Saxces    ----------------------------------------------------------------------------------------------------  000000
 102 Saxopp    ----------------------------------------------------------------------------------------------------  000000
 103 Saxriv    ----------------------------------------------------------------------------------------------------  000000
  18 Carbel    ----------------------------------------------------------------------------------------------------  000001
  21 Ceralp    111-2--21-------------------------1-1-----------------------------------------------------32--------  000001
  99 Saualp    ----------------------------------------------------------------------------------------------------  000001
 106 Silaca    ----------------------------------------------------------------------------------------------------  000001
  23 Cercer    --1-1--212-------------121--23241--21----------------2------------------------------------2-23------  000010
 107 Sildio    ----------------------------------------------------------------------------------------------------  000010
   6 Antdio    ---1---------------------------------------------------------------------------------------1--------  000011
  30 Desalp    -44------11------------------------3----------------------------------------------------------------  000011
  97 Sallan    ----------------------1-----------------------------------------------------------------------------  000011
 114 Tofpus    ----------------------------------------------------------------------------------------------------  000011
 118 Trispi    ------1---------------------------------------------------------------------------------------------  000011
  34 Epiana    ------------2121--21---1---1-----------------------------------------------------11-----2-----------  000100
  73 Oxydig    123-1---------2-132---4-2----32131---------------------------------------------1-3--------2---------  000100
 104 Saxste    --1----------1----1----22--1--1131-4-11--1---------------------------------------1--------2--1------  000100
 123 Veralp    ------------------------------12--------------------------------------------------------------------  000100
  13 Betnan    ------------------------1---------------------------------------------------------------------------  000101
  63 Luzspi    4554-35542423232--12--2-1212333225444-12-3415-------2-----1-------------------------2------4-2-2-2-3  000101
 105 Sibpro    --------1-3------------13-2--------1--11--11--------------------------------------------------------  000101
  96 Salher    -23----2----22111-3---22-24----------1-43223-2-2133-----1---------------1-2--12------11-------------  000110
  47 Harhyp    ------------------------------------------2--1------------------------------------------------------  000111
  53 Juntrf    -12----1---------------2--1--121-4-3-31122332242524-------------------------------1--1-------12-----  000111
  57 Loipro    ------------------------------------------11--------------------------------------------------------  000111
  76 Phycae    --------------------------------------131232-331-2--------------------------------------------------  000111
```

```
  9  Arapet    ----------------------------------------------------------------------------------------------------  00100
 81  Poaalp    322---1--24-14---2312-2---22-------1-------1------------------------------3-221----2---------1-1--2-  00100
 84  Polviv    -2------2--------1-----------1----------------------------------------------------------------------  00100
129  Visalp    -----------2----------------------------------------------------------------------------------------  00100
 59  Luzcon    ------2------------------2----14-222--------------------------------------------------------------1-  00101
 19  Carbig    --1-----------1--------1-2221----123-22---23111-221312----1-1---------------1-1--1--------33--------  0011
 40  Fesovi    -215445344355555555543-112-1-23242545331323332-1325342-1-433--11---22-1215422322222423323--5--552542  0011
 70  Omasup    -23-------2-33-1--32--24554----1-1-2-3314222-----11-------------------------------2--2----2--1-1----  0011
 90  Rumace    4-------------4--------4----23--32445----3-------------------------------------------------2-------1  0011
 48  Hiealp    ----------1------1--1-22-2---211-21-1212-3--21-21-----1----------2---12--1--3---123-11212---31------  0100
 29  Crycri    ----------------------1-1----------1-2-----------------------------------------------1--------------  01010
 33  Empher    --------------22------3-2------------21433442331232-1-----12-1-----2---1122--1---1--1---------------  01010
121  Vaculi    --------------1------------------------12111--1-----------------------------1-----------------------  01010
  7  Antodo    -1-3-1--1---32-41-34----12-1-1--1--1--21--23-------------------------------------------------2------  01011
 12  Athdis    ----------------------1------------------1---------------------------------------------------1------  01011
 22  Cerarv    ----------------------------------------------------------------11----------------------------------  01100
 35  Equsci    4------------------------------------------------------------------------------------------3------2-  01100
 17  Camrot    -----------------2------------------1----------------------------2------------------11-----4-2------  01101
 75  Phlalp    ---1--3-22--123--12423--------21-1-2--------------------------------------1---1--1------1-----2----2  01101
 91  Rumlla    545334223555341--24----24---1142-1---2-----------------------------------1-3-222232--3----4-44153553  01101
  3  Alcalp    -----------------1------2-----21-2-2---1-----------------------------------------11---------2-1-----  01110
 32  Desfle    45253-2-532-----431-5555455434525412-5555555555555534-532534555555555555545555555555555555-1-543-3333  01110
 68  Narstr    -1---31-2----------2-----------------------1-------42-----------------------------------12----------  01110
120  Vacmyr    --------------21------2--------------11-112223222-123--1----1-----12-2-2---------------------1---12-  01110
 55  Leoaut    -32--------------11--------2-1----------------------------------------------------------21---------4  01111
 67  Minbif    -----------------------------------------------------------------------------------1-----25---------  100
 69  Omanor    -----------------122--2--------1---------3------------------------------2--------12-----23---2----3-  100
 93  Sagsag    -12--4----4------------22-2-----------------------------------------------------------------3-4---1-  100
 16  Calvul    ----------------------2--------------1-1-----------21--------3-----1-1---------------1--------------  101
 58  Lotcor    --------------------------------------------------------4--1---------2-----1------------------1-----  101
 95  Salgla    -1----23-1--3-2312323143-4442223232223-223---2-------53551543324344454-352334453434442324332-232223-  101
108  Solvir    --------------------------------2----------------------------------1--1--1--2-------22212---21----2-  101
 10  Astalp    ---2------1-----------------------------------------------------------------------------------------  1100
 52  Junfil    ----------------------------------------------------------------------------------------------------  1100
 77  Pinvul    -----------------------------------1---1------------------------------------------------------------  1100
113  Taragg     -1-1------------------11--1---11-----------1----------------------------------------1---1-----31----  1100
 45  Gersyl    ---------------------------1---1--------------------------------------------------------------------  11010
 82  Poapra    ---355-5553------------------------------------------2-----1------1-----------------2----52-3---3---  11010
  1  Achmil    -------------------------------------------------------------------------------------1--------------  110110
  4  Alcglo    ----------------------------------------------------------------------------------------------------  110110
  5  Alninc    ---------------------------------------------------------------------------------------------1------  110110
 15  Calpur    ------------------------------------------------------------------------------------1---------------  110110
 20  Carova    ----------------------------------------------------------------------------------------------------  110110
 24  Cerfon    ----------------------------------------------------------------------------------------------------  110110
 25  Chaang    -------------------------------------------------------------------------------------------3--------  110110
 26  Chasua    --------------------------------------------------------------------------------------------------1-  110110
```

```
 27  Crecap   ----------------------------------------------------------------------------------------------------  110110
 28  Cretec   ----------------------------------------------------------------------------------------------------  110110
 41  Filuli   ----------------------------------------------------------------------------------------------------  110110
 42  Fraves   ------------------------------------------------------------------------------------------------2---  110110
 43  Galtet   ----------------------------------------------------------------------------------------------------  110110
 44  Gerrob   ----------------------------------------------------------------------------------------------------  110110
 50  Hypmac   ----------------------------------------------------------------------------------------------------  110110
 51  Junbuf   ----------------------------------------------------------------------------------------------------  110110
 62  Luzmul   ----------------------------------------------------------------------------------------------------  110110
 65  Maibif   ----------------------------------------------------------------------------------------------------  110110
 72  Oxaace   -----------------------------------------------------------------------------------------2----------  110110
 79  Plamaj   ----------------------------------------------------------------------------------------------------  110110
 83  Polavi   ----------------------------------------------------------------------------------------------------  110110
 86  Pruvul   ----------------------------------------------------------------------------------------------------  110110
 87  Ranacr   ----------1----------------4---11---------------------------------------------------------------2---  110110
 89  Rubida   ------------------------------------------------------------------------------------------------1---  110110
 92  Sagpro   ------------------------------------3---------------------------------------------------------------  110110
112  Stenem   ------------------------------------------------------------------------------------------------1---  110110
116  Tripra   ---------------------------2-------------------------------------------------------------------1----  110110
117  Trirep   ----------------------------------------------------------------------------------------------31----  110110
119  Urtdio   ----------------------------------------------------------------------------------------------------  110110
124  Veroff   ----------------------------------------------------------------------------------------------------  110110
125  Verser   ---------------------------------------------------3-------------------------------------23---------  110110
127  Viopal   ----------------------------------------------------------------------------------------------------  110110
128  Vioriv   -----------------------------------------------------------------------------------------11---------  110110
 11  Astnor   ----------------------------------------------------------------------------------------------------  110111
 36  Equsp    ----------------------------------------------------------------------------------------------------  110111
 37  Equsyl   --------------------------------------------------------------------------------------------------1-  110111
 38  Eriace   ----------------------------------------------------------------------------------------------------  110111
 39  Eupagg   -------------------------------------------------------------------------------------------2--3-----  110111
 49  Hieumb   -------------------------------------2------------------------------------------------------12---2--  110111
 56  Linbor   ----------------------------------------------------1-----------------------------------------------  110111
 64  Luzsyl   ----------------------------------------------------------------------------------------------------  110111
 74  Parpal   ----------------------------------------------------------------------------------------------------  110111
 80  Plamed   ----------------------------------------------------------------------------------------------------  110111
 85  Potcra   --------2-----------------------------------------------------------------------11-------1----1-----  110111
110  Stegra   ----------------------2--------------------------------------------------------------2------34----3-  110111
111  Stemed   ----------------------------------------------------------------------------------------------------  110111
115  Trieur   ----------------------------------------------------------------------------------------------------  110111
126  Viobif   ----------------------------------------------------------------------------------------------------  110111
  2  Agrcap   --------2-----32-4334224422--2---21-332------------31-5415554154342552-3115543212354-232142422324-23  1110
 31  Desces   -----2-----4221-2221-12-1-2555455453412------------45-2--1-1---41--22--1-132-2--33--44-1143344455345  1110
 66  Melsyl   ------------------------------------------------------------1--------------------------------1------  1110
 14  Betpub   --------------2-1-----11---------------1---1-------45455545555555455154552-34343---1445343333332332-  11110
 61  Luzcam   ---------------------------------------------------------------2------------------------------------  11110
 71  Ortsec   -----------------------------------------------------------1---------------------------1------------  11110
```

```
  109  Sorauc    -----------------1---------------------------------33---------------12--1---22--1-------122---------  11110
   54  Juntrg    ---------------------------------------------------3------------------------------------------------  111110
   78  Pinsyl    ---------------------------------------------------33-------1----------------------------12----1-3--  111110
   98  Salmyr    ----------------------------------------------------------------------------------------------------  111110
  122  Vacvit    ------------------------------------------------1--13--------------------2-----------------1------1-  111110
   46  Gymdry    ---------------------------------------------------------------------------------------------1------  111111
   94  Salcap    --------------------------------------------------------------------------------------------------1-  111111

                 0000000000000000000000000000000000000000000000000001111111111111111111111111111111111111111111111111
                 1111111111111111111111111111111111111111111111111110000000000000000000000000000000000000000000000000
                 0000000000000000000000000000000000000111111111111110000000000000000000000000000000000000011111111111
                 0000000000000011111111111111111111111000001111111110011111111111111111111111111111111111100111111111
                 11111111111111000000000000011111111110011100011111100000000000000000000001111111111111111  000000001
                 0001111111111100000000111110000001111        000111  0111111111111111111100000000000111110  01111111


TWO-WAY ORDERED TABLE

                    222 11 111111111 22222 22 222222222222 22           22222222222222222222         2        22
                 6667786456444555555356777278644444555555524722233333312312222222333333331221111122227    111114
                 6893903904678234568019012871156789023456753567935146774383456789012456789013456801234678901297412345

    8  Araalp    ----------------------------------------------------------------------------------------------------  000000
   60  Luzarc    23-------------1-----------------------------------------4--3-1-------------------------------------  000000
   88  Rangla    ----------------------------------------------------------------------------------------------------  000000
  100  Saxcer    ----------1-----------------------------------------------------------------------------------------  000000
  101  Saxces    ----------------------------------------------------------------------------------------------------  000000
  102  Saxopp    ----------------------------------------------------------------------------------------------------  000000
  103  Saxriv    ----------------------------------------------------------------------------------------------------  000000
   18  Carbel    ----------------------------------------------------------------------------------------------------  000001
   21  Ceralp    ------1------------------3-3------------------------------------1-----------------------------------  000001
   99  Saualp    ----------------------------------------------------------------------------------------------------  000001
  106  Silaca    --------------1-------------------------------------------------------------------------------------  000001
   23  Cercer    111--2------2-2---3--------1-----------2-------2--4------1------------------------------------------  000010
  107  Sildio    ----------------------------------------------------------------------------------------------------  000010
    6  Antdio    ----------------------------------------------------------------------------------------------------  000011
   30  Desalp    --2-------------------------------------------------------------------------------------------------  000011
   97  Sallan    ----------------------------------------------------------------------------------------------------  000011
  114  Tofpus    ----------------------------------------------------------------------------------------------------  000011
  118  Trispi    ----------------------------------------------------------------------------------------------------  000011
   34  Epiana    ---1------------------------------------1-----------------------------------------------------------  000100
   73  Oxydig    -1--------------------------------------------------------------------------------------------------  000100
  104  Saxste    ----2---------1--------------------------------1----1-----------------------------------------------  000100
  123  Veralp    -------------------1--------1-----------------------------------------------------------------------  000100
```

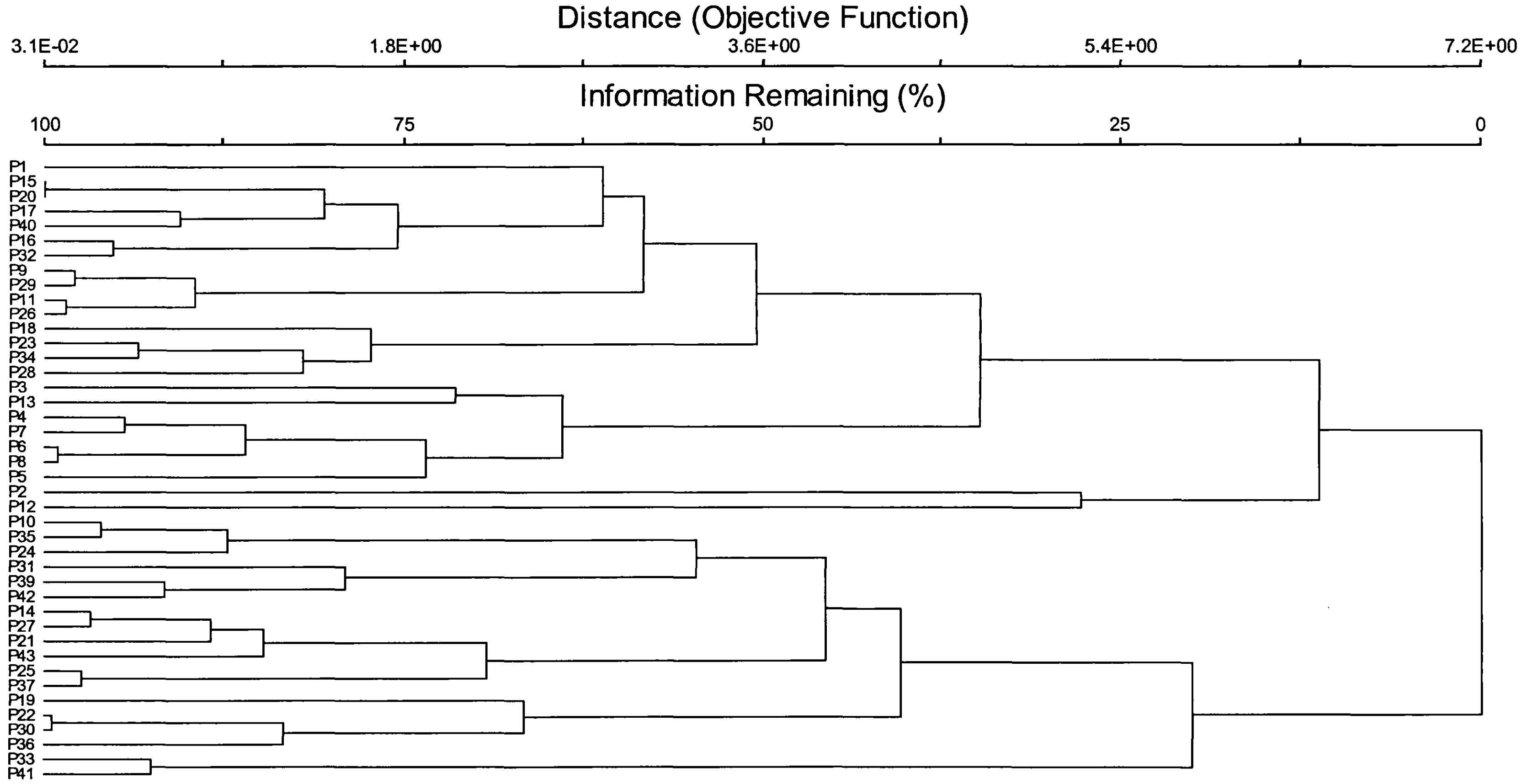
```
  13  Betnan  ----------------------------------------------------------------------------------------------------  000101
  63  Luzspi  443------------1-131----1-------1--------------------------------------2----------------------------  000101
 105  Sibpro  -12-------------------------------------------------------------------------------------------------  000101
  96  Salher  ----------------------------------------------------------------------------------------------------  000110
  47  Harhyp  ----------------------------------------------------------------------------------------------------  000111
  53  Juntrf  ----------------------------------------------------------------------------------------------------  000111
  57  Loipro  ----------------------------------------------------------------------------------------------------  000111
  76  Phycae  ----------------------------------------------------------------------------------------------------  000111
   9  Arapet  ------------1----1----------------------------------------------------------------------------------  00100
  81  Poaalp  -1-1--2-2------5445-3-----24-415444555555-12----------------------------------------3---------1-----  00100
  84  Polviv  211----55-3442-24----21-1--1-11-211----1----3---------------------------------------1---------------  00100
 129  Visalp  ----------1----2--2---------------------------------------------------------------------------------  00100
  59  Luzcon  -----1---3----332-4-----1--23---1-------------------------------------------------------------------  00101
  19  Carbig  ------------------------------------------------1---------------------------------------------------  0011
  40  Fesovi  2--22332-31-3523443-23331-11------------11-3---2------2132-23---1-13--23-12---------1---------------  0011
  70  Omasup  -----1---5---------------11----------------12332232-2---------1-------2------------1-2--12-----34413  0011
  90  Rumace  ----4-1---------------2----1------------------1---1-2---------------------------1-------------------  0011
  48  Hiealp  ------------------1------------------------3--1-----------------------------------------------------  0100
  29  Crycri  ----------------------------------------------------1-----------------------------------------------  01010
  33  Empher  11-----1-1------------------------------------------------------------------------------------------  01010
 121  Vaculi  ---------1------------------------------------------------------------------------------------------  01010
   7  Antodo  22------------1----------------------------1--------------------------------------2-----------------  01011
  12  Athdis  ----------------------------------------------------------------------------------------------------  01011
  22  Cerarv  ----------3---2-21----------------------------------------------------------------------------------  01100
  35  Equsci  -----3--3-----1------------3---------------4--------------------------------------------------------  01100
  17  Camrot  -11---2--2----1-------------------1------------------1------------1-------1-------21----------------  01101
  75  Phlalp  3-2234-------1---2-1--313-33-------211-1---2---2---1-------------------------------22-1-------------  01101
  91  Rumlla  -45-----1-52225--51----1--2-2------------1-3-----13--------13----------2--2-------3-3-11---3---2-3--  01101
   3  Alcalp  --3-------------------------1-----------------11----11-----------------------------1----------------  01110
  32  Desfle  431------1----------354342---331-1--1----35-1---2--442---2-2----111--------4----2-22-------------2-2  01110
  68  Narstr  ----------------------------------------------------------------------------------------------------  01110
 120  Vacmyr  ---------2-----------------------1------------------------------------------------------------------  01110
  55  Leoaut  -31------------------1-3---1------------------------1--3-----------1--2-221-------------------------  01111
  67  Minbif  ----------324243--1-----------------------------------------2-2-1-----------------------------------  100
  69  Omanor  ----2--------------2-----21--------------4--33-31---212-------2-2-----------------1-----------------  100
  93  Sagsag  ---155-------3---------2145543332232434545-4-3---445213--------------------23--2233-3332-13-2--3-21-  100
  16  Calvul  ----------1--------11-------------------------------------------------------------------------------  101
  58  Lotcor  -12-----------------------1-------------------------------------------------------------------------  101
  95  Salgla  43-3211-3434211242323312322-3-31331222-1-2--22321-----11-2-221---1-2-13---1-------1----1------------  101
 108  Solvir  -------1---------111---1-----------------1--1--21---------------------------------------------------  101
  10  Astalp  -------11-----1-212---------------------------------------------------------------------------------  1100
  52  Junfil  ----2----------------------------------1------------------------------------------------------------  1100
  77  Pinvul  ----1----1---------1----1-----------------------1----1----------------------------------------------  1100
 113  Taragg  ---12-5-33232244-31-33413321244---41333444542-1---1-2233----------------22131-32-21-4-2----1--1-----  1100
  45  Gersyl  ---2---1-------------------------------------2------2-----------------------------------1-----------  11010
  82  Poapra  ---3---------------1---------------------2-41524355542444454455544555455211----32332421-243--3-422--  11010
```

```
  1  Achmil   ------122---12----------------1--121-1--1-431--------------------------------------2--1----2-32-1-2-  110110
  4  Alcglo   -------------------------------------------------------------------------------1--------1---2--222-1  110110
  5  Alninc   -------------------------------------------------------------------------------1-------1------------  110110
 15  Calpur   --------------------------------1-------------------3-----------------------------------------------  110110
 20  Carova   ---------------------------------------------------------------------------1--324-------------------  110110
 24  Cerfon   -------------------3---2-22---3-2---22-----111---3--2-----------------------222--3--2-------1----1--  110110
 25  Chaang   ---221----23-----1-------122--2-3------------1-1--------321122-132------12-------------------4------  110110
 26  Chasua   -----------------------------4------133-5-41----------------------------------------232-413---2-2-23  110110
 27  Crecap   -------------------------------------------------------------------------------------3332333--------  110110
 28  Cretec   ------------------------------------------------------------------------------------------------323-  110110
 41  Filuli   ------------------------------------------------------------------------------------------------32--  110110
 42  Fraves   ----------------------------------------------------1------1---3--------253-2111-1-1--11----------21  110110
 43  Galtet   -----------------------------------------------------------------------------11---------------------  110110
 44  Gerrob   ---------------------------------------------------------------------------1-2----------------------  110110
 50  Hypmac   -----------------------------------------------------1-----------------------2212-21---------------1  110110
 51  Junbuf   ----------------------------------------------------------2-1------------32-------------------------  110110
 62  Luzmul   -----------------------------------------------------1-------------------------1--------------------  110110
 65  Maibif   ---------1----------------------------------1-------------------------------------------------------  110110
 72  Oxaace   ----------------------------------------------------------4-------------1----2----------------------  110110
 79  Plamaj   -----------------1---1------24142----2-1211111---1-1122551332455555555425555445455344555555545535555  110110
 83  Polavi   -----------------------------3-1----------------------------------------------------------2--3------  110110
 86  Pruvul   -----------------------------------------------------1-3---2-1-3234--------1--131-------------------  110110
 87  Ranacr   -1-2-1-42---2-1-2------121241--122-221---------------12--212-1-2-12--2--22---13332-3-32-11-24-233233  110110
 89  Rubida   -----------11----------------------1-----1-------------------------------1---1----------------1---1-  110110
 92  Sagpro   ----------------------------------------------------------2222424---252-------2---------------------  110110
112  Stenem   ----------4---3-----------------------------------------125-2-1----------3--------------------------  110110
116  Tripra   ---4-----------------3443---1------1-----------------------------------------2--2----2312--12-------  110110
117  Trirep   ---2-2254224254323235-423-4-4353245443444--1-------2---243-1-42--2222---334543-241443434444343541223  110110
119  Urtdio   ----------------------------1------------------------------------------------2----------------------  110110
124  Veroff   -------------------------1---1-142--2----3---1---2----1---------------------2-----21----------------  110110
125  Verser   --------------------------------------------1--------2421--22214--------11----2--21----------------2  110110
127  Viopal   -------------------1-------------------------21-2-----1---------------------1-1---1-----------------  110110
128  Vioriv   -----------------------------------------------------------3------1---------------------1------1-1--  110110
 11  Astnor   -----------------------1---------1------------------------------------------------------------------  110111
 36  Equsp    ---------------------31-3--2------------------------------------------------------------------------  110111
 37  Equsyl   ---3----2-1------2----------------------------------------------------------------------------------  110111
 38  Eriace   ---2------243---------------------------------------------------------------------------------------  110111
 39  Eupagg   ---------------21-2-1---2---3---2---212----------------------------------------1-1------------------  110111
 49  Hieumb   ----------------------23--2-----2-------------------21----------------------------------------------  110111
 56  Linbor   -----------------------3---------1------------------------------------------------------------------  110111
 64  Luzsyl   -------------------1------1---2---------------------------------------------------------------------  110111
 74  Parpal   ---------------------3-11---------------------------------------------------------------------------  110111
 80  Plamed   ----------1-3---------------------------------------------------------------------------------------  110111
 85  Potcra   -------1----1------1----1---11-2------1---4------------------2-----1-2-21---------1-----------------  110111
110  Stegra   --1313-------------1---33-4-2----------------2------4-------3-------------------1-311---------------  110111
111  Stemed   ------------------------------------12--------------------------------------------------------------  110111
```

```
115  Trieur    ----3-1--1------------------------------------------------------------------------------------------  110111
126  Viobif    ------2311------------------------------------------------------------------------------------------  110111
  2  Agrcap    2224445454342231321-41-145424-423532-2---2-4555-32-2-434434544444444455514444445-3524355544543-14555  1110
 31  Desces    5553-32-14--55145445545555-3444555554444355254455545555445455433554442355344555455354534455454554443  1110
 66  Melsyl    ---1------------------1------------------1------------------------------------21--------------------  1110
 14  Betpub    222444--32332223422121-21-221-3-121211-12---1111----2121-4-31-1----2-22-1------1-221---1------------  11110
 61  Luzcam    ----------------------------------------------------------------------3-----------------------------  11110
 71  Ortsec    ------------1-------------------------------1----------------------1--------------------------------  11110
109  Sorauc    ------1------------------------------1---1---------------------------1-------1----------------------  11110
 54  Juntrg    ---------------3------------------------------------------------------------------------------------  111110
 78  Pinsyl    -----------3-----------12-----2--2-2----------------------------------------------------------------  111110
 98  Salmyr    22-------------------2------------------------------------------------------------------------------  111110
122  Vacvit    -------31--------------2---------11---------1-------------------------------------------------------  111110
 46  Gymdry    -----------------------------------------------------------------------------1----------------------  111111
 94  Salcap    ---------------------------------------------------------------------------------1------------------  111111

               1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111
               0001111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111
               1110000000000000000000000000000000000000000011111111111111111111111111111111111111111111111111111111
               1110000000000000000111111111111111111111111100000000000000000000000000001111111111111111111111111111
               1110001111111111111000000000111111111111111100000000011111111111111111110000000000000111111111111111
                     0001111111111000000111000000000000011100000111100011111111111111110001111111111000000000011111
```

APPENDIX III Cluster analysis of glacier foreland pioneer sites

Linkage method: Flexible beta
Distance measure: Relative Sørensen
Flexible beta value selected is -0.250
Chaining = 5.65%



APPENDIX IV TWINSPAN of glacier foreland pioneer sites

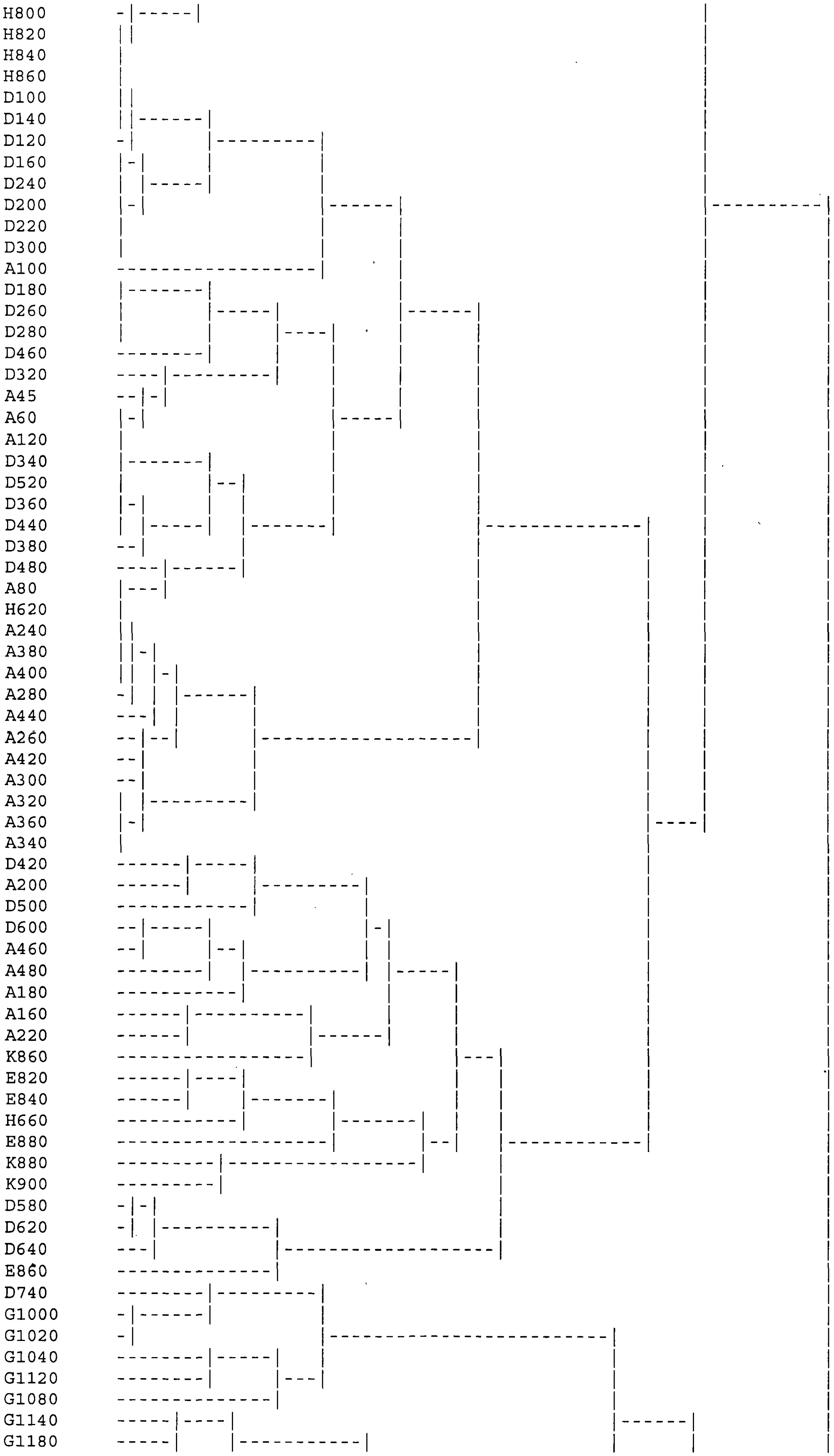
```
ORDER OF SPECIES INCLUDING RARER ONES
   5 Antdio  |  15  Cercer  |  23  Epihor  |  51  Sallan  |  53  Saxcer
  54 Saxces  |  56  Saxopp  |  57  Saxriv  |  65  Taragg  |   7  Araalp
  30 Lotcor  |  66  Trispi  |  67  Urtdio  |  11  Camrot  |  12  Carbel
  44 Rangla  |  70  Visalp  |   8  Arapet  |  25  Fesovi  |  31  Luzarc
  61 Silaca  |  14  Ceralp  |  42  Poaalp  |  19  Desalp  |  29  Leoaut
  38 Oxydig  |  50  Salher  |   1  Agrcap  |  55  Saxniv  |  32  Luzspi
  33 Minbif  |  35  Omanor  |  48  Sagsag  |  46  Rhoros  |  49  Salgla
  58 Saxste  |   6  Antodo  |  21  Empher  |  22  Epiana  |  27  Hiealp
  28 Juntrf  |  40  Phlalp  |  52  Saxazo  |  62  Sildio  |  63  Solvir
  10 Betpub  |  13  Carbig  |  16  Chaang  |  18  Crycri  |  36  Omasup
  37 Ortsec  |  41  Phycae  |   9  Athdis  |  20  Desces  |  64  Stearv
  68 Veralp  |  71  Wooalp  |  26  Gymdry  |   2  Alcalp  |  43  Polviv
  34 Narstr  |   3  Alcglo  |   4  Alninc  |  17  Cirhet  |  24  Equsci
  39 Petfri  |  45  Ranrep  |  59  Sedvil  |  60  Sibpro  |  69  Viobif
  47 Rumlla  |

ORDER OF SAMPLES
  31 P31     |  33 P33     |  38 P39     |  41 P42     |  19 P19
  30 P30     |  36 P36     |  14 P14     |  25 P25     |  37 P37
  10 P10     |  15 P15     |  20 P20     |  24 P24     |  35 P35
  39 P40     |  17 P17     |  27 P27     |  29 P29     |  16 P16
  23 P23     |  32 P32     |  34 P34     |  40 P41     |  22 P22
  18 P18     |  21 P21     |  28 P28     |  42 P43     |   1 P1
  11 P11     |  12 P12     |   5 P5      |   4 P4      |   8 P8
   7 P7      |   9 P9      |  26 P26     |   6 P6      |   3 P3
  13 P13     |   2 P2      |


TWO-WAY ORDERED TABLE


               33341331231122331221233421224 11     2  1
               138190645705045977963240281821125487966332

   5  Antdio   ------1-----------------------------------  000000
  15  Cercer   ----4-------------------------------------  000000
  23  Epihor   -------1----------------------------------  000000
  51  Sallan   1-----------------------------------------  000000
  53  Saxcer   --35-------1------------------------------  000000
  54  Saxces   4233422312122-1---1--1--1--21-------------  000000
  56  Saxopp   324341232-2-3-2--2---1-----1------------2-  000000
  57  Saxriv   ---3433--1--1-----------1-----------------  000000
  65  Taragg   2-----2-----------------11----------------  000000
   7  Araalp   1---455444-2324--142-31-5-1--1------------  000001
  30  Lotcor   -----------------------------2------------  00001
  66  Trispi   4--2213555-2221225--13--43545-3----2-2----  00001
  67  Urtdio   -----------------------------1------------  00001
  11  Camrot   ----------------11------------------------  0001
  12  Carbel   ---------------------1--------------------  0001
  44  Rangla   3545232---2231122-2354453-251-------------  0001
  70  Visalp   --------------1----------1----------------  0001
   8  Arapet   -------1---22----------------1---------1--  001
  25  Fesovi   22212--3-1443543431343231233222-2-342-31--  001
  31  Luzarc   ----1-----222-----------------24------1---  001
  61  Silaca   2---1-----22223--3-2231-----------12--1---  001
  14  Ceralp   2-32-33255-44343-354234-3325-45-2332453---  010
  42  Poaalp   5555345554554555544143434444523-45444444--  010
  19  Desalp   12--24-33-4543-55345241-1221255-4322444444  011
  29  Leoaut   ----------------------1---1--------------1  011
  38  Oxydig   22-135-12223222-5345555-5544-445444443434-  011
  50  Salher   22-----1----------2---1--413---------12-3-  011
   1  Agrcap   -----------------------------3-----2------  100
  55  Saxniv   --1-1--1---------------------------2------  100
  32  Luzspi   ----3--------2--22------2--------2422-41--  1010
  33  Minbif   -----------------11--------------2--------  1010
  35  Omanor   -------------------------21--2---12221---1  1010
  48  Sagsag   -------------------1----------------1-----  1010
  46  Rhoros   -------1---------1--------------------1--1  1011
  49  Salgla   3---21211-------2--------4-11---2432121233  1011
```

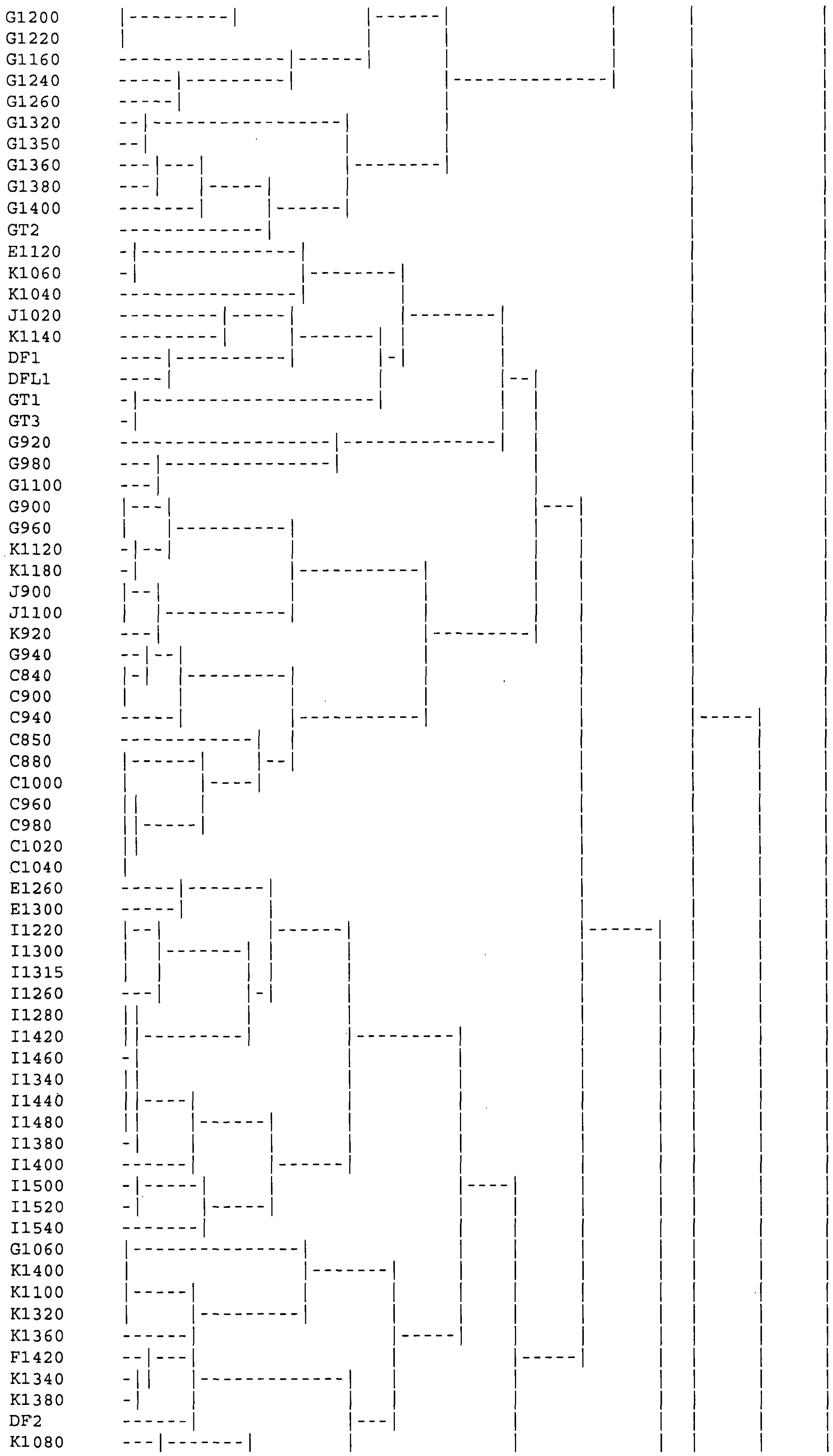
```
58  Saxste     -----------21---314---2-------2--444434442  1011
 6  Antodo     ----------------------------------1-------  110000
21  Empher     ----------------------------------1---1---  110000
22  Epiana     ------1-----------------11----2-3334332-2-  110000
27  Hiealp     ----------------------------------1-------  110000
28  Juntrf     ---------------------------------12-------  110000
40  Phlalp     -----------------1-----------3--42322-31--  110000
52  Saxazo     ---------------------------------1--2-----  110000
62  Sildio     ----------------------------------1-------  110000
63  Solvir     --------------------------------------1---  110000
10  Betpub     --------------------------------12-----1--  110001
13  Carbig     1-------------------------------3---1-----  110001
16  Chaang     ---------------------------------1-3--2143  110001
18  Crycri     --------------------------------212------1  110001
36  Omasup     -------------------------2------3121-3--22  110001
37  Ortsec     --------------------------------1---------  110001
41  Phycae     --------------------------------2---------  110001
 9  Athdis     -----------------------------2--322----23-  110010
20  Desces     ---------------------------------------5--  110010
64  Stearv     ---------------------------------------2--  110010
68  Veralp     -----------------------------1--1-------2-  110010
71  Wooalp     ----------------------------------------3-  110010
26  Gymdry     -----------------------------2--------12--  110011
 2  Alcalp     -----------------------------2----1---2--3  11010
43  Polviv     ---------------------1----------------2--3  11010
34  Narstr     --------------------------------1--------4  110110
 3  Alcglo     -----------------------------------------3  110111
 4  Alninc     -----------------------------------------3  110111
17  Cirhet     -----------------------------------------3  110111
24  Equsci     -----------------------------------------1  110111
39  Petfri     -----------------------------------------1  110111
45  Ranrep     -----------------------------------------4  110111
59  Sedvil     -----------------------------------------1  110111
60  Sibpro     -----------------------------------------1  110111
69  Viobif     -----------------------------------------3  110111
47  Rumlla     --------------------1--------4---------2-2  111

               000000000000000000000000000000001111111111
               000000000000000000000000000001110000000001
               00000000001111111111111111111   000000011
               00001111110000000000000001111   0111111
                   011111000000000111111        000001
                    00111000000111000001        00111
```

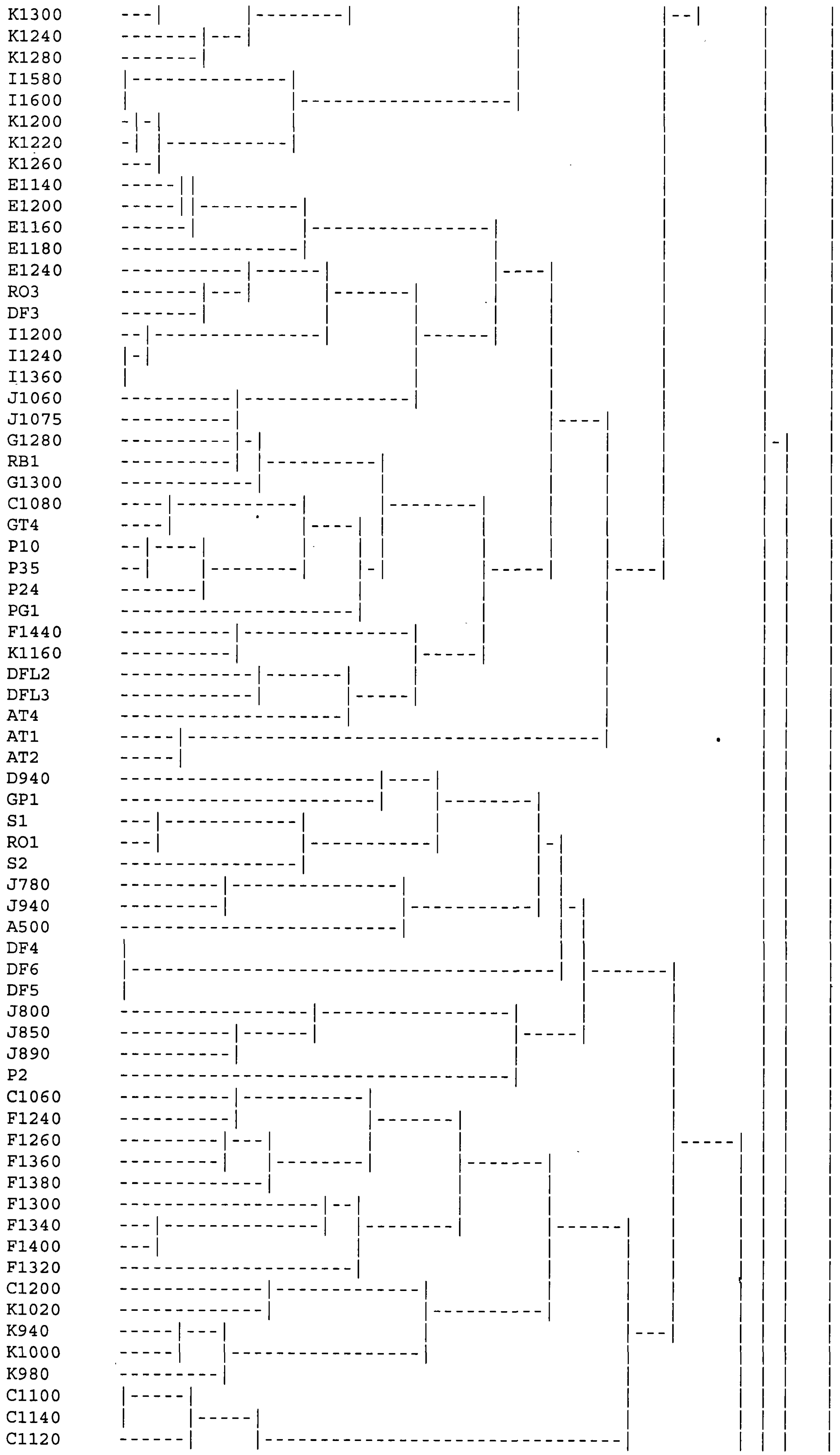
APPENDIX V Cluster analysis of all pioneer sites

Linkage method: Flexible beta
Distance measure: Relative Sørensen
Flexible beta value selected is -0.250
Percent chaining = 0.53

```
                        Distance (Objective Function)
         0.003         15.973          31.942          47.912          63.881
          |-------+-------+-------+-------+-------+-------+-------+-------+
                        Information remaining (%)
     100.000          75.000         50.000          25.000           0.000
          |-------+-------+-------+-------+-------+-------+-------+-------+
D80       ------|-------|
D780      ------|       |--------------|
D540      ----|--------||              |
D680      --|-|        ||              |
D720      --|          |               |
D800      -------------|               |------------|
D400      ||                           |            |
D760      ||---------------------|     |            |
D660      -|                     |     |            |
E900      --|------|             |     |            |
A140      --|      |-|           |-----|            |
E1000     |--------| ||          |                  |
E1020     |          ||          |                  |
E920      --|--------||----------|                  |
E940      --|         |                             |
E1080     ------------|                             |---|
D560      ------------------|------|                |   |
H600      ------------------|      |-----|          |   |
K800      -------||                |     |          |   |
K840      -------||----------------|     |          |   |
K820      --------|                      |          |   |
D700      |---------|                    |--|       |   |
D840      |         |------|             |  |       |   |
D820      ----------|      |---|         |  |       |   |
K780      -----------------|   |---------|  |       |   |
E1040     --------------|------|         |  |       |   |
E1060     ----|---------|                |  |-------|   |
E1100     ----|                          |  |           |
D860      -----|-------------|           |  |           |-----|
K960      -----|             |-----------|  |           |     |
E960      --------|----------|              |           |     |
E980      --------|                         |           |     |
A520      ----|-----------------------------|           |     |
A540      ----|                                         |     |
J840      -----------|----------|                       |     |
J920      -----------|          |-|                     |     |
H720      |----|                | |                     |     |
H760      |    |----------------| |                     |     |
H740      |----|                  |-------|             |     |
H780      |                       |       |             |     |
J960      ----|----|              |       |             |     |
J1040     ----|    |-------|      |       |             |     |
J1000     ---------|       |------|       |-------------|     |
J980      ------------|----|              |                   |
H700      ------------|                   |                   |
H640      ----|--------|                  |                   |
H880      ----|        |------------------|                   |
H680      -------|-----|                                      |
```


H800
H820
H840
H860
D100
D140
D120
D160
D240
D200
D220
D300
A100
D180
D260
D280
D460
D320
A45
A60
A120
D340
D520
D360
D440
D380
D480
A80
H620
A240
A380
A400
A280
A440
A260
A420
A300
A320
A360
A340
D420
A200
D500
D600
A460
A480
A180
A160
A220
K860
E820
E840
H660
E880
K880
K900
D580
D620
D640
E860
D740
G1000
G1020
G1040
G1120
G1080
G1140
G1180


G1200
G1220
G1160
G1240
G1260
G1320
G1350
G1360
G1380
G1400
GT2
E1120
K1060
K1040
J1020
K1140
DF1
DFL1
GT1
GT3
G920
G980
G1100
G900
G960
K1120
K1180
J900
J1100
K920
G940
C840
C900
C940
C850
C880
C1000
C960
C980
C1020
C1040
E1260
E1300
I1220
I1300
I1315
I1260
I1280
I1420
I1460
I1340
I1440
I1480
I1380
I1400
I1500
I1520
I1540
G1060
K1400
K1100
K1320
K1360
F1420
K1340
K1380
DF2
K1080


K1300
K1240
K1280
I1580
I1600
K1200
K1220
K1260
E1140
E1200
E1160
E1180
E1240
RO3
DF3
I1200
I1240
I1360
J1060
J1075
G1280
RB1
G1300
C1080
GT4
P10
P35
P24
PG1
F1440
K1160
DFL2
DFL3
AT4
AT1
AT2
D940
GP1
S1
RO1
S2
J780
J940
A500
DF4
DF6
DF5
J800
J850
J890
P2
C1060
F1240
F1260
F1360
F1380
F1300
F1340
F1400
F1320
C1200
K1020
K940
K1000
K980
C1100
C1140
C1120

```
C1160      |-----------|                                            | | |   |
C1180      |                                                        | | |   |
D1260      ------------|------------|                               | | |   |
I1785      ------------|            |--------|                      | | |   |
E1220      ----|-------------|      |        |                      | | |   |
E1280      ----|             |------|        |                      | | |   |
I1630      --|---------------|               |----------|           | | |   |
I1650      |-|                               |          |           |-| |   |
I1660      |                                 |          |           |   |   |
I1560      ---|-|                            |          |           |   |   |
I1615      |--| |----------------------------|          |           |   |   |
I1720      |    |                                       |           |   |   |
I1700      -|---|                                       |           |   |   |
I1760      -|                                           |           |   |   |
I1770      -|-----|                                     |------|    |   |   |
I1860      -|     |--------|                            |      |    |   |   |
P28        -------|        |----------|                 |      |    |   |   |
I1800      |---------------|          |                 |      |    |   |   |
I1820      |                          |----|            |      |    |   |   |
I1840      |                          |    |            |      |    |   |   |
P31        ----------|----------------|    |-----|      |      |    |   |   |
P39        ----|-----|                     |     |      |      |    |   |   |
P42        ----|                           |     |      |      |    |   |   |
P33        ----|---------------------------|     |------|      |    |   |   |
P41        ----|                                 |             |    |   |---|
PG2        |-----|                               |             |    |   |
PG3        |     |-------------------------------|             |    |   |
PG4        ------|                                             |    |   |
F1280      |-------|                                           |    |   |
P21        |       |-----------|                               |----|   |
P14        -|-----||           |                               |        |
P27        -|     ||           |----------------|              |        |
P43        -------|            |                |              |        |
P25        -|------------------|                |----------|   |        |
P37        -|                                   |          |   |        |
P19        ---------------------|               |          |   |        |
P22        |--------|           |---------------|          |   |        |
P30        |        |-----------|                          |   |        |
P36        ---------|                                      |   |        |
P1         ------------------------|                       |   |        |
P9         -|----|                 |                       |   |        |
P29        -|    |---------------| |----|                  |   |        |
P11        |-----|               | |    |                  |   |        |
P26        |                     |-|    |                  |   |        |
P15        |---------|           |      |                  |---|        |
P20        |         |-----------|      |-------|          |            |
P17        -----|----|                  |       |          |            |
P40        -----|                       |       |          |            |
P16        ---|---------|               |       |          |            |
P32        ---|         |----|          |       |          |            |
P23        ---|---------|    |----------|       |---|      |            |
P34        ---|              |                  |   |      |            |
P18        ------------------|                  |   |      |            |
P3         ----------------|--|                 |   |      |            |
P13        ----------------|  |--|              |   |      |            |
AT3        -------------------|  |              |   |      |            |
P4         ---|----|             |--------------|   |------|            |
P7         ---|    |------------||                  |                   |
P6         |-------|            ||                  |                   |
P8         |                    |                   |                   |
P5         --------------|------|                   |                   |
RO2        --------------|                          |                   |
P12        -----------------------------------------|                   |
D880       -------|                                                     |
D900       --||   |------|                                              |
D920       --||---|      |                                              |
D960       |--|          |--|                                           |
D1000      |             |  |                                           |
```

```
R04       ---------------|  |                                          |
B340      ||                |--------|                                 |
B860      ||--|             |        |                                 |
B880      ||  |             |        |                                 |
B980      -|  |-------------|        |                                 |
B845      |   |                      |                                 |
B1040     |---|                      |--|                              |
B1020     |                          |  |                              |
D980      |--|                       |  |                              |
B960      |  |----|                  |  |                              |
D1060     |--|    |                  |  |                              |
D1140     |       |                  |  |                              |
D1180     |       |------------------|  |                              |
D1200     |       |                     |                              |
B900      |       |                     |------------------------|     |
B940      |-------|                     |                        |     |
B560      |                             |                        |     |
B740      |                             |                        |     |
B920      |                             |                        |     |
D1020     |-----|                       |                        |     |
D1080     |     |---|                   |                        |     |
D1040     --|---|   |----|              |                        |     |
D1160     --|       |    |              |                        |     |
D1100     ----|-----|    |--------------|                        |     |
D1220     ----|          |                                       |     |
D1120     -----|---------|                                       |     |
D1240     -----|                                                 |     |
C920      |--------|                                             |     |
B415      |        |------|                                      |     |
B700      -|-------|      |                                      |-----|
B1000     -|              |                                      |
B360      |-|             |------------|                         |
B520      | |---|         |            |                         |
B460      | |   |         |            |                         |
B660      |-|   |---------|            |                         |
B580      |     |                      |                         |
B440      ------|                      |-----------|             |
B475      |                            |           |             |
B600      |                            |           |             |
B640      |                            |           |             |
B710      |--------|                   |           |             |
B490      |        |                   |           |             |
B540      |        |-------------------|           |             |
B760      ||       |                               |             |
B780      ||-------|                               |             |
B820      ||                                       |-------------|
B615      ||                                       |
B800      |                                        |
B380      |                                        |
GP2       |                                        |
B400      |                                        |
RL2       |------|                                 |
RL3       |      |---|                             |
RL1       -------|   |-----------------|           |
RL4       -----------|                 |-----------|
B680      -----------------------------|
```