

THESIS

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Grassland Dynamics on Revetments at RAF Caerwent,  
Monmouthshire, South Wales.

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for the degree of Doctor of Philosophy

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## SUMMARY

Title: Grassland Dynamics on Revetments at RAF Caerwent, Monmouthshire,  
South Wales.

### Abstract:

A chronosequence method was used to study plant community changes over successional time in a replicated design over an interval of 56 years. Artificial earthworks (revetments) constructed in 1939 and 1968 within a military manufacturing facility have been maintained under a constant regime of regular cutting and biomass removal. Predictions of species and community level change based on models of Odum, Grime and Peet are tested. Aspect and time are shown to be the major explanatory factors determining vegetational differences between samples. Diversity was seen to be significantly lower in older communities in conflict with Odum's model of community development. Partitioning of community structure by relative abundance suggests that the direction of development is contingent on physical conditions. Change in species types from ruderal to stress tolerators is consistent with Grime's successional model but is supported only weakly and by a minority of the species present. Peet's model of competitive sorting is strongly supported at the 1-3m scale but refuted at larger scales. It is apparent that older communities show a tendency towards divergence in structure. The influence of spatial factors on ecological research methods is examined and discussed and it is suggested that development of predictive community models will require a recognition of the multiple levels of community structure and the multiple scales of interactions between their components.

## DECLARATIONS

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

Signed B. Swagel ..... (candidate)

Date 4th July 2001 .....

### STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated.

Other sources are acknowledged by citations giving explicit references. A reference list is appended.

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## CHAPTER ONE: INTRODUCTION.

### 1.1 Background

This study is concerned with grassland succession on derelict land following disturbance generated by the construction of a series of earthworks. By studying the plant community compositions found on two series of artificial landforms, which differ in the time since a single episode of severe disturbance, it aims to further understanding of the processes involved in species replacements and community development over time. The possible effects of environmental factors on succession are studied by investigating the influence of aspect on this vegetational change.

This chapter describes the ecological background to succession in temperate grasslands and the role of environmental factors and disturbance. The study site and its history are described and the local and regional environments are outlined. The research problem is described with reference to predictions derived from successional models and the aims and objectives of the research are stated.

#### 1.1.1 Succession

The term “succession” here refers to the observation, frequently made, that, in the absence of active management, the plant species growing in an area are not constant, that some process of species change occurs over time and that this process gives rise to a predictable sequence of plant communities (Cowles, 1899; Tansley, 1935; Odum, 1969). The term community refers to all the living organisms within some defined area, though it is common practice, as here, to narrow the scope of an investigation to a subset of organisms such as the vascular plants (e.g. Watt, 1947; Wilson *et al.*, 1996).

Whilst successional studies in ecology are concerned with the sequence of plant species occurring at a site over time (Horn, 1981; Bazzaz, 1996), there is also a search for more general patterns of vegetation composition which may point to the processes underlying community change (MacArthur, 1972; May, 1975). It may be argued that a measure of the generality of such processes is that they do not result from the presence of particular species

but occur, with a degree of predictability, in a range of plant communities (Peet, 1992; McCook, 1994).

Attempts to obtain a general understanding of the process of succession have, for at least 100 years, failed to provide a satisfactory model (see Chapter Two). A number of mechanisms have been proposed and tested with differing degrees of success but these have generally been of limited use (Drury and Nisbett, 1973; Miles, 1987) and it is suggested that no single process is likely which can usefully explain all, or even most, of the observed community sequences (Odum, 1969; Miles, 1987; Crawley, 1997).

The development of theories of succession has reflected differences in the concept of the plant community itself: a dichotomy may be drawn between those ecologists who view the community as an integrated, self-regulating system (Clements, 1928; Odum, 1969) and those who consider that a particular assemblage of plants reflects only their common requirements for a particular set of conditions (Gleason, 1926; Whittaker, 1956). A conceptual scheme has nevertheless emerged from this debate within which the great number and variety of instances of vegetation change may be placed (Burrows, 1990). This successional context is outlined below.

Two views of the nature of the community are described (Sections 2.3 and 2.4) in terms of the perspectives of two early protagonists in the study of plant dynamics. One view states that a community is an assemblage of individuals each of which occupies a space in the community as a result of the many chance factors of dispersal, site availability and site conditions. Community development takes place as a process of species replacements resulting from similar chance events and opportunities with the consequence that all communities are different. The second view suggests that communities are structured by interactions between plants so that community composition is non-random, and that, from a given pool of available species, the same external conditions will give rise to the same communities because of the sorting process generated by plant interactions. The most extreme example of this holistic view (Section 2.3) suggests that local external conditions are themselves modified by interactions with the vegetation so that in any regional area the same community, the regional climax, will eventually develop.

This polarity of views has led ecologists to approach community development from two perspectives. The holistic, top-down view seeks to define communities as integrated



systems and describes them in terms of patterns or attributes characteristic of the whole community. Bottom-up explanations characterize the individualist approach which suggests that communities are built of individual plants and species and that characteristics of the community are therefore a reflection of the types of species which make up the community. This study considers models of vegetation change both from the perspective of a change in species type and as a development of community structure.

A framework for distinguishing the kinds of processes and mechanisms involved in successional change has been proposed (Peet, 1992) which defines a spectrum of initial conditions between the poles of primary and secondary succession and a range of processes within the limits between autogenic and allogenic change. A habitat in which primary succession may be said to occur is one in which there is no prior biological material present and the ecosystem is assembled from scratch. Such extreme conditions may be seen following volcanic eruptions, on deposits of lava or ash (Whittaker *et al.*, 1989) or on forelands following glacial retreat (Chapin *et al.*, 1994). An example of a secondary succession would be that found on an abandoned agricultural field (Bazzaz, 1975; Brown and Southwood, 1987) or in a forest gap (Finegan, 1984) where there is an existing, well developed soil which may already contain the propagules from which community reconstruction can proceed. In fact many successions fall somewhere between these extremes (Miles, 1979), the position within the spectrum being judged according to, firstly, the degree to which the soil has been returned to a raw mineral matrix by the initiating disturbance (Vitousek and Walker, 1987) and, secondly, the presence or proximity of regenerative plant structures (Miles, 1987).

A constant theme in ecological studies is the correspondence between the conditions characteristic of a particular habitat and the physiological and life-history attributes of the species which occupy that habitat (Drury and Nisbett, 1973; Whittaker, 1975); in successional studies change in species may follow predictably from a change in conditions at a site. A consideration of the causes of such changes in conditions suggests a second polarity in successional development between, on the one hand processes generated internally by the vegetation community itself and termed autogenic and, on the other hand, those changes in the vegetation brought about by external or allogenic factors. This spectrum of causative factors equates with the different conceptions of the nature of ecosystems as, either chance assemblages of species, largely driven by external change, or

as integrated holistic systems with self-regulating internal mechanisms generating change or development (McIntosh, 1980).

An autogenic process conforms broadly with that described by Clements (Section 2.3), and termed reaction, in which plants modify the local environment by, for example, producing changes in the microclimate or contributing to soil development, and, in so doing, generate different local conditions. If these conditions are less suited to the species own survival and more suited to an individual of another species then there is a probability that a species replacement will occur. Connell and Slatyer (1977 and Section 2.4.2) use the term facilitation to describe this sequential process. Reynolds *et al.* (1999) describe the case where an autogenic mechanism, nutrient cycling around a creosote bush generating “nutrient islands”, forms an important component in the change from prairie to sagebrush.

Allogenic vegetation change results from influences external to the community such as, for example, climatic cycles (Prentice, 1992) or a change in the level of a water table (Wheeler, 1992), in which case the sequence of species follows from a correspondence between the habitat’s environmental conditions and the plants adaptational preferences. Allogenic and autogenic factors are not, however, mutually exclusive (Glenn-Lewin and van der Maarel, 1992) and both may be apparent within a single sequence. In general, allogenic processes are thought to dominate in primary, and autogenic in secondary successions (Drury and Nisbett, 1973) though the notion that whole successions can be distinguished as resulting from one or other sets of factors has been criticised since processes of both kinds are often found in the same successional series (Glenn-Lewin and van der Maarel, 1992). They are suggested here as a way of locating the various mechanisms encountered in successional studies within a descriptive context.

In this work vegetation development is studied over a period of several decades, in a relatively constant habitat (Section 1.3) and under a relatively constant climate. Within the context of the above discussion therefore, change is likely to be the product of vegetation processes, either in modifying the local environment or as a result of interactions between individuals leading to, for example, competitive replacements.

### 1.1.2 Grassland ecology

Grasslands occupy a large proportion of the land surface in the British Isles and, in temperate regions, their dominance is almost always the result of repeated burning, cutting, animal grazing or other activities which prevent the establishment of shrub and tree cover (Duffey *et al.*, 1974). Pollen evidence suggests that, prior to human influence, mixed deciduous woodland was the major vegetation formation in the British Isles (Rackham, 1990). The development of agriculture led to the progressive clearing of land and the establishment of a largely graminoid-based economy (Duffey *et al.*, 1974). This was maintained, in pastoral areas by grazing and burning, and in arable systems by regular ploughing and reseeded (Ausden and Trewick, 1995). Where these activities cease or are reduced, fields rapidly revert to coarse grass, scrub and woodland (Duffey *et al.*, 1974). Grasslands represent therefore, an arrested succession or plagioclimax in the sense used by Rodwell (1990). In this study biomass removal was effected by regular, manual cutting of the vegetation (Section 1.1.5).

The classification of British grasslands is largely due to, and based upon, the work of Tansley (1939) who described three groups of grassland types which he referred to the underlying geologies and the level of acidity of the soils. Acidic grasslands are those which grow on soils formed from siliceous, peaty or sandy parent materials. These are to be found in upland areas in the north and west, and also on sandy heaths in the lowlands of England. All are characterized by soils of low pH. Calcareous, or basic, grasslands occur on chalk or limestone soils predominantly in the south-east quadrant of the British Isles. These are found where soils have a high calcium content and a high pH level. Mesotrophic, or neutral, grasslands occur on soils with a neutral range of pH, mainly on the clays and loams of lowland Britain. The definition of neutral grasslands is somewhat general and comprises those grasslands which are neither acidic nor calcareous. The grasslands in this study occupy a site characterized by moderately calcareous soils (Section 1.3).

This classification implies an association between community types and soil acidity, yet several authors have questioned the basis of this distinction. It has been shown, for example, that pH *per se* is not the reason for the exclusion of calcicolous species from areas of lower pH (Grubb *et al.*, 1969). Hodgson (1990) found no association between species distributions and soil pH in a large set of British grassland species and Grime (1990) reports that calcicolous species share traits which are adaptive for dry conditions and therefore

suggests that these species co-occur at present because they evolved in semi-arid habitats. Rodwell too, (1990) has argued that the distribution of calcicolous grasslands in Britain follows predominantly from a consideration of climate rather than geology. Nevertheless the basis of Tansley's classification remains in current usage, (Rodwell, 1992; Ausden and Trewick, 1995).

### **1.1.3 Grassland succession**

A number of factors have been associated with the onset of vegetation change in grasslands (Wells *et al.*, 1976; Usher and Jefferson, 1990; Gibson and Brown, 1991). The availability of colonizing organisms from outside the area may change such that, as opportunities for regeneration occur, new species "invade" the community. There may also be changes in the pattern of the creation of regeneration opportunities as, for example, when there are changes to the disturbance regime generated by grazing animals. There may be changes to the environment such that the conditions of soil or microclimate favour organisms with different life strategies. These environmental changes may result from outside influences, such as an increase in nutrient deposition in precipitation, or be generated from within by the community organisms as when an accumulation of plant litter modifies the pattern of humidity at the soil surface. The variation in plant size, form, biochemical composition and biotic relationships means that the presence of a particular plant species can alter the micro-environment in a particular way; it can differentially alter the soil, the sward architecture or the presence of particular insect species. Yet its presence may be due to largely random processes; the particular factors giving rise to the opportunity for colonization, the timing of the availability of a propagule and the conditions of temperature and moisture at the time, may all be essentially random. A single replacement may therefore be viewed as the result of a number of individual, stochastic events and inherently unpredictable. Whilst this is true at the level of the individual the impact of such individual events may be integrated for larger numbers (Pickett *et al.*, 1987) such that, at the community level, a coherent development is observed.

The removal of vegetable biomass by grazing animals effectively prevents the encroachment of scrub whilst maintaining a herb community. In addition the presence of macro-herbivores creates a heterogeneous pattern of local disturbance and nutrient enrichment which increases the range of microhabitats for colonizing plants. In this study the use of

stock to maintain the sward has been minimal or non-existent (Sections 1.3 ). The presence of ant mounds and the abundant cover of the rank grass *Arrhenatherum elatius* attest to the low impact of grazers (Wells *et al.*, 1976). Maintenance of the community has been the result of regular, manual cutting throughout the period 1939-1993 in an attempt to reduce the risk of fire (Defence Land Agents, 1993-96). Nevertheless, grazing impact by rabbits cannot be discounted. The presence of burrows and faeces indicates that rabbits are currently active on the site and were likely to have been present, as elsewhere, throughout the study period. Following the spread, in 1953, of the myxomatosis virus to the wild rabbit population in Britain there was a swift and severe fall in their numbers (Sheail, 1971) and, consequently, in the extent and severity of grazing impact on grasslands over large areas (Sumption and Flowerdew, 1985). Rabbit numbers have gradually recovered as they acquired immunity to the virus to the extent that by 1985 they were again having an impact on grasslands (Bacon, 1990). Grazing pressure is however highly variable from year to year as the virulence of the viral control fluctuates and the effects of grazing depend on climate, soil type and locally available alternative vegetation (Hillier *et al.*, 1990). The extent to which the reduction, and subsequent renewal, of herbivore pressure affected the plant communities in the study site is not known. The major change in vegetation reported from elsewhere (Hillier *et al.*, 1990) indicates that succession to coarse grassland and scrub was the most immediate consequence of reduced rabbit numbers. Since the site management already ensured that tall and woody vegetation was controlled by cutting the reduction in grazing was unlikely to have had a large effect. In addition since the site was the scene of intense human industry during the war years (Section 1.3) it is unlikely to have attracted large numbers of rabbits.

#### **1.1.4 Topography, aspect and microclimate**

Plant species vary in the characters which make them suited to one set of environmental conditions rather than another (Ellenberg, 1988) and conditions may change from place to place or over time at a single location (Geiger, 1965). They are limited, for example, by factors such as temperature, available moisture, light and nutrients (Begon, Harper and Townsend, 1990). These factors may be relatively constant, a given characteristic of the particular location, or they may be determined by other organisms in the area; their availability to one individual can be influenced by the presence of a neighbouring individual

with the result that species replacements can be the result of interactions such as competition (Tilman, 1985).

Differences in topography can influence levels of insolation, wind exposure, temperature and moisture availability and rates of moisture loss (Stoutjesdijk and Barkman, 1987), so producing a range of environmental conditions. As a consequence a range of plant communities may be present containing species which exhibit corresponding, adaptive traits (Whittaker, 1956). At a smaller scale, microtopography can be a factor promoting heterogeneity within a plant community through its effects on local environment and microclimate (Crawley, 1997).

Aspect has been shown to influence microclimate mainly as a result of the effect of differing levels of direct insolation (Austin *et al.*, 1984). Differences in the level of incident radiation translate to differences in temperature and moisture loss. Within a latitudinal region differences in insolation arise from differences in the angle of elevation of a slope and the compass direction of the slope face. In addition the height of the local horizon will influence the amount of direct solar radiation received by the surface over a diurnal interval. Indirect radiation has also been shown to account for a substantial proportion of the total radiation received by a surface, either scattered from a clear sky or reflected from cloud (Stoutjesdijk and Barkman, 1987). Slopes with differing aspect, slope angle and elevation may also be differentially affected by wind where the prevailing climate has a directional bias as is the case for much of the British Isles (Section 1.2). Evaporative loss of moisture from soil surfaces and mechanical damage to plant structures will therefore create additional stresses (Grace, 1981) to vegetation on slopes with a southerly or westerly exposure.

The angle of a slope will also influence a number of the factors determining the microclimate of the slope surface. A steeper slope will intercept a greater amount of wind energy with implications for temperature, surface moisture loss and mechanical damage. Slope angle will determine both the angle of open sky from which a face receives incident radiation and also, for south-facing slopes, alter the area of face which is normal to direct solar radiation. For this reason steeper, south-facing slopes will receive proportionally more direct solar radiation when the angle of the sun is low, as it is at dawn and dusk and during the early and later parts of the annual growing season. This will effectively increase the length of time, both diurnal and seasonal, during which radiation is intercepted and during which minimum levels of light and temperature for plant growth are attained; it will

likewise increase the probability of temperature stress during the hours of maximum irradiance.

From the above it may be supposed that slopes having different aspects would give rise to differing microclimates and they would therefore be expected to support vegetation communities comprising species whose life history traits were characteristic of these differing temperature and moisture regimes. Where communities are seen to develop over time it may further be questioned whether, such development is either, directed by environmental factors along different trajectories (Peet, 1992) or, that development shows consistent patterns which are not related to environmental differences. In this study vegetation on slopes having different aspects is compared over time in order to distinguish between the effects of these environmental factors on the presence of species types and on patterns of community development (Section 1.5.1).

Revetments with slope faces having differing aspects provide the opportunity to describe the change in species composition with respect to the environmental gradient represented by the different conditions found on those faces. Such a gradient may be used to describe the degree of segregation of species; a change in the preference shown by species for a particular environmental niche is predicted to change during the course of succession as a result of competitive interactions (Section 1.6.1).

### **1.1.5 Disturbance**

Disturbance is an important concept in successional ecology for two main reasons. At the level of the individual it is the removal or death of a plant which allows a replacement to become established (Horn, 1976). At the community level it is the wholesale destruction of a community, or a large scale change in the physical environment affecting a community, which initiates the process of secondary succession (Whittaker, 1975).

Disturbance is commonly seen as the starting point for a secondary succession where it results in space being made available within an existing community (Connell and Slatyer, 1977; Connell, 1987; Glenn-Lewin and van der Maarel, 1992). Clements (1928) used the term *nudation* to describe this process whereby a new succession is initiated though he considered that the role of disturbance was overemphasized in successional studies. The

term is usually taken to mean the destruction of existing vegetation and to imply its replacement or renewal from seed or regenerative fragments, either surviving within a disturbed soil, or migrating from an outside source (Grime, 1974; Crawley, 1997).

In addition, disturbance, acting continuously at a fine scale, is seen as a potent agent determining the composition and developmental pathway of a plant community (Pickett *et al.*, 1987). In this context it is defined as the partial or complete destruction of an existing plant by a mechanical interference of either the organism itself by, for example, burning, cutting or grazing, or a perturbation of the growth medium, by animals (e.g. soil insects, animal burrows and scrapes or hoof damage), by humans (e.g. ploughing) or by abiotic forces such as water, sun or frost (Grime, 1977). Such processes, in generating open space and opportunities for colonizing plants, are a prime mechanism of change in plant communities.

Thus the definition of disturbance and its influence on vegetation dynamics depends on the scale, severity and extent of its action. Prentice (1992) draws a distinction between landscape scale and patch scale disturbances, where a patch is an area of vegetation within which individual organisms interact. It is therefore useful to relate the extent of the disturbance to the size of the community on which it acts. Where this ratio is small the community may be regarded as a mosaic of patches each subject to its independent disturbance regime; at the community level this small scale disturbance operates to generate opportunities for colonists and therefore the potential for community development. Where the disturbance to community ratio is large and disturbance is infrequent then it acts as an initiator of succession. In this context a community may be operationally defined as an area of vegetation large enough to contain a sufficient number of patches such that patch-scale processes are averaged out at the community scale (Veblen, 1992; Wu and Levin, 1994).

In this study a severe disturbance event which reshaped the upper few metres of land surface over an area of several hundreds of hectares (Section 1.3) would certainly have been an effective initiator for a secondary succession. Thereafter vegetation on the revetments was allowed to regenerate and was regularly cut by hand-scything, the cut material being removed. In terms of the definitions given above the initial event constitutes a landscape scale disturbance with subsequent management being relatively unintrusive. Whilst plant material was continuously destroyed and removed this is likely to have been restricted to those stems exceeding around 20cm in height. This would have left the grasses and low



growing perennials intact and would have destroyed those species having meristems born high above the ground such as tree saplings, woody shrubs and tall forbs; annuals may well have had chance to set seed between cuts. Consequently it may be argued that, whilst maintaining a grassland plagioclimax, post-disturbance anthropogenic impacts on the revegetation communities were relatively minor.

The patch dynamics model (Pickett *et al.*, 1987; Prentice, 1992) emphasises the role of disturbance, at fine scales, in generating openings in which new colonists have an opportunity to become established. In this sense disturbance to the plant communities in the study area would have been restricted to those resulting firstly, from animal activities such as ant-hills (Wells *et al.*, 1976; King, 1977) and rabbit scrapes (Bacon, 1990), and secondly, from the effects of weather, either in directly killing plants by extremes of temperature or moisture deficit (Stoutjesdijk and Barkman, 1987), or indirectly as a result of soil erosion or wind damage (Grace, 1981).

#### **1.1.6 The scientific problem**

The scientific problem addressed in this study concerns the changes in vegetation which can be shown to occur, consistently and predictably over a successional time series during the decades following a disturbance which exposed a new surface. The possible influence of selected environmental factors on succession is addressed by investigating the effects of aspect on this vegetational change. The rationale for the experimental design, proposed as a means of addressing this problem, is described in Section 1.5.

### **1.2 The regional environment**

The Principality of Wales lies on the western margin of the largest of the British Isles on the north-west fringe of the European seaboard. The climate of the western parts of the British Isles is dominated by the oceanic influence of the north Atlantic weather systems. The combined effects of the warm, North Atlantic Drift ocean current and the mid-latitude westerly winds produce a characteristic weather pattern of warm, wet summers and cool, wet winters. There is generally an adequate and even supply of rain and a lack of extreme temperatures (Barrow and Hulme, 1997). The natural vegetation of the region is that

characterized as temperate forest with the maritime influence producing less extreme winter temperatures than those found in more continental examples of this biome (Cox and Moore, 1993).

Within the British Isles the main climatic gradient is that found between coastal and inland areas; those parts nearer the sea maintain a more humid atmosphere with less extreme temperature fluctuations than is the case in inland regions. In this regard the climate of the lowland regions of South Wales represent typical maritime conditions. Within this general regional climatic type Rodwell (1992) has distinguished those areas which receive strong summer sunshine as a result of their western or southern aspects producing "hot, unshaded and barren situations" (p. 112). The coastal area of eastern South Wales has a mean annual rainfall of around 1000mm, and mean monthly air temperatures of about 4.5° C in January and 17.0° C in July (Goudie and Brunnsden, 1994).

The geology of the South Wales region comprises sedimentary deposits of sandstones, coal measures and limestones overlain with Triassic Marls and more recent glacial, periglacial and river alluvium surface drifts, (Evans, 1970). The specific geology underlying the study site is described below (Section 1.3).

### **1.3 Royal Air Force Caerwent**

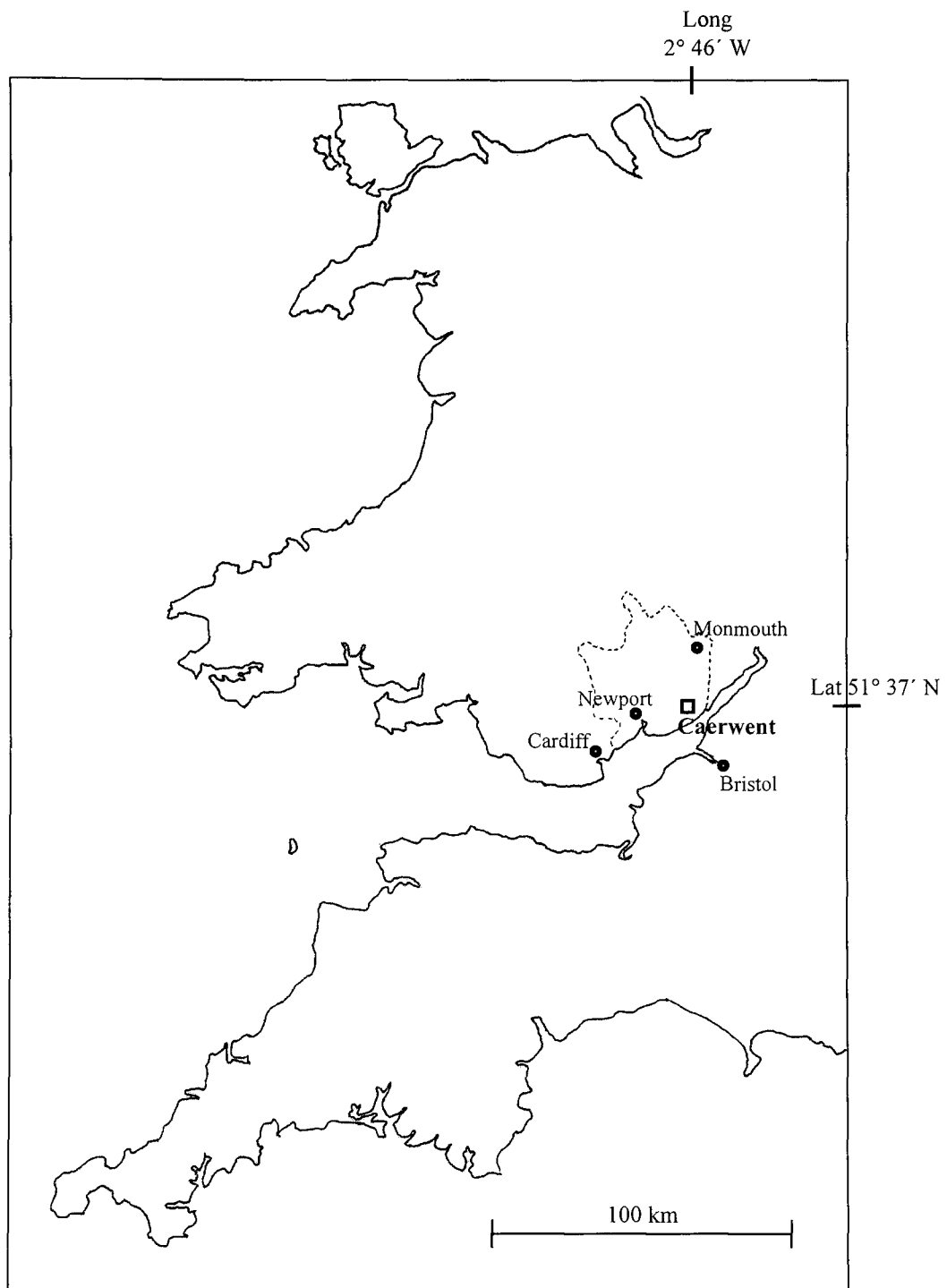
Royal Air Force Caerwent (the site) comprises a fenced area of 639 hectares of land close to the village of Caerwent in the county of Monmouthshire, South Wales (Figure 1.1) in an area of predominantly arable and pastoral agriculture. The site lies 15 kilometres east of the town of Newport, and 1 kilometre north of the village of Caerwent at longitude 2° 46' W, latitude 51° 37' N with the nominal centre of the study area at National Grid Reference (GR) ST 477 917, (Ordnance Survey, 1991). It lies 5 km north of the sea coast at Caldicot Pill on the Severn estuary and at an elevation of between 30 and 100 metres. Figure 1.1 indicates the location of the site in relation to the western coastal fringe of Great Britain.

Prior to 1937 the site consisted of a number of small holdings owned by Monmouth Borough Council. It was compulsorily purchased by the Admiralty in 1937 and has since been owned by the Ministry of Defence (MOD). From 1939 it housed the Royal Naval

Propellant Factory (RNPF), a manufacturing facility which employed some 6000 people in addition to the troops stationed there in a defensive role (Defence Land Agents, 1993-1996). The factory comprised over 700 buildings, each identified by number, and connected by a network of 30 miles of roads and 12 miles of rail track. Following the construction of the factory those areas away from the buildings and roads were re-seeded and used for cattle and sheep grazing. The site continued to be used for a variety of military functions after the war. In 1967 it was loaned to the United States Army, redesignated as Reserve Storage Activity Caerwent, and used as a store for conventional armaments. To effect this transfer to the US forces the site was first re-assigned to the Royal Air Force as RAF Caerwent; this nominal change of title was an administrative convenience and is the only association between the site and the RAF. This function ceased in July 1993 and the facility was formally closed on the 20th August 1993. Management of the site was then transferred to the Defence Land Agents (DLA) who currently hold it “under disposal”. The site perimeter has been maintained to the present day and all access and usage is restricted and controlled under the authority of the MOD. Safety concerns meant that permission to use the site for this vegetation study was granted with the express conditions that no metal implements were to be used nor any soil materials removed.

Current activities within the site include police and army training, a clay pigeon club and rabbit shooting. A number of the buildings are used for commercial warehousing and a small-scale charcoal manufacturing business operates in the wooded area. Grazing of sheep and cows by local farmers is permitted within designated areas under a scheme supervised by the Countryside Council for Wales (CCW). Four areas of unimproved grassland and one of semi-natural woodland were designated as Sites of Special Scientific Interest (SSSIs) in 1987. Locally-based conservation groups have special interests in the birds, bats and badgers inhabiting the site and the five SSSIs are managed by the MOD under the guidance of the CCW.

The site has an open southerly aspect and rises gently from south to north with the more abrupt rise of a wooded hill and ridge in the north. Between these two features lies a shallow, dry valley which corresponds to a sandstone bed. Figure 1.2 shows the main topographic features of the site. Whilst these general features are apparent today, large sections of the ground surface have been reworked during the extensive construction programmes in 1939 and 1967. The function of the site, as a factory manufacturing



**Figure 1.1 The location of Caerwent in relation to SW Britain and the county of Monmouthshire.**  
(redrawn from Ordnance Survey, 1966)

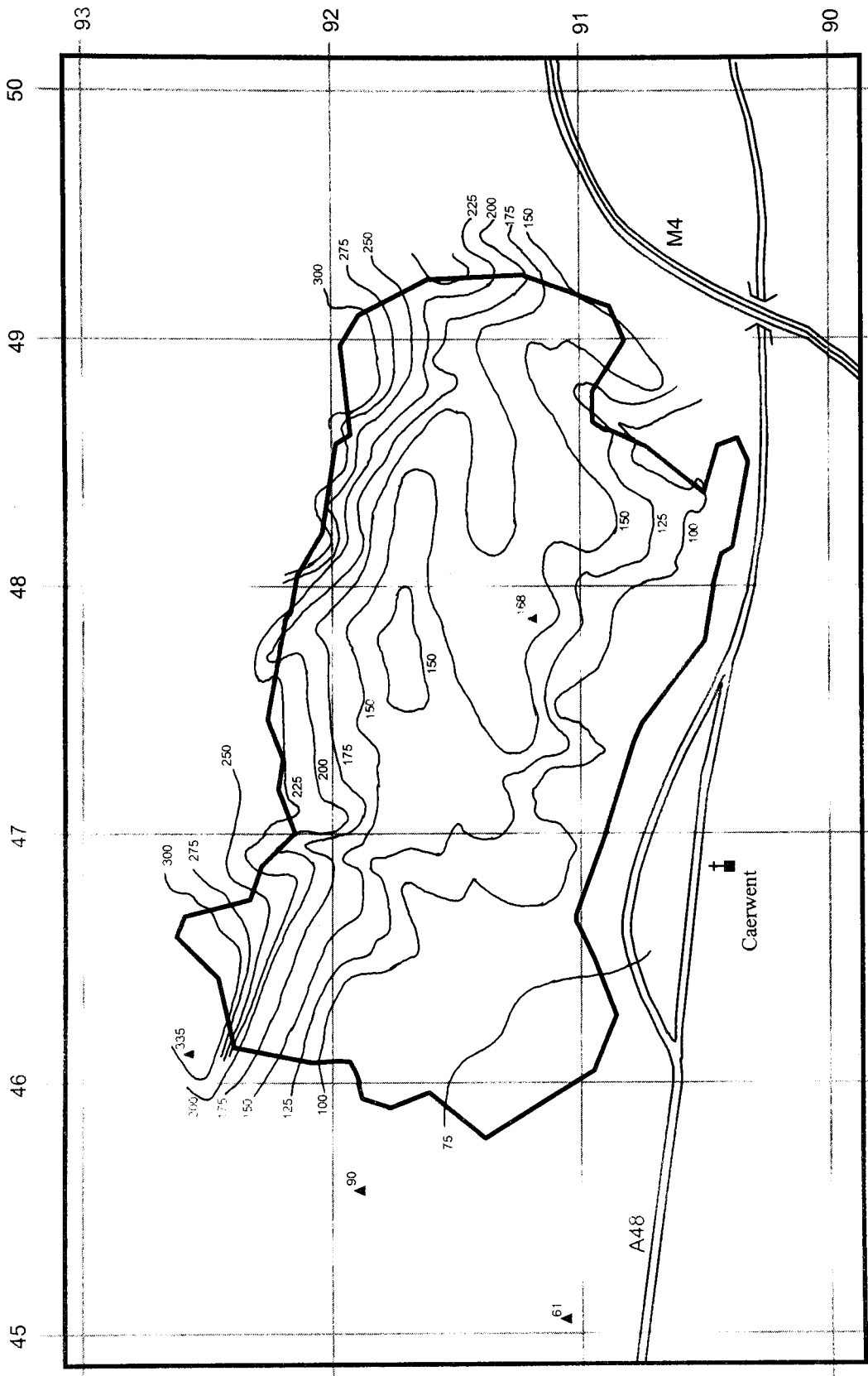
explosive material, imposed special constraints on the layout and design of the facility. To reduce the risk and extent of explosive or bomb damage, the buildings constructed in 1939 are spread over a large area and each is encircled by earthen mounds, or revetments, usually between 5 and 10 metres in height. Those built in 1967 form a more compact grouping but are similarly enclosed and isolated by revetments.

Predominantly on limestone rocks (Ordnance Survey, 1962), the site is overlain in the south by Keuper Marl and, to the north, there is a band of Drybrook Sandstone sandwiched between strata of Drybrook Limestone and Whitehead Limestone (Defence Land Agents, 1993-1996). These Carboniferous layers dip to the south at an angle of approximately 10°. Much of the eastern and western areas are covered by alluvium of third and fourth terrace drift. These deposits are composed of gravelly sands or clays. A geotechnical report by the Department of the Environment Soils Section in 1972, quoted in the RAF Caerwent Conservation Dossier (Defence Land Agents 1993-1996), indicates that these drift deposits are more extensive than is shown on the Geological Survey map. Figure 1.3 shows the geology of the site redrawn from the Geological Survey one-inch series (Ordnance Survey, 1962).

The site is generally very free draining as is evidenced by the occurrence of numerous swallow holes. These prompted an investigation by the Naval authorities in 1954 who reported that the increased incidence was likely to be associated with the use of large quantities of water on the site related to the manufacturing processes in use. As water drains down through the limestone strata it washes away the overlying drift material. This results in the formation of cavities which enlarge until the roof can no longer be supported, and this then collapses into the space beneath. The authorities found that the water table was 25 metres below the surface at that time, (Navy Works Report No 54, quoted in Defence Land Agents, 1993-1996).

An application for SSSI status for Dinham Meadows (GR: ST 475 915) and quoted in the RAF Conservation dossier (Defence Land Agents 1993-1996) describes soil types within the site;

Soil types range from deep coarse loams with slight seasonal waterlogging through fine loams of intermediate depths with a moderate calcareous influence to bare rock of Carboniferous Limestone.



**Key**

— Boundary Fence

~ Contour (height intervals in feet)

▲<sup>90</sup> Spot height (feet)

== A48 Roadway

Scale 1:25000

— 1 km

Figure 1.2 Topography of RAF Caerwent (redrawn from Ordnance Survey 1966).

It continues with a description of the vegetation;

Whilst the main grassland community type can be referred to the *Centaurea nigra* - *Cynosurus cristatus* mesotrophic grassland type, the range of soil types is reflected in the presence of other communities. On the deeper loams there are examples of the *Arrhenatherum elatius* coarse grassland community, whilst the shallower base-rich soils support a community with strong affinities to the *Koeleria macrantha* sub-community of the *Festuca ovina* - *Carline vulgaris* limestone grassland type.

The material of the revetments may be assumed to have originally comprised an amalgam of loams from a mesotrophic soil with a moderate calcareous influence mixed with material excavated from deeper, parent material, predominantly limestone and Keuper Marl mudstones, (Evans, 1970). The plant communities found in this study were largely of type MG1, *Arrhenatherum elatius* grassland, (Rodwell, 1992). As the revetments rise 5-10 metres (m) above a generally level land surface (see Plate 1.1) the vegetation on the upper parts of the slopes is likely to be more exposed to wind and radiation and therefore to experience a harsher microclimate (Section 1.1.4). In addition, it is assumed that, within a free-draining medium, plants located towards the top of a slope will suffer water stress more frequently than those in the lower part of the slope.

#### **1.4 The revetments and the study area**

Within the site an area was chosen (the study area) which allowed for an investigation of the influence on vegetation succession of some of the factors described above.

##### **1.4.1 Revetments**

Numerous revetments were present on the site (Plates 1.1 and 1.2): the vegetation stands which have developed on them form the objects of study in this work. It is assumed that the revetments were formed from the local surface material though no documentary evidence of the construction process has come to light. There are, however, areas within the site where it is apparent that the land surface has been removed to a depth of two metres or more, leaving a “scooped out” appearance (Plate 1.1) suggesting that this was the source material for the revetments. Moreover, in view of the urgency associated with the war effort, it is

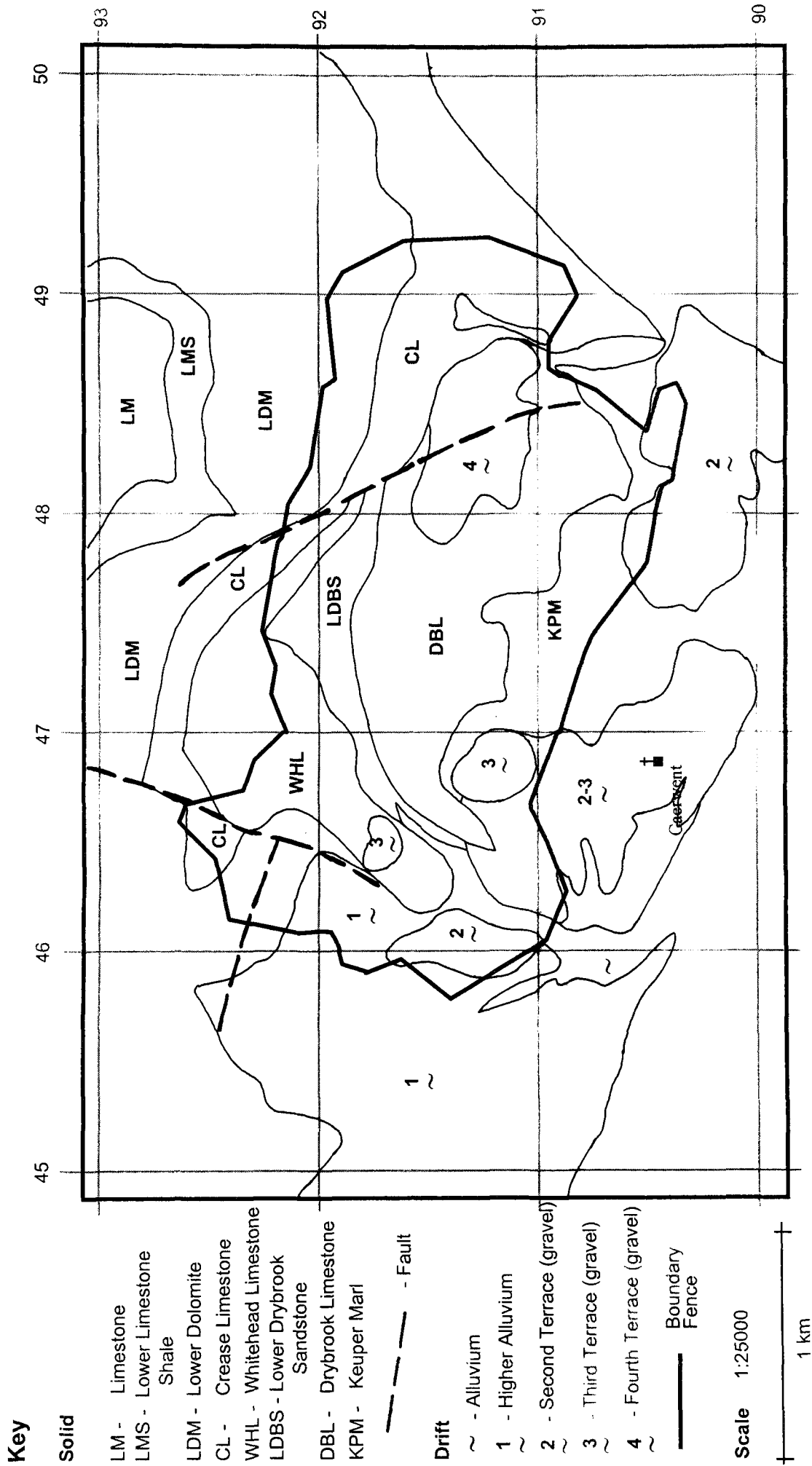


Figure 1.3 Geology of RAF Caerwent (redrawn from Ordnance Survey, 1962).



reasonable to assume that simple techniques and local materials were employed in the construction.

The revetments are the result of a major reforming of the land surface and therefore represent a massive soil disturbance event which must have involved mixing of an original soil surface, derived from a wide area, with subsoil and parent materials. As such they may be compared with other large scale engineering projects where new material is exposed or forms a large component of a new surface. This may be the case in mining and quarrying, (Bradshaw, 1977; Cullen *et al.*, 1998), and roadbuilding (Thompson, 1986) as well as in areas of natural landslips.

In 1967 a second group of buildings and their associated revetments was constructed. These differ from those erected in 1939 in terms of the following characteristics.

- They form a relatively compact group, separate from, though adjacent to, the rest of the site. (Figure 1.5)
- They were constructed as a series of six long, continuous embankments with many short side arms; each compartment, formed by two arms and a portion of the long embankment, contains a single building.
- They are generally taller than the earlier revetments, rising up to 15 m above the surrounding ground level.
- They form a very regular arrangement with all the embankments and side arms facing in the same respective compass directions.

Despite these differences it is apparent that the two sets of earthworks have many similarities in form and construction; in addition their adjacent locations within the same protected area makes it likely that they have been subject to the same conditions of management, climatic and environmental treatments.

For the purposes of this study it is considered that sections of the long embankments which are separated by a suitable distance may be taken as being equivalent to separate revetments and treated as independent replicates. The degree of separation deemed to be suitable was the subject of a pilot study, the results of which are reported below (Section 3.3.1). Ten sections from four of the embankments were included in the main study.



**Plate 1.1 General view of revetments at RAF Caerwent.**



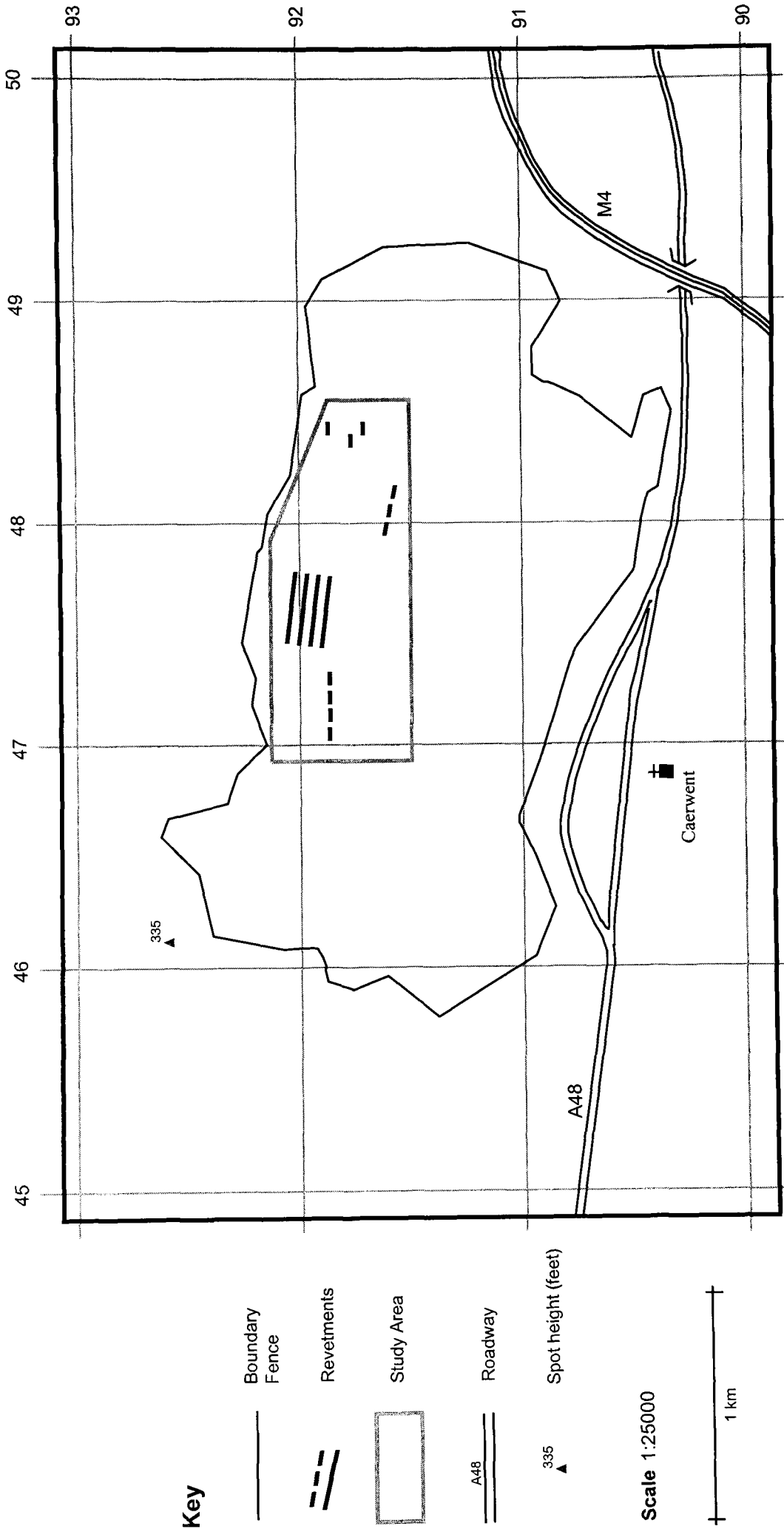
**Plate 1.2 Revetment number 200.**

### 1.4.2 The study area

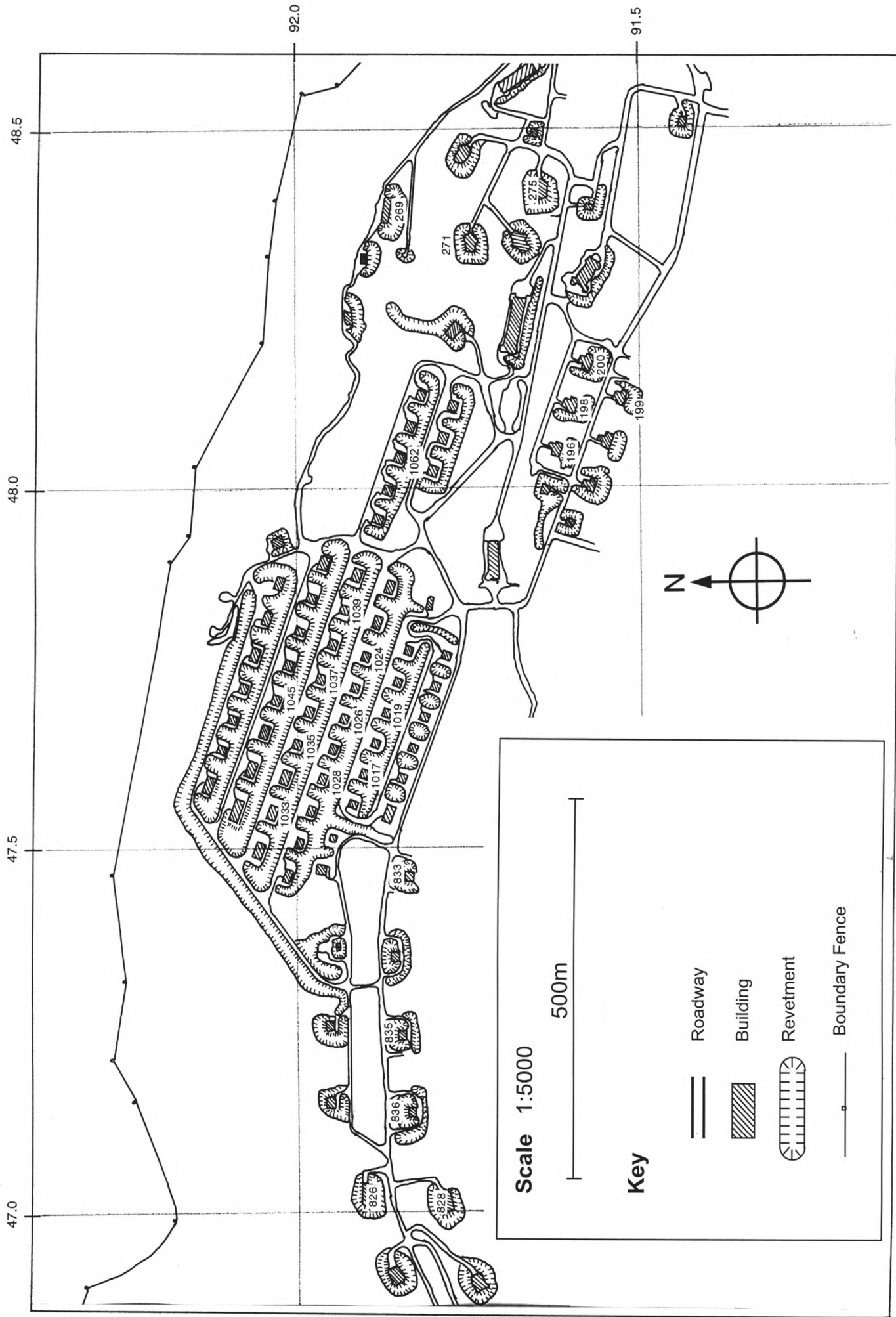
That part of the site containing the revetments included in this investigation is termed the study area (Figure 1.4). This study compares the plant communities which have developed on revetments belonging to two different age groups. In order to draw inferences regarding the effects of time on vegetation development, the design aims to reduce, isolate or eliminate the effects of other factors. To this end revetments were chosen for inclusion which were relatively close together and, since all the young revetments were located together, old revetments which were situated close to the young group were selected for study.

Since the topographical and geological gradients within the site are aligned in an east-west direction (Figures 1.2 and 1.3) and since the younger revetments are located to the north of the site, this approach meant that all the study revetments were located within the same sector with respect to those gradients. Since all the young revetments are aligned in the same compass direction, old revetments were chosen for inclusion which had the same or similar aspects. The sector of the site chosen as the study area is shown in Figure 1.4 and the detailed layout of the revetments within it is illustrated in Figure 1.5. All the revetments lie outside of the currently designated grazing areas.

The study area contains the equivalent of 10 revetments from each of the two age groups, young (Y) and old (O); each revetment having a north-facing (N) and a south-facing (S) slope. Upper (U) and lower (L) zones were identified within each slope face by a simple horizontal division midway between the top and bottom of the slope. The study utilizes the existing scheme by which each building is identified by a number (Section 1.3). Here individual revetments are identified by reference to the number of the associated building with the addition of a prefix letter "R".



**Figure 1.4 RAF Caerwent showing the location of the study area and revetments**  
 (redrawn from Ordnance Survey, 1966).



**Figure 1.5 The layout of the revetments in the study area**  
 (redrawn from Reserve Storage Activity Caerwent Drawing No. 1470, in Defence Land Agents, 1993-1996).

**Figure 1.5**

## 1.5 Experimental design

### 1.5.1 Environmental factors

The form and orientation of the revetments is such as to present symmetrical, uniform, plane surfaces facing in opposing compass directions. Clearly the influence of aspect on the vegetation communities developing on opposite faces could be an important factor in a comparative study (Section 1.1.4). The design incorporated the study of aspect as a major, though secondary, factor. The vertical position of the vegetation within the revetment slope is also considered since the upper parts of the slope may be more exposed to wind, receive greater levels of solar radiation due to a lower local horizon (Geiger, 1965), and be subject to a different soil moisture regime (Section 1.3). In addition, erosion of soils on slopes tends to lead to net removal from upper slopes and net deposition on lower slopes (White, 1987) leading, over time, to a thinner, denuded soil towards the top, and a thicker soil at the base, of a slope. Each of these physical factors associated with height may, additionally, be influenced by the elevation angle of the slope face (Section 1.1.4).

From the above discussion three major factors are defined, each being present at two levels, which may determine the nature of the vegetation communities currently seen on the revetments. The factor "age" defines communities from two age groups, developed over 27 years and over 56 years, respectively; the factor "aspect" defines those communities facing opposing compass directions; and the factor "height" those communities at two different heights within the revetment face. All the revetment communities can thus be classed into one of eight groups based on the three environmental factors;

AGE:	Young (27 years)	Old (56 years)
ASPECT:	North-facing	South-facing
HEIGHT:	Upper zone	Lower zone.

### 1.5.2 Inferences from chronosequence data

The assumption underlying the comparisons made in this study is that the two ages represented by the young and old revetments in the study area can be seen as two points along a single time sequence of vegetation development (Drury and Nisbet, 1971); it is argued that the older group passed through the successional phase represented by the present

condition of the younger group 27 years after construction, that is, in 1956. This chronosequence approach, though commonly used in ecological studies (Bazzaz, 1975; Aarssen and Turkington, 1985; Gleeson and Tilman, 1990; Terborgh *et al.*, 1996; Lichter, 1998), should not be used uncritically (Austin, 1981; Pickett, 1988). In particular the method is limited because of the implicit assumptions of common starting conditions and a uniform history at sites separated in time (Miles, 1979; Pickett, 1988). The particular nature of the site, its origins, its enforced and continuous isolation throughout the period covered by the investigation, and the uniform quality of the land management during that period (Section 1.3) suggest that such assumptions are justified in this case.

### 1.5.3 Replication

In any scientific, experimental study inferences drawn from the results of a single case are weakened by the argument that a single event, which led to a particular outcome, is no guarantee that, if the event were to be repeated, the same outcome would be seen to occur (Hairston, 1989; May, 1989). All natural systems exhibit variability and it may be argued that ecological systems, with their multiple factors and interactions, are more than usually afflicted (Crawley, 1993). Inferences are more credible where outcomes are seen to be repeated over a number of instances such that a more generally applicable result emerges. Hurlbert (1984) points out that many ecological studies utilize multiple samples taken from a single case in lieu of replicate treatments. Here each revetment is considered to be an independent, replicate, disturbance event. This study takes advantage of a fortuitous series of such events in which a number of revetments of similar size and shape were constructed at the same time and from similar materials, thus providing the replication required in a rigorous design (Eberhardt and Thomas, 1991).

Features of the site described above suggest that it is of particular value for this study in providing a replicated series of uniform, soil disturbance events, from two known dates, set within an enclosed, controlled area and subject to a known, minimal land management regime. It therefore presents the opportunity for a study of medium term successional processes based on a rigorous experimental design.

## **1.6 Successional models**

In this section a number of models related to vegetation development are first described (Section 1.6.1); the attributes with which they deal (Section 1.6.2), and the predictions they make (Section 1.6.3), are then outlined. There follows a discussion of the rates of successional change in managed grasslands and a statement of the research question.

Models are simplified descriptions of complex phenomena (Glenn-Lewin and van der Maarel, 1992). They aim to identify the important components of a system, to make explicit the relations between those components and, in so doing, describe, mimic, or predict the behaviour of the system. They have the advantage of being simple and therefore comprehensible but also carry the disadvantage of being removed from reality by the very process of simplification (North and Jeffers, 1991). Models may be formulated as words, graphical representations, mechanical constructions or mathematical equations (Jeffers, 1978); the degree of formalization reflects the extent to which quantitative information about the study system is available. The term model is here used to signify a description of successional change which may also be used to generate predictions.

### **1.6.1 Models of successional change**

Successional models may be usefully partitioned according to whether the community is viewed as either, an assemblage of individual species populations or, an entity displaying emergent, higher level properties (Section 1.1.1). In this section models of vegetation change based on species ecological traits and on community level attributes are described.

Species may be seen to have their origin from the operation of natural selection on organisms in a varied and varying environment (Maynard Smith, 1993). During the course of evolution, organisms have acquired traits, characteristic life-forms or life-histories (Whittaker, 1975), which make them better suited to one kind of environment rather than another and they are consequently more likely to succeed, to survive and produce viable offspring, in those environments to which they are better adapted. Plant species may be grouped according to the suites of traits which they possess, and these groupings correlated with the environments in which each group might be expected to be successful; such a classification of traits defines an ecological strategy (Southwood, 1977).



A spectrum of life-history traits was suggested by MacArthur and Wilson (1967), the poles of which are defined by, firstly the r-strategists, those organisms which utilize finite resources for fast growth and high reproduction and are characterized by their short lifespan and high dispersal rates, and secondly the K-strategists which maintain slow growth, low reproductive rates, employ defensive mechanisms and have long lifespans. The r-strategists are successful in transient or disturbed environments by virtue of their efficient dispersal but are unable to compete in stable conditions, whereas K-strategists persist in stable habitats where competition is intense. Where conditions change species selection may lead to vegetation development as a site is sequentially occupied by plants with different life-history strategies. Though the application of the r-K strategy spectrum to successional environments has been criticized (Grubb, 1987) it nevertheless forms the basis for the development of a classification of species traits and their corresponding environmental conditions.

#### **1.6.1.1 Grime**

A development of the r-K classification scheme is that seen in Grime's proposal (1974, 1977) of a two-dimensional strategy space defined by a pair of axes representing the levels of environmental disturbance and of resource availability. The position of a species within the space describes its strategy. Environments with high disturbance and high resources are occupied by "ruderal" plants, those characterized by low disturbance and low resources have "stress-tolerating" species and those with low disturbance and high resources have "competitors". Areas with high disturbance and low resources are deemed unsuitable for the persistence of any organisms.

Grime (1979) views plant succession following a disturbance as a process of species replacement in which the appropriate strategies for survival and persistence change as the environment changes. Thus the mechanisms generating successional change result from the evolutionarily determined plant characters. Ruderal species will be abundant in early succession since they have efficient dispersal mechanisms and fast growth rates, characters which are likely to be successful in a disturbed habitat. These will be replaced by those plants which are superior competitors; plants which are better able to forage for resources, outgrow and overtop other species.

The strength of the competitive environment, in which a plant's success is dependent on fast growth, is related to the available resource level. Grime suggests that in later successional stages nutrient levels are reduced as a result of the processes of leaching, biomass accumulation in living tissue and biomass removal, and these conditions will then favour plants which are adapted to survive in nutrient-limited conditions. Such stress-tolerating species are characteristically retentive with respect to nutrients; they have slow growth rates, long lives and well developed defences against herbivory; they show a tendency to sequester resources within their tissues. With slow rates of tissue turnover, there is reduced input of litter to the soil, and, with a higher level of anti-herbivore, polyphenol compounds in the plant tissues, decomposition rates are reduced. These factors serve to reduce rates of nutrient cycling and soil development (Grime *et al.*, 1997) with the result that soil nutrients remain low. Thus an end-point in the successional sequence would be a self-maintaining, stress-tolerant, low productivity community.

Grime *et al.* (1989) provide a listing of common British plant species together with a description of their position within the disturbance-resource strategy space. From this it is possible to generate predictions of a successional sequence in terms of plant functional types. In this study, since the site has been maintained as a grassland plagioclimax (Section 1.1.3) by removal of biomass, it is likely that soil resource levels have remained low. The predicted sequence of species types in Grime's model would therefore follow a trajectory from ruderal to stress-tolerator with little evidence of an intermediate competitive phase (Section 1.6.3).

#### **1.6.1.2 Tilman**

Tilman (1985) offers an explanation of succession in terms of the changing balance of plant resources over time. In particular the ratio of light and nitrogen is suggested to change from an initial state of high light levels and low nitrogen levels, when biomass and cover are low, to a later stage in which cover is more abundant and soil nutrients have accumulated, such that the light to nitrogen ratio is reversed. Vegetation change follows as different species are competitively superior at different ratios of the limiting resources. Thus it is a change in resources coupled with different competitive abilities which drives species replacements. This hypothesis was refuted by Tilman and Wedin (1991) when it was demonstrated that early successional grasses were excluded from poor nitrogen soils by later successional

species. The authors proposed an alternative explanation based on plant traits; specifically, that the allocation of greater resources to seed production in the weakly competitive, early-successional grass gave it the ability to colonize new sites more rapidly.

### **1.6.1.3 Odum**

Succession has been characterised as a community level process (Section 1.1.1) and a number of attributes have been considered in the search for general patterns in community development. Odum (1969) set out a list of 24 ecosystem attributes which are predicted to change during succession which he characterises as a orderly process of increasing control of the physical environment by the ecosystem. He cautions against combining the concepts of species numbers and evenness into the cover term diversity (Section 3.6.6) though both these components are predicted to increase during community development unless they are countered by increases in competition and organism size. In addition he expects that stratification will increase as communities become increasingly well-organized and, as a corollary to this, the niche breadth of species will narrow. Odum does not discuss the mechanisms driving the processes he describes although he seems to imply that, as a consequence of the increase in species numbers, resources will be shared more equitably. In this study measures of diversity, species numbers and evenness together with the degree of stratification at two time intervals in a successional sequence allow a test of these predictions to be made.

### **1.6.1.4 Peet**

Peet (1992) has suggested that mechanisms operating during secondary successions may be grouped into two general models; the gradient-in-time (GT), and the competitive sorting (CS), models. In the GT model the species present during a successional sequence are those having adaptations suited to the changing habitat conditions. Succession is thus seen to be the result of the evolutionary forces of natural selection which gave rise to species having those adaptations (Section 1.6.1). The competitive sorting model proposes that species interactions, in a constant environment, lead to a progressively more ordered community. Here the processes are “ecological” in that the sequence results from a species abilities to colonize, establish and grow in a habitat already occupied by other organisms. The

consequent interactions between species leads to winners and losers and it is predominantly this competitive environment which generates the stages of a successional sequence. In the CS model dominance is seen to change as the nature of the habitat is reformed by the organisms occupying the site. In this study species preferences for a particular set of conditions, represented by slopes with opposing aspects, are measured and the change in preference over successional time is used to indicate the utility of these models (Section 3.6.8).

#### **1.6.1.5 Greig-Smith**

Greig-Smith (1952) described patterns of species abundances in tropical rainforest plots using samples from primary forest, secondary successions after cultivation and degraded forest. He characterized three phases of successional change in terms of the departure from a random distribution and also by the degree of interspecific association found. Though he used the variance to mean ratio as a measure of non-randomness this method has been criticised by Hurlbert (1990) who demonstrated its lack of effectiveness for this purpose. Additionally Greig-Smith described patterns of species association and, in comparing these patterns between sites suggests a descriptive, three-phase model of succession in which early stages are characterised by weak levels, middle stages have strong levels and late or climax stages have, once again, weak levels of species association. He does not suggest reasons for this pattern which would require detailed knowledge of the ecology of the species. Nor does he relate the differences between positive and negative associations to successional processes within the study plots. He does suggest that the patterns found can be used to distinguish between environmental influences and those generated by species interactions. Given that individuals are located randomly in early stages and associations develop over time the change in association levels, it is concluded, must be the result of species interactions rather than being driven by the species environmental tolerances. In this study differences in the level of species associations are compared between communities from two age classes (Section 3.7) and the observed community structure is compared with that generated by a random distribution of individuals and species (Section 5.3.5).

### **1.6.1.5 Gitay and Wilson**

The model of Greig-Smith has been adopted and developed by Gitay and Wilson (1995). They applied this, and the models of Peet (1992), to a grassland succession following disturbance by fire and were able to distinguish three phases during a 30 year series. They found that during the early, pioneer phase, species associations were predominantly negative. This they suggest is the result of small-scale environmental heterogeneity, at the level where interactions between species might occur, generated by historical factors and also due to patchiness imposed by the nature of the disturbance. During a middle or building phase, when species are spreading, species association was close to zero suggesting that interactions are unimportant, whereas in the third, mature phase species interactions were more in evidence and associations are again negative. The use of patterns of association, coupled with a knowledge of site history, can thus be used to generate a descriptive model of vegetation development.

This study investigates the differences in species associations at two stages of successional development following disturbance and at three areal scales. Predictions of change in community structure generated by the models of Peet (1992), Greig-Smith (1952) and Gitay and Wilson (1995) are thereby tested (Section 3.7).

### **1.6.2 Community attributes**

Whilst an ecological community refers to the entirety of the organisms living in a given area (Southwood, 1996), the usefulness of the concept depends on the degree to which these organisms display unifying characteristics and the extent to which interactions between them generate community level processes (Section 2.3.1).

Plant communities have been characterized in a number of ways which allow for a comparison between communities in space and over time (Whittaker, 1962). Attributes used to generate such descriptions may be based on the floristic structure of the community (Greig-Smith, 1983), they may be process-based as, for example in studies of community productivities (Whittaker, 1965; Odum, 1969) or they may be based on the growth form of the vegetation components (Whittaker, 1953; McCook, 1994). In this study features related to the compositional structure of grassland communities are used to investigate differences

over time and between aspects and slope positions in order to test the predictions of successional models. The structural attributes which are predicted to change during succession are described below.

#### **1.6.2.1 Relative abundance distribution**

Whilst a community is composed of constituent species its structure is more accurately described in terms of the relative proportions of each species. Patterns of species abundances relate to the questions of why some species are common and others rare so that an overall description of relative abundances integrates inter-species and environment-species relationships (Grubb *et al.*, 1982). The abundance relations within a community can be efficiently summarized in a diagram of the rank abundance distribution (RAD) in which each species' abundance value is represented in turn, and in decreasing rank order, on a logarithmic scale (Whittaker, 1965). The shape and interpretation of such plots have been the focus of considerable debate (MacArthur, 1960; Preston, 1962; Bazzaz, 1975; May, 1975; Gray, 1987; Tokeshi, 1993) as attempts have been made to describe the mathematical (May, 1975; Pielou, 1975) and ecological (Whittaker, 1965; Tokeshi, 1993) mechanisms by which plots of a given shape are likely to have been generated. Bazzaz (1975), for example, describes community changes in old-fields in terms of the progression seen in a series of these plots characterized by increasing species numbers and more even distribution of abundances. Whilst the question of the interpretation of RAD plots remains unresolved (Murray *et al.*, 1999) they are used here (Section 5.3.5) to present summary information on both species richness and equitability in an accessible and readily understood format.

#### **1.6.2.2 Diversity and evenness**

Measures of diversity are described in Chapter Three where it is shown that the concept consists of two separate components; those of species richness, that is the number of species present in an area, and of evenness or equitability. Evenness refers to the degree of equality in the abundances of the species. Two communities containing the same 10 species would differ in their levels of evenness, and therefore also in their diversities, if one contained a single highly dominant species and nine rare species, whilst the other contained 10 equally abundant species; the latter would be considered to have the maximum evenness.

Community structure can be described according to the relative abundances of the component species (Section 1.6.2.1) though attempts to encapsulate this attribute as a single numerical index, that is the diversity of the community, require the combination of the two concepts of species richness and equitability. Measures of diversity are described below (Section 3.6.6).

The processes associated with plant colonization, niche preference and competition and predation are predicted to generate characteristic levels of evenness (Kent and Coker, 1992; Crawley, 1997). The pattern of colonization by plant propagules is a function of the species which are regionally available and their rates of dispersal (Gibson and Brown, 1985). Immigration into an extensive bare area may, for example, be dominated by a single species which is able to take advantage of the occurrence of new sites by producing large numbers of well dispersed propagules, so leading to an even-aged community which has a low evenness value. Within an existing, closed-canopy, community microsite availability may occur infrequently and essentially at random such that propagules from a large number of species having a range of habitat preferences and dispersal times, may be added to the community over time. Where these are able to persist, the community tends towards increasing species richness and evenness with time.

Where species are limited by their tolerances to physical conditions the range of micro-environments within a site can determine relative species abundances. Underlying environmental heterogeneities can generate a range of microsites within a community such that species distributions result from local, edaphic or microtopographic factors (Armesto *et al.*, 1991). Where species occurrences are a reflection of such influences then diversity and evenness are likewise environmentally determined and, if these determining factors change over time, species replacements will occur and community structure will be altered accordingly (Vivian-Smith, 1997).

Competitive relations with existing community members may determine the fate of colonists and so generate characteristic patterns of diversity (Whittaker, 1965; Usher and Jefferson, 1990). A competitive dominant, forming a closed canopy, will exclude most potential colonists so generating a community structure having high dominance and low evenness values. Where such a dominant species is subject to frequency dependent predation by herbivores, colonists are more likely to gain a foothold so that herbivore

effects may result in a higher level of evenness and diversity in a community (Olf and Ritchie, 1998).

In this study changes in evenness and diversity are related to the successional models of Peet (1992) and Odum (1969).

### **1.6.2.3 Rank consistency**

Within a single vegetation sample the abundance measures of the component species may be ranked, as described above (Section 1.6.2.1); when the species rank order is compared between replicate samples from the same community, the constancy of the species' ranks may be interpreted as a measure of the degree of ordering in the community (Mitchley and Grubb, 1986; Naeem, 1996). A measure of this attribute has been proposed by Watkins and Wilson (1994) and applied in an attempt to distinguish between ecological and evolutionary community processes. Though this index is intended to be used in a single community at a point in time using replicate samples (Mitchley and Grubb, 1986), as a measure of order in a community, it lends itself for use in a comparison between communities of different successional age where the degree of order is predicted to undergo a directional change (Watkins and Wilson, 1994). In addition, it has been proposed (Wilson *et al.*, 1996) that the predominant processes operating during succession change during a three phase process in which each phase has a characteristic level of rank consistency (Section 1.6.1.5). It is used here as a means of comparing levels of community order or predictability between communities of differing aspect and successional age (Section 3.6.8.1).

### **1.6.2.4 Interspecific associations**

The degree to which species in a community co-occur has been suggested as a characteristic which may be used to describe the degree of ordering within that community (Greig-Smith, 1983; Peet, 1992; Gitay and Wilson, 1995). Peet (1992) has suggested that the development over time of interspecific associations is a reflection of the forces structuring the community. Where species are pre-adapted to a particular set of environmental conditions they will occur together as a result of their sharing the same range of ecological tolerances (Begon, Harper and Townsend, 1990). Where community structure is determined



predominantly by direct interactions between species these will tend to generate stronger associations (Greig-Smith, 1983). One species may exclude others by competition for resources (Begon, Harper and Townsend, 1990) thus giving rise to a negative association, or it may enhance the survival of others by providing some resource, in which case a positive association results (*op cit.*).

Each of Peet's two models (Section 1.6.1.4) suggests that the strength of the association will change in characteristic directions as successional communities develop. Where succession is seen as a change generated by a changing environment the level of association between species will remain constant though the species themselves may change. Under the competitive sorting model the level of associations, both positive and negative, will become stronger over time. In this study the distinction between these processes is tested in this study by comparing measures of interspecific association from old and young samples (Section 3.6.7).

#### **1.6.2.5 Environmental stratification**

This term refers to the degree to which species are segregated into areas distinguished by microenvironmental conditions. Where species distributions are limited by their range of tolerance to a particular physical or chemical variable their actual distribution may be further confined by biotic factors such as competition (Begon, Harper and Townsend, 1990). Within a successional development it is likely that initial colonization within a site is largely random (Gleason, 1926) but that, if competitive interactions operate, a species range will become progressively more limited to those microenvironments where conditions most nearly approximate the species optima or where exclusion by a superior competitor is relaxed (Whittaker, 1975). Within a given, fixed environmental gradient competition is likely to lead to a narrowing of species niche breadth resulting in a greater number of species, each occupying a narrower range of microenvironments (Crawley, 1997).

In this study north- and south-facing revetment slopes, and upper and lower zones within them, furnish differences in regimes of light, temperature, moisture and exposure (Section 1.1.4) representing environmental gradients to which species having different tolerances may be expected to respond (Peet, 1992). Where community structure results from ecological interactions the degree of sorting between microenvironments is expected to

become increasingly apparent over successional time (*op cit.*). If, on the other hand, plant-plant interactions have little or no impact on community structure then the extent of segregation between microenvironments will remain the same over time. This distinction is tested (Section 3.6.8.2) by comparing a measure of species preference for one or other microenvironments between slopes of different age. In addition, numbers of species present on a combination of a north- and a south-facing slope may be expected to increase, under competitive sorting, over time.

#### 1.6.2.6 Predictability and convergence

The mechanisms of successional change proposed by Peet (1992) and Gitay and Wilson (1995) suggest that fundamental differences between ecological and evolutionary processes give rise to communities having characteristic structures and degrees of order. A community with greater structure would show a higher degree of predictability, or constancy (Mitchley and Grubb, 1986). Predictability, as a measure of order or structure within a community, is inversely related to the amount of spatial variation (McGrady-Steed *et al.*, 1997); in this sense a community with greater predictability would be the one in which repeat samples have greater similarity of composition. Where development is driven by species interactions the degree of order increases over time, whilst if species occurrences and replacements result from inherent genetic characters, developed over evolutionary time, then community order would remain unchanged over ecological time scales.

Changes in predictability may be apparent as changes in the amount of variation within a set of repeated measures of some community attribute. For example, a decline in variance of measures of diversity would constitute evidence of increasing predictability. Both rank consistency and stratification (Sections 1.6.2.4 and 1.6.2.5) might also be used to indicate changes in the degree of community order (Wilson *et al.*, 1996). In addition more general patterns exhibited by vegetation samples are displayed in ordination plots (Sections 4.3) where community composition is used to define a multi-dimensional space within which each sample is plotted according to the numerical abundance value recorded for each species. Samples with similar compositions are therefore located close together in ordination space whilst dissimilar species assemblages are far apart. Numerical analyses may be applied using ordination scores generated for each sample along each axis. Increasing levels of predictability over time are then indicated by greater clumping of older

Model	Diversity	Evenness	Spp. Assoc.	Rank Cons.	Predict.	Funct. Types
Odum <sup>1</sup>	+	+			+	
Gradient in time <sup>2</sup>		0	0 <sup>6</sup>	0	0	
Competitive sorting <sup>2</sup>		-	+ <sup>6</sup>		+	
Greig-Smith <sup>3,4</sup>			i- weak ii- strong iii- weak			
Gitay and Wilson <sup>6</sup>			i- -ve ii- weak iii- -ve	i- high (P) ii- low (B) iii- high (M)		
Grime <sup>5</sup>						i- Ruderal ii- Competitor iii- Stress tol.

**Table 1.1 Community attributes predicted to change during succession**

- notes: + increases during succession  
 - decreases during succession  
 0 shows no change during succession  
 i, ii, iii. level of attribute during early, mid and late succession  
 P, B, M Pioneer, Building and Mature phases of development  
 1 Odum, 1969  
 2 Peet, 1992  
 3 Greig-Smith, 1952  
 4 Wilson *et. al.*, 1996  
 5 Grime, 1979  
 6 Gitay and Wilson, 1995

sites whereas lower predictability may be inferred from a more dispersed pattern amongst the older sites.

The CS and GT models proposed by Peet (1992) generate predictions, respectively of, increasing order and of no change in order over time. Furthermore Peet predicts that under competitive sorting different sites subject to the same conditions will tend to converge in their compositional structures. Under the operation of a GT mechanism differences between sites would remain. Community divergence is not predicted to occur by either of the successional models yet such an outcome has also been reported (Matthews, 1979; Inouye, *et al.* 1987; Rydin and Borgegaard, 1988; Vankat, 1991).

It is useful to distinguish between, firstly, predictability or constancy within a site or vegetation stand and, secondly similarity between sites subject to the same environmental and historical processes. Convergence within a vegetation stand leads to a community characterized by increasing order. It may arise as an initially random selection of colonists become ever more restricted to microhabitats in which they are best able to persist (Christensen and Peet, 1984). Convergence between sites may be supposed to arise because this same sorting process re-occurs in the same manner within each site. Such a co-occurrence could only be envisaged if driven by external constraining forces such as regional climate or a limited set of regionally available colonists (Section 2.2.2). In this study community compositions from ten replicate communities within each of two age groups are sampled thus allowing for an analysis of convergence between sites as well as within site predictability. As is the case for measures of predictability, convergence between sites may be inferred, either from direct measures of similarity between pairs of samples, or from their relative positions in ordination space.

### **1.6.3 Model predictions**

Those changes in species attributes and community structure discussed above (Sections 1.6.1 and 1.6.2), predicted to occur over successional time, are listed in Table 1.1. The experimental design (Section 1.5) allows these predictions to be tested. They may be summarized by:

- Different species are present at different successional stages. Such a sequence relates to the species “type” where species have been characterized by their strategies, vital attributes or life history types (Section 1.6.1) and these types are predicted to correspond to the habitat conditions experienced at different stages of a succession.
- Community structure may be characteristically different at different ages (Sections 1.6.2.1, 1.6.2.2 and 1.6.2.3).
- Interspecific associations will be stronger in older sites (Section 1.6.2.4) under the action of competitive sorting.
- The differentiation of species along an environmental gradient will be more marked in older sites as competitive interactions have forced species into narrower niche spaces (Section 1.6.2.5). The division of zones between north- and south-facing slopes and between upper and lower parts of the revetment slope each represent two different points along two environmental gradients. As niche width narrows more species will be accommodated within a given environmental gradient.
- The compositional predictability of the sites will increase with time (Section 1.6.2.6). This means that vegetation samples from sites having the same aspect and height, will be more similar in composition in the older sites than in the younger. There will also be less variability within the old sites compared with the young sites.

#### **1.6.4 Successional time-scales**

If successional models are to predict vegetation change then they should be explicit about the time scale of that change. A test for the validity of a prediction must likewise be made at the appropriate temporal scale (Connell and Slatyer, 1977). Ecological systems change by the replacement of individuals (Section 1.1.1; but see discussion below) so it follows that rates of change are largely set by the lifespan of the individual organism (Odum, 1969; Brown and Southwood, 1987) since this defines the timing of the availability of new space for potential colonists (Section 1.1.5). Since plant lifespans vary over several orders of magnitude, rates of change are specific to the compositional type of the plant community

and may themselves change as the community membership changes. An individual's lifespan may be reduced by disturbance or interference by one or more factors such as competition, herbivory, inhibition (allelopathy), physical damage from abiotic, animal or human interventions.

This study investigates differences in species composition between two age groups representing two points within a presumed ecological time series (Section 1.5.2) and it makes inferences about community development in relation to the successional models described above. Since the attributes associated with species replacements (Section 1.6.1) and community development (Section 1.6.2) are not necessarily predicted to change as a consistent, monotonic trend (Greig-Smith, 1952; Odum, 1969; Whittaker 1975), it is necessary to consider the time scale associated with grassland community development so that differences between two given points in a time series can be related to predicted changes over ecological time. The time scales associated with succession may be related to life history aspects of the species comprising a community such as their longevity, mode and rates of dispersal, seed production, germination requirements, environmental requirements (Grime, 1979; Bazzaz, 1996) or to aspects of soil development (Jastow *et al.*, 1984), or to changes in microclimate such as exposure to light, humidity levels and temperature ranges (Section 1.1.4).

Whilst many early successional species exhibit annual or biennial life histories, perennial herbs and grasses have a less clearly definable life span. In these species vegetative and flowering shoots which appear on an annual cycle do not correspond to the genetic individual or genet (Harper, 1981). Such individuals may, or may not, produce above-ground structures in any particular season and may spread by rhizomes giving rise to clones (or ramets) which can form separate, and independent, plants. Thus genets can survive almost indefinitely (Grubb, 1990), though not necessarily by occupying the same point in space. It is therefore meaningless to refer to the spatial replacement of individuals and a definition of vegetation change must be restricted to those aspects of a species which signify their ecological importance by maintaining an above-ground presence related to occupation of space (Whittaker, 1965). Thus, whilst the true abundances of species on a site may be impossible to determine without extensive and destructive sampling, a species importance value may be measured by inspection of above-ground structures. Successional change is thus seen as a change in the identity and relative importance of those organisms monopolising the resources of space and light and this may be inferred from measures of

above-ground biomass or counts of shoots. The occupation of a point in space by a perennial species, and its replacement, can therefore be defined and measured without reference to the individual's lifespan.

A number of studies (Wells *et al.*, 1976; Gibson and Brown, 1991; Mehrhoff and Turkington, 1995; Hemsley, 1996; Wilson *et al.*, 1996) have followed or inferred the development of grass and herb communities over periods as short as 7 and 13 years (Wilson *et al.*, 1996) and as long as several centuries (Gibson and Brown, 1991). There is little agreement over the time-scale of the processes involved. Wilson *et al.* (1996), in experimental studies of grassland development, find evidence of the three successional stages of pioneer, building and mature in even the shortest time series whilst Gibson and Brown (1991) report that fields abandoned in late Medieval times “may still be recognisably in a ‘young’ stage”. In discussing the re-creation of ancient calcareous grassland, these latter authors conclude that, “the succession takes at least several decades and probably over a century to stabilise” (page 308). They divide the successional process on ex-arable land, according to time since abandonment, into young ( $\leq 10$  years), medium (11 -100 years) and late ( $> 100$  years) stages and suggest a list of species characteristic of each stage.

Wells *et al.* (1976) compare, and find identifiable differences between, grasslands aged 30-50, 50-100 and 100-130 years since abandonment; they also review studies by Cornish (1954) and Lloyd and Piggott (1967) in which colonization of, respectively, 3-10 and 20-30 year old grasslands are reported. On the basis of these studies conclusions are drawn which suggest the rates and pathways of succession on chalk grassland in relation to grazing pressure and nutrient status; these follow a timescale of 130 years and assume an increase in soil nutrient levels with time. Under conditions of no grazing Wells *et al.* (1976) predict the presence of an open *Arrhenatherum* grassland with prostrate herbs after 25 years which develops after 120 years to form a tall *Arrhenatherum* grassland with scrub.

Mehrhoff and Turkington (1995) compare competitive interactions between grassland species from five pasture communities representing an old-field successional sequence of 0, 3, 8, 27 and 46 years since abandonment. They too report significant changes occurring over timescales of several decades. Hemsley (1996) reports a very dynamic plant community on the slopes of an artificial earthwork at a chalk grassland site in Wiltshire. At the Overton Down archaeological project a single bank 2m high and 25m long was

constructed from material excavated from an adjacent 2m deep pit; this being set within a fenced enclosure measuring 45m by 30m. The author indicates that substantial changes in species abundances were apparent in surveys made 24 and 32 years after construction. This suggests that, where relatively severe disturbance has been inflicted, the establishment of a stable plant community may take more than a few decades.

From a comparison of studies of grassland succession outlined above it may be argued that successional processes are likely to have continued to occur in the study site over the timescale of this study and, further, that because of the severity of the disruption and the consequent lower nutrient status, the rate of change is likely to have been slower (Connell and Slatyer, 1977; Dvorak, 1984; Tilman, 1988) than that found on abandoned agricultural fields. Within the context of the successional ages described by Wells *et al.* (1976) and Gibson and Brown (1991) the expectation is that the two age groups in this study represent, respectively, young and middle successional stages.

## **1.7 Aims and objectives**

### **1.7.1 The research question**

Within the context set by the region, the site, and the features of its layout, topography and history, the question of successional change raised in Section 1.1.6 can be addressed by a comparison of vegetation on the revetments of the two age groups. Specifically, by referring the particular vegetational changes represented by differences in the communities currently found on revetments aged 27 and 56 years and those differences between slopes having opposing aspects and between samples from different heights within those slopes, to the outcomes predicted to occur by the ecological models described in Section 1.6.2, the utility of those models may be tested.

### **1.7.2 Aims**

The main aim of this study is to improve knowledge and understanding of the factors controlling grassland succession in an artificially created habitat.



### **1.7.3 Objectives**

To achieve this aim the following objectives are defined;

- 1)- to devise an appropriate and efficient method of sampling the vegetation at the revetment sites,
- 2)- to describe the variation in the vegetation in terms of species components and community structure,
- 3)- to analyse the effects of age and topographic factors,
- 4)- to evaluate the role, and usefulness as descriptors, of ecological types and plant strategies in the succession,
- 5)- to test the predictions of successional models and, if necessary, develop new models in the light of the findings.

### **1.8 Scope and limitations**

Succession is a large and multifaceted area of study (Miles, 1987) and it is therefore beyond the range of a project of this nature to explore more than a limited number of those facets. The research question therefore reflects the fact that questions about succession can be answered only to the extent that they can be derived from the analysis of the particular vegetation present at the site. The developmental series took place over a few decades and in the particular set of conditions described for the study site (Section 1.3).

The findings of this study may be found to be applicable to vegetation development in situations where;

- embankments formed of relatively plane surfaces are exposed over scales of a few tens of metres following relatively large scale, severe disturbance
- slopes have inclinations of between 20° - 40°
- subsoil material forms a large component of the newly exposed surface
- the soil is of low nutrient quality and is moderately calcareous

- the area is subject to the maintenance of a low stature herb vegetation with removal of excess biomass and with no added nutrients
- development of vegetation proceeds over several decades
- the area is well drained with no external inputs of water other than rainfall
- the area is ungrazed except by rabbits and insects.

These conditions mirror those found following large scale construction projects which leave embankments, spoil, bulldozed ground or landscaped slopes (Section 1.4.1). Such slopes may be found following road and rail constructions, strip mining, and also where areas of ground are exposed following naturally occurring landslips. Revegetation and medium to long term maintenance of cover on such areas is an important part of a reclamation process (Dvorak, 1984; Marrs and Bradshaw, 1993) because of the effects of plant cover on surface water flow and infiltration with consequences for soil erosion and slope stability.

## **1.9 Outline of the work**

The following chapters provide;

- an historical overview of the successional paradigm and the current status and utility of the concept in plant ecology,
- Chapter Three introduces the methods used in data collection and analysis. It provides a description of some of the problems associated with vegetation sampling, the relation between species-area and the choice of quadrat size, and the issue of spatial dependence between samples. It further describes the sampling design, the pilot study and the field methods used, together with an introduction to the techniques of data analysis employed in the interpretation of the data,
- the findings and results of the work are described in Chapters Four and Five,
- a final chapter offers an evaluation of the work together with a discussion of the implications of the work for successional studies, lists the conclusions and suggests directions for extending the research.

## **CHAPTER TWO: LITERATURE SURVEY**

The main themes of this research described in Chapter One represent some of the most recent stages in an historical development of ideas about the processes of vegetation change. In order to underpin the reasons for the research described, and the problems which it addresses, it is instructive to consider these themes as part of an ongoing enquiry into the nature of succession and its place within the field of vegetation ecology.

### **2.1 Introduction**

In the description, study and investigation of vegetation a constant observation (Section 1.1.1) has been the changing pattern of organisms which inhabit an area which is denuded of vegetation and subsequently left untended. This sequence has engaged the minds and efforts of ecologists for at least 100 years (Golley, 1977), yet remains contentious; the explanations offered, the mechanisms proposed, the methods of study and description, have all themselves developed and changed over this period (Miles, 1987; Burrows, 1990; Glenn-Lewin and van der Maarel, 1992). It is the aim of this review to chart the main events in this process and to describe the major ideas used in descriptions, definitions and explanations of succession. The works of selected authors are reviewed as a means of illustrating the concepts which underpin the work described in this study. Reviews of the literature relating to other specific topics are included in the appropriate sections.

### **2.2 Early workers in successional theory**

#### **2.2.1 Cowles**

An early attempt to provide a full description of the changing vegetation patterns within an identifiable ecosystem was made by Cowles (1899) in his study of the dune vegetation around Lake Michigan. His work serves to introduce some of the major themes in the study of vegetation change.

Cowles' study emphasises the dynamic nature of vegetation processes and, as a trained geologist, he understood the problems of studying a long-term process. For this reason he chose to study a dune habitat that is subject to exceptional rates of change and in which vegetation is subject to extreme conditions. His account consequently emphasises the ever changing environment and it is perhaps inevitable that the major force driving vegetation development is seen to be the nature of the physical environment. Cowles described the vegetation flux as a continuous adaptation to physical conditions which are themselves moderated by topographic features. The interactions described are all those occurring between the plant and its environment. The conditions of heat, wind and soil water determine which plants can establish and survive and which, subsequently, are able to modify the dune structure; in altering the dune topography those same physical conditions are changed as a consequence.

This alteration of the physical conditions by the developing vegetation includes the fixation of sand, increased shelter, decreased wind erosion, an increase in soil organic matter and increased soil water availability. This change follows a general pattern of decreasing severity and results in an orderly sequence of vegetation adapted to this temporal gradient. This sequence culminates in "the most genial of all conditions" producing the "normal climax type", a deciduous woodland. Whilst the essentially deterministic relationship between conditions and vegetation is emphasised, the progress of stages toward an endpoint does not necessarily proceed as an uninterrupted sequence. Cowles relates how even a long established forest can be destroyed by a slight alteration in physical conditions such as a change in wind direction.

By tracing the processes taking place in new dune formations on the beach, on the active, wandering dunes further inland and finally on the established dunes, Cowles was able to reconstruct the temporal sequence by analysing a spatial one. In so doing he described how the rate of change varies along the sequence, starting rapidly and slowing as the climax is approached. This same sequence was also characterised by a change from xerophytic to mesophytic conditions. In describing a plant which is especially well adapted to the extreme conditions he notes those attributes which contribute to its success. The bugweed is an annual which is capable of rapid dispersal due to its winged seeds. Its rapid germination also allows it to establish in the very freely draining dune sands. Stability in the dunes depends however on longer lived plants which are able to develop more extensive

and less transient root systems, and it is these biennials and perennials which slow the dune's advance and allow its "capture".

Cowles' work illustrates the idea of succession as an orderly sequence of stages culminating in an end-point. At each stage plants are matched, in their attributes and physiologies, to the prevailing physical environment which is described as a multi-factored gradient of increasing levels of soil moisture and organic matter and of decreasing levels of disturbance. The interaction between plant and environment is seen as the fundamental cause of the successional sequence. Though plant-plant and animal-plant interactions are of little importance in Cowles' scheme, the process he describes nevertheless includes an autogenic component in that the plants modify the environment in ways that make the habitat less extreme and more receptive to later colonists.

### **2.2.2 Clements**

A contemporary of Cowles, F.E. Clements developed a theory of plant succession based on studies of the mid-western prairies (Clements, 1916; 1928). Prairies are more stable systems than the dunes studied by Cowles and Clements considered that they were typical of highly stable formations remaining unchanged for millions of years (Clements, 1936). His studies tended therefore to emphasize the stability and finality of this end-point, the climax. He established the climax concept as the foundation of vegetation studies suggesting that, given sufficient time and freedom from human interventions, all formations would develop towards a climax state identifiable by the life-form type of its dominant species and determined solely by the prevailing, regional climate. His system of vegetation classification (Clements, 1936) is based on climax types and includes numerous subordinate and intermediate categories. Underlying this theory of vegetation development is the presumption that change necessarily proceeds by convergence to uniform climax types. Despite criticism (Gleason, 1926; Tansley, 1935) Clements' comprehensive system was to dominate American ecology for many decades.

A central concept in Clements' theories is that of the plant formation and, later (Clements, 1936), the biome as a whole, as an entity in its own right. This super-organism has a life-cycle of its own; it has stages of growth, development and maturity; it is composed of component organs; it reproduces, dies and regenerates itself. This organismic idea is more

than an illustrative metaphor in Clements' work as he argues that plant communities develop according to the same laws as organisms. This presumed homology defines the structure and functioning of the formation at a stroke and is presented as self-evident fact without debate, argument or evidence.

Equally important in Clementsian philosophy is the mechanism of change in plant communities. Succession is the result of a constant interplay between the plants and their habitat; the interactions are reciprocal and, in time, a stable state is achieved, a dynamic equilibrium. This climax state is subsequently self-sustaining and is independent of the initial species composition, the soil and the geology. The force that drives succession, and generates the internal structure of the climax formation, is the competition between plants of similar life-form. Clements argues that tree species for example, being similar in form, will be of similar function and, as a result, be more directly in competition with each other than with plants of different life-form. Such differential competitive interactions would generate a dominance hierarchy in which the levels are defined by the life-form of the dominant. A single plant species would tend to dominate both within its own level and over those levels representing lower life-forms. The development of the hierarchy over time is characterised by an increase in complexity and stability. Such a scheme is intuitively attractive until one considers that members of the same species are likely to compete with one another more than would two individuals of different species (Begon *et al.*, 1990), even those of similar life-form.

Clements work is prescriptive; rather than being based on observational evidence it has the flavour of a pronouncement of the way things ought to be. Subsequent amendments and new terms were added to his scheme so as to include all new records (Whittaker, 1953), in order to preserve the monumental structure of the "idea" rather than to further an understanding of what actually is (Golley, 1977). One is left with the impression of a scientist who starts out with the need, perhaps the mission, to find order in the complexity of nature (Miles, 1987) but who in actuality imposes his own pre-conceived structure.

### **2.2.3 Gleason**

Where Clements looked at a plant formation and perceived an essential unity between its parts, Gleason (1926) maintained that although two areas of vegetation may have a degree

of similarity, there is never a precise uniformity and therefore it is variation which is the dominant feature of plant associations rather than unity. He argued that, although an attempt may be made to correlate plant types with their respective environments, the same plant association may be found in different environments and also different environments within the same association. Though individual plant species do have particular requirements the variety of organisms and environments is such that the collection of plants assembled in any one place is largely a matter of accident.

Gleason's paper (1926) proposes that the species making up an actual plant association are the result firstly, of a fluctuating environment and secondly, the constant influx of seeds from the surrounding vegetation. The majority of seeds will originate from within the area of the association but over time all seeds from the wider vicinity will have arrived and all those that are able to survive will be represented in the flora. This description is an attempt to explain his previous findings (Gleason, 1917), which had showed that the distribution of species and individuals in a community was largely that expected from chance alone. This conclusion does not allow for a mechanism whereby plants establishing at one time may be later excluded by competitive interactions with other species; rather Gleason maintained that, given the constantly fluctuating environment, over time there will be opportunities for any plant that can arrive and tolerate the average conditions. On the basis of this mechanism those plants becoming established earlier will be more widespread, and later arrivals more sporadic, in their distributions. Once established the later, minority species will continue to spread and so give rise to a constantly changing community composition.

Gleason (1926) next introduces the notion of a sorting action which he terms environmental selection. An initial, randomly selected set of plants in a new habitat first begin to spread, covering the bare ground till they become dense enough to influence conditions of light, moisture and soil humus; from this stage "permanent differences in the vegetation may appear" (p. 20) as a result of these altered conditions. Gleason distinguishes between the early stage, when differences between patches may arise because of chance migration and a later stage, when plants have sufficiently modified the environment that they provide different conditions. It is not clear if he anticipates that competition will exclude some members of the established set or that further immigrants will be more heavily sorted. In either case this represents a different phase distinct from the purely chance events described above; by allowing that the modifying action of the vegetation on the local environment

will influence the later composition of the vegetation he is describing a facilitation process (Section 2.4.2) which will influence the next phase in the sequence.

Environmental changes lead to the point where established species are less able to spread and reproduce and it is at this stage, Gleason argues, that further establishment by immigrant plants becomes more likely as they find the changed environment more amenable. However the same chance factors of migration and environmental fluctuations apply. The timing of this critical stage and the particular species which are most able to take advantage of the opportunity are both matters of chance so that there is no predisposing factor which determines the successional sequence. In fact, as Gleason allows, where conditions change gradually neighbouring areas provide the most likely source of seeds. It is therefore probable that plants from adjacent areas will appear to spread into a declining association but this is no more than would be expected by chance and does not represent any inherent, organizing process. It appears that Gleason ignores the possibility of direct plant interactions, that a plants individual response may be altered by the influence of its neighbours (Burrows, 1990; but see also Matthews, 1996); interaction effects are apparent only through the indirect action of changes made to the environment. Thus the plant and its environment are the only variables; there are no higher order processes to be considered in his scheme.

Gleason is, in effect, proposing that succession as a sequence of identifiable stages of development in a plant community does not exist. There is a process by which a plant community changes but this is based on chance fluctuations in conditions and chance migrations; it is not directional and there is no end-point since fluctuations in both these factors continue.

#### **2.2.4 The Clements-Gleason debate**

Clements and Gleason's views represent the two extremes of a debate in ecology which continues to have repercussions through to the present (Miles, 1987; Matthews, 1996). For Clements plants and species are merely the cellular components making up the organism which is the plant association, an organized and integrated system which generates behaviour at the level of the formation. In contrast Gleason takes the view that each plant is a law unto itself; it knows only the conditions in which it can grow, it knows nothing of



other plants and any apparent unity of response of a collection of species is an insignificant aberration in the eye of the ecologist.

Perhaps of equal significance is the difference in the formulation of their two theories. Gleason proposes that the observed patterns and responses, previously measured and quantified, results from the two simple processes, environmental fluctuations and chance migration, which can be readily understood and which give rise to testable, and therefore falsifiable, hypotheses. Thus, for example, seed dispersal will follow a particular pattern in which the majority of propagules will originate from nearby sources. Clements' view, in contrast, requires acceptance of an all encompassing theoretical structure which is so inclusive that no number of observed exceptions can refute it; all deviations are accounted for as some variant of a climax, being a modification or proclimax which "simulates the climax to some extent" (Clements, 1936, p.262). Clements does not argue from observation but only states axiomatically so that adherence to his point of view is a matter of faith (Tansley, 1935) rather than reason.

### **2.3 Developments of the successional paradigm**

In this section a number of studies are described which demonstrate a trend towards a more analytical approach in the relation between ideas and observations in successional investigations.

#### **2.3.1 Tansley**

The Clementsian dogma and its extension by Phillips (1934, 1935a, 1935b) were heavily criticised by Tansley (1935) for their lack of scientific argument. Though Tansley rejected the organismic concept, he nevertheless argued for a treatment of vegetation processes at a level above that of the individual plant species. His concept of a vegetation community is one in which the components interact with each other (they have horizontal connections) in ways which generate system-level behaviours rather than one which is merely the sum of many individual behaviours. To this extent it lies somewhere midway between the extremes of Clements and Gleason (Section 2.2)

Tansley's definition of succession (1935) is that of a vegetation change consisting of a sequence of continuous phases. He distinguished autogenic and allogenic factors (1929) driving succession and was keen to exclude catastrophic disturbances from the study of succession proper; he further narrowed his definition by suggesting that development, as applied to a "quasi-organism", can include only autogenic factors though succession may result from internal or external forces. His working definition of succession (1935) was thus refined to,

... any series of vegetational phases following one another in one area, repeating themselves everywhere under similar conditions and clearly due in each case to the same or a similar set of causes, .... (p. 287).

He further argued (p. 290) that established plant communities have enough "of the characters of organisms" to be called "quasi-organisms", a term which he initially equated with the well developed and integrated community of the climax. This description is justified, he maintained, by the "close inter-relations of the parts....and.... on their behaviour as wholes". By substituting a physical model, the system, in place of the contentious organismic one, he retained the sense of an entity which is made up of component parts to form an organised whole. He stopped short, however, of the holistic view, that the whole system generates behaviour, as a result of interactions between components, which cannot be predicted from an examination of those parts. Such emergent properties are not, he contended, the result of some mysterious, holistic factor but only an indication of the current limits to our knowledge; it is nevertheless valid, he argued, to study the behaviour of these whole systems which he described, coining the term ecosystem, as "the basic units of nature" (p 299).

By defining the system and its behaviour as expressions of an integrated whole he focused on the interactions of its components, that is the biotic interactions and their mutual relations with climatic and edaphic factors, as the driving forces of vegetation change. Stable ecosystems result from a process of selection from amongst a number of incipient systems; those that achieve an equilibrium through an integration of these forces are the ones which survive, the climax systems. He described an example in which animal grazing is used to illustrate how a dynamic equilibrium between multiple interactions is achieved in a grassland system. Similarly when applied to a forest system grazing action may convert an ecosystem from one equilibrium type to another. This idea is generalised by Tansley

into the proposition that a dynamic equilibrium, that is a climax, may result from a balance between any number or combination of such biotic interactions.

Tansley has described how a stable climax may be sustained in an ecosystem as a dynamic equilibrium between biotic factors acting within the limits imposed by climate and soils.

Whilst this idea forms a conceptual framework for successional studies the specific processes leading to the climax remain unexamined except in the general terms of a sequence of stages each of which show a tendency towards greater stability. This suggests that the climax represents that stage in a series in which all the factors are balanced and in which change, consequently, is no longer apparent. The climax may be seen, in this sense, as the persistence of a plant community in contrast to a successional stage in which a community fails to persist under the controlling influence of some unbalanced factor.

Whilst Tansley views succession as a progressive process, in which the community becomes more integrated, this conceptual framework represents a progression only to the extent that the forces remain the same; under a stable set of forces the plant community gradually adapts to become an integrated system defined by those forces. Wherever the forces are the same and the sources of plant colonists remain the same then there is an implied convergence of communities.

### **2.3.2 Watt**

In a series of case studies describing the internal dynamics of a range of plant community types and summarized in his presidential address Watt (1947) showed that, at the appropriate scale, even stable climaxes show dynamic behaviour. His work suggested that it is within the context of the small scale cycle of plant replacement and regeneration that a community persists. Thus although Watt's perspective is that of understanding how a stable, climax, community maintains itself, it is within the internal dynamics and the mechanisms of species replacements that he seeks an answer. Consequently, as succession may be viewed as the replacement of a community which fails to persist in time, it is from an explanation of the mechanisms of persistence and the circumstances of their failure that allow an understanding of successional change at this mechanistic level to be achieved. Such a failure is a prerequisite for community development.

Watt accepts that the object of study, whether plant community or ecosystem, is a collection of objects or components and that its behaviour is to be understood by tracing the interactions between these components. His work focuses at the small scale of the patch, an aggregate of individuals and species which are in constant flux and which move through a number of stages of orderly change. The plant community as a whole is seen as a mosaic of many such patches. A single point within a patch displays cyclic change in plant type, species and numbers whilst the composition of the patch itself remains constant.

He describes details of these processes from a range of ecosystems and so is able to argue for its generality. In one example, he describes a four phase cycle within a patch dominated by *Festuca ovina*. Bare ground, the hollow phase, is initially colonized by grass seed from a neighbouring *F. ovina* plant which, during the subsequent building phase, establishes and grows, spreading laterally to form a tussock. This structure accumulates fine soil particles and detritus, and continues to expand as the vigorous young plant produces more shoots during this mature phase. As the parent plant becomes older, senescent and less vigorous, the lateral branches attain independence but the central portion of the tussock decays and the accumulated mound of soil is subject to erosion. During this degenerate phase the spaces between shoots are invaded by a sequence of lichens which, as the hummock is gradually worn down, then give way to the hollow phase of bare ground.

The distribution of the various plants suggests to Watt that grass seedlings are effectively restricted to the hollow phase and that, since establishment is so limited, both in time to that part of the sequence and in space to those particular areas, the result is a sequence of even-aged plant groups in any one phase; these develop through the sequence whilst resisting invasion from other nearby phases. Watt is therefore able to argue that the assumption made by Gleason (1926), that seed migration and establishment is entirely a matter of chance, is unsupported in many plant communities. In addition, this spatial pattern of interactions and successions sets a lower limit to the scale at which the plant community can be studied and the temporal scale is likewise set by the longevity of the dominant organism. Again this undermines Gleason's unitary view in which the individual plant is restricted in its distribution by chance fluctuations alone; rather, its opportunities for colonizing an area, Watt suggests, are set, in part, by the internal dynamics of the patch which are non-random.

Watt's contribution to the concept of the plant community was to suggest that Tansley's ecosystem, and the reductionist approach to it, can be realized at the level of interactions between groups of plants within a patch. His work supports the idea of a stable plant community as a dynamic equilibrium between the processes of colonization, establishment, growth and degeneration occurring under constant climatic and edaphic conditions. His emphasis on the small-scale pattern both undermines Gleason's concept (Section 2.2.3) of a fortuitous assemblage of plants, and sets an agenda for autogenic successional studies at both the spatial scale of local interactions between plants and the temporal scale of individual life-spans.

### **2.3.3 Whittaker**

The extensive work of R.H. Whittaker (1953, 1956, 1962) both reviewed and synthesized the disparate notions of succession in addition to providing the first rigorous refutation of the Clementsian monocl原因 paradigm. In redefining the concept of the climax this work laid the foundations for the subsequent development of the successional paradigm

Whittaker's analysis of vegetation patterns in the Great Smoky Mountains (1956) provided evidence which supported the Gleasonian hypothesis of individualistic plant responses to the environment (Section 2.2.3). He plotted vegetation groups along axes representing moisture and elevation gradients and showed that population patterns were generally constrained by environmental factors. His results showed that species occurred, not in relation to other species, but rather wherever the environment matched their physiological requirements. He was therefore able to conclude that the plant community as an identifiable unit of associated species does not exist. His findings therefore supported the individualistic hypothesis of plant distribution patterns.

In his work on climax theory Whittaker (1953) criticised the monocl原因 of Clements as being overstretched and he distinguished between those concepts based on vegetation structure and those dealing with interacting species populations, electing to concentrate on the latter. His ideas of species populations were extended in relation to environmental gradients to propose that climax vegetation is similarly continuous in nature and that its patterns are likewise environmentally determined. He viewed such climax patterning as being at a higher level of organisation than the irregularity and "temporal instability" (p.

46) due to internal dynamics of the sort described by Watt. He reviewed the systems approach which attempts to characterize the successional sequence in terms of community level attributes such as productivity, stability and diversity but clearly prefers the less abstract and more species-based definition of the climax, recognition of which is by reference to “what populations actually replace other populations and then maintain themselves” (p57).

For Whittaker all factors which impinge on a site are capable of determining the composition of the vegetation and therefore any number of climax states may be possible; the term "prevailing climax" is suggested. Consequently the terms climax and succession are useful, and may be distinguished, only in a relative sense; the climax being that state in which populations are relatively stable and in which vegetation change is relatively non-directional. By providing a population-based definition of these terms Whittaker points the way towards a quantitative exposition of the climax as that state of stability within which different vegetation stands tend to have similar compositions; that is there is regularity of composition between stands when a degree of stability in relation to the environmental factors has been achieved. Greater uniformity between samples from within a single stand is also proposed as a feature of the stable climax state in contrast to successional, unstable vegetation which is characterized by patchy and irregular composition.

Whilst this conception of the climax as one of relative stability in the relations between the vegetation and the numerous factors which impinge upon it, the emphasis nevertheless remains on the environment as the ground state to which the system comes, through successional development, into an equilibrium condition. This emphasis reflects Whittaker's (1956) findings of vegetation change along gradients of moisture and elevation. The combination of the quantitative, population approach and this causal relation to the environmental conditions led Whittaker to the development of the gradient analysis method for the investigation of vegetation (Whittaker, 1967). This approach was to have a dominant influence on the methods of ecological study during the following decades (Mueller-Dombois and Ellenberg, 1974; Section 3.6.2).

The works described in this section have been used to illustrate how an emphasis on rigorous definition of terms, on detailed and intensive observations from a range of plant community types, and on quantitative methodologies have led to the generation of new

insights into the nature of vegetation development. This more analytical approach paved the way for further, recent advances in defining the processes of change.

## **2.4 Modern developments in successional theory**

The trend towards explaining successional patterns in terms of population dynamics has led to considerations of the proximate causes of change. Mechanisms and models may be seen as being of two general types; first the effects of one plant population on another either indirectly via changes in the environment or by direct influence of plants on each other, and secondly, where plant interactions are due to differences in the inherent properties of the plants themselves, that is attributes such as life-form, life-history, modes of regeneration and dispersal.

### **2.4.1 Drury and Nisbet**

In a review of the successional concept Drury and Nisbet (1973) find a lack of supporting evidence for Whittaker's ideas of the continuum of climax types and focus instead on aspects of individual species attributes for an explanation of successional sequences.

Egler's paper (1954) had paved the way for this change of perspective by restating in concise terms the twin poles of the successional debate and the discrepancies between theory and observation. He referred firstly to the sequence of identifiable stages of succession, in which each stage prepared the way for the next, as relay floristics; in fact this is equivalent to the Clementsian process of reaction (Miles, 1987). Secondly he contrasted this with the evidence from many successions which showed that late successional species were often present from an early stage and from which he argued that the series actually consisted of a change in the relative conspicuousness of the various plants. This process, which resulted from the differing growth rates and growth forms of the component species, he summarised using the term initial floristic composition.

Drury and Nisbet (1973) laid emphasis on the different species attributes developed over evolutionary timescales by natural selection. Their review suggests that geomorphological processes, acting continuously, generate a diverse range of habitat types to which different

plant species have evolved specialist adaptations and within which they each tend to dominate as a result of their competitive superiority. This range of environments they describe as representing stress gradients, and plants having different architectural life forms are better suited to one level of stress rather than another. Large structures which hold their growing organs away from the shelter of the ground and which maintain a relatively large proportion of non-productive tissue tend to be more vulnerable to stress. It is the match between environmental stress levels and plant life form which generates the observed correlation between species and successional stage.

The argument of Drury and Nisbet contains an implied consideration of the spatial dimension. A plant exists at a point in space and vacant sites likewise arise at finite points in a more or less random manner so that, in order to occupy a newly vacant site, a plant must be able to disperse. Plants already occupying the site have an advantage over colonizers but this advantage is reduced in proportion to the level of disturbance. New sites become available as a result of some disturbance and are subject to higher levels of environmental stress; they will therefore be occupied preferentially by species which are stress tolerant but only if those species are also able to disperse to the site. This relation between stress and dispersal has meant that the two plant attributes tend to be positively correlated and are combined in Drury and Nisbet's term colonizing ability.

These authors present the further hypothesis that the attributes of, firstly colonizing ability and, secondly growth rates and size at maturity, are negatively correlated. The observed correlation of slow growth, large size and long lifespan (Section 1.6.1), together with the attributes associated with stress and disturbance, constitute a sufficient explanation of observed successions. It was the predicted correlations associated with this hypothesis that led to Grime's scheme of a species-attribute space (1979; Section 1.6.1.1) in which succession is described in terms of the change in species strategies along an environmental gradient in time.

#### **2.4.2 Mechanisms: Connell and Slatyer**

Connell and Slatyer (1977) describe succession as a continuous process of species replacements which, because of the constant presence of disturbance, is itself continuous; they therefore reject the notion of a successional endpoint and conclude that succession



never stops. Using a systems approach they relate the concept of succession to that of community stability. Where a stable system is subject to a perturbation then recovery may be a consequence of either resistance to change or adjustment to change; succession describes the process of system adjustment. The process takes place as a sequence of species replacements and it is the mechanisms which drive that sequence which are the subject of Connell and Slatyer's analysis.

In addition to the process by which species enable replacement to occur by modifying local conditions (Section 2.2.1) Connell and Slatyer (1977) outline two other possible species interactions which may tend either to prevent or to have no net effect on species replacements. They describe three possible mechanisms which they propose as promoting successional change by autogenic means. In all three models a newly available site is colonized by species with specialist dispersal adaptations which make them more likely to arrive at the site. The conditions at the site are altered by the presence of these colonizers and it is their subsequent replacement by "early" and then "late" successional species which is driven by the proposed mechanisms termed facilitation, tolerance and inhibition.

Facilitation corresponds to the traditional view of succession in which the early colonizers are able to survive relatively harsh conditions and modify the environment such that it becomes more favourable for other species and relatively less suitable for themselves. These early arrivals are usually thought of as poor competitors which are easily displaced when other species begin to establish. The tolerance model suggests that those species present at a site in the early successional period are all equally likely to establish but that some are better able to tolerate low resource levels; these species grow slowly, tolerating competition, until they are able to exclude other species by shading. A third model suggests that plants actively inhibit the growth of potential competitors by, for example, leaching a growth suppresser into the soil. Inhibition prevents other species occupying the site until the original plant dies; release from inhibition can then lead to replacement by a new species. Some studies (Hils and Vankat, 1982; Bornkamm, 1988) have found this three-way classification useful though in other cases it has been difficult to isolate a single mechanism (Miles, 1987); many workers report all three processes, either between a single pair of species over time, or simultaneously within the same patch (Walker and Chapin, 1986; DeSteven, 1991; Gill and Marks, 1991).

The distinction between models generates predictions related to the community features produced by successive species replacements. Facilitation derives from a view of the community as a highly organized system in which structure develops over time as an accumulation of species interactions. There is therefore a time gradient in community structure such that species stratification increases and niche width decreases (Section 1.6.2.5). Under the action of the tolerance model the mature community is composed of those species which have a high resource use efficiency; succession is represented by a gradient of resources and species sequences derive from life history attributes rather than by biotic interactions (Section 1.6.1.1). Communities structured by inhibitory mechanisms are composed of species which acquire and monopolize space and so prevent further invasion. This process is non-sequential, in the sense of Gleason's chance assemblages (Section 2.2.3), but leads nevertheless to a predominance of long-lived species which are characterized by attributes, such as defensive adaptations, which promote longevity.

These differences may, it is suggested, have applications in the management of the recovery process in damaged ecosystems. Successional rates are likely to be faster under the action of facilitation, slower when tolerance is predominant and slowest of all when species inhibit replacement. Where inhibition is apparent in early succession restoration may be accelerated by selective species removals whilst in degraded or primary successions re-establishment may require facilitation in which case early species may be actively encouraged or planted. Despite the growth of interest in restoration ecology (see for example Jordan *et al.*, 1986) there is little reported evidence of restoration techniques based on these concepts being applied in reclamation schemes (but see Vieira *et al.*, 1994; Powers *et al.*, 1997; Walker and Powell, 1999).

Connell and Slatyer consider the three proposed mechanisms within explicitly defined scales of space, time and disturbance intensity. They note that the mechanisms involved are likely to be dependent on scale and also that judgements about the stability of a system must be based on measures made at an appropriate scale. Where, for example, disturbance is severe and over a large spatial area then facilitation is likely to be the more predominant mechanism and colonization processes are likely to favour species with high dispersal rates. A site which is similarly disrupted but over a limited area is likely to be colonized by local species which need not be adapted for long range dispersal.

Walker and Chapin (1987) review Connell and Slatyer's paper and describe evidence from recent studies which further illustrate the processes involved in successional replacements. They point out that Connell and Slatyer's mechanisms are each composed of amalgams of other processes with the result that it is difficult to treat them as single, alternative mechanisms acting in isolation. In deconstructing the three mechanisms into components related to life history traits and competitive interactions they extend the range of processes impacting on successional sequences to include the outcomes of random influences such as differential seed and site availabilities during colonization. They suggest that replicate cases may be used as a measure of the importance of such stochastic factors.

### **2.4.3 The status of the successional concept in modern ecology**

During recent decades studies of vegetation dynamics and ecosystem processes have led to a rejection of the climax as a useful concept (Miles, 1987) though much of the terminology associated with Clements classification remains in use (e.g. Gilbert and Anderson, 1998). Increasingly, it has been recognised that vegetation communities are always subject to change and that disturbance is a constant part of an organisms habitat, being variable on scales of severity, extent and frequency (Pickett *et al.*, 1987; Bazzaz, 1996). Such a recognition leads to the investigation of those adaptational traits which allow species to persist in varying conditions: species may be adapted to levels of disturbance as well as to levels of resources. Southwood (1977) proposed a scheme for classifying habitats in terms of their variability or durational stability and also in relation to their favourableness or resource levels. Within this framework vegetation change follows from changes in the habitat and succession is the process by which species adapted to high levels of disturbance are gradually replaced by those with attributes suited to persistence in low disturbance environments. This scheme was developed by Grime (1979) who added the dimension of competition and applied the resulting three-way strategy classification to a large number of British plant species (Grime *et al.*, 1989; Section 1.6.1.1).

Pickett (1976) also suggested that succession follows from species adaptational responses to a changing environment over time. He considered that the suite of traits which characterize any one species are a fixed, evolutionary-derived inheritance and that a species persistence at a site is determined by the match between those traits and the environment. Community change follows as the environmental conditions change - a gradient in time. At

the same time “successional sorting” acts through the mechanism of competition and other ecological processes to limit the portion of temporal gradient able to be occupied by any one species. Pickett draws the same conclusion as Southwood in describing succession as a replacement process in which later species are characterised progressively less by opportunist, and more by equilibrium strategies. Despite the contention that “succession can be understood ..... without reference to a deterministic progression toward climax” (p112), the mechanism and sequence described by Pickett are both deterministic and progressive. Further, he describes how a climax state is attained when resident species have a greater level of adaptation to conditions than do potential colonizers.

In Pickett’s description this sequence may be interrupted by a variety of disturbance mechanisms which continually form patches of more successional juvenile vegetation. The composition of new patches is dependent on the proximity of other, similar patches and the colonizing ability of their constituent species. For Pickett the vegetational landscape is an array of such patches in which local, within-patch processes are to be distinguished from landscape-scale dynamics.

Pickett's later work (Pickett *et al.*, 1987) also addresses the issue raised by Connell and Slatyer (1977) of scale. They point out the problem of confounding processes at the spatial level of the individual, where the species replacements which comprise succession actually occur, with community level phenomena. As a solution they propose a tabulation of the causes of succession arranged hierarchically in order to aid an appropriate match between the factor or mechanism investigated and the predicted outcome.

Tilman (1985) also described a gradient in time as the basis for succession. However, he emphasised competition between species as the mechanism generating change. For primary, and low-nutrient secondary, successions Tilman’s gradient in time is a joint one, a ratio between the negatively correlated resources of soil nutrients (typically nitrogen) and light. Initially nitrogen is highly limiting whereas light is abundant. As vegetation establishes soil nutrients increase and above ground biomass increases so producing shade. As the ratio between these two resources changes so species replace each other as competitive dominants. The model assumes an equilibrium state between plants and environment for each stage and, though not necessarily directional, it is predictive given a time-scale long enough to avoid transient dynamics.

In a brief review of succession Miles (1987) proposed that, having abandoned the search for an all encompassing theory of succession, vegetation research has concentrated on, amongst other things, exposing the mechanisms which determine the mix of species in a community. An uncovering of these mechanisms would allow for an understanding of vegetation development since it is when these mechanisms are altered that community change occurs. Similarly, Glenn-Lewin *et al.* (1992), in an overview of successional studies, suggested that modern studies are characterised by a move away from holistic, systems approaches to a more pragmatic, reductionist approach in which it is accepted that vegetation dynamics are both non-equilibrium and multi-factorial in nature.

## 2.5 Conclusion

This review has selected a number of works in order to illustrate the ideas which form the conceptual foundations for the research proposal described in Chapter One and to offer a description of the historical development of those ideas in order to provide a context for the current state of knowledge of successional dynamics.

This series of portraits has shown that the concepts currently held to be central to the field (species-environment relations, the chronosequence methodology, species interactions, the multi-factorial nature of the processes, the non-equilibrium approach and the importance of chance factors) were present in the earliest descriptions (Section 2.2.1) but that the perception of their relative importance has not been constant. The early polarity between community-level, top-down descriptions and the reductionist view of processes at the level of individual plants (Section 2.2.4) has remained but it may be argued that the development has been characterised by a shift in the preoccupation of mainstream ecology from the community to the species level. This shift has been brought about by an increasing acceptance of observational evidence of natural communities and its application to accepted theory and, more recently, the initiation of field-scale trials (Bakker, *et al.* 1996) to answer specific questions.

In addition two aspects are apparent in recent work which are under represented in the earlier literature; the importance attributed to disturbance (Section 1.1.5) and the explicit consideration of scale (Section 3.3 and 3.4).

## CHAPTER THREE: EXPERIMENTAL DESIGN AND METHODOLOGY

By describing and examining differences between plant communities which have developed over periods of 27 and 56 years this study aims to interpret them in the light of recent theories of ecological succession and so achieve an improved understanding of the factors driving vegetation development. The first objective towards this goal was that of devising methods for the collection and analysis of appropriate data (Section 1.7.3). In this chapter the rationale behind the experimental design and the methods used to record species abundances are described and the analytical methods are introduced.

### 3.1 Vegetation sampling

This study views succession as a species replacement process and a community as an assemblage of species within an area (Section 1.1.1). It was therefore necessary to record the presence of each of the species within each of the communities under study. In addition to a list of the species present it is of value to measure the abundance of each species in order to quantify the relative importance of each in the community (Goldsmith *et al.*, 1986). A full enumeration of all the individual plants in even a small site is, however, impractical because of the time required and so consideration must be given to methods of obtaining a representative sample (Mueller-Dombois and Ellenberg, 1974).

A number of quantitative measures of abundance are available; Kershaw and Looney (1985) discuss the suitability of density, cover, frequency and yield as methods of obtaining quantitative information. In view of the difficulties in identifying individual plants (Section 1.6.4) in a grassland community, the relatively large areas covered, the time constraints within which sampling could occur and the restrictions placed on removal of materials from the site it was decided that counts of local, rooted frequency would be the most practical method of recording relative abundances. Consideration was given to the size of the plants and the pattern of spatial distribution in determining quadrat size (Section 3.3).

Taking a sample from a vegetation stand in lieu of a measure of the whole community makes the assumption that the vegetation is homogeneous and that the sample therefore contains the same amount of information as is present in the complete stand. This assumption may be invalid because vegetation is rarely homogeneous (Kershaw and

Looney, 1985). The extent to which one may make valid inferences about areas outside of the sample is directly related to the degree of community homogeneity (Leps and Stursa, 1989).

Homogeneity within a community may be considered at a number of scales. Individual shoots have a finite size and there is a space between one shoot and the next. Clearly a sample should be large enough in area to even out this type of heterogeneity. It is also apparent that heterogeneity of this kind is related to the size and growth form of the individual so that a study of, for example, lichens requires a different sampling scheme from one which investigates herbs or trees (Kent and Coker, 1992). The vegetation in this study is dominated by grass and herb species with separation between stems of a few centimetres and the sampled area contained within the quadrat frame is  $200 \times 200$  cms (Section 3.3). Since this linear dimension is at least one order of magnitude greater than the shoot separation typically found in this type of vegetation the data collected are unlikely to be biased by this form of heterogeneity.

Even within a visually homogeneous area, vegetation may be found to change over a scale of a few metres. This may be the result of the action of a number of processes. Clusters of species may arise from the process of vegetative spread resulting in an aggregated or contagious distribution (Greig-Smith, 1983). Where there are small-scale differences in substrate, topography or microclimate, then conditions may differentially favour particular species or groups (Section 1.1.4). This patchiness of the vegetation may be examined by spatially explicit sampling, whilst environmental differences can be minimized by suitable choice of sample area. In this study regularly-spaced samples were used to investigate the spatial variation of samples within revetment slopes (Section 3.3.1).

The relationship between the number of species found in a sample and the size of the sampled area also bears on the design of a sampling programme and has been the subject of some debate amongst ecologists (Arrhenius, 1921; Gleason, 1922; Dony, 1977; Shmida and Wilson, 1985; Palmer and White, 1994). It is commonly found that, in an homogeneous area, as the sample size increases so does the number of species recorded but that the rate of increase declines markedly for sample areas above a certain size (Hopkins, 1955; Kilburn, 1966; Kershaw and Looney, 1985; Goldsmith, *et al.*, 1986). In a perfectly homogeneous, model system a point would be reached where an increase in the area sampled would no longer result in additional species being encountered. That perfectly homogeneous systems

do not occur in nature explains why new species continue to be found in larger sample areas without apparent limit (Kilburn, 1966; Crawley, 1997).

Clearly a smaller quadrat will give a less representative record of a community than a larger one due to there being fewer sampled individuals. The degree of inaccuracy obtained will depend on, amongst other things, the size of the individuals and the extent to which their distribution deviates from that of a purely random one. However the extra effort required in sampling a larger area may be inefficient when judged against the additional information gained (Gauch, 1982). In this study the relation between the number of species recorded and the size of the sampled area was investigated by sampling areas of increasing size (Section 3.3).

### **3.2 The species-area relation in ecology**

The species area relation has been the subject of numerous studies in ecology which have sought, variously, to determine the minimum area which may be representative of a particular community, the smallest quadrat able to include either a specified proportion of the constituent species or, more generally, a representative sample of that community. Investigators have also sought to understand the pattern, by modelling it mathematically, and by proposing biological mechanisms which might be responsible for generating it; they have used the relationship as an empirical description of particular communities, to predict species numbers in larger areas and also species losses from areas following habitat destruction and the size of reserves required to preserve a given level of biodiversity.

In 1921 Arrhenius proposed a mathematical description of the species-area relation, based on his sampling of 12 vegetation communities. His formula, relating species number ( $S$ ) and area ( $A$ ), was to be later modified into the power function  $S = cA^z$  where  $c$  and  $z$  represent constants which are functions of the particular community under study. The studies described by Arrhenius show observed species numbers which deviate from those predicted to occur in the larger sampled areas but he nevertheless felt justified in proposing that the relation embodied in this formula was universally applicable.

Gleason (1922) pointed out this shortcoming and argued that for larger areas the formula produced unrealistically large predicted species numbers. He proposed an alternative,



logarithmic relation between species and area symbolized by the equation  $S = a + b \times \log A$  in which the constants  $a$  and  $b$  are again parameters specific to the community being studied.

Subsequent studies (Hopkins, 1955; Kilburn, 1966; Dony, 1977; Rydin and Borgegaard, 1988) have generated much debate over the utility of these and other formulae until, in recent decades, a consensus view has developed which accepts the power law as being the most widely applicable mathematical description (Diamond and May, 1981; Colinvaux, 1986). At the same time it has been argued that the relation, however well modelled, has no significant meaning in ecology but is, rather, a mathematical result generated by the multiplicative effects of several independent factors operating on species distributions (May, 1981). It has come to be accepted that no single ecological process can be envisaged which generates the relation and that different processes are likely to operate over different spatial scales (Auerbach and Shmida, 1987; Leps and Stursa, 1989).

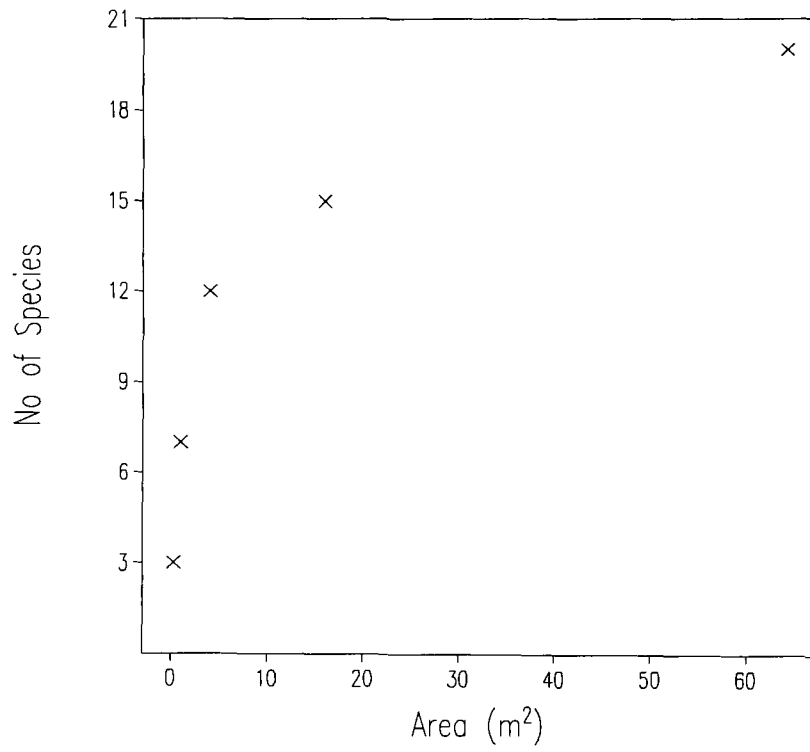
Nevertheless the species-area relation is still considered useful as a means of describing the pattern of species distributions within a community and as an empirical guide for determining the most appropriate areal sample size (Greig-Smith, 1983; Kershaw and Looney, 1987; Kent and Coker, 1992); this despite a general acceptance that it lacks any firm theoretical or ecological basis (Bullock, 1996; Crawley, 1997).

### **3.3 Vegetation sampling: the species-area curve**

A preliminary investigation was carried out to quantify the relation between sample area and species number with the aim of characterising the pattern of species within the community and for use as a guide in determining the optimum quadrat size (Kershaw and Looney, 1985). From the argument above (Section 3.1) it may be accepted that the chosen quadrat size will inevitably involve a compromise between one that is large enough to include a representative community sample yet small enough to allow the efficient collection of species abundance data with minimum redundancy (Greig-Smith, 1983).

A location for this investigation was chosen so as to avoid any obvious environmental gradients. Since the study zones were on sloping revetment faces of limited size, typically 5m by 15m, a larger, level area was chosen in order to eliminate the possibility of variation due to a gradient associated with varying height. This was located adjacent to building 199 (Figure 1.5) on a plot which was visually judged to be of uniform composition. The method

Area (m <sup>2</sup> )	0.25	1	4	16	64
No. of species	3	7	12	15	20



**Figure 3.1 The relationship between area and the number of species recorded from nested plots at site 199.**

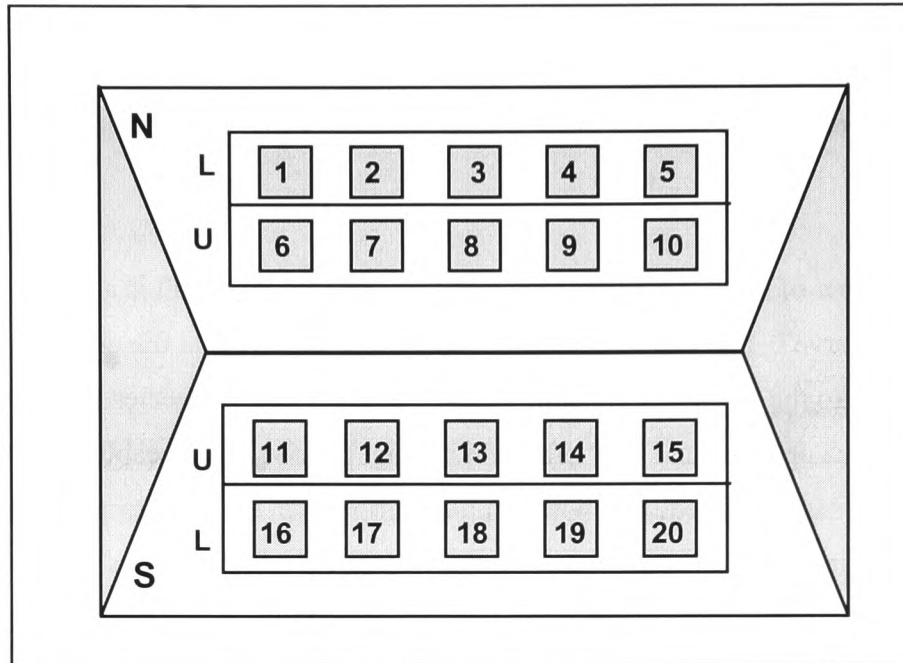
is described by Kent and Coker (1992). A square area, 8 m by 8 m, was marked, from a point chosen at random, using wooden pegs and string. Using the same origin a 4 m by 4 m plot was similarly marked within the larger square. This smaller plot was similarly divided and the process was repeated to give a nested set of square plots of side lengths 0.5, 1, 2, 4 and 8 m. In the smallest square the number of plant species was recorded. Moving to the next larger square and excluding the area already sampled the number of additional species found was recorded. The process was repeated for all squares and the results are presented in Figure 3.1.

When the number of species is plotted against area sampled the result is a characteristic “species-area curve”. It is apparent from the shape of the curve that the use of larger sample areas is subject to the law of diminishing returns. The number of species found increases sharply with area up to around 4 m<sup>2</sup> after which point the rise is noticeably less steep. If the size of the area sampled is equated with sampling effort then the extra time required to sample, for example, a 4 m by 4 m area compared with a 2 m by 2 m area, yielding as it does an increase in species numbers from 12 to 15, is unlikely to be worthwhile (Greig-Smith, 1983). For this reason a sample area of 4 m<sup>2</sup> is used in these studies. This choice is in agreement with the general recommendations for sampling areas in coarse grasslands (Kent and Coker, 1992; Bullock, 1996) and is also the same as that used in the National Vegetation Classification (NVC) survey of British vegetation (Rodwell, 1992).

### **3.4 The pilot study**

It is apparent from the species area curve (Figure 3.1) that the number of species encountered continues to increase with increasing sample area above the 4 m<sup>2</sup> level even within a visually homogeneous area, albeit at a reduced rate. For a theoretical, perfectly homogeneous community the curve would become flat beyond some particular areal size at which point all the species in the community would have occurred within the sample (Kershaw and Looney, 1985). That this is not the case here, and for the majority of such curves representing actual field communities (Kilburn, 1966; Crawley, 1997), suggests that the effect of space on species counts remains at this larger scale. It may be inferred that some factor operates in this range which influences the number and distribution of species.

In order to investigate this spatial factor and its relation to vegetation sampling on the revetment faces a regularly spaced grid of quadrats was delineated and sampled. This pilot



**Figure 3.2. Schematic plan view of a revetment showing north (N) and south (S) faces, upper (U) and lower (L) zones and the layout of the pilot study quadrats.**

study aimed to quantify the relation between community composition and spatial separation within the scale and context of the revetment slopes. The study employed a grid of 20 quadrats laid out on each of three revetments (R200, R833 and R1062; Figure 1.5). The design is illustrated in Figure 3.2.

Each revetment in the study is composed of a north- (N) and a south-facing (S) slope or face. Within each face a sampling plot is described by that rectangular area which lies no closer than 2 metres from any edge of the revetment. Thus areas close to the top, bottom and ends of the revetment faces are not included. This plot typically comprised an area of approximately, 10 by 20 metres. Each plot was divided into an upper (U) and a lower (L) zone and five quadrats were arrayed along an horizontal line within each zone.

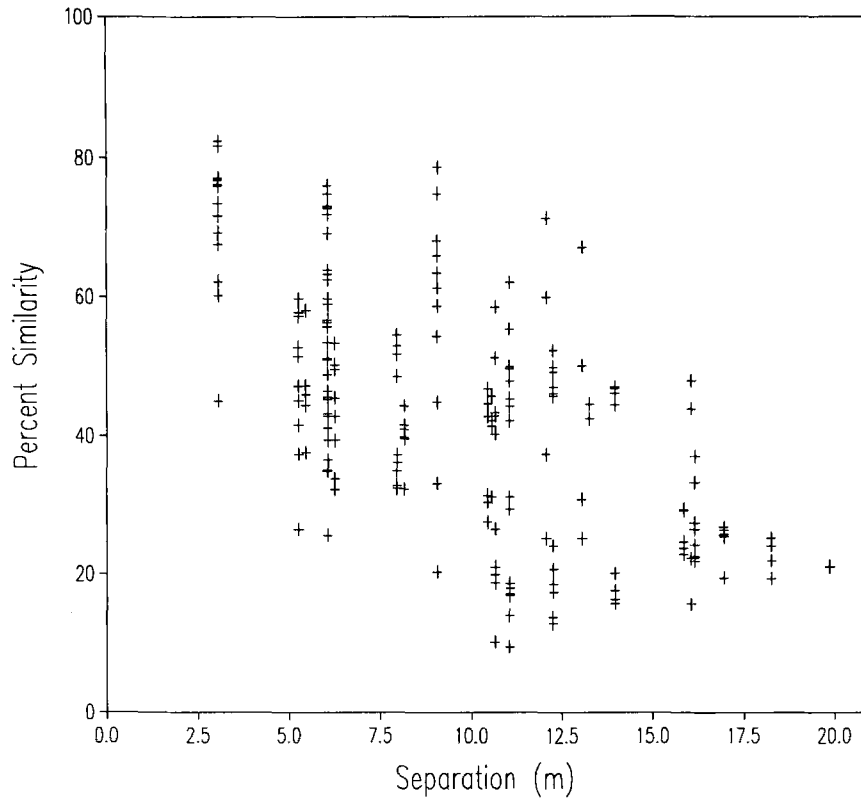
For all possible pairs of quadrats, from the 20 on each revetment, a measure of the degree of similarity of vegetation was computed. The index used was the Percent Similarity (van Tongeren, 1987; Kovach, 1995); this was chosen because of its simplicity, widespread use and its capacity for the utilization of quantitative species data (Mueller-Dombois and Ellenberg, 1974). The index (PS) is calculated as,

$$\text{Percent Similarity} = 200 \times \frac{\sum_{k=1}^n \min(y_{ki}, y_{kj})}{\left( \sum_{k=1}^n y_{ki} + \sum_{k=1}^n y_{kj} \right)}$$

where all pairs of sites *i* and *j* are compared and  $y_{ki}$  is the abundance of species *k* at site *i*.

A scale drawing of each revetment was used to determine the physical distance between each pair of quadrats. Thus for each combination of a pair of quadrats, two measures were obtained, similarity and separation.

The data were sorted to remove elements which tended to bias the comparison. For example a rectangular matrix of similarities necessarily contains duplicates of each quadrat pair: quadrat 20 is compared with quadrat 1 and quadrat 1 is compared with quadrat 20. These duplicates were removed to give a triangular data matrix. Furthermore, each quadrat has a similarity with itself of 100 and a separation distance of zero. These pairs also unduly influence the computed relationship and they too were removed.



**Figure 3.3 The relation between similarity and separation of 20 vegetation samples from revetment R200.**

Nearest pairing (m)	Number of cases	Correlation coefficient (r)	Significance level (p)	Mean similarity
3.0	190	- 0.638	< 0.001	43.31
5.2	174	- 0.538	< 0.001	40.73
9.0	106	- 0.436	< 0.001	35.56
12.0	59	- 0.418	< 0.001	31.71
16.0	24	- 0.370	< 0.05	26.27
18.0	6	- 0.382	> 0.10	22.25

**Table 3.1 Correlation between separation and similarity of pairs of quadrats**

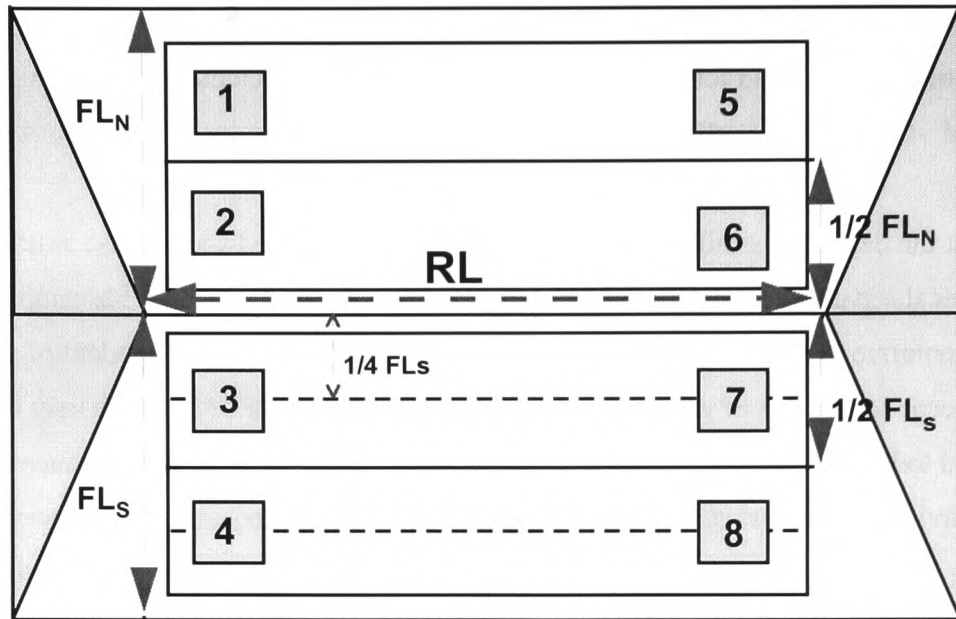
The remaining data consists of 190 cases for each revetment and comprises measures of separation and similarity. The data for revetment R200 are displayed as a scatterplot in Figure 3.3 which shows a decrease in similarity for larger separation distances. The correlation coefficient associated with these variables is -0.638 which is significant at  $p < 0.001$  indicating a strong, negative correlation. The procedure was repeated for the data sets from revetments R833 and R1062 which gave correlation coefficients of, respectively, -0.228 and -0.377 (both coefficients are significant at  $p < 0.01$ ).

Given that the degree of similarity in species composition of any two quadrats is related to their physical separation and that a sampling scheme is required which yields samples which are representative of the community in any one zone, and therefore independent of samples from adjacent zones, it is of value to know at what distance a pair of quadrats may be considered to be no longer subject to this spatial factor. To determine this distance for the data set having the highest correlation coefficient, cases were progressively removed, beginning with those quadrats closest together, and correlation coefficients recalculated at each step. The results are shown in Table 3.1. It can be seen from this table that the negative correlation between similarity and separation ceases to decline for distances greater than around 16 m and that at separations greater than this the degree of correlation is no longer significant at the 5% level. The percent similarity at this distance is generally of the order of 25%.

The inference from this exercise is that quadrats which are closer than around 16 m may not be considered to be independent. A factor or factors appears to operate within this range, in this grassland, which may be considered to be equivalent to a variable having a measureable effect and the intensity of which is inversely related to the distance between any two points. The methodology outlined below for the main study includes measures to reduce or eliminate the effect of this variable from the experimental design.

### **3.5 The main study**

In Section 3.2 the reasons for adopting a 2m × 2m quadrat for sampling vegetation of the type found at the site were explained and Section 3.3 has described how quadrats may be located so as to minimise the effects of spatial dependence. Under the constraints set by the size of the revetment faces and the requirements to take one sample from each of the four zones and to place quadrats at least 16 m apart it follows that there are eight possible



**Figure 3.4 Schematic plan view of a revetment showing the quadrat sampling layout of the main study (see text for explanation).**

Key:

- RL - Revetment length
- FL - Face length
- N - North facing
- S - South facing



positions for a quadrat on any one revetment numbered 1 to 8 in Figure 3.4. The choice of actual quadrat locations is therefore limited to a set of four from these eight. The possible combinations are; either quadrats numbered 1, 3, 6 and 8, or quadrats 2, 4, 5 and 7.

### 3.5.1 Revetment faces and zones

For the purposes of this study the revetments are identified by reference to the number allocated to the building with which they are associated (Section 1.3) with the addition of a prefix letter R. The faces are denoted by the letters N and S, signifying north- and south-facing respectively, and height zones are referred to as upper (U) and lower (L) in order to distinguish those positions towards the top or bottom of the revetment slopes. Faces were delineated according to the following method (Figure 3.4). Two pegs were placed on the revetment ridge at a distance of at least 15m though in one case this was reduced to 14m to ensure that zones did not extend to the revetment edge. The length along the revetment ridge between the pegs was measured and recorded as RL. Next the length from the revetment ridge to the base of the slope was measured along a line, from each peg, perpendicular to the line of the ridge, on each of the north- and south-facing slopes and recorded as face lengths,  $FL_N$  and  $FL_S$  respectively. This face length was halved to give the position of a horizontal line of division between the upper and lower zones. Each of these lengths was again halved to give the position of the midline of each zone. A peg was positioned 1 m below this line to mark the location for the lower edge of the quadrat frame. For example the position for the base line of quadrat 3 (Figure 3.4) from the top of the revetment is given by,

$$\frac{1}{4} FL_S + 1 ; \quad \text{and that for quadrat 8 by,} \quad \frac{1}{2} FL_S + \frac{1}{4} FL_S + 1$$

In some cases the geometry and size of the revetment resulted in a face length which was shorter than desirable and which meant that some quadrat pairs were located less than 16m apart. Those quadrats on opposite faces and in upper and lower zones respectively at the same end of a revetment (e.g. quadrat positions 1 and 3, or 2 and 4) were, on some revetments, separated by between 10 - 13m . In no case was a quadrat pair on the same face less than 15m apart.

### 3.5.2 Quadrat sampling

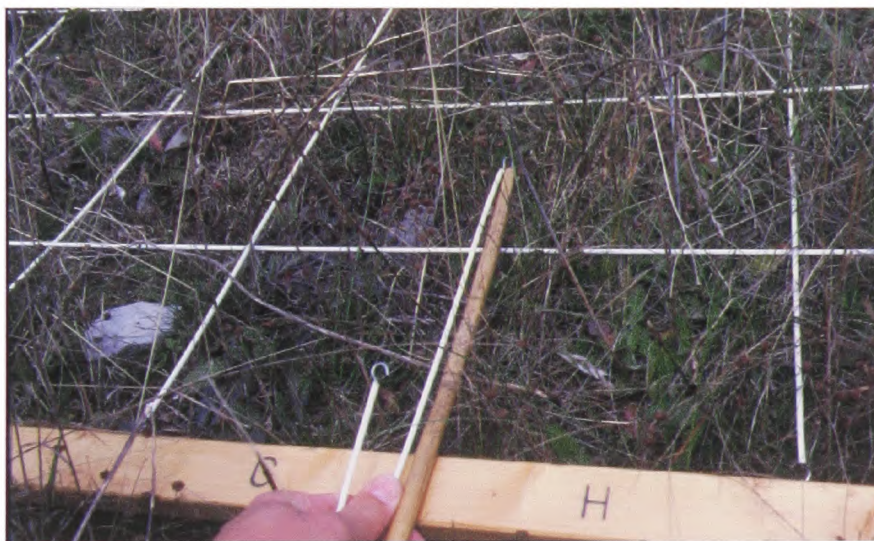
The quadrat frame comprised four wooden battens, each 230 cm in length, and 18 two-metre lengths of curtain wire (Plate 3.3). The four battens formed the base, top, left and right sides of the quadrat; at each end they were shaped to a rounded point and drilled to take bolts; eyelets were attached along the edge at intervals of 20 cm. When assembled the frame had internal dimensions of 2 m along each side. The curtain wire lengths were carefully adjusted so that when hooks were inserted into each end they could be attached, under tension, to the frame so dividing the area into well-defined cells. The base and top battens were marked with letters A - K and the left and right battens with numerals 1 - 10 as an aid to referring recorded data to individual cells.

The quadrat and dividing wires were constructed *in situ* for each sampled area. This ensured minimal disturbance to the vegetation enabling accurate and consistent counts to be achieved. Experience showed that it was not possible to position the quadrat in a “ready-made” form in vegetation of more than 15-20 cm in height without damage to the plants and a consequent difficulty in locating shoots within the quadrat cells. This problem has more than purely practical consequences since the data recording process relies on locating individual plant stems within both the quadrat frame and the cell formed by intersecting dividing wires. The “edge effect” refers to the error introduced in quadrat sampling of vegetation when shoots cannot be accurately or consistently assigned to one division or another (Kershaw and Looney, 1985). This can arise because of a lack of standardization in locating the quadrat flat on the ground surface or because the plant shoots do not stand perpendicular to the surface. The degree of error introduced by the edge effect is in proportion to the amount of edge presented to the vegetation by the quadrat and is also exacerbated by damage to the shoots from wind-throw, trampling or rough treatment in placement of the quadrat. All parts of the quadrat in this study were designed to be passed through the vegetation, in a shuttle-like manner, at ground level to avoid this disruption.

Having marked the position for the sample area the quadrat was placed according to the following method. As sampling was undertaken on slopes with inclinations of 30 - 40° there was a need to support the quadrat frame to prevent it slipping under gravity. The base section was placed first along a horizontal line using the location peg as a guide and hammering in two wooden support pegs. The two side battens were similarly threaded perpendicular to the base and attached to the base by bolts and wing nuts. Further pegs were inserted in the outside corners of the frame to lock the quadrat in place. The top batten was



**Plate 3.1** The dividing wire is hooked onto the end of the cane.



**Plate 3.2** The dividing wire and cane are pushed through the vegetation.



**Plate 3.3** The completed quadrat frame.

next threaded and bolted. The dividing wires were each threaded from the top and sides of the quadrat using a 2.5 m length of bamboo cane (Plate 3.1). The hooked end of a wire was inserted into the end of the cane and, keeping a tension on the wire, the two components were together pushed through the vegetation at ground level, at right angles to the frame which also acted as a guide (Plate 3.2). The cane could then be withdrawn leaving the wire in place. Finally the wires were attached under tension to the frame by means of the eyelets and hooks. At the majority of the sampling locations the vegetation was more dense than that shown in the plates, being typically between 50-120 cm in height, and, in such circumstances, the method described was very effective in leaving the vegetation undisturbed.

The completed quadrat frame thus enclosed a gridded area of 4 m<sup>2</sup> with 100 subdivisions or cells each measuring 20 by 20 cm (Plate 3.3). Those vascular plant species present and rooted in each cell were recorded along with data for the location, zone and aspect of the quadrat and incidental notes relating to the site description and to species identification. Appendix B contains a sample record sheet of the type used. Plant species were denoted by *ad hoc* labels and specimens collected for later identification. Floras used for species identification included; Stace (1991), Wade (1970), Rose (1981), Clapham, Tutin and Warburg (1959) and Hubbard (1984). Nomenclature follows Stace (1991). In a number of cases, where a plant, rooted outside the quadrat frame, overhung the sampled area this too was noted. Other features present and recorded are described below (Section 3.5.4).

### 3.5.3 Bryophytes

Whilst this study restricted its scope to the investigation of differences signified by the presence of vascular plants (Section 1.1.1) a number of other plant forms were found and recorded for their potential value as ecological indicators. In the pilot study the numbers of species and frequencies of lichens and fungi found were extremely small; moss specimens, however, were encountered in almost all quadrats and cells.

Identification and recording of moss specimens presented a number of problems. Moss species are notoriously difficult to identify in the field (Watson, 1954). Visual inspection of field specimens showed that two groups of moss specimens could be distinguished, here termed type I and type II. Several samples of each type were collected and identified with the help of the staff of the National Museums of Wales. All samples of type I were found to

be *Pseudoscleropodium purum* and type II were *Polytrichum formosum*. It was decided that identifying mosses to species level in the field would be too time-consuming in relation to the information value achieved. Further it has been argued that growth-form within a single moss species is somewhat variable and therefore growth-form may be a better indicator of habitat or of environmental factors than taxonomic categories (Gimingham and Birse, 1957; Grace, 1995). Consequently it was decided to record mosses as *Pseudoscleropodium purum* if they had type I form and *Polytrichum formosum* if they had type II form. In fact all moss specimens recorded in the main study appeared to be of type I form.

The method used in the pilot study, of scoring species frequencies within the 2 × 2 m frame, was found to be very effective for grass and forb species where the size and spread of the plant shoot was of the same order of magnitude as the cell in which it was located. However this was not the case when moss and lichen specimens were recorded. In many instances moss was found to be present as tiny filaments which were very much smaller than the 20 × 20 cm cell. The pilot study nevertheless applied a consistent criteria to the recording of all plants, namely presence/absence in each cell of the quadrat. This approach led to a number of weaknesses:

- Moss occurrences recorded in this way consistently produced very high frequency counts and so could make almost no contribution to the analysis of differences within or between sites.
- There were however clear differences in the extent of moss cover, when judged by eye, between sites and between cells within single quadrats.
- The decision in any one instance, to record a presence for moss was dependent, to an indeterminate degree, on the observer effort. Given the often sparse yet constant distribution of moss, the harder or longer that one searched each cell, the more likely the chance of finding a moss filament. Since it was difficult to apply the same degree of recording effort to each cell consistently over a fieldwork season, it was likely that this method would introduce noise into the recorded abundances.
- The method was highly inefficient in terms of use of time.

These considerations led to a decision to change the method for recording moss presence. In the main study it was recorded as present in those cells where it formed a continuous cover over at least 50% of the cell area as judged by eye. The occurrence of lichens in the sampled areas was extremely low and this group was recorded as present wherever it occurred in a cell regardless of areal cover.

### **3.5.4 Sampling and seasonality**

Field data for the main study were collected between July and September of 1996. Since this period extends over a large proportion of the growing season it is possible that relative species abundances may appear to change over the course of the season as each species attains its maximum biomass at a different time. The possibility of such phenological differences confounding the question of differences in species compositions between revetment age-groups led to a sampling programme design in which data were collected alternately from young and old revetments. It may also be noted that data derived from a record of rooted frequency, rather than estimates of cover or shoot frequency, are less likely to be influenced by seasonal changes in differential plant growth (Thompson *et al.*, 1998).

### **3.5.5 Other factors**

In addition to the plant species present, a number of other features relating to the area enclosed by the quadrat frame were recorded. The presence of bare ground, ant hills, burrows, disturbed ground and signs of repair work to the slope face were noted as potential indicators of the level of soil disturbance. The presence of dominant plants growing over the sampled area but not rooted within it (e.g. *Rubus spp.* and *Clematis vitalba*) were also considered worthy of inclusion where they were judged to form a sufficiently closed canopy as to alter conditions of light and microclimate for the vegetation below.

The angle of slope of the revetment face was recorded by measuring the angle of inclination above the horizontal at the centres of each of the two side battens of the quadrat frame using an Abney level; the mean value for each quadrat is listed in Appendix A. Aspect was recorded as a categorical factor (North or South).

### **3.5.6 Data set compilation**

Species abundance values, represented by counts of local frequencies, were calculated for each quadrat as the total number of cells in the quadrat which were positive for each species. Hence all species abundances are recorded for each quadrat as an integer score in the range 0 - 100. A complete listing of species abundances for each of the 80 quadrats is given in Appendix A.

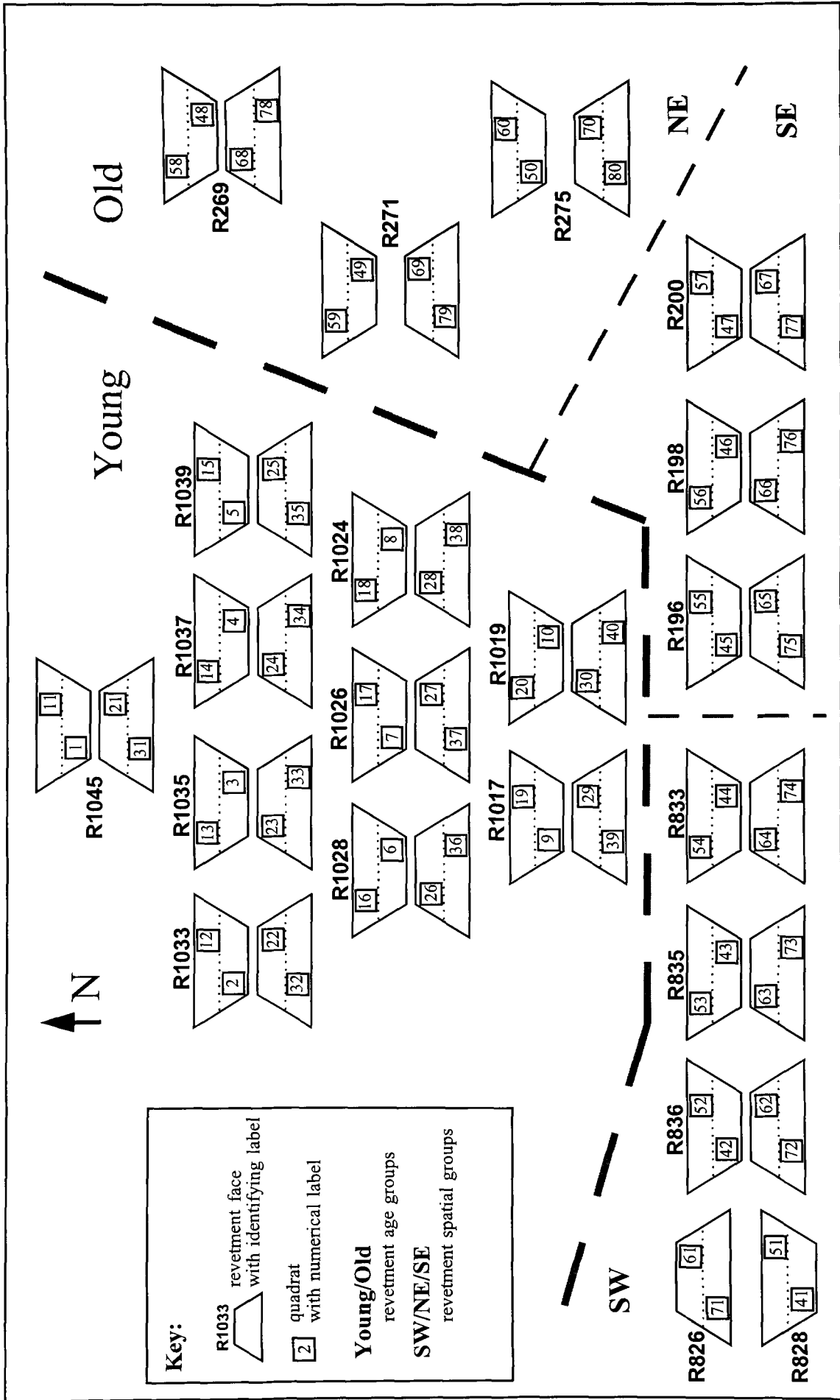


Figure 3.5 Schematic diagram of the study area showing the layout of the quadrats

Each individual quadrat was denoted using a numbering scheme in which the categories of age, aspect and height zone (Section 1.5.1) are easily recognized. Thus, for example, quadrat samples from young revetments are numbered 1-40 and those from old revetments, 41-80. The quadrat numbers relating to zones, aspects and age groups are shown in Table 3.2.

In this study species local frequencies are termed species abundance scores. The term species frequency is used in the conventional sense (Kent and Coker, 1992) to refer to the number of whole quadrats in which a species occurs and therefore indicates a measure of the commonness of a species occurrence on revetments in the study area or within some subdivision of it. Species frequencies, denoted by an integer value in the range 1 - 80, are listed in Appendix A. The factors age, aspect and height associated with each case are treated as categorical variables and, since each may be present at one of two levels, they are allocated scores of 1 or 2 according to the scheme shown in Table 3.2.

The analysis below (Section 4.2.7) makes reference to the spatial arrangement of the revetments. Spatial groups are distinguished according to their locations within different parts of the study area; these groups are denoted by labels referring to the south-west (SW), south-east (SE) and north-east (NE) quadrants of the study area. The layout of the quadrats, revetments and their groupings within the study area are illustrated schematically in Figure 3.5 together with the numbering scheme for each.

Quadrat No.	1-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80
Zone	U	L	U	L	U	L	U	L
score	2	1	2	1	2	1	2	1
Aspect	N		S		N		S	
score	1		2		1		2	
Age	Y				O			
score	1				2			

**Table 3.2 Quadrat reference numbers and factor scores in relation to zone, aspect and age groups.**

Key:

- U - upper
- L - lower
- N - north
- S - south
- Y - young
- O - old



### **3.6 Analytical methods**

Having compiled an appropriate data set, the questions posed in Section 1.7.3 may be reformulated as an investigation of the variation in vegetation between sites representing gradients of age, aspect and height. This requires an analysis of that variation applying particular, numerical techniques. This section describes and discusses the techniques in the context of the particular problems that commonly arise from the analysis of vegetation data.

#### **3.6.1 The nature of the data**

Vegetation sampling typically generates a sites by species matrix in which the sites may be represented as objects, cases or quadrat samples and the species as variables or attributes: each species at each site is characterized by an abundance value or species score (Section 3.5.6). Such data commonly contain high levels of redundancy and noise (Gauch, 1982a).

##### **3.6.1.1 Redundancy**

Many sites represented in a data set typically contain similar groups of species having similar abundance values. The inclusion of additional numbers of these sites would not increase the amount of information in the data in the sense that it would not add to the structure revealed by the existing data. Such sites, which repeat information already present in the data set, are said to contain redundant data (Kent and Coker, 1992). Whilst it is inevitable, where samples are taken from many sites, that duplication will appear, it is desirable to minimise redundancy so as to make the data more amenable to interpretation (Gauch, 1982a). It is one of the aims of multivariate analysis to reduce the amount of data without loss of information from the data set; that is, to reduce the level of redundancy (Kent and Coker, 1992).

##### **3.6.1.2 Noise**

Data is said to be noisy where there is variation between sites which does not serve to distinguish between them in a structured way. Gauch (1982a) describes noise as being

present where “ ... samples from identical sites are not identical in species composition” (p.7). Whilst this statement merely begs the question of what constitutes identical sites it does perhaps suggest variation which cannot be explained by reference to known factors (Kent and Coker, 1992). Noise can arise in numerous ways such as the chance distribution and establishment of individuals, heterogeneity at a scale smaller than the sampled area, or local disturbance due, for example, to animal activities (Section 1.1.5). Gauch (1982a) defines noise as “variation in a species abundances not co-ordinated with variation in other species”. He goes on to explain that co-ordinated variation gives data a structure, whereas noise tends to mask that structure. This is an operational definition and can be meaningful only in respect of the scale and objectives of the particular investigation. Within the context set by this discussion, multivariate analysis aims to eliminate noise and reveal structure in the data.

### **3.6.1.3 Outliers**

Variation in species compositions between samples may also give rise to more extreme differences where, for example, one site is very unlike the others in the sample. These extreme cases or outliers can arise for reasons similar to those for noise. However, results from multivariate methods can be distorted by the presence of outliers (Kent and Coker, 1992) and Gauch (1982a) advises that they be identified and removed from the analysis. The decision as to what may constitute an outlier may be based on field evidence and experience, in which case it can be avoided when samples are recorded, or it may be apparent during the initial, exploratory analysis of the data (Kershaw and Looney, 1985). In this study collection of field data followed a systematic methodology such that subjective decisions about the placement of samples did not occur. The data exploration stage revealed a number of sites which may be considered to be outliers and so which, potentially, may detract from the inherent structure in the data. These are discussed below (Section 4.1); the possible influence of outliers is tested by comparing the outcomes from analyses run with and without the inclusion of atypical cases.

#### 3.6.1.4 Weighting of relative abundances

A potential problem in using species abundance data is apparent when consideration is given to the relative abundances of the species recorded. The investigation of differences between groups based on factors relies on differences in the relative compositions of the communities they are purported to represent: differences, for example, between age groups, representing vegetation development, require an analysis of differences in species abundances found in samples from the communities observed on old and young revegetations. Yet it is apparent from inspection of the whole data set (Appendix A) that some species are typically common or abundant whilst others are typically rare; for example, *Arrenatherum elatius* is often present with abundance scores greater than 80 whilst *Vicia sativa*, though widespread, is rarely recorded with a score greater than 30.

For some of the analytical procedures described below this difference in typical abundance values between species results in a distortion whereby derived differences between groups are more likely to be based on differences in the more abundant species than differences in the rarer species. Given that communities typically consist of species with a range of abundances it is desirable, when describing differences between communities, to ensure that the common and the rare components have equal weighting (van Tongeren, 1987).

It must, however, also be recognised that, as a result of the sampling process, rare species may be included which are not typical of the community as a whole. The rarities appear as transient anomalies and it is customary to remove or downweight such rare occurrences (van Tongeren, 1987). A decision must be made, for each analytical test, as to whether or not abundances should be rescaled, either to give less abundant species a higher weighting, or to remove the influence of rare species from the calculations. In the analyses presented below (Section 4.3) a number of options for differentially weighting the data are employed and the results compared.

#### 3.6.1.5 Multivariate analyses

Species abundance data typically contain high levels of noise and redundancy and it is therefore appropriate to employ multivariate methods of analysis to uncover structure in the data. Nevertheless the nature and history of the site in this study suggest that an

experimental approach may also be usefully applied to the data (Section 1.4). Since the study units, the revetments, were constructed at the same time from the same local surface material and according to the same design, they share a set of initial conditions that may be regarded as identical (Section 1.5.2). Those conditions represent an episode of severe disturbance such as may result from large scale construction or mining processes. The revetments also share a near identical management; essentially, other than the cutting and removal of woody growth, they have been left to develop with little or no direct anthropogenic influence. They may therefore be regarded as replicate experimental units. The second set of revetments, constructed 29 years after the first may, within the limitations discussed above (Section 1.4), be considered to be equivalent to the older group but representing an earlier stage in the same developmental sequence. This gives a basis for the direct comparison of attributes between age groups and for inferences to be drawn relating to changes in those attributes over time. Thus the present study has, fortuitously, been able to combine the strengths of multivariate analysis with experimental control in a field situation.

### **3.6.2 Ordination**

Ordination refers to the placing in sequence, or ordering, of vegetation samples along some gradient of variation, either measured or derived (Whittaker, 1967), with the aim of simplifying and summarizing the data (Austin, 1977; Manly, 1994) and revealing the structure or inherent pattern within it (Ludwig and Reynolds, 1988). A number of numerical ordination procedures have been developed which transform a set of data containing a relatively large number of variables, each being recorded from a number of sites, into a concise format which allows a more accessible survey of relationships between the variables and the sites to be formulated (Kent and Coker, 1992). Ordination is a data reduction exercise which summarizes the data and which also allows it to be presented in the form of a readily understood, graphical plot. In this study the variables are represented by species abundance values, each having a measured abundance score at each site (Section 3.6.1). The ordination combines these species variables into four composite variables such that each site, instead of having abundance scores for each species, is allocated an axis score for each of the four derived variables.

The technique is based on, and derives from, a community model in which species show characteristic distributions in relation to one or more environmental variables or combinations of such variables. Each species may be supposed to display a Gaussian pattern of tolerance to such factors, which is reflected in its abundance scores, such that a difference in a species abundances between two or more sites is a reflection of the level of the factor at those sites (Whittaker, 1967; Ter Braak and Prentice, 1988).

It is recognized that species respond to a large number of both environmental and biotic influences and it is suggested that the actual species abundances at a particular site embody an integrated representation or summation of those influences and so contain the information necessary to interpret conditions at, and between, sites. Ordination methods attempt to extract and present that information.

Ordination, as described above, therefore infers information about theoretical factors from measured species abundance data; as such it is termed indirect ordination (Whittaker, 1967). In this study an indirect ordination technique called Correspondence Analysis (CA) is used (Section 4.2). It is also possible to include measured environmental data explicitly within an ordination procedure (Sections 3.6.3 and 4.4), in which case the method is referred to as direct ordination. Indirect methods generate an ordering based solely on vegetational measures and make no initial assumptions about causative agents; the relation to environmental or other variables is subsequently investigated by correlation techniques in a secondary analysis (Kent and Coker, 1992). In contrast, direct methods make explicit reference in the ordering procedure to known, predetermined variables. Although it may appear from the above that indirect methods are superior in allowing the vegetation, as it were, to speak for itself, both methods report the amount of variation which can be attributed to any given environmental variable. Direct methods may therefore be seen as being appropriate where previous analysis has already narrowed the focus of an investigation to the effects of a given set of variables. In this study indirect ordination is reported as a means of providing an overview of the vegetation structure (Section 4.2); this is then related to the factors of interest and these factors are subsequently included in an analysis using direct ordination techniques (Section 4.4).

The ordination technique proceeds by using species abundance data to calculate scores for each site; these site scores represent the levels of a theoretical variable at the site (Ter Braak, 1987). Sites may then be ordered on a presumed gradient of this derived variable. Within

this gradient species abundances may then be weighted according to the value of the theoretical variable, that is the score of the site in which the species occurs, to produce new species scores; the weight, in combination with the abundance value, may be taken to represent the operational level of the variable at that site. If the species scores are then used to recalculate the site scores, then the ordering of the sites on the theoretical variable may be refined. This successive refinement can be repeated indefinitely though it is usually found that site scores quickly converge (Digby and Kempton, 1987). A numerical illustration is described below (Section 4.2.1). These site scores represent a single derived variable (the first ordination axis) which maximizes the variation between sites as represented by differential species occurrences. The method may be visualized as the projection of a set of points from a multidimensional space onto a single axis where the axis is chosen so as to maximise the spread of the points (Randerson, 1993). Further axes may be derived which are uncorrelated with the first and so represent secondary, and higher, gradients of variation; it is not normally considered useful to extract more than four axes (Kent and Coker, 1992). Since both site scores and species scores are recalculated the ordination may be viewed, either as sites plotted within a species-space, or as species within a sites-space and both sites and species can be represented graphically on the same coordinate system.

The ordering of sites along the derived axis represents the major gradient of variation in species compositions and therefore the most important factor structuring the plant community. The occurrence of a correlation between site scores along a given axis and known variables is thus a strong argument for the potential importance of that known variable and may be the basis for hypothesis formulation and further investigation (Goldsmith, *et al.*, 1986; James and McCulloch, 1990). In this study the major question relates to the differences between groups (Section 1.7.1) which have defined levels of the factors age, aspect and height (Section 1.5.1). It is therefore useful to consider the ordering procedure, and the axes generated, in relation to these known gradients. If the gradients so defined have an influence on the community structure then cases will be seen to segregate along the axis according to their value for the particular factor.

A number of features associated with CA and other ordination methods have been criticised. In particular, although the method of calculation of the higher axes ensures that they are uncorrelated with the first axis they are not necessarily independent of it. This may be apparent as an arched appearance in a plot of the first and second axes (Hill, 1979a). In cases where the effect is extreme the distortion compresses the ends of the ordination so that

the spacing between sites is non-linear; where the arch is more exaggerated the ends may be involuted to form an "horseshoe" shape to the extent that the ordering of sites within each of the end portions may be reversed (Digby and Kempton, 1987). Corrections to these failings were applied by Hill (1979a) in an ordination algorithm termed Detrended Correspondence Analysis (DCA). This program includes, within each iteration, a routine by which the axis is divided into a number of segments. Within each segment the axis scores along the lower axis are rescaled such that the cases are evenly spaced and scores along the higher axis are recalculated to have a mean value of zero so effectively removing the arch effect.

More recently the CA algorithm has been shown to contain a flaw which makes the results sensitive to the order in which data is read by the program (Oksanen and Minchen, 1997). The possible influence of this problem on the analyses presented here (Sections 4.2, 4.3 and 4.4) is discussed below (Section 6.1.7).

DCA has become the most widely used of ordination techniques in ecological studies (Kent and Coker, 1992; Manly, 1994) and, despite developments in the methods of analysis available, has remained the method of choice for studies in a diverse range of applications (for example; Greenacre and Vrba, 1984; Charles, 1985; Glaser, 1992; Williams *et al.*, 1996; Heikkinen *et al.*, 1998). The method is used here (Section 4.2) to provide an overall description of the vegetation on the revetments in the study area, to expose the patterns of variation in the data and to relate those patterns to age and topographic factors (Section 1.7.1).

The software package MVSP (Kovach, 1995) was used to perform the analysis. In this study the initial analysis (Section 4.2.1) utilized the program's default options, namely:

- data were untransformed
- the reciprocal averaging algorithm was used without detrending
- rare species were not downweighted
- the number of segments used in the detrending procedure was 26
- the number of rescaling cycles was limited to four.

Additional analyses were performed using the detrending and downweighting options and also for the analyses of subsets of the data. These are described in Sections 4.2.3 - 4.2.7.

The DCA program results in the generation of an ordination space defined by four axes within which each site and species may be located; a site's position in the space is defined by the scores of the species which it contains. The relative importance of each axis in accounting for variation in the original data is represented by a number termed the eigenvalue. The eigenvalue is a numerical representation of the length of the gradient or axis of variation in the data and hence of the importance of that particular axis in explaining the main trends in the data. The concept may be visualized in that, if the data set is represented by a cloud of points in  $n$  dimensions (conventionally we may limit  $n$  to 2 to allow easy representation on a flat page) and an ellipse is drawn so as to include all the data points, then the eigenvalue represents the length of the major axis, that is the long radius, of the ellipse (Fielding, 1993). A second axis defines a lesser gradient of variation normal to the major axis and progressively shorter axes, or radii, may be similarly defined for each higher dimension occupied by the ellipsoid. The CA algorithm contains routines for standardizing and rescaling the data. Standardization means that the axes remain comparable with one another so that their relative explanatory power can be seen from a comparison of their eigenvalues. Rescaling ensures that the data set, the ellipse defining the cloud of points, remains centred within the coordinate system at the point (0, 0).

The scale by which distance along the gradient is measured derives from the species scores. A species will have an optimum level of the derived factor represented by the axis and its abundance will fall on either side of this optimum. Different species, having different optima, will be seen to appear, rise to their optima, and disappear progressively along the axis (Hill, 1979a). This spread of species abundances over the gradient may be measured in units of standard deviations (sd) of the species scores and the scaling is calculated such that, on average, a species' rise and fall will occur over 4 sd units. In the particular CA implementation used here (Kovach, 1995) scores are calculated in sd units multiplied by 100 (Appendix C; Figures 4.2- 4.14). It may be noted that the relative importance of each axis is not translated into the axis scores so that interpretation must take account of eigenvalues when reading axis scores.

Diagrams (e.g. Figure 4.2) showing the sites plotted on pairs of axes are used to interpret the degree of similarity or resemblance of groups of sites. Analyses may be repeated with reduced data sets to determine the impact of particular groups of sites or individual sites or species.



### 3.6.3 Constrained ordination (Canonical Correspondence Analysis)

Canonical Correspondence Analysis (CCA) is an ordination technique which combines correspondence analysis directly with environmental data in a multiple regression. Consequently it derives an ordination space in which the site scores are constrained to be functions of the environmental variables (Ter Braak, 1986; Palmer, 1993). This technique is an example of direct gradient analysis wherein the factors thought to be important in determining community structure are measured and related directly to the species data (Section 2.3.3). It is the most widely used analytical technique in the study of species-environment relations (Palmer 1993; Waite, 2000) and has been applied in the investigation of a range of ecological studies.

Zhang and Oxley (1994) compared the results from indirect ordination (DCA) with detrended CCA and Fuzzy Sets Ordination in an analysis of UK montane grasslands. They report that all three methods give consistent results but note the ease of interpretation offered by the combined plots of species, samples and environmental factors in CCA. They suggest that CCA may perform better than other methods when large differences in vegetation and environmental factors are present.

Aguado-Santacruz and Garcia-Moya (1998) used CCA to evaluate the role of climatic factors in generating variation in semi-arid grassland vegetation over time. Using partial CCA they were able to subtract the effects due to differences in soil and management factors to reveal the extent of the influence of temperature and rainfall gradients.

McIntyre and Lavorel (1994) employed CCA to investigate the role of disturbance in mediating patterns of invasability of non-native species in temperate grasslands in Australia. By using axes representing levels of disturbance they were able to group species by their occurrence in sites having characteristic disturbance regimes and showed that alien species had particular preferences. Management aimed at the conservation of native grasslands could therefore focus efforts towards preventing the occurrence of those habitats.

Dinsdale *et al.* (1997) employed CCA to investigate the community and habitat relations of an endangered heathland plant with the aim of defining conditions for its conservation. They showed that the species occurrence in the UK was dependent on the limited availability of suitable sites rather than on community or environmental tolerances.

In this study CCA is used to address three problems. First it provides a summarizing overview of the data including the relation between the factors age and aspect and the species data. In this it provides an alternative to the DCA method of highlighting the role of these factors in structuring the vegetation in the study area. This is useful as a check on other methods of analysis. Secondly CCA allows a deeper analysis of the role of the factors of interest. Whilst retaining the full data set the effects of chosen variables may be selectively investigated by removing the influence of other dominant, possibly confounding, factors. Using partial CCA the effect of selected factors may be removed from the analysis by entering them as co-variables. Thirdly the degree to which individual species show a preference for a particular factor level can be emphasised by analysing species scores generated when all variables except the one of interest are entered as covariables. This approach allows for an analysis of species ecological types in relation to successional age and acts as a check on the other methods (Section 4.3) used to investigate species differences between age groups.

The CCA method is implemented using the software package CANOCO (Ter Braak, 1987-92). The program generates an output including a number of tables containing information which may be used to interpret the analysis. The program typically generates four ordination axes; the eigenvalue associated with each is a measure of the axis's importance in explaining the variation in the species data. The total variation in the data is termed the "total inertia" and each eigenvalue is a measure of the amount of variance associated with each axis. Because of noise much of the variance in the data is often not accounted for by the derived axes. Nevertheless even axes with low eigenvalues can be useful as indicators of the major trends in a data set. Ter Braak (1987-1992) suggests that values greater than 0.02 may be informative.

The species-environment correlation (e.g. Table 4.19) indicates, for each axis, the degree of correlation between the species and the environmental variables. It is a measure of the correlation between two sets of sample scores. One set of scores is derived from the species abundance data as in CA; the second is calculated as linear combinations of the environmental variables. Within the limits set by the amount of variance explained by the axis (that is its eigenvalue), this correlation indicates the extent to which species data reflect environmental data and so indicates the importance of the environmental variables as predictors of species distribution. This figure can, however, be misleading; where an axis's

eigenvalue is low, even a high species-environment correlation may not signify a strong explanatory power of the axis (Ter Braak, 1987).

The information generated by CCA is summarized in a diagram in which sites and species are jointly plotted within a two-dimensional ordination space. As in CA the axes are defined by the ordering of the site scores, these being derived from species scores in such a way as to maximize the dispersion of the species scores. Additionally, a tri-plot illustrates the above features and also includes arrows denoting environmental axes. This allows the relations of the species and sites to the environmental variables to be analysed. The length of the arrow denotes the relative importance of the represented variable, and its direction describes the environmental characteristics of the sites and species associated with it. Furthermore, the angle between any two arrows gives an indication of the degree of correlation between the represented environmental variables (Palmer, 1993). The method is also used to distinguish those species having a preference for one or other age group. Where the analysis is constrained by the single factor age, the resulting species scores represent a measure of species age preferences and are therefore useful as an aid to investigating the extent of species replacements over time (Sections 4.5.4.3 and 5.1.2.3)

The primary benefit of CCA ordination is that it facilitates the exposure of those environmental variables which most strongly influence the species abundances. Clearly it can only distinguish amongst those variables for which data is available and to this extent an interpretation may fail to highlight the most significant factors if they have not been measured. In this study the technique is used to verify the results of DCA, as a general description of the species-environment relations and to determine the extent to which successional time has influenced the pattern of vegetation.

#### **3.6.4 Classification**

Classification refers to the process of creating groups of similar objects from amongst a larger, diverse collection of objects. It aims to collect together into discrete groups those objects which are similar to each other such that objects in a group have a common identity which serves to distinguish them from objects in other groups (Gordon, 1981). In order to achieve this it is necessary that features or attributes associated with the objects are defined and recorded. In plant taxonomy individuals may be grouped into species based on

morphological or genetic features; in ecology vegetation samples may be grouped into communities based on the measured abundances of each species within each sample.

The formation of groups may serve a number of purposes. Classification can be used to simplify a complex data set. Where the number of objects is so large as to be unmanageable, they may be reduced to a smaller number of classes of objects to which subsequent analyses may be applied more efficiently. The process of forming groups can also serve to reduce noise and redundancy in a data set (Gauch, 1982b). Where there are many objects which contribute little extra information or where they contain extraneous information these problems can be eliminated by agglomerating objects into groups defined by the more important attributes. The process can also be useful in highlighting cases which are very different from the majority. These outliers may then be the subject of more intense scrutiny (Section 3.6.1).

Groups formed from similar vegetation samples may be taken to represent community types (van Tongeren, 1987) so that the classification process is equivalent to that of defining plant communities from a collection of vegetation samples. Such a set of groups, forming a reduced number of derived objects, serves to simplify and summarize the data.

Classification is also a process of generating order in a set of samples and, as such, it aims to uncover the “true” or natural groupings within the data (Kent and Coker, 1992). If there is little prior knowledge concerning structure within the data then classification can be a useful technique for generating hypotheses (Howard, 1991). Where, as here, definite classes are known to exist amongst the objects then classification can provide an objective method of testing for the degree of influence exerted by these groupings.

Different approaches to the technique of classification are possible. All the objects may, initially, be considered as a single group which is then divided into subgroups; alternatively the procedure may start by treating each object singly and form groups by a process of agglomeration. The classification may be accomplished as a single operation or it may be applied sequentially in which case it generates groups in a tree-like, hierarchical series. Furthermore the criteria for the formation of groups may be based on, either a single attribute or on several attributes; the former is termed a monothetic, and the latter a polythetic method. The features associated with each of these possible methodologies are discussed in Gordon (1981), Greig-Smith (1983), Digby and Kempton (1987) and Howard (1991). Any particular method requires; a measure of similarity between objects, a

mechanism for forming groups of similar objects and a means of ordering the final groups into a sequence.

It is desirable for a classification method to achieve a stable and objective output (Gordon, 1981) in which small changes to the data, such as may result from recording errors or the addition of new cases, do not substantially alter the structure revealed in the groupings. A classification should also display objectivity in the sense that the same results should be revealed by different clustering methods. Gauch and Whittaker (1981) compared a number of hierarchical classification techniques using both simulated and field data sets. They found that Two Way Indicator Species Analysis (TWINSPAN; Hill, 1979b) was effective, objective and robust though they noted a tendency for early divisions to be dominated by extreme cases when the data set was very diverse. The method, used here (Section 4.4), includes a comparison of results from analyses which either include or omit such outliers.

Where classification is applied to samples which have a truly continuous distribution, as it is argued is the case for many vegetation types, then the method, termed dissection, will impose a structure which is not inherent (Howard, 1991). The extent to which this limitation applies must be a matter of judgement for each study though the distinction between continuous and discontinuous variation in vegetation is considered by some to be artificial (Digby and Kempton, 1987). Having detected meaningful structure by classification, the groups may be used, in a predictive process, to uncover correlations between vegetation and external variables (van Tongeren, 1987).

In this study classification is used to provide a simplified, ordered description of the data for the purpose of checking the findings of the ordination analyses. In addition, the investigation of the relations between the plant communities and the binary factors age, aspect and height implies the existence of distinct groups within the vegetation. It is proposed that, if these factors have a determining influence on the pattern of vegetation, then there will be a correspondence between natural groupings and those defined by factor levels (Section 1.5.1).

### 3.6.4.1 Two Way Indicator Species Analysis

The classification method employed in this study is that of Two Way Indicator Species Analysis or TWINSpan (Hill, 1979b; van Tongeren, 1987). This technique is widely used in ecology (Kent and Coker, 1992; Waite, 2000) and includes features which make it especially useful for the analysis of a species by sites data set (Kershaw and Looney, 1985). It is used as a means of providing a general survey, of simplifying the data set, as a means of data reduction, as a check on other analytical procedures and as a way of highlighting the role of particular species as indicators of community types. If vegetation groups do show some relation to age groups, the TWINSpan program explicitly indicates those species which show the strongest preferences for one side of a division. This allows a meaningful interpretation of groups based on the ecology of these indicator species. In this study it is employed to;

- summarize the data in a readily interpretable form
- relate groups based on known factors of age, aspect and height to those derived from vegetational composition
- highlight those species which best distinguish between groups.

Carter *et al.* (1987) used TWINSpan to generate a classification of vegetation types as a systematic and objective means of exploring the possible reasons for the existence of a rare habitat type in Shetland. Vegetation found on sites classed as open debris suggested seasonal drought was a major factor in maintaining this habitat. Curry and Slater (1986) classified 370 riverine sites by their vascular plant species in an attempt to provide an overview of the biological resources of Welsh rivers. They found that site groups generated by TWINSpan reflected differences in the factors of shade, altitude and geology. Luff *et al.* (1992) employed TWINSpan in conjunction with DCA and Discriminant Function Analysis to construct a grassland habitat classification on the basis of *Carabidae* abundances. They were able to relate the groups to the different management regimes employed and to use the classification to predict the group membership of new sites by reference to the ground beetle species found there. Collinson *et al.* (1995) compared invertebrate assemblages in ponds having different levels of permanence. The major division of their classification coincided with the level of permanence in pond types and they were able to use TWINSpan to identify species whose presence was indicative of a temporary habitat. Learner and Chawner (1998) used abundances of invertebrate species to

construct a method for monitoring the condition of sewage beds. They produced a classification of 67 sewage filter beds based on populations of invertebrates and related this to the physical and chemical conditions of the beds. They found that species assemblages reflected the level of organic material within the beds and suggested that particular species may be used to indicate the condition of the beds.

#### **3.6.4.2 The TWINSpan program**

The TWINSpan algorithm (Hill, 1979b) works by repeated divisions of the sites on the basis of their species compositions. Initially, an axis is generated using the CA method and this axis is divided into two equal halves. Species which have a strong preference for one or other side of the division are identified and used to refine the point of division. The resulting two groups are repeatedly divided by the same method to generate four, then eight and 16 groups. There is no formal stopping point; rather it is usual to set a limit to the minimum size of the groups to be divided. This determines the point at which a group may no longer be subdivided and when all groups contain fewer cases than this minimum size the procedure terminates. Cases within groups are ordered so that adjacent samples in the output are most alike even when they may be in different groups (van Tongeren, 1987). The program is especially useful in reporting the species with strong preferences for one side of a dichotomy. Once the site classification is complete the species are classified on the basis of their group membership. Again there is an ordering within the classification which groups similar species together.

The method is divisive in that initially all sites form a single group which is repeatedly divided. A hierarchical series of divisions results (e.g. Figure 4.15) the levels of which denote an order of importance to the groups. Lower order divisions signify groups which are less strongly differentiated. The method uses a default number of up to five differential species in defining the dichotomies. Thus, in this polythetic method, divisions are less likely to be influenced by anomalous, single occurrences than would be the case using a monothetic method.

A particular feature of TWINSpan is the use of pseudospecies to define quantitative levels of species abundance. In essence the classification method works on presence-absence data but, by dividing quantitative data into a number of cut levels, species abundance groups are

defined and each group is treated as a separate species termed a pseudospecies. The cut levels may be chosen by the user to give abundance groups appropriate to the nature of the data. Thus, in the example given by Hill (1979b, p. 7), for abundances measured on a percentage scale, cut levels may be defined at 0, 5, 26, 51 and 76 giving abundance groups corresponding to the Braun-Blanquet scale. To illustrate, if a species (e.g. SPA) is present in a sample at a level of 18% it would be represented as two pseudospecies *viz.* SPA1 (abundance group 0-5) and SPA2 (abundance group 6-26). The same species present in a second sample at an abundance level of 36% would generate the additional pseudospecies SPA3 (abundance group 26-51). The degree of similarity between the two samples would then be calculated based on the common presence of two pseudospecies (SPA1 and SPA2) and the differential presence of one pseudospecies (SPA3). Though the abundance level of the species in sample 2 is twice that in sample 1 the two samples would be seen to have more features of similarity than of difference.

Further details of the TWINSPAN classification method and the program options utilized are given in Section 4.3.

### **3.6.5 Discriminant function analysis**

An investigation of vegetation development over time may be approached by an analysis of species differences between age groups (Section 1.6.3). For example Grime's model of succession (Section 1.6.1.1) predicts a change in species ecological types from a ruderal (R) strategy to, either a competitive (C), or a stress tolerator (S) strategy.

The classification technique outlined above generates groups of sites from species data and so allows for an investigation of the role of the factors age, aspect and height in structuring the vegetation by comparing the degree of correlation between groups based on species data and those defined by the factors. It also indicates those species which have a particular preference for each division. However these indicator species reflect age preferences only where this factor corresponds to the groups generated by divisions based on species abundances. If other factors predominate then species age preferences may remain hidden. In order to answer the specific question of what changes in species occur over time it is necessary to analyse species differences between age groups and to isolate those species which show the greatest age preferences. Discriminant Function Analysis (DFA) is the



technique which measures each of the variables power to distinguish between pre-defined categories. This information will enable an analysis of species types in relation to successional age.

The technique may be visualized within an ordination space in which each axis represents a species and each quadrat is represented by a point located within that space by its position on each axis by the species abundance score recorded in that quadrat (Afifi and Clark, 1990). DFA constructs a new variable which, in this study, may be taken to represent age. Each quadrat has a known age group membership so it is possible to arrange for this new axis to maximally discriminate between samples from different age groups. The new axis is constructed as a weighted combination of the existing axes (i.e. species scores) in such a way as to maximize the difference between groups. If, as here, there are only two groups then there will be a single discriminant function of the form,

$$D = W_1 \cdot Z_1 + W_2 \cdot Z_2 + W_3 \cdot Z_3 + \dots + W_i \cdot Z_i \quad \text{Equation 3.1}$$

where,  $Z_1, Z_2$  are the existing species scores for species 1 and 2, and  $W_1, W_2$  are the weights applied to each species score in order to calculate the discriminant score,  $D$ . For a given sample,  $D$  represents its position along the discriminant axis, its level of the factor "age". If the function is constructed so as to maximize the difference between groups then the species with the highest absolute weights are those which best discriminate between groups. It is therefore the weights given to the species scores which are of interest in answering questions about species age preferences.

DFA is also applied, in this study, to the analysis of DCA axis scores (Section 4.2). Where axis scores represent new, derived variables the degree to which each is able to account for known differences in age, aspect and height is assessed as a means of interpreting the DCA output.

### 3.6.6 Diversity

A comparison of vegetation samples may be approached either at the species, or the community, level. In this study measures of diversity (Section 1.6.2.2) are used to compare communities from old and young revegetations. It is common practice to characterize a plant community by defining a quantitative measure of its level of biological variety which

represents both the number and relative abundance of its species (Whittaker, 1965; Greig-Smith, 1983; May, 1981; Gray, 1987). Diversity is predicted to increase over time by Odum's (1969) model of succession (Section 1.6.1.3) and diversity measures are used here to test that prediction (Section 5.3).

There are many measures of diversity and a great deal of debate as to their relative merits (see reviews in Peet, 1974; Pielou, 1975; Magurran, 1988; Tokeshi, 1993). It may be said that the debate results from attempts to encapsulate a complex concept in a single numerical index and, for that reason, is unlikely to be resolved. All diversity measures include components relating to both species richness and relative abundance or evenness with different indices giving different weights to these two elements (Magurran, 1988). This work does not attempt to resolve the issue but rather employs a number of commonly used methods of representing diversity, species richness and evenness.

An alternative method of characterizing the species composition of a community is the graphical representation termed, variously, a rank abundance diagram (Magurran, 1988) or a dominance-diversity curve (Whittaker, 1965) in which each species abundance value is represented, in turn, by its value on a vertical axis and, in decreasing rank order, along a horizontal axis (e.g. Figure 5.9). The method of summarizing community structure as a display of the ranked abundance distributions (RAD) of the species is used here (Section 5.3.5) as it allows for a readily accessible comparison between communities and does not suffer the loss of information which results from the calculation of a single, numerical diversity value. Furthermore, the RAD curve may be analysed by calculating the degree to which it conforms to a community model based on a random distribution of numbers of species and individuals. An interpretation of deviations from the random model can give insights into the processes generating community structure.

### **3.6.7 Interspecific association**

This section outlines the method used to calculate a measure of the level of association between species within a community. This index is used (Section 5.4) to distinguish between the successional models of Peet (Section 1.6.2.4).

Where a number of vegetation samples are recorded, and it is required to know whether or not two species, X and Y, show some association, it is usual (e.g. Kershaw and Looney, 1985) to define a 2 × 2 contingency table of the form;

		Species Y		totals
		Present	Absent	
Species X	Present	a	b	a+b
	Absent	c	d	c+d
	totals	a+c	b+d	n

where,

- a represents the number of samples in which both species are present,
- b represents the number of samples in which species X is present and species Y is absent,
- c represents the number of samples in which species Y is present and species X is absent,
- d represents the number of samples in which both species are absent.

It can be seen that the total number of samples, n, is equal to a + b + c + d and that the frequency of species X is given by (a+b)/n, and that of species Y by (a+c)/n.

An index of association ( $\chi^2$ ) may be calculated as;

$$\chi^2 = \frac{(ad - bc)^2 \times n}{(a + b) \times (a + c) \times (b + d) \times (c + d)} \quad \text{Equation 3.2}$$

The index may be calculated for all possible species pairs in a set of samples.

Hurlbert (1969) criticized the use of this index for the reason that its value is dependent on the frequencies of the component species; he also described an alternative index (Coles C7) which he showed is subject to the same fault and proposed a third index (C8) which he shows to be independent of species frequencies.

Hurlbert's C8 index is defined as;

$$C8 = \frac{ad - bc}{|ad - bc|} \times \sqrt{\frac{Obs\chi^2 - Min\chi^2}{Max\chi^2 - Min\chi^2}} \quad \text{Equation 3.3}$$

- where  $Min\chi^2$  is the minimum possible value for  $\chi^2$
- $Max\chi^2$  is the maximum possible value for  $\chi^2$
- $Obs\chi^2$  is the actual value calculated for  $\chi^2$  by Equation 3.2

In this index the term to the left of the multiplication sign serves to give the index the correct sign (+ or -), whilst the part to the right defines the range of possible values of  $\chi^2$  and generates the relative level of the observed  $\chi^2$  within this range between the maximum and minimum values. Where the observed level is equal to the maximum the index has a value of unity and when it is equal to the minimum value the index is equal to zero.

Greig-Smith (1983) has discussed the difficulties of interpreting measures of association derived from quadrats of a single size. Since the values represented by a, b, c, and d are frequencies their magnitude is dependent on quadrat size. As a check on the method used here therefore, measures of association are calculated for quadrats of three different sizes (Section 5.4). The large (L) size is represented by the  $2\text{m} \times 2\text{m}$  used throughout this study (Section 3.5.2) and which contains 100 cells. A medium size quadrat (M) is that defined by the  $1\text{m} \times 1\text{m}$  formed by the 25 cells at the top left of the large quadrat and a small quadrat (S) by the 9 cells at the bottom right of the medium quadrat. Association measures are thus made at the three areal scales of  $4\text{m}^2$ ,  $1\text{m}^2$  and  $0.36\text{m}^2$ .

### **3.6.8 Predictability**

Section 1.6.2.6 describes how the predictability of species composition between replicate samples is a characteristic of different models of succession, with increasing predictability over time being the result of biotic interactions described by the competitive sorting model whilst the gradient in time model suggests that, with environmental factors determining composition, predictability would remain unchanged over time. Predictability is measured in this study in two ways; firstly by the degree of rank abundance consistency of species between replicate samples and secondly by the degree of stratification of species along an environmental gradient.

#### **3.6.8.1 Spatial rank consistency**

The index of spatial rank consistency, Cr (Watkins and Wilson, 1994), is a measure of the degree to which species retain their rank abundance order between samples (Section 1.6.2.3). It is calculated according to the formula,

$$C_r = 2 \times \frac{V_{species}}{V_{species} + V_{interaction}} - 1 \quad \text{Equation 3.4}$$

where V represents the variance components of ranks due to species and due to the interaction between species and quadrats. The formula generates a value between +1, when species retain the same rank orders throughout, and -1 when rank orders are as different as they could be. An index value of zero indicates the null model occurrence of randomly distributed rank orders.

Although spatial rank consistency is a new analytical tool a similar approach was used by Mitchley and Grubb (1986) to argue that chalk grasslands have highly stable compositions so making them well suited to studies of relative abundance distributions. Watkins and Wilson (1994) devised the Cr index as a means of comparing community structures and suggest its usefulness as a method of distinguishing between communities assembled by either ecological or evolutionary processes (Section 1.6.2.3).

In order to make comparisons between rankings from different age groups the species abundance data from 80 quadrats are first grouped by aspect (N and S) and age (Y and O) and abundances within each quadrat are replaced with species rank orders. Thus each species has 20 replicate rank orders within each of the four data sets representing the groups designated as YN, YS, ON and OS. Equation 3.4 generates a single value for each group representing the degree to which species over all 20 replicates retain their ranking. The Cr index may be compared between age groups to indicate a change in rank consistency over time. The resulting values of the index are reported in Section 5.5.1.

### 3.6.8.2 Stratification

The term stratification is used in this context to describe the degree to which species are segregated along an environmental gradient. This is predicted to change with time by the competitive sorting model (Section 1.6.1.4) as competition results in narrower, realized niches for species, whereas, under the operation of the gradient in time model, the degree of stratification will remain unchanged under constant environmental conditions.

In this study the measure of species preference for north-facing or for south-facing slopes is calculated in a manner similar to that used for species age preferences (Section 5.1.2). Only those species which have frequencies of at least one in each of the four groups are included in the analysis. The 49 species which meet this criterion are listed in Appendix F. Species environmental preference scores ( $E_p$ ), which represent a species preference for either N-facing or S-facing slopes, are calculated, for each age group, as the sum of the abundances in quadrats on north slopes ( $A_N$ ) minus the summed abundances from south-facing quadrats ( $A_S$ ) divided by the total summed abundances from all the quadrats ( $A_T$ ) within the age group; thus for species on young slopes.

$$E_{pY} = (A_{YN} - A_{YS})/A_{YT} \quad \text{Equation 3.5}$$

The preference score represents the proportional preference and is independent of the actual total abundance value. Where a species abundances on south-facing slopes gives a total greater than that on north-facing slopes the preference score is negative. The change in  $E_p$  values over time is tested for significance (Section 5.5.2) using a Wilcoxon signed ranks test (Sokal and Rohlf, 1995).

## **CHAPTER FOUR: RESULTS I - ORDINATIONS AND CLASSIFICATION**

Fieldwork produced a data set containing 80 quadrats or cases and abundance scores for 113 species or attributes. Each quadrat was also characterized by three binary factors - age, aspect and height - arising from the underlying experimental design (Section 3.5.6). In addition to the species abundance values a number of other attributes were recorded for each quadrat: these included measures of the slope angle and the areal extent within the quadrat of bare ground, ant hills and features related to disturbance of the soil surface. The full data set is listed in Appendix A. The aim of the analyses described here was to summarize the data, to reveal structure within the data and to relate it to the factors age, aspect and height.

The data set may be treated either as a whole or divided into subsidiary sets based on the factor levels. The factor aspect was likely to be a major influence on the pattern of vegetation and, since the main question relates to differences in age, it was considered useful to divide the data set into two subsets based on aspect. In this way the influence of aspect in structuring the data is controlled and the two separate data sets may each be examined with regard to changes over time. Changes over time can then be compared between slopes having opposing aspects.

### **4.1 The nature of the data**

It has been suggested (Section 3.6.1) that extreme cases or outliers within a data set can cause problems for some analytical methods and that it is therefore beneficial to identify and remove such outliers from the data before proceeding with an analysis. A preliminary examination of the data, with a view to identifying anomalous cases, was therefore undertaken.

#### **4.1.1 Anomalous cases resulting from known factors**

Anomalous cases were considered likely to arise as a result of ;

- invasion of scrub
- disturbance resulting from repair work to the revetment slopes or animal activities.

Quadrat no.	BD	DA	DR	N	RF
29		15			
32					38
33					72
39		12			
40		21			
43			15		
53	11				
58					39
62		18			
63	44				42
64				4	
70			12		
72		10			27
74			27	1	
76	7				
77				4	

**Table 4.1 Anomalous features recorded during the vegetation survey**

Key to abbreviations:

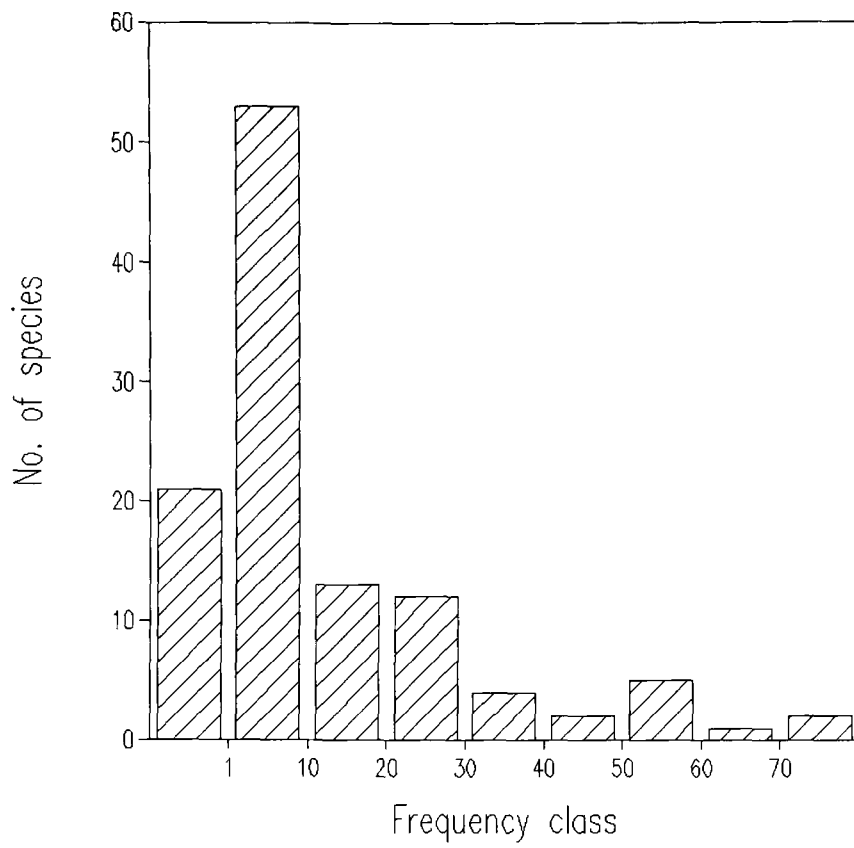
- BD bare or disturbed ground
- DA ant hills
- DR ground disturbed by rabbit burrows
- N repair netting visible
- RF *Rubus fruticosus*



This study investigates changes to vegetation over several decades under a constant management of regular cutting which maintained a low stature grassland community. The cutting and removal of vegetation ceased in 1993, since when there has been the opportunity for invasion of woody species. Where the herb community has been overgrown by scrub this may represent a very different community, a successional stage which is recent and no longer represents the community under study. Such cases can add little to an understanding of the differences between 56 year old and 27 year old slopes since the scrub must have arisen in the three years previous to the study. Several quadrats were located in areas containing high levels of bramble *Rubus fruticosus*, (RF). Cases which have high scores for these factors are listed in Table 4.1.

Netting (N) was found in three quadrats. The presence, above ground, of plastic netting suggests that repair work has been carried out which is likely to have involved a substantial part of the revetment surface even though the netting itself is apparent only within a small area. Bare or disturbed ground (BD) signifies disturbance of the soil surface with no obvious, identifiable cause.

Ground disturbed by ants (DA) was noted in many parts of the site. The network of chambers constructed by ant colonies protrude above ground as mounds of soil 10-40 cm in diameter. This feature has been described by Wells *et al.* (1976) and is common in areas where grazing by large animals is absent or of low intensity. The mounds consist of fine-grained, friable soil and are easily disturbed by trampling. It was considered that this feature may play a role in soil development and was judged worthy of inclusion in the investigation. Those quadrats with scores of 10 or greater are shown in Table 4.1. The presence of ant hills was also included as a factor in the canonical analyses (Section 4.4.3). The abundance scores of ant hills were not significantly different between young and old age groups, as judged by a Mann-Whitney test, neither when the data were analysed as a whole ( $p = 0.82$ ) nor when north- and south-facing data sets were separated ( $p = 0.13, 0.49$  respectively). However there was a significant difference in their abundances between north and south faces ( $p < 0.001$ ) with greater numbers being found on the south-facing slopes; this was very likely to be a result of the warmer and drier conditions found there (Wells *et al.*, 1976).



**Figure 4.1** Frequencies of species occurrences  
(lowest frequency class represents single occurrences)

#### 4.1.2 Anomalous cases identified from ordination analyses.

From an inspection of plots produced by ordination procedures (Section 4.2; Figures 4.2 and 4.4), five quadrats are seen to have extreme positions and may be considered to be outliers; these are quadrats 17, 31, 33, 42 and 78.

Quadrat 17 is remarkable in having a high level (69) of *Equisetum arvense*, a species which occurs in only 5 other quadrats and in which it achieves a maximum abundance of 7.

Quadrat 31 contains relatively high levels of *Epilobium hirsutum* (20), *Carex hirta* (80) and *Hedera helix* (49); this last species occurs in only 2 quadrats. Similarly quadrat 33 contains a high abundance (72) of *Rubus fruticosus*. Quadrat 42 also has a high abundance score for *Hedera helix* (76) and a similarly high score for *Viola riviniana* (65), a species which occurs only rarely, being recorded in eight quadrats, and with generally much lower scores: quadrat 72 is the only exception to this pattern having an abundance score of 45 for this species.

Quadrat 78 contains a number of species which are either rare elsewhere or are present in this sample with unusually high abundances. *Hypericum maculatum*, *Primula veris* and *Bellis perennis* all achieve their maximum abundance scores in this quadrat whilst the lichen, *Peltigera canina* occurs only in this quadrat where it has an abundance score of 12.

Four quadrats were considered as candidates for removal from the analysis because of the potential influence of anomalies. Three contained netting which was taken as evidence of repair work and therefore as representing a significant disturbance to the soil and vegetation: these were quadrats 64, 74 and 77. One (quadrat 33) contained a high level of *Rubus fruticosus* and was considered to be no longer representative of the herb community which has been maintained on the revetments until 1993. Repeat analyses were performed using data sets with, and without, the extreme cases.

#### 4.1.3 Rare species

It is a characteristic of vegetation communities, and of samples taken from them, that they contain many rare and a few common species (e.g. Whittaker, 1965). Figure 4.1 shows the distribution of species frequencies within the data set. It can be seen that there is a high proportion of species with frequencies of less than 10; in this histogram those species occurring in only a single quadrat are displayed as a separate frequency class. A rare species

may occur, either because it is an anomaly and not characteristic of the plant community under study, or it may be a representative species which is typically found at low frequency (Gauch, 1982a). In the former case the recorded presence can contribute little to an analysis of the pattern of species composition for that community. In the second case its rarity means that its occurrence within a particular sample is somewhat arbitrary. A finite sample will record rare occurrences with a reliability which depends, firstly on the size of the sampled area in relation to that of the community and, secondly the degree of rarity of the species. Except where the sampled area is a large fraction of the study area and the species is not at extreme rarity, a sample is unlikely to include the rarity except by chance. As was demonstrated above (Section 3.3) new species continue to be encountered in plots of up to 64m<sup>2</sup>. The recorded presence of rare species in a sample therefore adds little to the pattern of species composition. It is apparent that in both these instances rare species are a source of noise in the data and for this reason it is common practice to reduce their effects or eliminate them from the analysis (Greig-Smith, 1983; Kershaw and Looney, 1985). The presence of rare species within a community sample and the possible approaches to their interpretation is discussed below (Sections 5.3.5 and 6.3).

An option within the DCA program used to analyse the data (Section 4.2) is the downweighting of rare species. This subroutine is described by Hill (1979a). It operates on those species whose frequencies are less than one fifth that of the most common species. Frequency, (“f”) refers to the overall frequency of a species in the data set and is defined as the number of quadrats in which the species is present. Since there are 80 quadrats in this study frequency values lie in the range 0-80. The abundance, (“a”), denotes the species count in any single quadrat; this is the same as the local frequency and lies in the range 0-100. For the purpose of downweighting, the maximum frequency, AMAX, is defined as the frequency of the most common species which in this study is *Arrhenatherum elatius*, this being present in 79 of the quadrats. Downweighting is applied to those species which have frequencies of one fifth, or less, of AMAX; that is  $79/5 = 15.8$

Where the downweighting option is used those species with overall frequencies of 16 or more will remain unaltered. A species, s, with a frequency ( $f_s$ ) of 15 or less will have each of its scores ( $a_s$ ) downweighted; it will be replaced by;  $(a_s \times f_s) / 15.8$

A species with a frequency of 10 and a quadrat score of 6 will have that score downweighted to  $(6 \times 10)/15.8 = 3.8$ . Were this same species to record an abundance score of 50 it would be downweighted by an equal proportion to  $(50 \times 10)/15.8 = 31.6$ .

Downweighting reduces the eigenvalues and increases the percentage variance explained. The eigenvalues generated by the ordination program may be thought of as defining the lengths of the major axes of a multidimensional ellipse which encloses the data set. A measure of the power of the downweighting algorithm may be seen from a comparison of the eigenvalues from a data set without and with the downweighting procedure. This may be seen from a comparison of Tables 4.3 and 4.4 where the full data set is ordinated first without, and then with, downweighting of rare species. The eigenvalues for each of the four axes are reduced by about one third of their original level signifying the elimination of noise from the data. The amount of variance in the data which is explained by the ordination axes is consequently increased substantially.

## 4.2 Correspondence analysis

Correspondence analysis of the data set was performed using Detrended Correspondence Analysis (DCA) which is included as part of the software package MVSP (Kovach, 1995). The use of the DCA ordination aims to summarize the data and uncover any latent structure. It is a dimension-reducing procedure such that the variation contained within 113 species dimensions is reduced to four uncorrelated axes. The interpretation of these four axes, in relation to the known factors associated with the 80 cases, seeks to highlight those variables which, in the context of this study, give rise to differences in age, aspect and height. A number of program variations were used in order to explore the effects of detrending and of downweighting of rare species and also as a means of analysing subsets of the data. These seven different analyses each generated a set of results which are described below as Runs 1 to 7.

### 4.2.1 The CA algorithm

In CA sites are ordered by reference to the species abundances which they contain. The algorithm performs a weighted averaging procedure on the sites by species data table. From an initially arbitrary set of site scores, species scores are derived such that the score for any particular species is the weighted average of the abundances where it occurs; the weight applied being the site score. Thus, for example, from 10 quadrats (sites) given initial scores of 1 to 10, in which Species A occurs in quadrats Q3, Q7 and Q8 with abundances respectively, of 5, 22 and 15, the species score for this species would be given by;

$$\frac{(3 \times 5) + (7 \times 22) + (8 \times 15)}{5 + 22 + 15} = \frac{289}{42} = 6.88$$

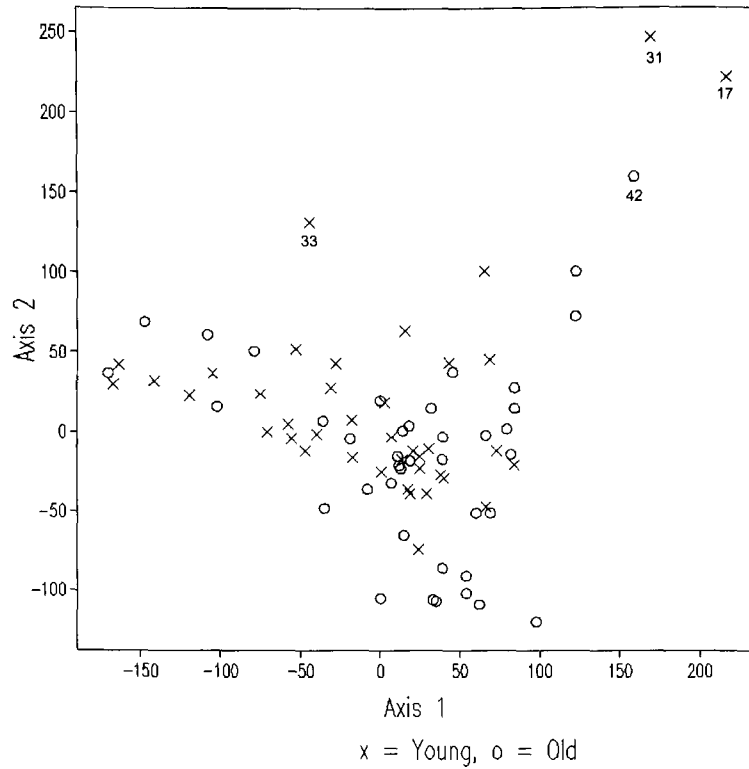
Each of the species A abundance values is weighted according to the site score of the quadrat in which it occurs. These weighted abundances are summed and the average is obtained by dividing by the summed abundances. This process is equivalent to deriving a species score which describes the species optimum level of some factor amongst the sites. If the sites are arranged in an order corresponding to some tangible entity such as a measured environmental gradient, with each site having a score which positions it within that gradient, then the species score refers to the species preferred level for the variable represented by that gradient. In the case illustrated species A has an optimum level along the presumed gradient of 6.88. This can be confirmed by simple inspection of the data

where the species has a relatively high abundance in quadrat 7. Up to this point the hypothesized gradient is based on arbitrarily assigned numbers represented by sites scores, so there can be no meaningful interpretation of the site scores. Species scores are calculated in this same way for all species in the data set. New site scores are then calculated as average weighted species scores in a similar manner to that described for species scores. In CA the cycle of calculating new species scores and new site scores is repeated until the scores converge towards a set of values which no longer change with recalculation. This set of values are the site and species scores along the first CA axis.

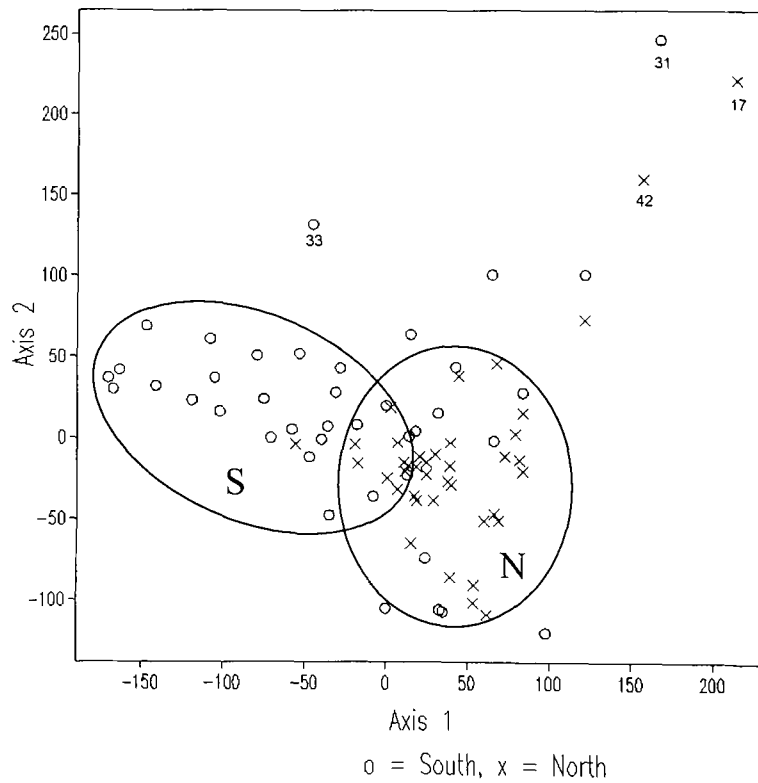
### 4.3 CA results

Output from each analysis consists, for each of the 80 cases (vegetation samples or quadrats), of a score on each of four axes. A full listing of the axis scores for each run can be found in Appendix C. Each of the four sets of axis scores, from each run, has associated with it an eigenvalue which gives a measure of the amount of variation in the data along that axis (Section 3.6.2). This is complemented by a measure of the percentage variation in the data which is explained by the axis in question. These measures of axis score power together with the results of analyses of the scores in relation to the factors are presented for each run (Tables 4.2 - 4.8), and for all seven runs together (Table 4.9). Diagrams, showing cases plotted within an ordination space defined by pairs of axes, are illustrated in Figures 4.2 - 4.14. In these diagrams each case is plotted using symbols which denote the level of one of the binary factors, age, aspect or height chosen to illustrate a particular pattern or relationship. Lines have been added to the diagrams to suggest natural partitioning between cases, and circles indicating groupings; individual quadrats are, in some cases, identified by their number for ease of reference.

Each set of axis scores is tested for a possible relation with each factor using both a Mann-Whitney U test (MW) and Discriminant Function Analysis (Section 3.6.5). The Mann-Whitney procedure tests for differences in mean rank of axis scores between for example, old and young samples. Mean rank differences are reported (Tables 4.2 - 4.8) together with an indication of the significance of the result; significance levels at  $p < 0.05$ , and  $p < 0.01$ , are shown in bold type and denoted by single and double asterisks respectively.



**Figure 4.2 Ordination from Run 1. Cases are plotted using symbols denoting age**



**Figure 4.3 Ordination from Run 1. Cases are plotted using symbols denoting aspect.**



DFA coefficients are the weights which, when applied to the axes scores, give the best separation between the levels of each factor. Large weights associated, for example, with the factor age, indicate a powerful influence of the axis scores in separating the two groups of young and old quadrats. The sign associated with the weight is arbitrary and merely results from the order in which the groups are entered into the algorithm.

Slope angle is tested for a possible relation to axis scores using a Spearman Rank Correlation test (Sokal and Rohlf, 1995). The resulting coefficient is reported with an indication of the level of significance in the same manner as that described for the Mann-Whitney test.

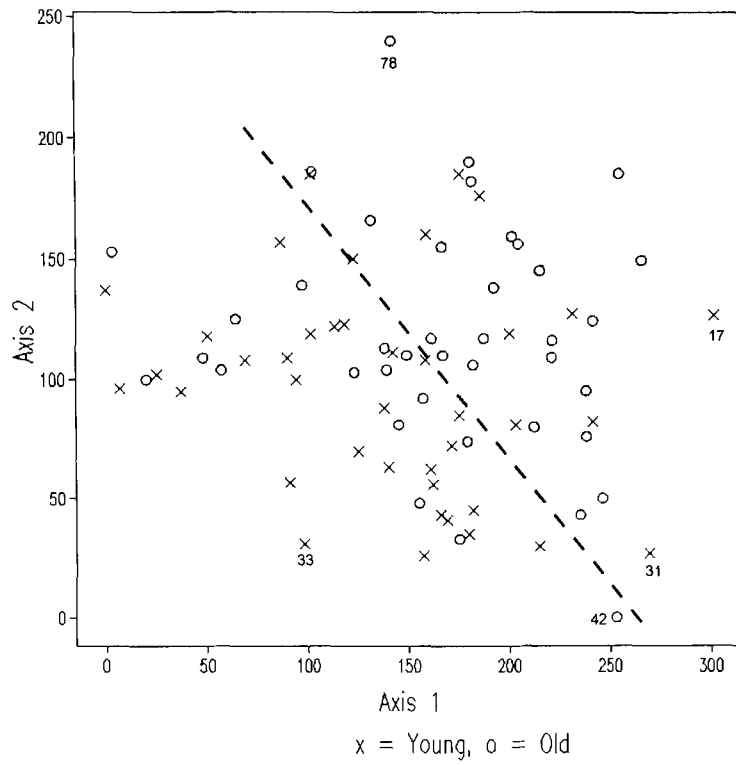
#### 4.3.1 Correspondence Analysis: Run 1

Run 1 uses the options for Correspondence Analysis without detrending and without downweighting of rare species. The resulting graphical output of axis 1 and axis 2 (Figure 4.2) shows cases coded by symbols indicating age group. Cases are seen to form a large single, central cluster with several outliers though no general pattern is observed to the distribution. Outliers are identified as quadrats 17, 31, 42 and, in a less extreme position, quadrat 33. Table 4.2 shows that axis 4 shows a significant relation with age.

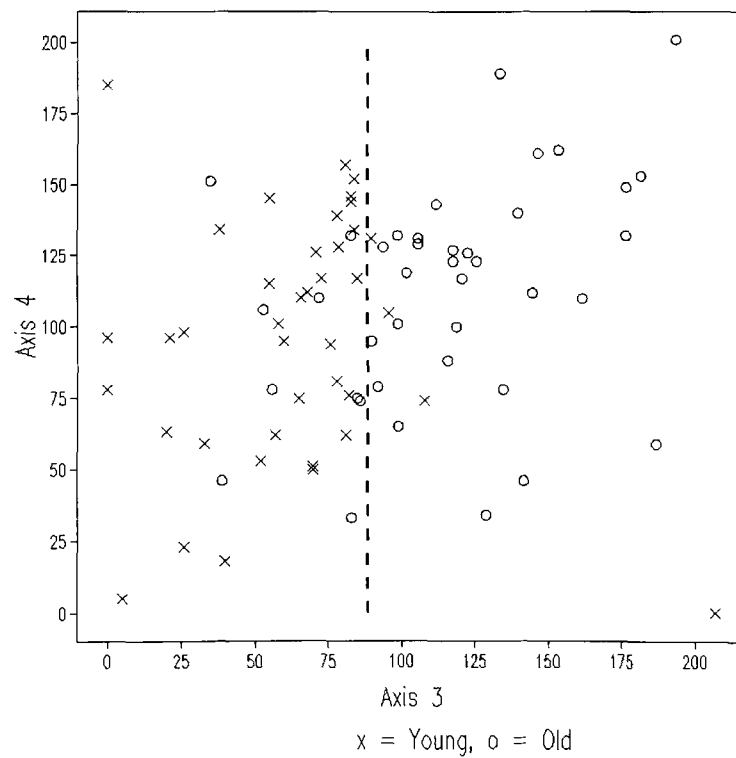
When the same data are analysed by aspect (Figure 4.3) cases are seen to be divided into two subgroups which correspond, broadly, to those quadrats facing north (N) and south (S). There is a strong correlation between aspect and CA score for all four axes (Table 4.2).

Full data-set; no detrending or downweighting (80 cases)	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.370	0.313	0.272	0.266
% variance explained	7.69	6.50	5.66	5.52
Age: mean rank difference	9.8	9.4	2.2	<b>21.6**</b>
DFA weight	-0.4861	0.5722	-0.1490	0.9030
Aspect: mean rank difference	<b>21.8**</b>	<b>17.8**</b>	<b>26.0**</b>	<b>19.7**</b>
DFA weight	-0.9633	0.4667	0.9413	-0.6484
Height: mean rank difference	6.4	2.2	2.2	4.6
DFA weight	-0.6551	-0.4471	-0.4910	0.3234
Slope: rank correlation coefficient	-0.1427	-0.1821	<b>-0.2778*</b>	0.1374

**Table 4.2 Analyses of CA scores from Run 1**  
(\* -  $p < 0.05$ ; \*\* -  $p < 0.01$ )



**Figure 4.4 Ordination from Run 2 with detrending (DCA). Cases are plotted on axes 1 and 2 using symbols denoting age.**



**Figure 4.5 Ordination from Run 2 with detrending (DCA). Cases are plotted on axes 3 and 4 using symbols denoting age.**

### 4.3.2 Correspondence Analysis using detrending: Run 2

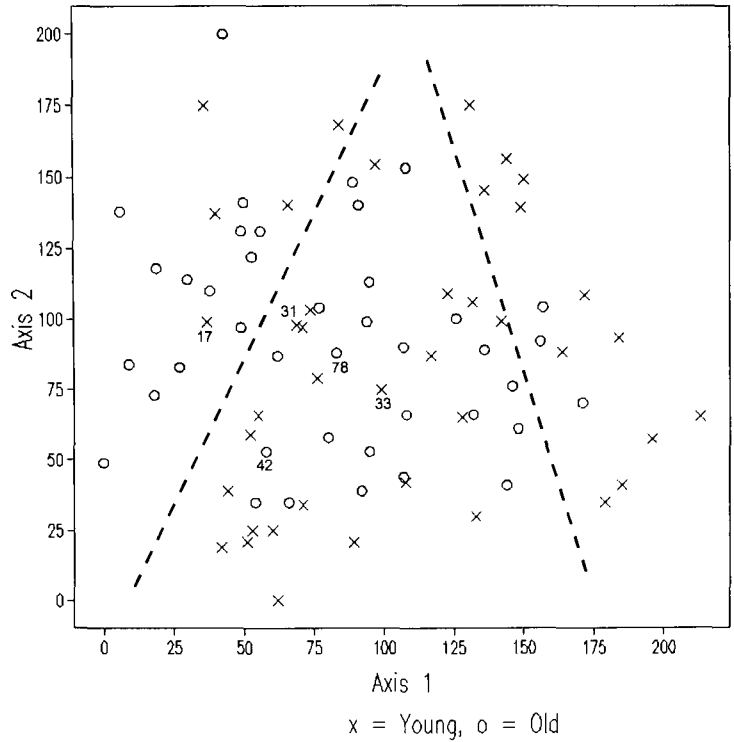
With the introduction of the detrending option (DCA), but without the downweighting of rare species, the cases can be seen to be more evenly distributed within the ordination space (Figures 4.4, 4.5). This change results from the rescaling algorithm described above (Section 3.6.2). Table 4.3 shows that axes 1, 2 and 3 are significantly related to the factor age and this is also indicated (Figure 4.4) when quadrats are plotted on axes 1 and 2; a dashed line indicates a suggested division between old and young quadrats. Old quadrats have generally higher scores than those of young quadrats on both axes 1 and 2. Quadrats 17, 31 and 42 remain at the extremes of the ordination space as also is quadrat 78.

Axis 3 is also strongly related to age (Table 4.3) and this is illustrated in a plot of axes 3 and 4 (Figure 4.5) where the lower part of axis 3 is dominated by young, and the upper part by old quadrats.

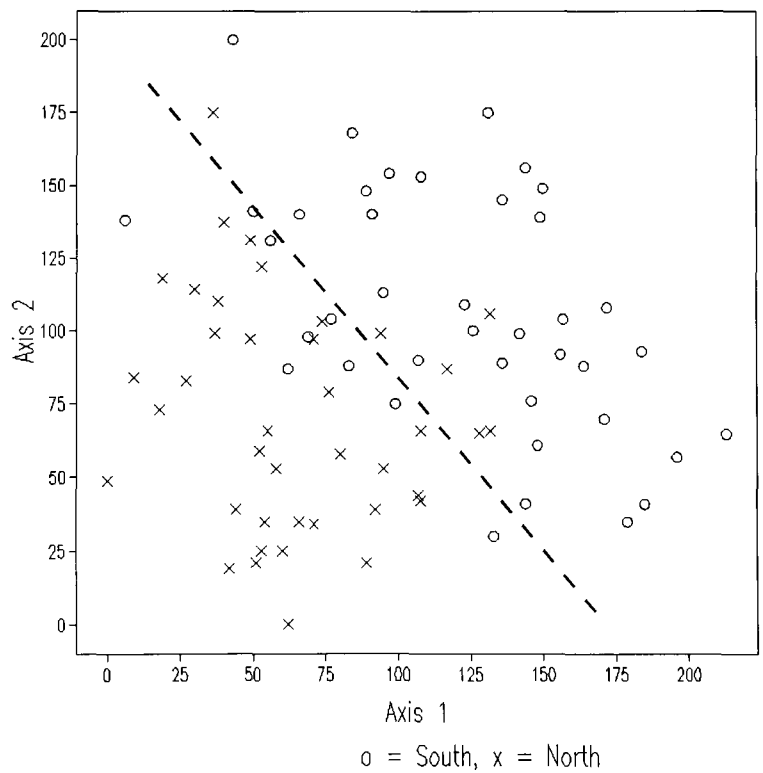
Table 4.3 also shows that, as was the case in Run 1, axes 1 and 2 are strongly correlated with aspect. It may also be noted that axis 4 shows a strong correlation with slope angle; however this axis contributes only 4% of the explained variance.

Full data; detrended; no downweighting (80 cases)	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.370	0.264	0.211	0.145
% variance explained	7.69	5.49	4.39	3.00
Age: mean rank difference	<b>10.6*</b>	<b>10.2*</b>	<b>30.0**</b>	8.2
DFA weight	0.5096	0.5517	1.0747	0.2816
Aspect: mean rank difference	<b>20.2**</b>	<b>22.4**</b>	2.6	9.4
DFA weight	0.9727	-0.7475	-0.1423	0.7009
Height: mean rank difference	5.2	2.4	4.2	3.4
DFA weight	0.3984	-0.0678	0.8156	-0.5435
Slope: rank correlation coefficient	-0.137	-0.189	0.168	<b>0.339**</b>

**Table 4.3 Analyses of DCA scores from Run 2**  
(\* -  $p < 0.05$ ; \*\* -  $p < 0.01$ )



**Figure 4.6 Ordination from Run 3 with detrending and downweighting. Cases are plotted on axes 1 and 2 using symbols denoting age.**



**Figure 4.7 Ordination from Run 3 with detrending and downweighting. Cases are plotted on axes 1 and 2 using symbols denoting aspect**

### 4.3.3 Correspondence analysis using DCA with downweighting of rare species: Run 3

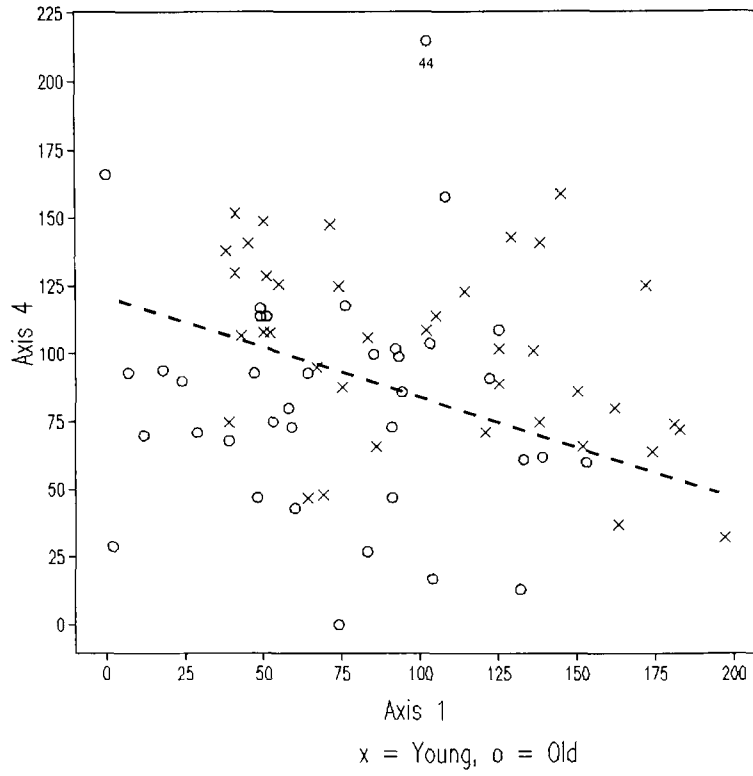
The third DCA run uses the options both for detrending and the downweighting of rare species. Table 4.4 shows that the use of downweighting results in lower eigenvalues (*cf.* Table 4.3) and that the proportion of the variation explained is increased. Figure 4.6 shows the results of the ordination plotted on axes 1 and 2. It can be seen that the downweighting routine has successfully reduced the effects of the anomalously high abundances of rare species which occurred in quadrats 17, 31, 33, 42 and 78. These quadrats now lie within the main body of the ordination space. The ordination space is shown partitioned to indicate a left-hand section dominated by old, and a right-hand section by young, quadrats. Table 4.4 shows that axis 1 remains significantly correlated with the factor age.

The strong influence of aspect in structuring the ordination space is again apparent in the mean rank differences of axes 1, 2 and 4. This is illustrated for axes 1 and 2 (Figure 4.7) where south-facing quadrats are predominant in the upper right, and north-facing quadrats in the lower left, of the plot.

Axis 2 scores show a significant negative correlation with slope angle in this analysis. This suggests a possible relation between slope angle and aspect. When slope angle values were analysed by a two-sample t-test, however, no systematic relation with aspect was found ( $p = 0.258$ ).

Full data with downweighting (80 cases) Run 3	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.251	0.160	0.126	0.073
% variance explained	17.18	10.95	8.60	4.96
Age: mean rank difference	<b>10.2*</b>	4.0	8.6	5.3
DFA weight	0.8177	-0.3371	-0.7518	0.5509
Aspect: mean rank difference	<b>27.0**</b>	<b>19.2**</b>	6.6	<b>16.5**</b>
DFA weight	1.1305	0.8901	-0.0723	0.5171
Height: mean rank difference	5.2	2.6	1.2	1.6
DFA weight	-0.8543	-0.3692	-0.1836	0.5792
Slope: rank correlation coefficient	-0.0428	<b>-0.452**</b>	0.0832	0.118

**Table 4.4 Analyses of DCA scores from Run 3**  
(\* -  $p < 0.05$ ; \*\* -  $p < 0.01$ )



**Figure 4.8** Ordination from Run 4 with four quadrats excluded. Cases are plotted on axes 1 and 4 using symbols denoting age.

#### 4.3.4 DCA analysis with reduced data set: Run 4

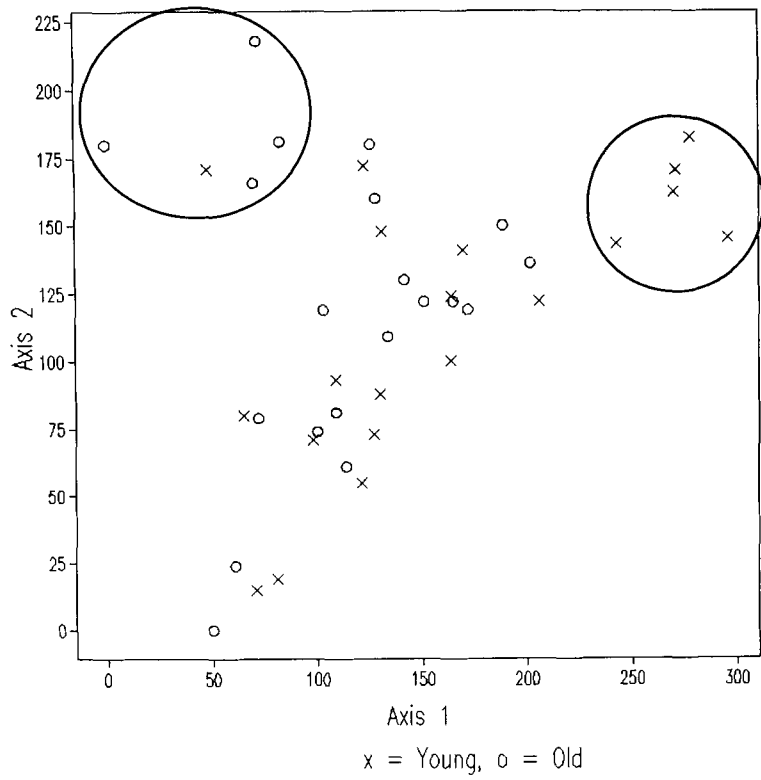
In Run 4 those quadrats (numbers 33, 64, 74 and 77) which had been identified (Section 4.1.2) as being unrepresentative of the grassland community were excluded from the data set and the run 3 analysis repeated. Table 4.5 shows that this change results in a small increase in the correlation between axis 1 scores and age and that axis 4 now also shows a correlation with this factor. It may be noted that axis 4 contributes only a small percentage of the explained variance in the data. Aspect remains a significant factor in relation to axes 1 and 2 though with a slight decrease in the significance of the correlation. Figure 4.8 shows the ordination space generated by axes 1 and 4 with a line inserted to indicate the separation of age groups along axis 4. Quadrat 44 can be seen to occupy an extreme position on axis 4. This quadrat is remarkable in having a very high abundance (100) of the species *Holcus lanatus*. Whilst this species is very common on the site it achieves abundances greater than 50 in only two other quadrats.

It is clear from a comparison of Tables 4.5 and 4.4 that the removal of the four anomalous quadrats does not alter the overall pattern shown to be present in the data by the DCA analysis utilizing detrending and downweighting.

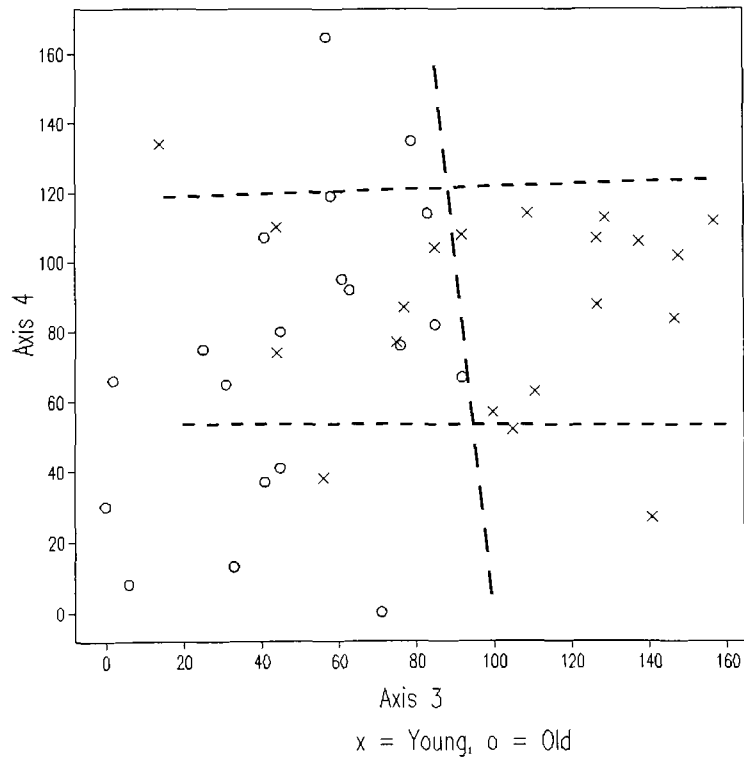
Reduced data with down-weighting (76 cases) Run 4	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.240	0.167	0.131	0.069
% variance explained	16.92	11.76	9.21	4.83
Age: mean rank difference	<b>12.1*</b>	6.6	5.9	<b>11.5*</b>
DFA weight	0.9541	-0.3406	-0.3564	0.6446
Aspect: mean rank difference	<b>25.3**</b>	<b>18.2**</b>	4.6	<b>19.9**</b>
DFA weight	-1.0957	-0.8500	0.0204	0.6621
Height: mean rank difference	5.9	0.6	0.2	4.0
DFA weight	0.8502	0.1858	-0.0284	0.7047
Slope: rank correlation coefficient	-0.137	<b>-0.4513**</b>	0.077	-0.0025

**Table 4.5 Analyses of DCA scores from Run 4**

(\* -  $p < 0.05$ ; \*\* -  $p < 0.01$ )



**Figure 4.9 Ordination from Run 5: south-facing quadrats. Cases are plotted on axes 1 and 2 using symbols denoting age**



**Figure 4.10 Ordination from Run 5: south-facing quadrats. Cases are plotted on axes 3 and 4 using symbols denoting age**



### 4.3.5 Ordination of south-facing data: Run 5

In view of the strong influence of aspect in structuring the data it is considered that vegetation changes over time may be more clearly seen if this factor is controlled. To this end DCA analysis was performed separately on the south- and north-facing data.

Run 5 analyses south-facing quadrats and Table 4.6 shows that the factor age is strongly related to axis 3 scores though this axis accounts for only 6.73% of the variation. Figure 4.9 shows the ordination space formed by axes 1 and 2 with the positions of 40 south-facing quadrats, which are plotted using symbols denoting age. Some separation by age is indicated by the presence of a group of 5 young cases with high axis 1 scores and a somewhat diffuse group containing 4 old and 1 young case which have low axis 1 and high axis 2 scores. In other respects there appears to be little distinction between age groups.

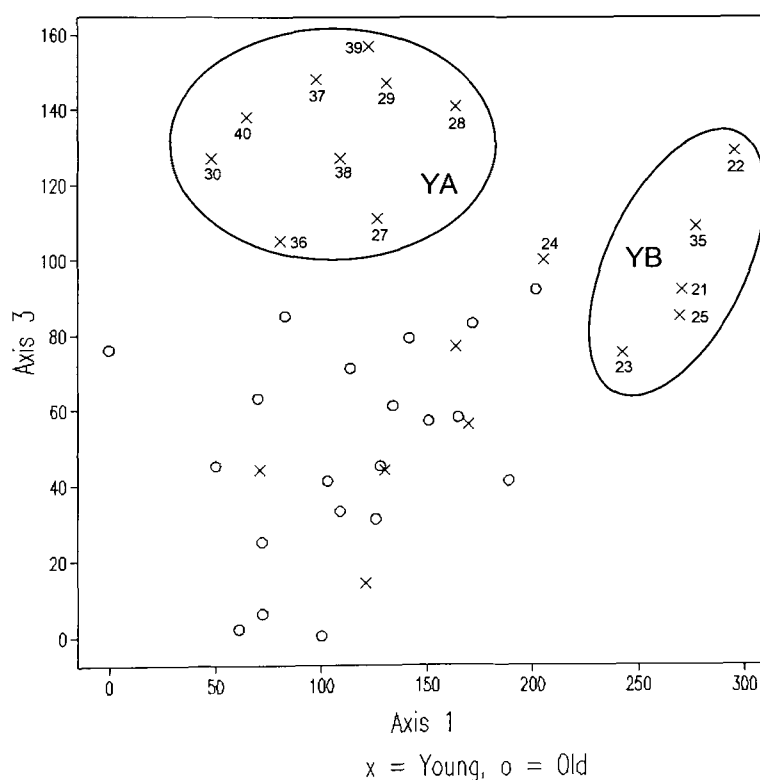
Figure 4.10 displays axes 3 and 4 from Run 5. Age groups are well separated in the space defined by axis 3, with young cases having high, and old cases low, scores. Young cases are relatively confined along axis 4 to a central band whilst old cases are spread more evenly over this axis.

Slope angle is shown (Table 4.6) to be significantly correlated, positively with axis 1 and negatively with axis 3, in this run. This suggests the possibility that, on south-facing slopes, steeper slopes support a vegetation community identifiably different from that found on shallower slopes. This relationship is further investigated in the canonical ordinations (Section 4.5.2).

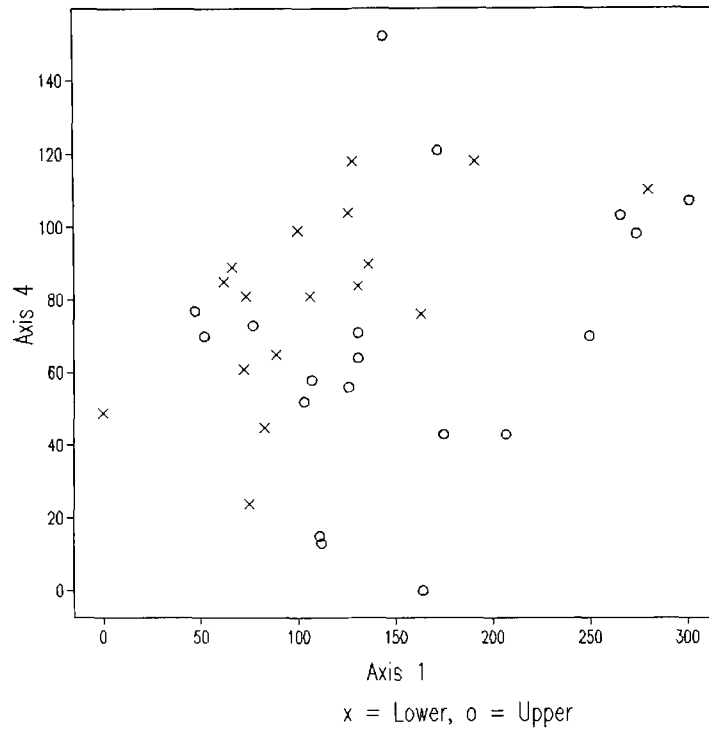
South-facing data; with down-weighting (40 cases) Run 5	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.347	0.188	0.122	0.080
% variance explained	19.16	10.39	6.73	4.44
Age: mean rank difference	6.0	1.2	<b>13.8**</b>	4.4
DFA weight	-0.5702	0.6144	-1.1727	-0.1153
Height: mean rank difference	6.0	2.0	0.9	4.5
DFA weight	-0.8285	-0.3397	-0.0599	0.8793
Slope: rank correlation coefficient	<b>0.4251*</b>	0.1939	<b>-0.3098*</b>	0.1312

**Table 4.6 Analyses of DCA scores from Run 5**  
(\* -  $p < 0.05$ ; \*\* -  $p < 0.01$ )

The patterns described above are emphasized in a plot of axes 1 and 3 (Figure 4.11). Here the old cases form a relatively coherent group confined to the lower left quadrant, having low scores on both axes, whilst the majority of young cases form two distinct groups, one (YB) with high axis 1 scores, and the other (YA) with low to mid axis 1 scores. Group YA consists of 9 quadrats having axis 3 scores greater than 100 and axis 1 scores less than 200; this group contains quadrats, 27-30 and 36-40. Group YB contains quadrats 21, 22, 23, 25 and 35. Referring to Figure 3.5, it is apparent that group YA quadrats lie in the southern half of the young revetments and that group YB contains quadrats from the northern part of the young group. Group YA contains 4 upper and 5 lower quadrats whilst group YB has 4 upper and a single lower quadrat. Quadrat 24, the “missing”, upper case from the YB group, lies midway between groups YA and YB. There is therefore evidence of a correspondence between groups in ordination and geographical space. An interpretation of the significance of the spatial separation of these groups is discussed below (Section 6.5).



**Figure 4.11 Ordination from Run 5: south-facing quadrats. Cases are plotted on axes 1 and 3 using symbols denoting age.**



**Figure 4.12 Ordination from Run 6: south-facing quadrats. Cases are plotted on axes 1 and 4 using symbols denoting height**

### 4.3.6 DCA of south-facing quadrats with anomalous cases omitted

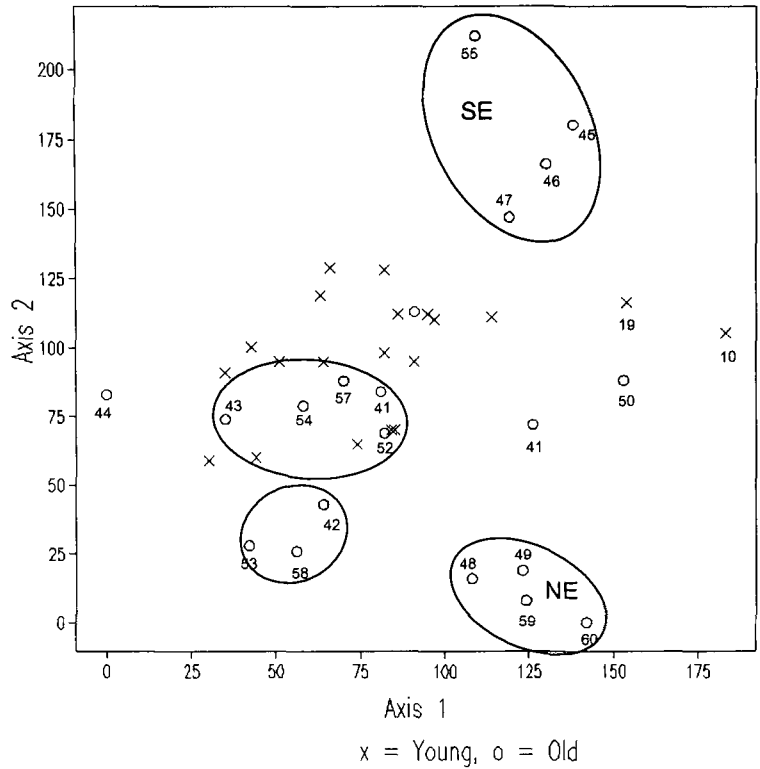
Run 6 of the DCA analysis repeats that of Run 5, the south-facing quadrats with the four anomalous quadrats (Section 4.1.2) omitted; a comparison of Tables 4.7 and 4.6 shows results which are very similar to those of Run 5. There is a small increase in the percentage variance explained by axes 1, 2 and 3 and a small increase in the mean rank difference between age groups on axes 1 and 3, with axis 3 again shown to be significant in separating levels of this factor.

There is also a significant difference in mean rank of groups based on the factor height with respect to their axis 1 scores (Table 4.7). This is also shown in Figure 4.12 which displays axes 1 and 4 from Run 6 with cases plotted by height and where the majority of the lower cases are contained in a large grouping in the left centre of the plot. Upper cases show a more widespread distribution.

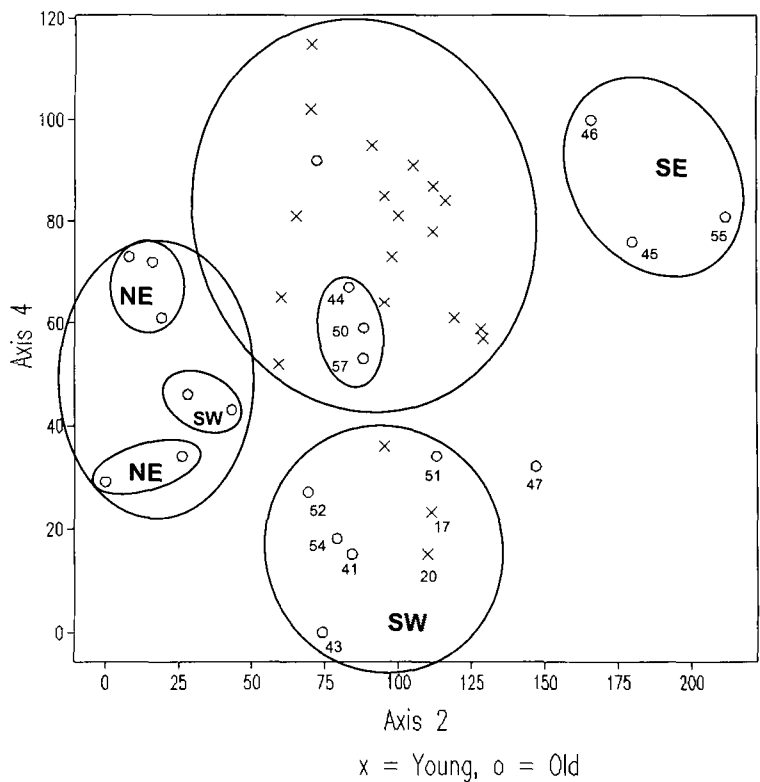
Axis 1 scores are again correlated with slope angle and, since this axis is also related to the factor height, this suggests that height may be systematically related to slope angle. A t-test procedure was used to test for differences in slope angle between upper and lower quadrat groups. The test was performed for both the whole, and for the south-facing, data sets. In neither case was there a significant difference ( $p = 0.311$ ;  $p = 0.161$ , respectively).

South-facing with down-weighting (36 cases) Run 6	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.365	0.190	0.120	0.062
% variance explained	20.96	10.89	6.90	3.56
Age: mean rank difference	6.8	0.8	<b>15.0**</b>	2.6
DFA weight	0.6922	-0.6519	1.4284	-0.1932
Height: mean rank difference	<b>6.8*</b>	0.9	0.2	5.3
DFA weight	-1.0204	-0.1441	0.1575	0.8170
Slope: rank correlation coefficient	<b>0.3990*</b>	0.2115	-0.3196	0.1134

**Table 4.7 Analyses of DCA scores from Run 6**  
(\* -  $p < 0.05$ ; \*\* -  $p < 0.01$ )



**Figure 4.13 Ordination from Run 7: north-facing quadrats. Cases are plotted on axes 1 and 2 using symbols denoting age**



**Figure 4.14 Ordination from Run 7: north-facing quadrats. Cases are plotted on axes 1 and 4 using symbols denoting age**

### 4.3.7 DCA analysis of north-facing quadrats

DCA in run 7 is restricted to the N-facing quadrats. In this run the factor age shows a significant correlation with the axis 4 scores (Table 4.8) though this axis explains only 4.45% of the variance in the data. However, there is evidence of some separation of cases by age group in the ordination space defined by other axes. A plot of axes 1 and 2 (Figure 4.13) shows a large, central group of cases containing the majority of the young quadrats with the old quadrats forming four, widely separated groups. These relatively discrete groupings of old quadrats appear to show some relation to their spatial separation in physical space (*cf.* Figure 3.5). The group comprising quadrats 45, 46, 47 and 55 belong to the group of revetments in the SE of the study area whilst the group having low axis 2 scores and containing quadrats 48, 49, 59 and 60 are from the NE. Of those five old quadrats from the central group four belong to the SW section and one to the SE. Quadrats 42 and 53 are from the SW group but quadrat 58 is from the SE group of revetments.

In Figure 4.14 cases plotted by age on axes 2 and 4 again show this same pattern with a central concentration of young quadrats and with three separate groups of old quadrats having low, mid and high axis 2 scores, respectively. The group with the low axis 2 scores contains five quadrats from the NE group of revetments and two from the SW group together with three young quadrats whilst the group with high axis 2 scores contains three quadrats from the SE revetment group. The group with mid-range axis 2 scores contains five quadrats from the SW sector together with three young quadrats. The large group of young quadrats lies in the upper central portion of the space and this probably accounts for the significance of the factor age in relation to axis 4 scores seen in Table 4.8.

Axis 3 scores show a strong correlation with slope angle in this data set.

North-facing data; with down-weighting (40 cases) Run 7	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.167	0.126	0.075	0.043
% variance explained	17.45	13.13	7.83	4.45
Age: mean rank difference	4.0	6.6	2.6	<b>8.2*</b>
DFA weight	0.6458	-0.3808	-0.3210	-0.8662
Height: mean rank difference	0.8	0.6	3.0	5.8
DFA weight	0.1728	-0.0344	0.6637	-0.9125
Slope: rank correlation coefficient	0.0097	0.1764	<b>0.5895**</b>	0.01344

**Table 4.8 Analyses of DCA scores from Run 7**

(\* -  $p < 0.05$ ; \*\* -  $p < 0.01$ )

<b>Run 1; 80 cases</b>	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.370	0.313	0.272	0.266
% variance explained	7.69	6.50	5.66	5.52
Age: mean rank difference	9.8	9.4	2.2	<b>21.6**</b>
DFA weight	-0.4861	0.5722	-0.1490	0.9030
Aspect: mean rank difference	<b>21.8**</b>	<b>17.8**</b>	<b>26.0**</b>	<b>19.7**</b>
DFA weight	-0.9633	0.4667	0.9413	-0.6484
Height: mean rank difference	6.4	2.2	2.2	4.6
DFA weight	-0.6551	-0.4471	-0.4910	0.3234
Slope: rank correlation coefficient	-0.1427	-0.1821	<b>-0.2778*</b>	0.1374
<b>Run 2; 80 cases, detrended</b>	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.370	0.264	0.211	0.145
% variance explained	7.69	5.49	4.39	3.00
Age: mean rank difference	<b>10.6*</b>	<b>10.2*</b>	<b>30.0**</b>	8.2
DFA weight	0.5096	0.5517	1.0747	0.2816
Aspect: mean rank difference	<b>20.2**</b>	<b>22.4**</b>	2.6	9.4
DFA weight	0.9727	-0.7475	-0.1423	0.7009
Height: mean rank difference	5.2	2.4	4.2	3.4
DFA weight	0.3984	-0.0678	0.8156	-0.5435
Slope: rank correlation coefficient	-0.137	-0.189	0.168	<b>0.339**</b>
<b>Run 3; 80 cases downweighted</b>	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.251	0.160	0.126	0.073
% variance explained	17.18	10.95	8.60	4.96
Age: mean rank difference	<b>10.2*</b>	4.0	8.6	5.3
DFA weight	0.8177	-0.3371	-0.7518	0.5509
Aspect: mean rank difference	<b>27.0**</b>	<b>19.2**</b>	6.6	<b>16.5**</b>
DFA weight	1.1305	0.8901	-0.0723	0.5171
Height: mean rank difference	5.2	2.6	1.2	1.6
DFA weight	-0.8543	-0.3692	-0.1836	0.5792
Slope: rank correlation coefficient	-0.0428	<b>-0.452**</b>	0.0832	0.118
<b>Run 4; 76 cases</b>	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.240	0.167	0.131	0.069
% variance explained	16.92	11.76	9.21	4.83
Age: mean rank difference	<b>12.1*</b>	6.6	5.9	<b>11.5*</b>
DFA weight	0.9541	-0.3406	-0.3564	0.6446
Aspect: mean rank difference	<b>25.3**</b>	<b>18.2**</b>	4.6	<b>19.9**</b>
DFA weight	-1.0957	-0.8500	0.0204	0.6621
Height: mean rank difference	5.9	0.6	0.2	4.0
DFA weight	0.8502	0.1858	-0.0284	0.7047
Slope: rank correlation coefficient	-0.137	<b>-0.4513**</b>	0.077	-0.0025
<b>Run 5; S-facing data (40 cases)</b>	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.347	0.188	0.122	0.080
% variance explained	19.16	10.39	6.73	4.44
Age: mean rank difference	6.0	1.2	<b>13.8**</b>	4.4
DFA weight	-0.5702	0.6144	-1.1727	-0.1153
Height: mean rank difference	6.0	2.0	0.9	4.5
DFA weight	-0.8285	-0.3397	-0.0599	0.8793
Slope: rank correlation coefficient	<b>0.4251*</b>	0.1939	<b>-0.3098*</b>	0.1312
<b>Run 6; S-facing data (36 cases)</b>	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.365	0.190	0.120	0.062
% variance explained	20.96	10.89	6.90	3.56
Age: mean rank difference	6.8	0.8	<b>15.0**</b>	2.6
DFA weight	0.6922	-0.6519	1.4284	-0.1932
Height: mean rank difference	<b>6.8*</b>	0.9	0.2	5.3
DFA weight	-1.0204	-0.1441	0.1575	0.8170
Slope: rank correlation coefficient	<b>0.3990*</b>	0.2115	-0.3196	0.1134
<b>Run 7; N-facing data (40 cases)</b>	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.167	0.126	0.075	0.043
% variance explained	17.45	13.13	7.83	4.45
Age: mean rank difference	4.0	6.6	2.6	<b>8.2*</b>
DFA weight	0.6458	-0.3808	-0.3210	-0.8662
Height: mean rank difference	0.8	0.6	3.0	5.8
DFA weight	0.1728	-0.0344	0.6637	-0.9125
Slope: rank correlation coefficient	0.0097	0.1764	<b>0.5895**</b>	0.01344

**Table 4.9 Summary of DCA ordinations**

#### 4.3.8 Summary of DCA ordinations

The findings presented above (Sections 4.3.1 - 4.3.7) indicate that;

- the options for detrending and downweighting improve the spread of the data within the ordination space
- the removal of anomalous cases from the data does not produce any major change in the pattern of the ordinations or the arrangement of the groups in ordination space.
- there is a strong influence of the factor aspect in partitioning the cases
- there is a secondary influence generated by the factor age in partitioning the cases
- the Discriminant Function Analysis of ordination scores shows good definition of groups by factors and gives results which confirm those of the Mann-Whitney tests.
- the factor height does not show consistent correlation with the groups of similar quadrats
- the variable slope angle is shown to have a significant correlation with axis scores in all of the ordination runs
- when the data are divided by aspect the influence of age is apparent only on minor axes this being strongly represented on S-facing slopes
- the factor height achieves a significant relation with axis 1 in a single ordination, that of the reduced, south-facing data
- when the factor aspect is controlled there is evidence of groups corresponding to the spatial arrangement of the revetments.



#### 4.4 Classification

The data were classified using Two-way Indicator Species Analysis (TWINSPAN) described above (Section 3.6.4.1) and the results of these analyses are presented below (Figures 4.15 - 4.19; Tables 4.10 - 4.14). The figures each show a dendrogram in which the end-groups, generated by the repeated division of the data set, are displayed. Species and pseudospecies used as indicators, together with their cut levels, are listed in the dendrogram at the point of division, to the left for species with a preference for the negative group and to the right for the positive preferentials. Species names are abbreviated in the dendrograms to two or three letters: the full names for each indicator species are given in Table 4.15. The quadrats forming the end-groups, after five divisions, are denoted, not by their quadrat number, but by letters signifying their age (Y/O) and aspect (N/S) group. Successive divisions are designated as D1, D2, etc. and the new clusters of cases formed at each level of division as A, B, C, &.

Since the divisions are based on differences in the species composition of the samples, it is of interest to relate the factors of age and aspect associated with each quadrat to their final group membership. Any such association is indicative of the potential influence of age and aspect in determining community types. The strength of this relationship is quantified using a chi-square test of association and the results displayed in Tables 4.10 - 4.14. The tables include the number of cases in each group at each of the first four divisions and the number in each class, at each level, of the factors age and aspect. The  $\chi^2$  statistic is a measure of the degree of association between group and factor, and  $p$  is the probability that this degree of association could arise by chance. By convention associations are considered to be significant where  $p$  is less than 0.05. The chi-square test is ineffective for small groups and is therefore not employed for groups derived from the fifth division. In no case was there a significant association between the classification groups and the factor height; test results for this factor are not included in the tables or dendrograms.

Five runs of the TWINSPAN program were employed (referred to here as T1 - T5) in order to explore the effects on the classification of; different program options, the selective removal of anomalous cases and also the use of different subsets of the data. For each run the program is limited to five divisions and groups with fewer than five members are not subject to further division. Cut levels, used to define abundance levels of pseudospecies, are set at; 0, 2, 5, 10, 30, 60. This allows a species to be treated within the program as present at up to six abundance levels. Pseudospecies are given weights (1, 1, 2, 2, 2, 2) which reduce

Division	Group	Cases	Old	Young	$\chi^2$	South	North	$\chi^2$
D1	A	35	14	21	2.49	32	2	45.15
	B	45	26	19	$p = 0.111$	8	37	$p < 0.000$
D2	A	18	7	11	7.85	16	2	46.62
	B	17	7	10	$p = 0.049$	16	1	$p < 0.000$
	C	24	10	14		1	23	
	D	21	16	5		7	14	
D3	A	11	1	10	22.74	10	1	42.91
	B	7	6	1	$p = 0.0024$	6	1	$p < 0.000$
	C	14	4	10		13	1	
	D	3	3	0		3	0	
	E	19	7	12		0	19	
	F	5	3	2		1	4	
	G	13	11	2		5	8	
	H	8	5	3		2	6	
D4	A	6	0	6	17.84	6	0	35.81
	B	5	1	4	$p = 0.17$	4	1	$p = 0.001$
	C	3	2	1		3	0	
	D	4	4	0		3	1	
	E	7	1	6		7	0	
	F	7	3	4		6	1	
	G	3	0	3		0	3	
	H	16	7	9		0	16	
	I	4	2	2		1	3	
	J	1	1	0		0	1	
	K	6	6	0		3	3	
	L	7	5	2		2	5	
	M	6	4	2		0	6	
	N	2	1	1		2	0	

**Table 4.10 Group compositions after TWINSpan classification (run T1)**

the influence of those abundance classes having scores of less than 5; this is equivalent to the downweighting of rare species (Section 4.1.3). Further options utilized are described for each run.

#### **4.4.1 Results of TWINSpan Run T1**

In the first run the full data set is used and all pseudospecies are allowed to act as indicators for defining groups.

The resulting dendrogram (Figure 4.15) shows that aspect is a dominant influence in determining the end-group membership; the majority of the groups consist of cases having the same level of the this factor. Table 4.10 confirms that aspect has a highly significant association with group membership at each of the four divisions. The factor age has a significant influence on the end-group identities at the lower divisions D2 and D3.

It can be seen from the dendrogram that 26 of the 50 pseudospecies used as indicators are represented at the lowest cut level 1. This suggests that species with single occurrences make a large contribution to the classification. It has been suggested (Section 4.1.3) that rare species do not generally contribute meaningful structure to the data yet here many of them are utilized in defining groups despite being downweighted. In order to investigate this question it is considered useful to further limit the influence of rare species by restricting the choice of indicator species to those with abundance levels greater than five.

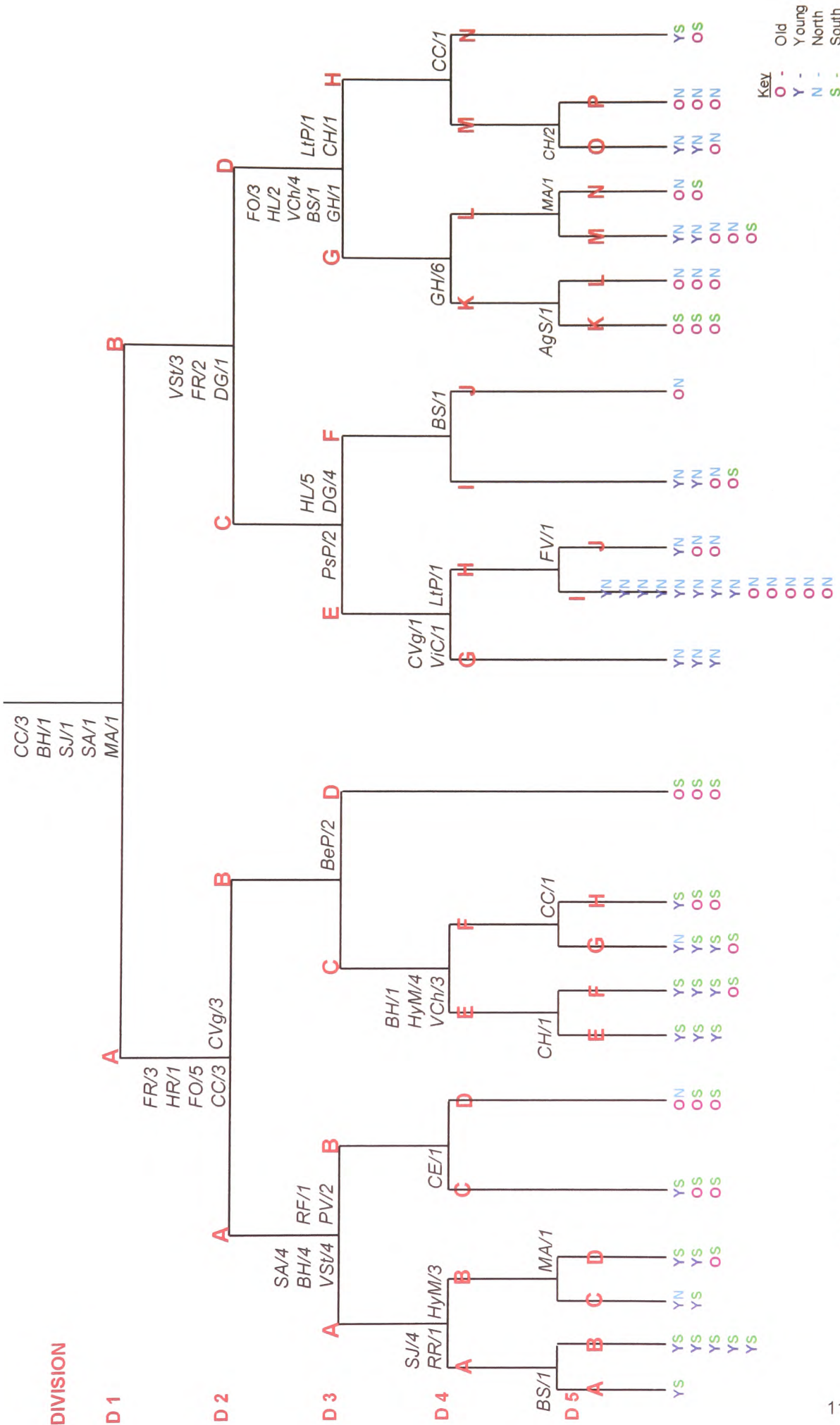


Figure 4.15 Classification showing indicator species and end-group members listed by age and aspect (run T1).

Division	Group	Cases	Old	Young	$\chi^2$	South	North	$\chi^2$
D1	A	35	14	21	2.49	31	4	37.03
	B	45	26	19	$p = 0.111$	9	36	$p < 0.000$
D2	A	13	4	9	9.29	12	1	40.62
	B	22	10	12	$p = 0.026$	19	3	$p < 0.000$
	C	21	8	13		0	21	
	D	24	18	6		9	15	
D3	A	4	2	2	14.48	4	0	35.40
	B	9	2	7	$p = 0.044$	8	1	$p < 0.000$
	C	2	2	0		2	0	
	D	20	8	12		17	3	
	E	18	5	13		0	18	
	F	3	3	0		0	3	
	G	17	13	4		7	10	
	H	7	5	2		2	5	
D4	A	1	1	0	21.66	1	0	33.66
	B	8	1	7	$p = 0.011$	7	1	$p < 0.000$
	C	10	1	9		9	1	
	D	10	7	3		8	2	
	E	3	0	3		0	3	
	F	15	5	10		0	15	
	G	6	5	1		4	2	
	H	11	8	3		3	8	
	I	5	4	1		0	5	
	J	2	1	1		2	0	

**Table 4.11 Group compositions after TWINSPAN classification (run T2)**

#### 4.4.2 Results of TWINSPAN Run T2

In this run the effects of removing the influence of low abundance species (having frequencies of less than five) from the analysis are investigated by omitting them from the list of potential indicator species. In addition those “woody” species which are associated with the development of a scrub vegetation are excluded from the analysis. These are species *Rosa agg.*, *Rubus fruticosus*, *Crataegus monogyna*, *Quercus robur*, *Fraxinus excelsior*, *Cornus sanguinea*, T1 and T9. The results are shown in Figure 4.16 and Table 4.11.

This classification shows a similar pattern of relations between group identities and factors as that seen in Run T1. The divisions again show the dominant effect of aspect in the identity of the groups with a significant association being present in each of the first four divisions shown in the table. Age is seen to be significantly associated with group membership at divisions 2, 3 and 4.

This comparison suggests that the classification method is not sensitive to the presence of many rare species and that the pattern revealed is not dependent on particular species presences. To that extent the community structure uncovered may be supposed to be general within the site and the attribution of the influence of aspect and age to be robust to changes in the component species.

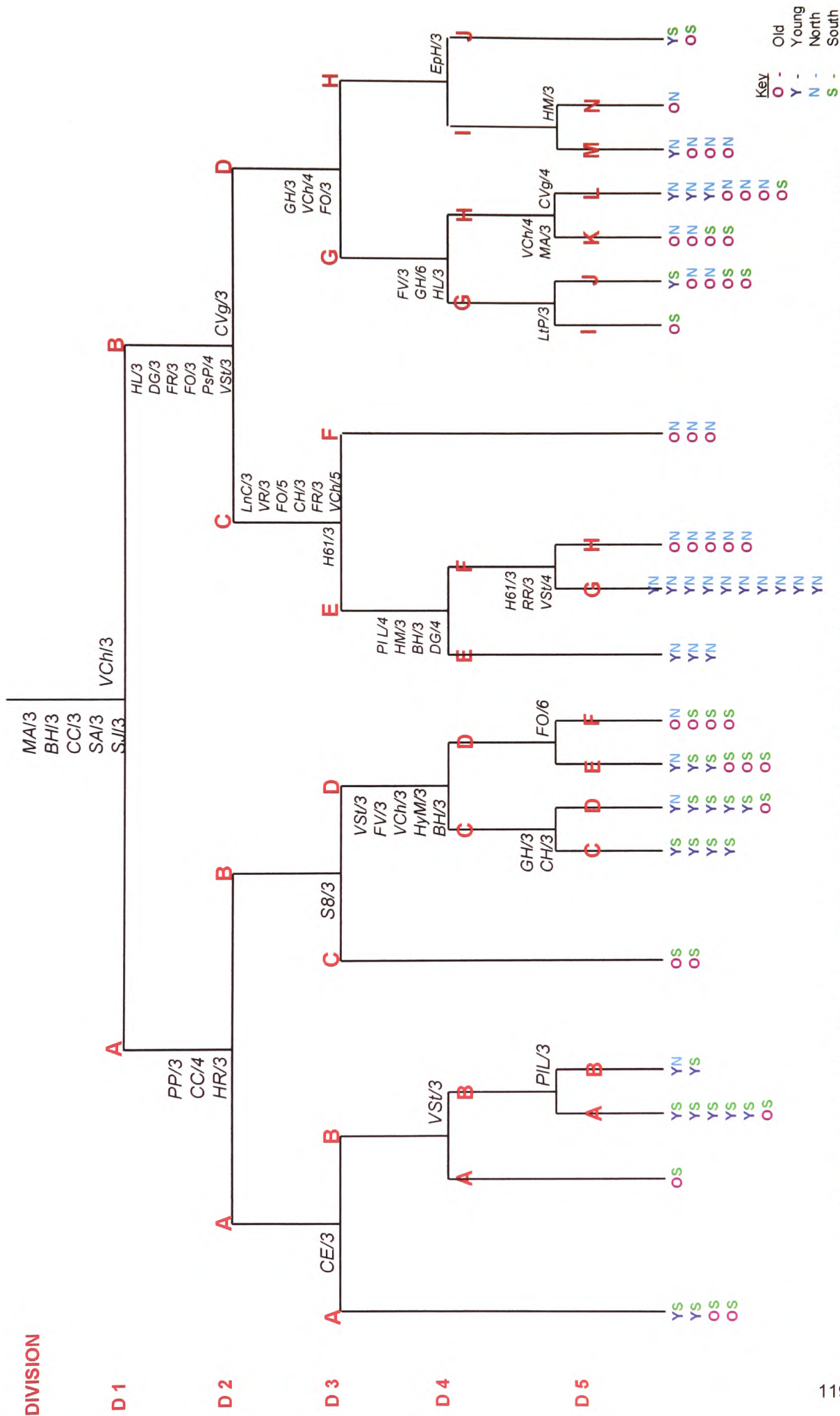


Figure 4.16 Classification showing indicator species and end-group members listed by age and aspect (run T2)

Division	Group	Cases	Old	Young	$\chi^2$
D1	A	15	5	10	2.67
	B	25	15	10	$p = 0.099$
D2	A	9	1	8	10.85
	B	6	4	2	$p = 0.013$
	C	14	6	8	
	D	11	9	2	
D3	A	5	0	5	11.56
	B	4	1	3	$p = 0.12$
	C	4	2	2	
	D	2	2	0	
	E	5	4	1	
	F	9	2	7	
	G	8	6	2	
	H	3	3	0	
D4	A	2	0	2	6.1
	B	3	0	3	$p = 0.53$
	C	4	4	0	
	D	1	0	1	
	E	4	0	4	
	F	5	2	3	
	G	6	4	2	
	H	2	2	0	

**Table 4.12 Group compositions related to age after classification of south-facing quadrats (run T3)**

Division	Group	Cases	Old	Young	$\chi^2$
D1	A	12	2	10	6.74
	B	24	15	9	$p = 0.009$
D2	A	9	0	9	10.31
	B	3	2	1	$p = 0.016$
	C	14	7	7	
	D	10	8	2	
D3	A	5	0	5	10.13
	B	4	0	4	$p = 0.072$
	C	4	0	4	
	D	10	7	3	
	E	7	5	2	
	F	3	3	0	
D4	A	2	0	2	5.076
	B	3	0	3	$p = 0.41$
	C	5	5	0	
	D	5	2	3	
	E	4	2	2	
	F	3	3	0	

**Table 4.13 Group compositions related to age after classification of 36 south-facing quadrats (run T4)**



#### 4.4.3 TWINSPAN classification of south-facing data

As noted above the dominant influence of aspect can be removed by considering the north- and south-facing data sets separately. The analysis was therefore applied to the two subsidiary data sets containing north- and south-facing cases. Classification of the south-facing data was performed both for all 40 quadrats (Run T3) and also after removal of anomalous cases (Run T4).

The results of the classification of south-facing data are shown below (Table 4.12; Figure 4.17). The second division is seen to be significantly related ( $p = 0.013$ ) to the factor age.

Four south-facing quadrats have been identified as having anomalous features which may make them unrepresentative of the normal vegetation (Section 4.1.1). Quadrat 33 has high levels of *Rubus fruticosus* and quadrats 64, 74 and 77 have evidence of repair work to the eroded surface. These quadrats were removed from the data set and the classification repeated using the same program options described above for run T3. The results of run T4 are shown below (Table 4.13; Figure 4.18).

Figure 4.18 shows a very similar classification structure to that of Figure 4.17. Two old cases and one young case have been removed from D1/A and one case (quadrat 73) from this group has been re-assigned to D1/B. A comparison of the  $\chi^2$  values in Tables 4.12 and 4.13 shows that there is an increase in the strength of the association with age for groups formed at D1, D3 and D4 in Table 4.13. The association at level D2, though weaker, remains significant.

With the influence of aspect removed the primary division (Table 4.12) is not significantly related to age. It is unclear if an explanatory factor can be assigned to account for this division of the south-facing data. When the four anomalous quadrats are removed (Run T4) then age is shown to be the dominant influence at divisions D1 and D2. The difference between these two classifications is the use, at the first division, of the pseudospecies representing *Festuca ovina* at abundance levels greater than 30. The inclusion of anomalous quadrats seems, in this instance, to add noise to the data so making the classification less interpretable.

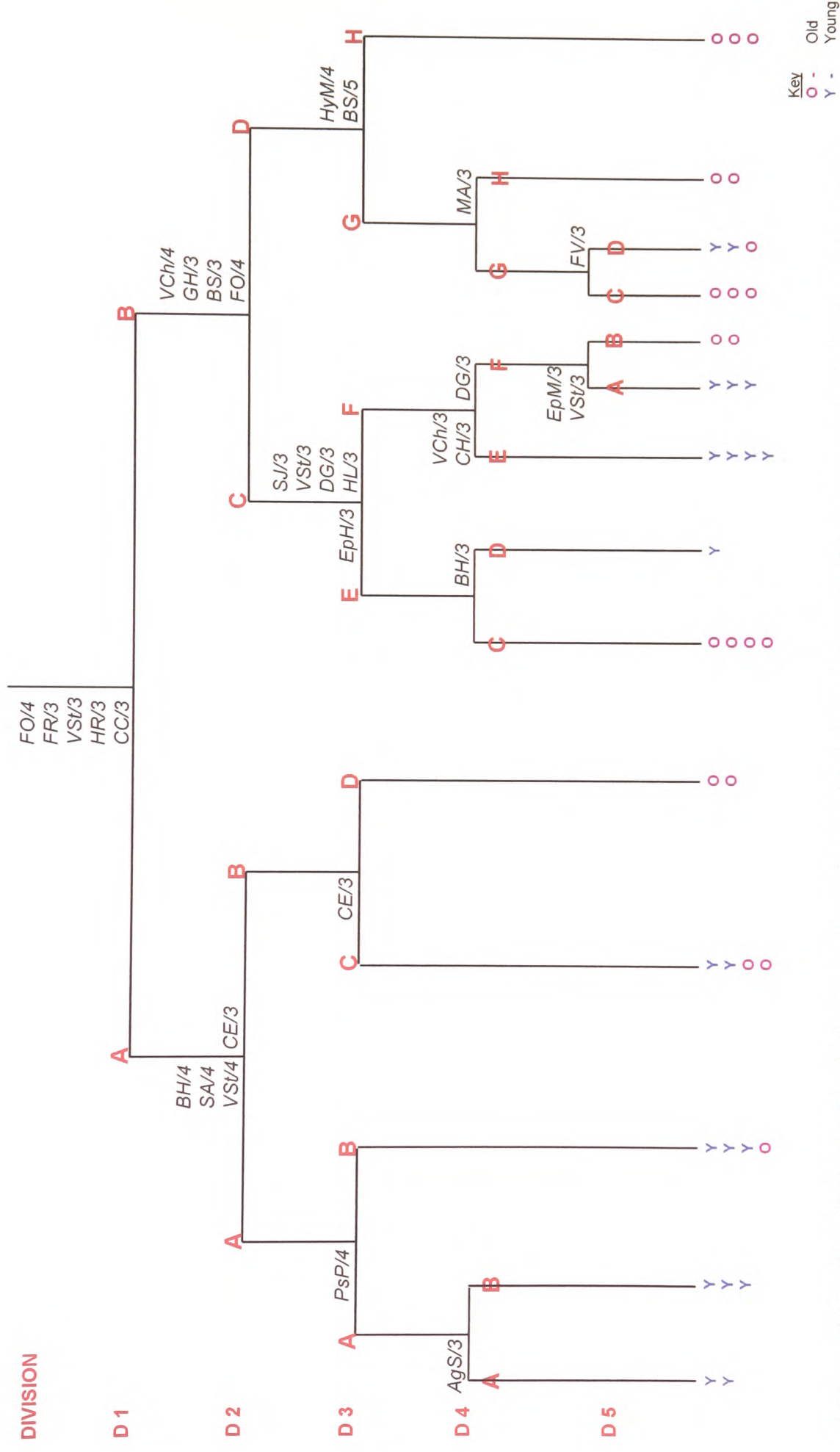
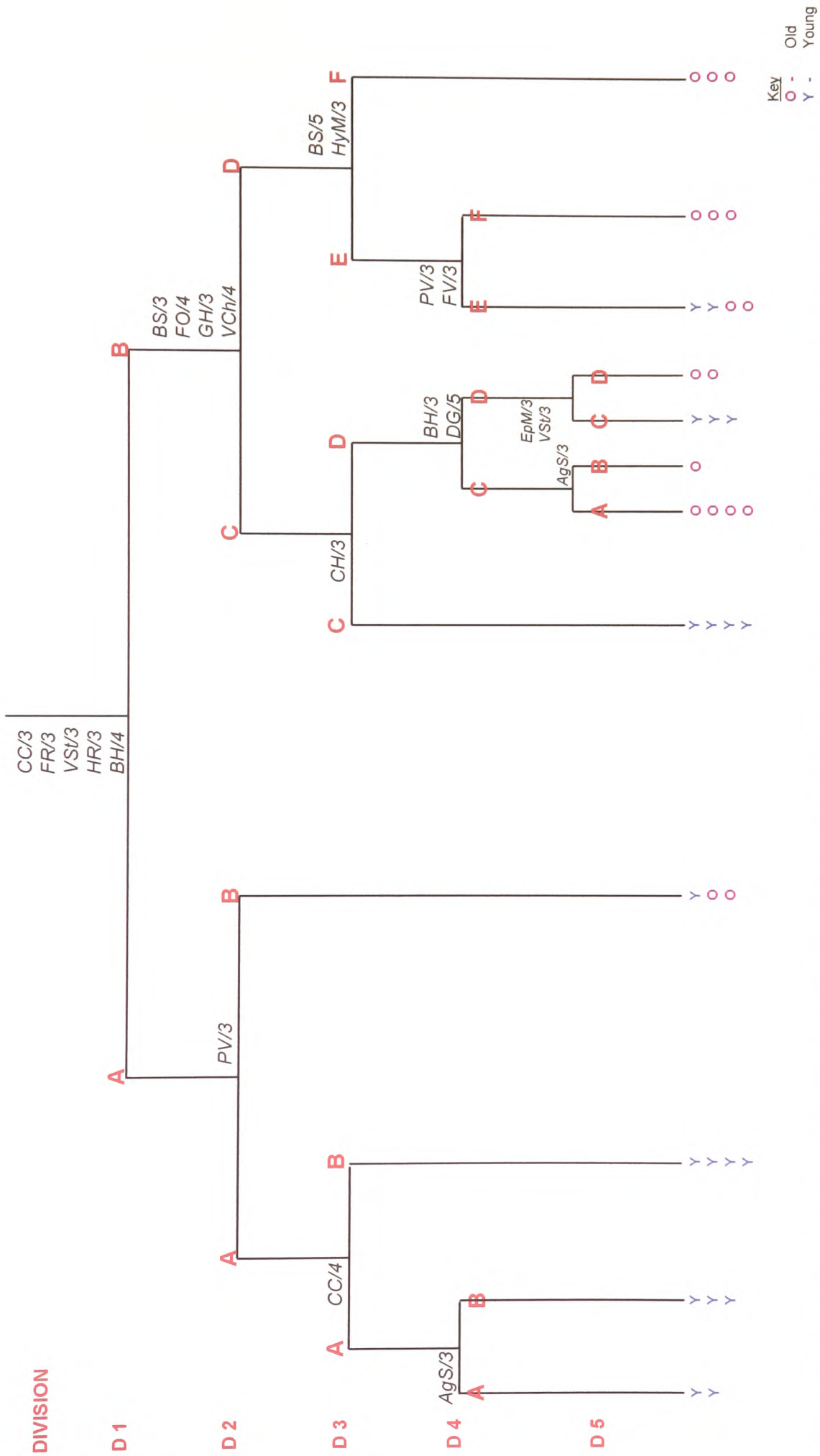


Figure 4.17 Classification of south-facing quadrats showing indicator species and end-group members listed by age (run T3)



122 **Figure 4.18** Classification of 36 south-facing quadrats showing indicator species and end-group members listed by age (run T4).

Division	Group	Cases	Old	Young	$\chi^2$
D1	A	25	9	16	5.23
	B	15	11	4	<b>p = 0.021</b>
D2	A	13	3	10	7.17
	B	12	6	6	p = 0.066
	C	10	7	3	
	D	5	4	1	
D3	A	1	0	1	11.00
	B	12	3	9	p = 0.14
	C	7	1	6	
	D	5	5	0	
	E	8	5	3	
	F	2	2	0	
	G	4	3	1	
	H	1	1	0	
D4	A	5	3	2	10.96
	B	7	0	7	p = 0.14
	C	2	0	2	
	D	5	1	4	
	E	4	4	0	
	F	1	1	0	
	G	4	1	3	
	H	4	4	0	

**Table 4.14 Group compositions related to age after classification of north-facing quadrats (run T5)**

#### **4.4.4 TWINSPAN classification of north-facing data**

With the influence of aspect removed, classification of the 40 north-facing quadrats (Run T5) shows that the primary division generates groups closely related to age (Figure 4.19; Table 4.14). In addition, though not statistically significant overall, three of the four groups (A, C and D) formed by division D2 also show evidence of this association.

Analyses by chi-square tests of groups formed at lower divisions is limited by the low numbers of cases. The test is considered unreliable when expected numbers of cases fall below 5 (Sokal and Rohlf, 1995). Such a limitation is therefore likely to occur at divisions D3 and D4 for data sets with 40 cases.

#### **4.4.5 Summary of classifications**

Results from classification indicate a general pattern characterized by a strong association between community structure and aspect with a secondary pattern associated with age. These patterns are consistently displayed in each of the analyses and appear relatively stable when the program parameters are changed and when subsidiary data sets are employed. The removal of anomalous cases does, however, generate different results in this analysis.

Abbreviation	Species
<i>AgS</i>	<i>Agrostis stolonifera</i>
<i>BeP</i>	<i>Bellis perennis</i>
<i>BS</i>	<i>Brachypodium sylvaticum</i>
<i>BH</i>	<i>Bromus hordeaceus</i>
<i>CH</i>	<i>Carex hirta</i>
<i>CE</i>	<i>Centaureum erythraea</i>
<i>CVg</i>	<i>Cirsium vulgare</i>
<i>CC</i>	<i>Crepis capillaris</i>
<i>DG</i>	<i>Dactylis glomerata</i>
<i>EpH</i>	<i>Epilobium hirsutum</i>
<i>EpM</i>	<i>Epilobium montanum</i>
<i>FO</i>	<i>Festuca ovina</i>
<i>FR</i>	<i>Festuca rubra</i>
<i>FV</i>	<i>Fragaria vesca</i>
<i>GH</i>	<i>Glechoma hederacea</i>
<i>HL</i>	<i>Holcus lanatus</i>
<i>HM</i>	<i>Holcus mollis</i>
<i>HyM</i>	<i>Hypericum maculatum</i>
<i>HR</i>	<i>Hypochaeris radicata</i>
<i>LtP</i>	<i>Lathyrus pratensis</i>
<i>LnC</i>	<i>Linum catharticum</i>
<i>MA</i>	<i>Myosotis arvensis</i>
<i>H61</i>	pea seedling
<i>PIL</i>	<i>Plantago lanceolata</i>
<i>PP</i>	<i>Poa pratensis</i>
<i>PV</i>	<i>Prunella vulgaris</i>
<i>PsP</i>	<i>Pseudoscleropodium purum</i>
<i>RR</i>	<i>Ranunculus repens</i>
<i>RF</i>	<i>Rubus fruticosus</i>
<i>SJ</i>	<i>Senecio jacobaea</i>
<i>SA</i>	<i>Sonchus asper</i>
<i>S8</i>	undetermined sedge
<i>VCh</i>	<i>Veronica chamaedrys</i>
<i>ViC</i>	<i>Vicia cracca</i>
<i>VSt</i>	<i>Vicia sativa</i>
<i>VR</i>	<i>Viola riviniana</i>

**Table 4.15 Abbreviations used to designate species used as indicators in TWINSpan classifications.**

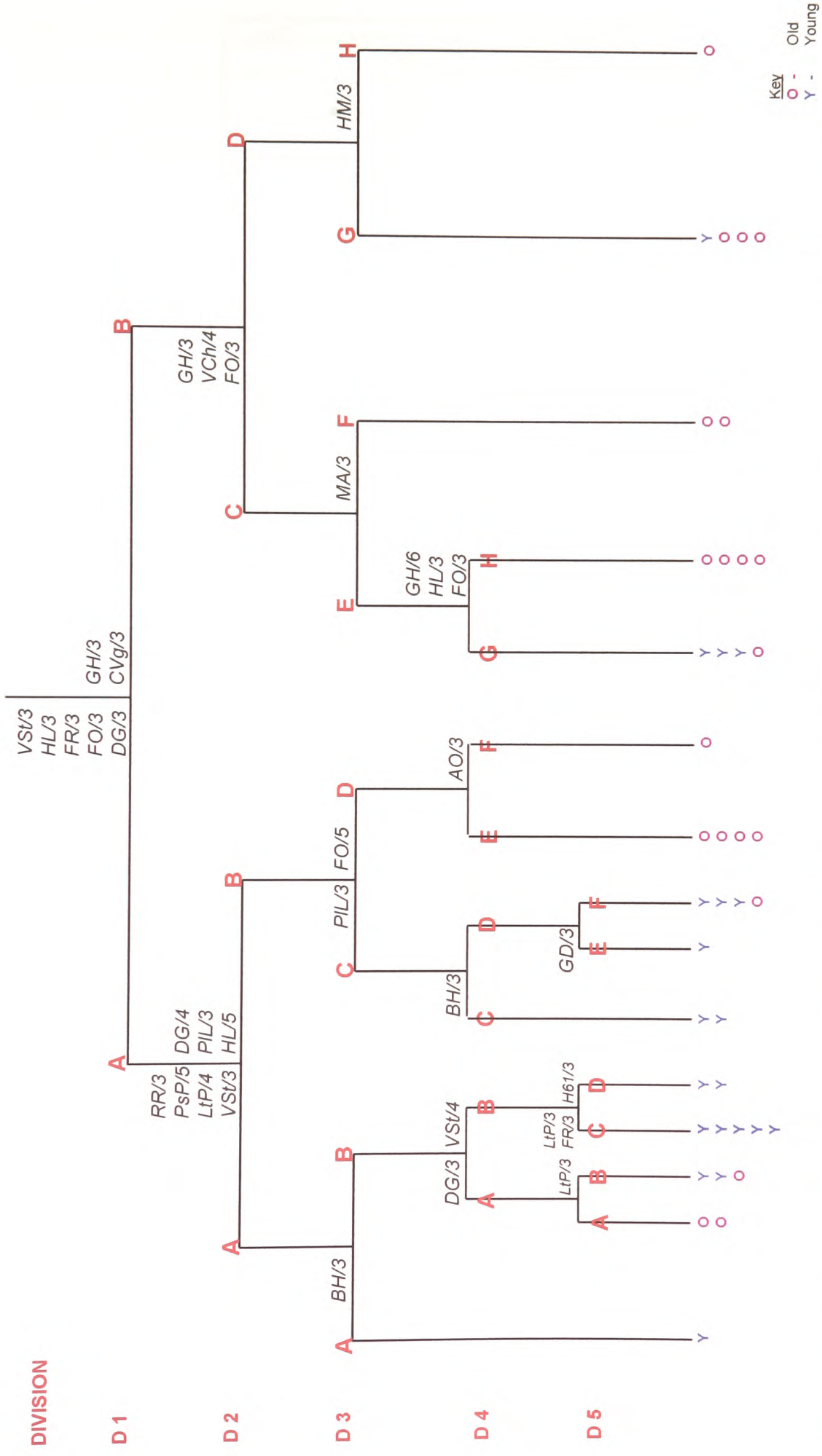


Figure 4.19 Classification of north-facing quadrats showing indicator species and end-group members listed by age (run T5)

T3 division D1	Young	Old
A/B	<i>FO/4</i> <i>FR/3</i> <i>VSt/3</i> <i>HR/3</i> <i>CC/3</i>	
division D2		
A/B	<i>BH/4</i> <i>SA/4</i> <i>VSt/4</i>	<i>CE/3</i>
C/D		<i>VCh/4</i> <i>GH/3</i> <i>BS/3</i> <i>FO/4</i>
T4 division D1		
A/B	<i>CC/3</i> <i>FR/3</i> <i>VSt/3</i> <i>HR/3</i> <i>BH/4</i>	
division D2		
A/B		<i>PV/3</i>
C/D		<i>BS/3</i> <i>FO/4</i> <i>GH/3</i> <i>VCh/4</i>

**Table 4.16 Indicator species age preferences generated from classifications of south-facing quadrats**

T5 division D1	Young	Old
A/B	<i>VSt/3</i> <i>HL/3</i> <i>FR/3</i> <i>FO/3</i> <i>DG/3</i>	<i>GH/3</i> <i>CVg/3</i>
division D2		
A/B	<i>RR/3</i> <i>PsP/5</i> <i>LiP/4</i> <i>VSt/3</i>	<i>DG/4</i> <i>PIL/3</i> <i>HL/5</i>

**Table 4.17 Indicator species age preferences generated from classification of north-facing quadrats**



#### 4.4.6 Indicator species

Where the classifications of quadrats form groups which are significantly related to revegetation age it is of interest to note those species or pseudospecies which are the major indicators used in generating dichotomies. An examination of these species can be used to assign age preferences to individual species and such species may thus shed light on the attributes most characteristic of particular successional stages.

Since the primary interest relates to species differences between age groups those classifications which control for the factor aspect are more likely to indicate species' age preferences. Indicator species for runs T3, T4 and T5 are listed in Tables 4.16 and 4.17.

In the classification of south-facing quadrats (Runs T3, T4), age discrimination is most apparent at divisions D1 and D2 (Figures 4.17, 4.18; Tables 4.11, 4.12). In run T5 the age discrimination on north-facing slopes is best shown by the groups formed at divisions D1 and by groups A and B at division D2 (Figure 4.19; Table 4.13).

It can be seen that, with the exception of the grasses *Festuca ovina* (FO/4), *Holcus lanatus* (HL/3, HL/5) and *Dactylis glomerata* (DG/3, DG/4), the species used as indicators show a consistent association with one or other age group, that is, they have high age-group fidelity. Of the three exceptions only the pseudospecies FO/4 occurs as an indicator in both old and young groups. The remaining two species occur as indicators representing higher abundances in old groups and lower abundances in young groups. This suggests that, except for *Festuca ovina*, the listed species and pseudospecies may be used to indicate attributes associated with particular ages and, consequently, with successional stage. The question of species age preferences is considered further in Section 5.1.2.

## 4.5 Canonical Correspondence Analysis

This section describes Canonical Correspondence Analysis (CCA) as an extension of Correspondence Analysis (CA) and its use in highlighting the role of aspect and age in structuring the vegetation communities. CCA is the method of choice for investigating environment-species relations (Ter Braak, 1986; Palmer, 1993). In this study the layout of the samples is designed to highlight differences in species compositions between sites having binary levels of the factors age, aspect and height. These factors are used within the CANOCO program (Section 3.6.3) as environmental variables together with a number of other attributes related to the measured variables recorded for each quadrat.

### 4.5.1 The CCA algorithm

Canonical Correspondence Analysis performs a data analysis which combines Correspondence Analysis with a regression or multiple regression (Section 3.6.3). The term “canonical” here refers to the selection of particular variables as being of prime importance in the analysis of species-environment relations; the ordination is constrained by these variables (Ter Braak, 1987-1992).

The CCA technique is a development of the CA method of numerical analysis of species abundances and sites (Section 4.2.1). It contains an additional step within the iteration cycle. After the new site scores are calculated they are fitted in a multiple regression procedure in which the independent variables are the measured environmental factors. Regression analysis seeks to describe the response variable (in this case the site scores) as a function of one or more explanatory variables (the environmental variables). The site scores calculated from the species scores are replaced by the fitted values predicted from the regression equation. The iteration proceeds with a recalculation of the species scores from which new site scores are calculated these being again replaced by values fitted by multiple regression. From the final iteration site scores calculated by both methods are available for interpretation. The weights given to the environmental variables in the final iteration are reported as the regression, or canonical, coefficients. Site scores calculated by the algorithm containing the regression element form the first canonical (or environmental) axis. Site scores calculated from species scores, without the regression procedure, form the first species axis. The correlation between these two sets of sites scores represents a measure of

the degree of association between the species and the environmental variables (e.g. Table 4.21) termed the species-environment correlation (Ter Braak, 1987).

In addition to the species-environment correlation the CCA output contains a number of elements which describe the relationships within the data and which may be used to interpret the analysis. These are;

i)- The eigenvalues for each axis indicate, as in CA, the extent of the variation in the data explained by that axis. Because of the added constraint of the regression algorithm these are generally lower than those from CA. Ter Braak (1987-92) suggests, however that eigenvalues as low as 0.02 may contain useful information.

ii)- The cumulative percentage variance explained by each axis reflects the relative importance of the axis and the overall explanatory power of the procedure. The variance inflation factor measures the degree to which each environmental variable in the analysis is correlated with other environmental variables. A warning is given by Ter Braak (1987-92) that an inflation factor of 20 or greater indicates that a variable is almost perfectly correlated with other variables and that “its regression coefficient is unstable and does not merit interpretation” (p. 40).

iii)- The canonical coefficients are the weights given to each environmental variable in the final regression equation and as such represent the relative power of that variable in explaining the species distributions.

iv)- The t-values reported for each of these coefficients are analagous to those conventionally generated by regression procedures but are not suited for use in a t-test in the case of canonical analyses because of their greater levels of variance. Nevertheless they may be useful in interpreting the coefficients; those variables with a t-value of less than 2.1 do not make an additional contribution to the fit in the regression equation (Ter Braak, 1987-92).

The program output is summarized in an ordination diagram (e.g. Figure 4.20) in which sites, species and environmental variables are displayed in such a way as to illustrate the relations between them. Sites (quadrats) are shown as open circles, species as filled circles and environmental variables as arrows or vectors. The length of a vector indicates the

variable's relative explanatory power and its direction the degree of correlation between it and the ordination axes and the other variables. Sites and species may be related to their levels of each environmental variable by reference to their orthogonal positions along the appropriate vector. Nominal variables are also indicated by a triangular symbol showing the position of the centroid for sites possessing that feature.

#### **4.5.2 Choice of variables for CCA**

A consideration of the nature of the factors used in CCA is useful in order to clarify the methods of analysis applied in this study.

The CCA program, in common with CA and DCA, assumes an underlying statistical model in which species occurrences display a non-linear, unimodal distribution with respect to an environmental gradient (Section 3.6.2). This assumption is generally accepted (Palmer, 1993) and the model is appropriate where gradients relate to specific physical or chemical variables; there is ample evidence showing that species abundances decline on either side of some optimum value for a given combination of species and variable (Kent and Coker, 1992). In this study the factors age, aspect and height are treated as environmental variables. A successional model may characterize community compositions as changing over time in a directional manner. In this context, and by accepting this assumption, time may be considered to be an environmental factor in the same way as, say, a moisture gradient, where sites may be scored for high or low moisture levels and species compositions related directly to levels of this factor. That is, sites have known, measured levels of the factor time associated with them and it therefore makes sense to refer to older sites having a higher level of time than the younger sites. If however the assumption of a linear sequence of community change through time is not made then it is no longer appropriate to regard old sites as having a greater level of the factor time but rather that sites have different classes of age. Time in this sense becomes a categorical variable rather than an ordinal one.

A similar consideration may be applied to the factor aspect. In this study this factor takes one of two values, north or south, but each may be seen as representing an amalgam of a number of physical variables. Levels of solar radiation (direct and indirect) are likely to be higher on south facing slopes with the consequence that day time surface temperatures will

be higher and evaporative moisture loss more pronounced (Section 1.1.4). This factor may be modified by the degree of shelter and shade offered by adjacent features such as buildings and other revetments and also by the angle of the slope. Each of these factors may also influence the exposure of the slope to wind with a further consequence for evaporative losses. A presumed gradient from south-facing to north-facing slopes may be representative of a change in a number of these factors. In this study south-facing slopes may be characterized as hot, dry and exposed whilst those facing north are relatively cool, moist and sheltered. With such a combination of variables it may not be appropriate to assign an ordinal division between the sites since it is unclear which group has a greater level of which factor. To assign a level of 2 to south-facing and 1 to north-facing sites is to imply that light is the factor under consideration; if the reverse then it is more likely to represent a measure of available moisture.

In a similar way the factor height may be considered to combine factors related to moisture level determined by the action of gravity, exposure to solar radiation and to wind and again each of these factors may be modified by aspect. Again the characterization of this factor by the use of an ordinal scale is questionable.

For the reasons discussed above the factors age, aspect and height were represented in the data as nominal variables rather than as ordinal gradients. Where nominal variables are to be included in a CCA analysis Ter Braak (1987-92) recommends that each level of the variable is represented in the data as a separate variable with values 1 and 0 being assigned to cases where the variable is present or not. Thus in the case of the factor age, two variables are defined, young and old and each quadrat is scored separately for each. However, since such pairs of variables have perfect, negative correlations one of each pair was omitted from the analyses. The same consideration applies to the factors north, south, upper and lower.

CCA provides the option of investigating the effects of interactions between variables by defining a new variable as the product of two measured variables. Thus the effect of, say, height on aspect discussed above could, in principle, be included by constructing a variable "asp  $\times$  hgt". However where the variables are nominal and represented by 1 or 0, such product variables are unlikely to provide a meaningful separation between classes (Table 4.18).

	product value
South × Upper	1 × 1 = 1
South × Lower	1 × 0 = 0
North × Upper	0 × 1 = 0
North × Lower	0 × 0 = 0

**Table 4.18 Example products of nominal variables**

Following the same argument these four new classes are each defined as a new nominal variable which is represented in the data as a 1 or 0. In a similar way product variables are defined for interactions between pairs of all three factors giving a total of twelve new product variables identified as; SU, SL, NU, NL, YS, YN, OS, ON, YU, YL, OU, OL.

The CCA analyses included 28 variables comprising the three factors age, aspect and height, together with; slope angle, a number of physical features present in the sample quadrat and recorded during the vegetation survey (Section 3.5.5), and the twelve defined product variables included to test for interactions between the factors. All data representing environmental variables were standardized within the CANOCO program to a mean of zero and unit variance (Ter Braak, 1987-1992). The full list of variables and their original values is contained in Appendix A.

#### **4.5.3 Forward selection of variables for canonical analysis**

CANOCO contains an option for the selection and testing of variables prior to their inclusion in the canonical analysis. Variables are selected stepwise, in the order of the extra species variance explained by the variable. For each variable included a Monte Carlo permutation test is performed (Sokal and Rohlf, 1995). This procedure generates 99 random data sets in each of which samples are allocated at random to the species data. The difference in explanatory power produced by inclusion of the variable in the regression equation is compared with that obtained for each of the random data sets. The analysis tests the hypothesis that the addition of the selected variable does not increase the fit of the regression equation to the data significantly more than to the random data sets. If this null hypothesis can be rejected at the conventional level of significance ( $p = 0.05$ ) then the variable is deemed worthy of inclusion. Each variable is selected and tested in turn until the null hypothesis can no longer be rejected.

	SpAX1	SpAX2	SpAX3	SpAX4	EvAX1	EvAX2	EvAX3	EvAX4	B	DA	Yng	Nth
SpAX1	1											
SpAX2	-0.0845	1										
SpAX3	0.0731	-0.0755	1									
SpAX4	-0.0206	0.0311	-0.003	1								
EvAX1	0.8666	0	0	0	1							
EvAX2	0	0.7342	0	0	0	1						
EvAX3	0	0	0.7411	0	0	0	1					
EvAX4	0	0	0	0.6619	0	0	0	1				
B	0.5743	-0.297	0.3793	0.2435	0.6627	-0.4045	0.5118	0.3678	1			
DA	0.3236	0.4529	-0.3114	0.3647	0.3734	0.6168	-0.4202	0.5509	-0.0145	1		
Yng	0.2751	-0.4261	-0.5547	-0.0303	0.3175	-0.5803	-0.7485	-0.0458	0.0452	0.0499	1	
Nth	-0.7735	-0.3014	-0.022	0.1219	-0.8926	-0.4106	-0.0297	0.1841	-0.3729	-0.4726	-0.0313	1

**Table 4.19 CCA1: species-environment correlation matrix**

SpAX = sample score axes derived from species data

EvAX = sample score axes calculated as a linear combination of environmental variables.

Environmental variables:

B = areal measure of bare ground

DA = areal measure of ant hills

Yng = age; quadrats on young slopes have positive values of age.

Nth = aspect; quadrats on north slopes have positive values of aspect.

Name	(Weighted) Mean	Stand. dev.	Inflation factor
SpAX1	0.0000	1.1539	
SpAX2	0.0000	1.3620	
SpAX3	0.0000	1.3494	
SpAX4	0.0000	1.5107	
EvAX1	0.0000	1.0000	
EvAX2	0.0000	1.0000	
EvAX3	0.0000	1.0000	
EvAX4	0.0000	1.0000	
B	4.9811	8.8119	1.2310
DA	2.4016	4.0790	1.3651
Yng	0.5373	0.4986	1.0048
Nth	0.5047	0.5000	1.5816

**Table 4.20 CCA1: canonical variables and axes**

SpAX = sample score axes derived from species data

EvAX = sample score axes calculated as a linear combination of environmental variables.

Environmental variables:

B = areal measure of bare ground

DA = areal measure of ant hills

Yng = age; quadrats on young slopes have positive values of age.

Nth = aspect; quadrats on north slopes have positive values of aspect.

As discussed above, where nominal variables are denoted as present or absent, then pairs of variables, such as north and south, occur which show perfect negative correlation. In this analysis only one of each such pair is included in the regression model, despite the indication of substantial “extra fit” by the forward selection algorithm. Using these criteria four variables were found which gave significantly greater extra fit to the regression; these were north, young, DA and bare. DA refers to the number and extent of ant hills, and bare to the area of bare ground, recorded in the vegetation survey. It is notable that neither height nor slope angle gave an improved regression and none of the interaction products showed a significant contribution.

#### **4.5.4 CCA analyses**

The results from three CANOCO runs are described below. Each included all quadrats and all species, utilized the option for downweighting of rare species, and used the four environmental variables referred to above.

##### **4.5.4.1 CCA run 1**

The first run (CCA1) aimed to generate an overall description of the data which explicitly includes the environmental factors. A summary of the CCA1 output is shown below (Tables 4.19 - 4.23; Figures 4.20 and 4.21). Table 4.19 shows the correlations between the ordination axes derived from species data and those derived as linear sums of environmental variables together with the environmental variables selected for inclusion in the analysis. Table 4.20 lists these axes and variables together with a summary of their means and standard deviations and the variance inflation factor associated with each of the environmental variables. Table 4.21 shows a summary of the ordination and includes measures of the eigenvalues associated with the species and environmental axes together with the amount of the variance explained by each of the axes and the overall correlation between the species and environmental components for each axis. Table 4.22 displays the canonical or regression coefficients derived for each environmental variable; the relative importance of each of the chosen variables may be compared. Table 4.23 gives the t-values from these regression functions for each of the environmental variables together with the fraction of the variance explained (Fr. Exp) by them for each axis.



	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.222	0.117	0.086	0.042	2.700
Species-environment correlations	0.867	0.734	0.741	0.662	
Cumulative percentage variance					
of species data	8.2	12.6	15.7	17.3	
of species-environment relation	47.4	72.6	90.9	100.0	
Sum of all unconstrained eigenvalues					2.700
Sum of all canonical eigenvalues					0.467

**Table 4.21 CCA1: summary of the CCA ordination**

	Axis 1	Axis 2	Axis 3	Axis 4
B	38	-53	52	73
DA	2	44	-40	101
Yng	28	-59	-75	-10
Nth	-74	-42	-5	93
Eigenvalue	0.222	0.117	0.086	0.042

**Table 4.22 CCA1: regression/canonical coefficients ( $\times 100$ ) for standardized variables**

Environmental variables:  
 B = bare ground  
 DA = ant hills  
 Yng = age  
 Nth = aspect

Name	Axis 1	Axis 2	Axis 3	Axis 4
B	510	-445	451	506
DA	23	354	-325	659
Yng	415	-553	-719	-76
Nth	-879	-310	-35	566
Fr Exp	0.474	0.251	0.183	0.091

**Table 4.23 CCA1: t-values ( $\times 100$ ) of regression coefficients**

Environmental variables:  
 B = bare ground  
 DA = ant hills  
 Yng = age  
 Nth = aspect  
 Fr Exp = fraction of variance explained

Table 4.19 shows relatively strong correlations ( $r = 0.8666, 0.7342, 0.7411$  and  $0.6619$ ) between each of the four axes derived from species data (SpAx) and the respective axis generated as a combination of environmental variables (EvAx). These figures indicate the strength of the relation between species data and environmental data. However the importance of the variables in explaining the data is best expressed by the eigenvalues associated with each axis. It may be seen (Table 4.21) that the eigenvalues due to the environmental data give a total variance of 0.467 which is small in relation to the total inertia in the data of 2.700. Axes 1 and 2 together explain 12.6%, and all four axes represent 17.3% of the total variance. This is somewhat less than the explained variance in DCA (Table 4.4) as a result of the constraining nature of the algorithm (Ter Braak, 1987-1992). Table 4.19 indicates that the factor aspect has a strong correlation with environmental axis 1 (EvAx1), and age with EvAx2 and EvAx3 confirming the findings of DCA that both factors have a strong influence on the ordination.

The inflation factors (Table 4.20) are small, very much less than 20.0, indicating that the four selected variables do not demonstrate collinearity and may therefore be usefully interpreted (Ter Braak, 1987-1992). In addition to the factors age and aspect, the variables bare and DA are also shown to have a significant influence. Bare is, however, necessarily correlated with species occupying sparsely vegetated ground and so may be regarded as reflecting an effect rather than an influence. Ant hills are known to show a bias towards south-facing slopes (Wells *et al.*, 1976); they are negatively correlated with the factor Nth (Table 4.19). The presence of ant hills and their possible influence on community composition is discussed below (Section 6.1.3).

Figures 4.20 and 4.21 summarize the ordination in graphical form; they each illustrate the co-relations between the environmental variables, quadrats and species within a two dimensional space defined by pairs of axes. They indicate the relative strength of the factors as agents in structuring the community. Figure 4.20 shows the dominant influence of aspect indicated by the nominal variable north (Nth) which is seen to be correlated with axis 1. The factor age, represented by the vector young, is correlated with axis 2 and is orthogonal with respect to aspect. The abundance of ant hills (DA) has a negative correlation with north indicating its association with south-facing sites. Filled triangular symbols indicate the position of the centroids of each of the nominal variables north and young.

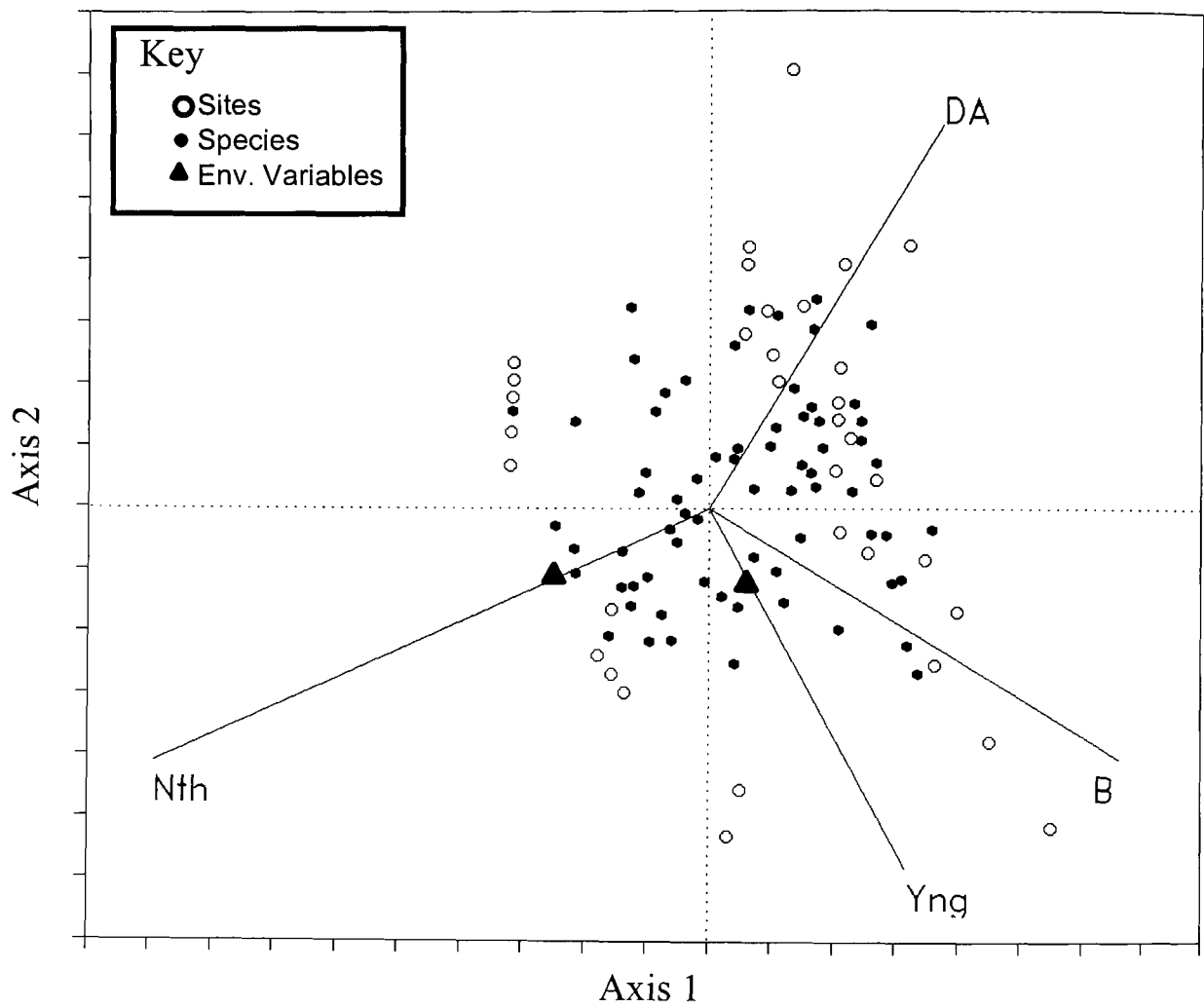


Figure 4.20 CCA ordination (run 1) of sites, species and environmental variables: axes 1 and 2

Figure 4.21 shows the ordination results on the minor axes 3 and 4. Axis 3 is strongly associated with the factor young and axis 4 with north. However, since these axes explain only 3%, and 1.6% respectively, of the total variance, an interpretation is unlikely to be of value.

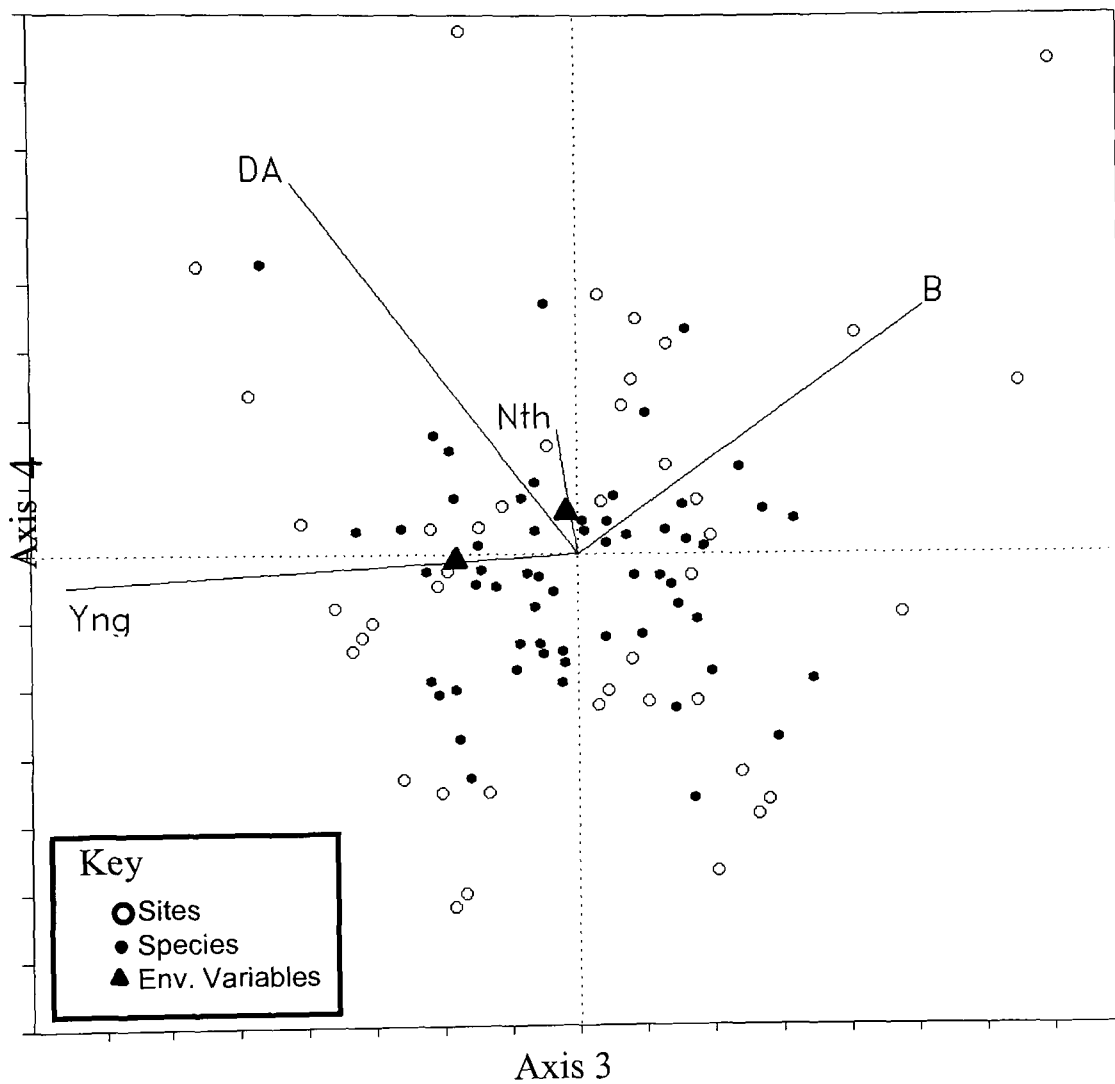


Figure 4.21 CCA ordination (run 1) of sites, species and environmental variables: axes 3 and 4

	SpAX1	SpAX2	SpAX3	SpAX4	EvAX1	EvAX2	EvAX3	EvAX4	B	DA	Old
SpAX1	1.000										
SpAX2	0.1007	1.000									
SpAX3	-0.0487	0.0105	1.000								
SpAX4	-0.2514	-0.4535	-0.2286	1.000							
EvAX1	0.7418	0.0	0.0	0.0	1.000						
EvAX2	0.0	0.7331	0.0	0.0	0.0	1.000					
EvAX3	0.0	0.0	0.6779	0.0	0.0	0.0	1.000				
EvAX4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0			
B	0.5425	0.3900	0.2894	0.0	0.7313	0.5320	0.4269	0.0	1.000		
DA	-0.2968	-0.3690	0.5192	0.0	-0.4001	-0.5033	0.7659	0.0	-0.2333	1.000	
Old	-0.5149	0.5244	0.0544	0.0	-0.6941	0.7154	0.0802	0.0	-0.0928	-0.0209	1.000

**Table 4.24 CCA2: species-environment correlation matrix**

SpAX = sample score axes derived from species data

EvAX = sample score axes calculated as a linear combination of environmental variables.

Environmental variables:

B = areal measure of bare ground

DA = areal measure of ant hills

Old = age; quadrats on old slopes have positive values of age.

Name	(Weighted) Mean	Stand. dev.	Inflation factor
SpAX1	0.0	1.3480	
SpAX2	0.0	1.3641	
SpAX3	0.0	1.4752	
SpAX4	0.0	1.000	
EvAX1	0.0	1.000	
EvAX2	0.0	1.000	
EvAX3	0.0	1.000	
EvAX4	0.0	0.0	
B	4.9811	8.8119	1.2409
DA	2.4016	4.0790	1.3644
Old	0.4526	0.4977	1.0134

**Table 4.25 CCA2: canonical variables and axes**

SpAX = sample score axes derived from species data

EvAX = sample score axes calculated as a linear combination of environmental variables.

Environmental variables:

B = areal measure of bare ground

DA = areal measure of ant hills

Old = age; quadrats on old slopes have positive values of age.

#### 4.5.4.2 CCA run 2

As in previous analyses the effect of age on community compositions may be better illustrated if the influence of aspect is removed. Whereas in DCA and TWINSpan it was necessary to divide the data set in order to treat each aspect separately, CCA allows for the effects of a variable to be subtracted from the analysis. To this end a second CCA run (CCA2) was performed in which the same four environmental variables were included but in which the factor north was declared as a co-variable. The results of the analysis are shown in Tables 4.24 - 4.28 and Figure 4.22. The variance due to the canonical variables is considerably reduced (Table 4.26) as a consequence of the removal of the effects of aspect.

Figure 4.22 shows the environmental variables plotted in relation to the sites. A polygon is drawn around the groups of young and old sites. It can be seen that, with a single exception, the sites are well segregated along the age vector. The exception to this pattern is quadrat 74 which occupies a position within the area of the young sites. This quadrat was previously identified as one having anomalous features (Section 4.1.1) in that it contained relatively large areas of ground disturbed by rabbits and it also contained "netting" indicating that repairs had been made to the revetment slope. These features suggest that more than usual levels of disturbance have been experienced at this site. The quadrat is also unusual in having the only occurrence of *Cruciata laevipes* and a moderate level of *Hypochoeris radicata*, a species associated in this study with young sites (see Appendix D).

Figure 4.23 shows species plotted in the same ordination space defined by the three environmental variables. This representation allows individual species to be located along environmental gradients denoting a preference for each of the significant factors. Abbreviations used to designate species are given in Appendix D. The reliability of this measure may, however, be limited by the frequency score of the species. Thus, for example, the species *Cruciata laevipes*, noted above, shows a high score for the variable bare yet this is based on data from a single quadrat. Frequencies for each species are also shown in Table 4.35 and Appendix D.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.135	0.084	0.047	0.213	2.700
Species-environment correlations	0.742	0.733	0.678	0.0	
Cumulative percentage variance					
of species data	5.4	8.8	10.7	19.2	
of species-environment relation	50.8	82.2	100	0.0	
Sum of all unconstrained eigenvalues					2.502
Sum of all canonical eigenvalues					0.267

**Table 4.26 CCA2: summary of the CCA ordination**

	Axis 1	Axis 2	Axis 3	Axis 4
B	66	56	71	0
DA	-31	-42	105	0
Old	-64	76	16	0
Eigenvalue	0.135	0.084	0.047	0.213

**Table 4.27 CCA2: regression/canonical coefficients ( $\times 100$ ) for standardized variables**

Environmental variables:

B = bare ground

DA = ant hills

Old = age

Name	Axis 1	Axis 2	Axis 3	Axis 4
B	564	466	508	0
DA	-253	-333	716	0
Old	-613	702	127	0
Fr Exp	0.508	0.314	0.178	0.000

**Table 4.28 CCA2: t-values ( $\times 100$ ) of regression coefficients**

Environmental variables:

B = bare ground

DA = ant hills

Old = age

Fr Exp = fraction of variance explained

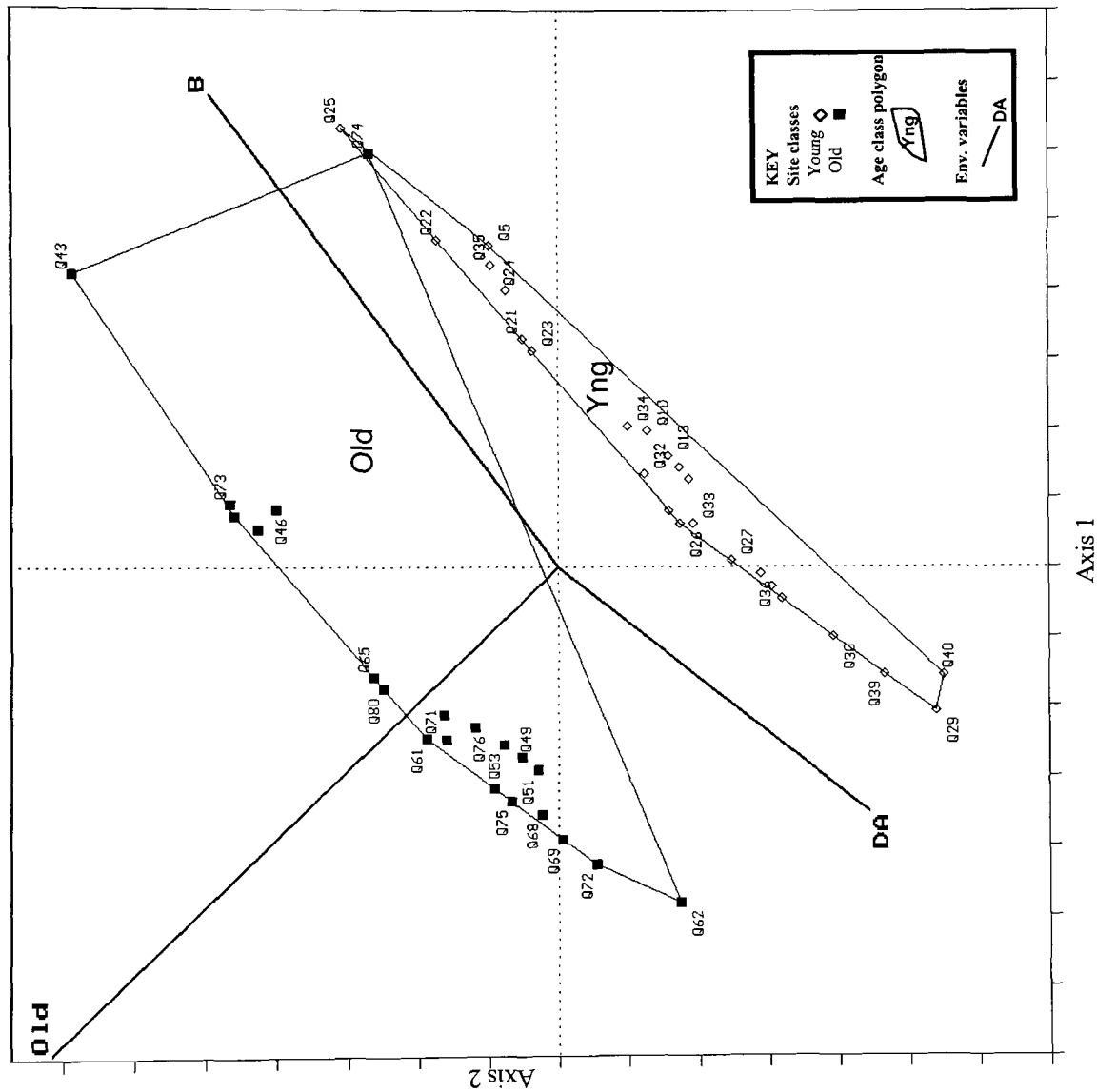


Figure 4.22 CCA ordination (run 2) showing quadrats plotted and classified by age group on axes 1 and 2



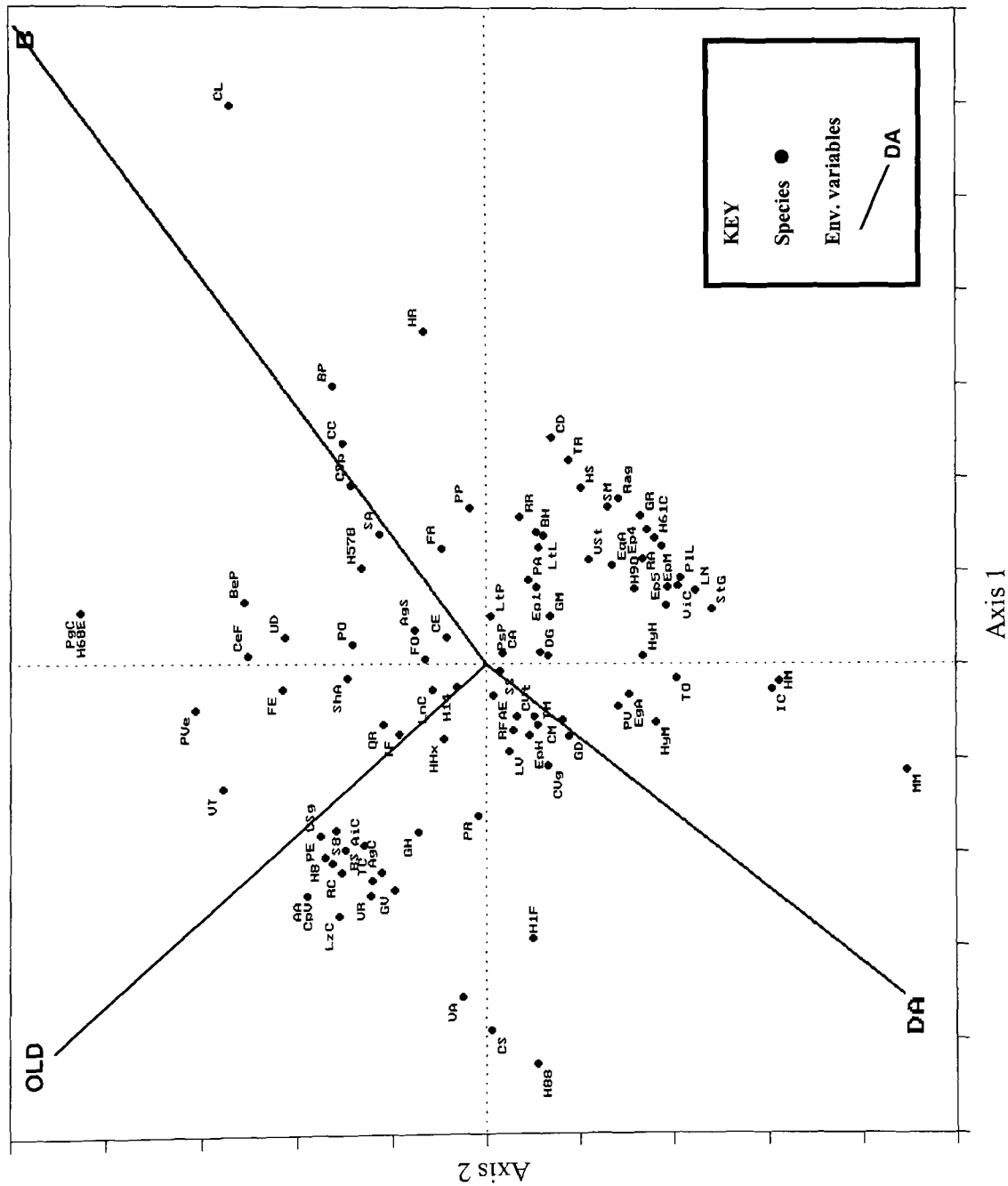


Figure 4.23 CCA run 2; species plotted in relation to age on axes 1 and 2

	SpAX1	SpAX2	SpAX3	SpAX4	EvAX1	EvAX2	EvAX3	EvAX4	Old
SpAX1	1.000								
SpAX2	-0.0382	1.000							
SpAX3	-0.3591	0.0	1.000						
SpAX4	0.3128	0.0	0.0	1.000					
EvAX1	0.7649	0.0	0.0	0.0	1.000				
EvAX2	0.0	0.0	0.0	0.0	0.0	1.000			
EvAX3	0.0	0.0	0.0	0.0	0.0	0.0	1.000		
EvAX4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.000	
Old	0.7649	0.0	0.0	0.0	1.000	0.0	0.0	0.0	1.000

**Table 4.29 CCA3: species-environment correlation matrix**

SpAX = sample score axes derived from species data

EvAX = sample score axes calculated as a linear combination of environmental variables.

Environmental variables:

Old = age; quadrats on old slopes have positive values of age.

Name	(Weighted) Mean	Stand. dev.	Inflation factor
SpAX1	0.0	1.3074	
SpAX2	0.0	1.000	
SpAX3	0.0	1.000	
SpAX4	0.0	1.000	
EvAX1	0.0	1.000	
EvAX2	0.0	0.0	
EvAX3	0.0	0.0	
EvAX4	0.0	0.0	
Old	0.4526	0.4977	1.0470

**Table 4.30 CCA3: canonical variables and axes**

SpAX = sample score axes derived from species data

EvAX = sample score axes calculated as a linear combination of environmental variables.

Environmental variables:

Old = age; quadrats on old slopes have positive values of age.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.107	0.213	0.198	0.161	2.700
Species-environment correlations	0.765	0.0	0.0	0.0	
Cumulative percentage variance					
of species data	4.5	13.3	21.5	28.2	
of species-environment relation	100	0	0	0	
Sum of all unconstrained eigenvalues					2.407
Sum of all canonical eigenvalues					0.107

**Table 4.31 CCA3: summary of the CCA ordination**

#### 4.5.4.3 CCA run 3

In order to relate species occurrences directly to age class it is preferable to eliminate the influence of all factors except age; the third CCA run (CCA3) uses this approach. It again uses the same four environmental variables this time with the variables north, bare and DA as co-variables to exclude their influence; only the factor age was allowed to influence the ordination. With only this single variable, the species scores for the environmental axis are equivalent to a measure of the species preference for successional age. As such this score represents one method of determining age-discriminant species (Section 5.1.2). The results are illustrated below (Figure 4.24; Tables 4.29-4.33). Table 4.34 shows those age scores ( $A_{CCA}$ ) for species with an absolute age score greater than 50; it also excludes those species which occur in only a single quadrat, that is, those having a frequency of 1. Scores are listed in numerical order and denote the strength of a species preference for the nominal factor old; negative values therefore represent a preference for young sites. A full list of species age scores and frequencies is contained in Appendix D.

	Axis 1	Axis 2	Axis 3	Axis 4
Old	102	0	0	0
Eigenvalue	0.107	0.213	0.198	0.161

**Table 4.32. CCA3: regression/canonical coefficients ( $\times 100$ ) for standardized variables**

Environmental variables:  
Old = age

Name	Axis 1	Axis 2	Axis 3	Axis 4
Old	103	0	0	0
Fr Exp	1.0	0.0	0.0	0.0

**Table 4.33. CCA3: t-values ( $\times 100$ ) of regression coefficients**

Environmental variables:  
Old = age  
Fr Exp = fraction of variance explained

Species	Abbrev.	Freq.	Age score (A <sub>CCA</sub> )
<i>Aira caryophyllea</i>	AiC	2	130
<i>Primula veris</i>	PVe	6	121
<i>Verbascum thapsus</i>	VT	2	118
	H8	6	118
	S8	3	112
<i>Viola riviniana</i>	VR	8	111
<i>Galium verum</i>	GV	2	109
<i>Luzula campestris</i>	LzC	2	108
<i>Carex flacca</i>	CF	6	107
<i>Dryopteris felix-mas</i>	DFm	5	107
<i>Agrostis capillaris</i>	AgC	12	101
<i>Brachypodium sylvaticum</i>	BS	20	96
<i>Cerastium fontanum</i>	CeF	4	93
<i>Rumex crispus</i>	RC	3	92
	H1F	3	87
<i>Fraxinus excelsior</i>	FE	27	84
<i>Glechoma hederacea</i>	GH	22	75
<i>Bellis perennis</i>	BeP	11	72
<i>Potentilla reptans</i>	PR	4	51
<i>Ranunculus repens</i>	RR	26	-54
<i>Bromus hordeaceus</i>	BH	29	-55
<i>Lathyrus linifolius</i>	LtL	5	-59
<i>Stachys sylvatica</i>	SS	2	-60
<i>Carex hirta</i>	CH	13	-63
<i>Hypochaeris radicata</i>	HR	16	-66
<i>Hypericum humifusum</i>	HyH	9	-69
<i>Vicia sativa</i>	VSt	53	-69
<i>Rosa</i> agg.	Rag	4	-72
<i>Equisetum arvense</i>	EqA	6	-76
<i>Carex divulsa</i>	CD	3	-78
<i>Erigonum acer</i>	EgA	2	-78
<i>Malva moschata</i>	MM	3	-83
<i>Sanguisorba minor</i>	SM	6	-84
<i>Holcus mollis</i>	HM	2	-88
<i>Trifolium repens</i>	TR	9	-88
<i>Plantago lanceolata</i>	PIL	19	-90
<i>Geranium rotundifolium</i>	GR	4	-91
<i>Lathyrus nissolia</i>	LN	22	-91
<i>Vicia cracca</i>	ViC	9	-91
<i>Stellaria graminea</i>	StG	8	-92
	Ep4	5	-93
<i>Epilobium montanum</i>	EpM	6	-93
<i>Heracleum sphondylium</i>	HS	3	-96
<i>Stellaria pallida</i>	StP	5	-98
<i>Vicia sepium</i>	VSp	4	-99
	H61C	2	-99
	T1	2	-99

**Table 4.34. CCA run 3: species age scores and frequencies**

Freq. - number of quadrats in which the species occurs

Age score (A<sub>CCA</sub>) - species score on the age axis (+ve values indicate a preference for old slopes)

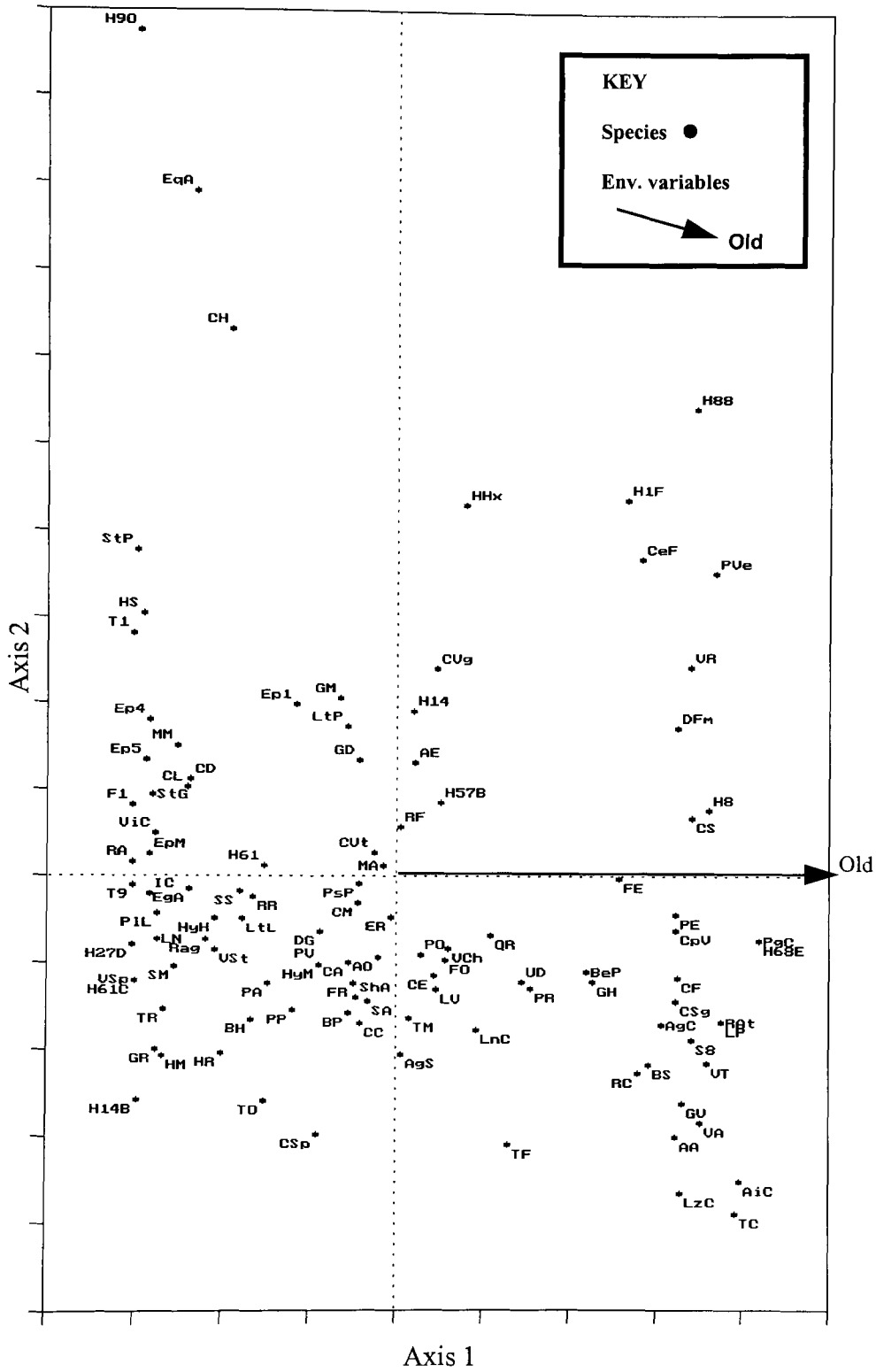


Figure 4.24 CCA run 3: species plotted in relation to age

#### 4.5.5 CCA conclusions

The results from CCA provide

- a concise summary of the data both for the species and environmental variables.
- an efficient method of removing the effects of a selected factor from the analysis
- an efficient method of highlighting relevant factors and variables
- a method for characterizing species with respect to a single factor.

The results show

- a large amount of unexplained variance
- the dominant influence of the factors aspect, age and the variables DA and bare
- that the variables height and slope do not have a large influence.

## **CHAPTER FIVE: ANALYSES OF SPECIES AND COMMUNITY ATTRIBUTES**

In the previous chapter the data have been viewed as a whole and, using CA, CCA and TWINSpan, the analyses have attempted to expose the underlying structure and to relate that structure to the major factors of aspect and age and to other potentially relevant variables. The approach adopted in this chapter attempts to uncover relationships at the species and community level. Individual species have been characterized by their life history types, typical habitats, both environmental and successional, and strategies (Section 1.6.1) and communities by features related to the relative abundances of species (Section 1.6.2). Analyses are employed here with the aim of testing predictions made about successional changes in species, in plant traits and in community attributes by the models described in Chapter One.

Section 5.1 deals with changes in species between age groups and the calculation of age preferences for species. Predictions relating to changes in species traits, life cycle type and plant strategies over successional time are analysed in Section 5.2. Section 5.3 includes tests for changes in community level attributes and the findings are compared with the expectations of the models of Odum and Peet described in Section 1.5. Section 5.4 deals with evidence of differences in the degree of interspecific associations between young and old revegetations and its relation to the predictions of Peet (Section 1.6.2.4). The final analysis (Section 5.5) describes the evidence for changing levels of community predictability over successional time.

### **5.1 Changes in species over successional time**

Changes over time have been described and modeled at the level of the species and the community. This section describes how differences in species assemblages may be characterised by an inspection of the species which favour one or other age group.

Spp.	Species	Abbrev	Freq	Avg abund	U value <sup>1</sup> North	U value <sup>1</sup> South	Habitats <sup>2</sup>
7	<i>Bellis perennis</i>	BeP	11	11	-160.0*	+169.0	P
8	<i>Bromus hordeaceus</i>	BH	29	25	-160.0*	-64.0**	WS
10	<i>Brachypodium sylvaticum</i>	BS	20	25	+147.0*	+140.0*	WD
16	<i>Carex flacca</i>	CF	6	17	+160.0*	+180.0	CG
17	<i>Carex hirta</i>	CH	13	31	+191.5	-140.0*	G/WD
26	<i>Dryopteris felix-mas</i>	DFm	5	10	+150.0*	-	WD
27	<i>Dactylis glomerata</i>	DG	54	9	-102.5*	-151.0	P/R
48	<i>Hypochaeris radicata</i>	HR	16	16	-170.0	-122.0*	P/R
51	<i>Hypericum maculatum</i>	HyM	22	18	-172.5	-134.0*	R/WD
53	<i>Lathyrus nissolia</i>	LN	22	3	-100.0**	-80.0**	WS
56	<i>Lathyrus linifolius</i>	LtL	5	1	-160.0*	+190.0	WD
65	<i>Plantago lanceolata</i>	PL	19	13	-95.0**	-130.0**	WS
69	<i>Pseudoscleropodium purum</i>	PsP	55	31	-164.5	-101.5**	CG <sup>3</sup>
72	<i>Quercus robur</i>	QR	9	1	+189.0	+160.0*	WD
74	<i>Rosa</i> agg.	Rag	4	1	-	-160.0*	WD
78	<i>Ranunculus repens</i>	RR	26	10	-127.5*	-192.5	C/R
81	<i>Senecio jacobaea</i>	SJ	35	9	-170.0	-128.0*	P/WD/WS/B
82	<i>Sanguisorba minor</i>	SM	6	7	-180.0	-160.0*	B/R/CG
84	<i>Stellaria graminea</i>	StG	8	16	-178.5	-160.0*	R/B
87	<i>Trisetum flavescens</i>	TF	10	7	+191.0	+150.0*	P/R
90	<i>Trifolium repens</i>	TR	9	2	-140.0*	-170.0	WS
91	<i>Urtica dioica</i>	UD	4	9	-	+160.0*	R/WS/WD
95	<i>Viola riviniana</i>	VR	8	17	+160.0*	+160.0*	WD
97	<i>Vicia sativa</i>	VSt	53	10	-77.0**	-30.0**	WS
105	pea seedling	H61	34	4	-85.0**	-154.0	-
108	? <i>Picris</i>	H8	6	3	-	+150.0*	-

**Table 5.1 Species showing a significant change in abundance between age classes**

1- Postive U values denote a preference for old, and negative values for young, revegetments.

\* - U values significant at  $p < 0.05$

\*\* - U values significant at  $p < 0.01$

2- Habitats (Wade, 1970)

P - pasture

CG - calcareous grassland

G - grassland

WS - waste ground

WD - woodland

R - roadsides

C - cultivated ground

B - banks

3 - Watson (1971)



### 5.1.1 Species replacements

Succession may be seen as a species replacement process (Section 1.1.1) and theories of succession are based on the notion of a predictable sequence of replacements. It therefore follows that successional development may be represented by predictable changes in species abundances over time. In controlled conditions the changes in species composition ought to be the same, when the experiment and conditions are replicated. The initial conditions described for this study offer, it is argued, a close approximation to replicate conditions and treatments for periods of 27 and 56 years. So it is reasonable to ask if species replacements have been consistent and predictable between stages in the chronosequence represented by young and old revegetations.

For each species an abundance level on young slopes (N and S; 20 replicates) and on old slopes (N and S; 20 replicates) was recorded (Section 3.5.6). The question to be answered, therefore, is whether or not succession, as defined, has occurred, i.e. if there has been a consistent change in abundance over time for each species. The hypothesis to be tested is that species replacement has led to a change in abundance of species between young and old slopes. Since it has been shown that aspect is a major influence on the vegetation (Sections 4.3-4.5) it is appropriate to consider conditions separately for each aspect.

An appropriate method for testing this hypothesis must take into account the pattern of distribution of the species abundance data which, in common with most vegetation data, is highly skewed. A method of testing for differences in median abundance in non-normal data is the Mann-Whitney U test (Sokal and Rohlf, 1995). This test generates a U-value which may be taken to indicate the strength of a species preference for a particular age group. Results are shown in Table 5.1 for those species which have a significant difference in abundance between old and young slopes on one or both compass aspects: negative values denote a preference for the young age class. The U-values for all species are shown in Appendix D. U-values denoting a significant difference are shown in bold, suffixed by a single asterisk where  $p < 0.05$ , and a double asterisk where  $p < 0.01$ . It can be seen (Table 5.1) that 26 species, from a total of 113, show a significant change in abundance between young and old slopes indicating that species replacements have occurred and that these species may be said to show an age class preference.

The habitat types in which each species is typically found within Monmouthshire (Wade, 1970) is also shown in Table 5.1. Whilst species found on young sites in this study are characteristic of a range of habitats, including both woodland and wasteland, those species with a preference for old sites are typically woodland species with none from wasteland habitats. A possible correspondence is therefore suggested between young sites and wasteland habitats and between old sites and woodlands. It may also be noted that 19 species show a preference for the same age class on both north- and south-facing slopes; of these species six show a significant preference on both aspects. The four species from this group which show a preference for young slopes are described by Wade (1970) as being typical of waste-ground habitats whilst the two species having a preference for old slopes are characteristic of woods and hedgebanks. Three species, *Bellis perennis*, *Carex hirta* and *Lathyrus linifolius*, show age preferences which are different for each of the two aspects.

These results suggest that succession, as a process of species replacement over time, has occurred in the study area in respect of 26 of the 113 recorded species. By highlighting individual species in this manner it is possible to describe those traits which are typical of particular stages of a successional sequence. The majority of species do not, however, show a strong age preference and this is true of the two most widespread species *Arrhenatherum elatius* and *Festuca ovina* which form the dominant components of much of the vegetation of the site.

### 5.1.2 Calculation of species age preferences

The previous section showed that certain species show a significant change in abundance between age groups and that this distinction may form the basis for characterizing successional age in terms of species habitat types. In this section methods of assigning age preference scores to all species are described.

Species have been classified and characterized by features of their ecology and life history type and plant features have been described as typifying particular stages of succession, (Grime *et al.*, 1989; Gibson and Brown, 1991). It is useful to determine those species in this study which show the strongest association with one or other of the two age groups in order to ascertain if plant attributes show some consistent pattern between old and young revegetations. Such a study would indicate the validity of the assumption of a successional

time series being present at the study site. This section describes those species and species' attributes which best characterize young and old revegetations.

#### 5.1.2.1 Discriminant Function Analysis

The method of discriminant function analysis (DFA) proposed above (Section 3.6.5) was found to be inappropriate in the analysis of species abundances between age-groups because of the highly skewed nature of the data and the bias introduced by those species with very low abundance scores. Thus, for example, inspection of the raw data (Appendix A), shows some species having strong age preferences; *Plantago lanceolata* (PIL) and *Lathyrus nissolia* (LN) have a strong preference for young sites; yet the DFA program gave these two species discriminant scores of -0.030 and +0.648 respectively in a data set having a range of +/-10.86. Furthermore the method is limited when the number of variables is large in relation to the number of cases (ter Braak, 1987; Tabachnick and Fidell, 1996). Ter Braak (1987, p. 148) describes this problem and suggests that a form of CCA may be applied to perform this analysis without the necessity of omitting species (Sections 3.6.3, 4.4.4.3). Here an alternative measure of species age preference was derived and is outlined below.

#### 5.1.2.2 Age preference scores

Species age preferences may be formulated from a comparison of abundances from sites representing different age classes. In this method the summed abundance scores for each species in each age group was determined and the difference between the summed abundances for each age group calculated for each species; these scores are examined with respect to their potential as indicators of age preference. For example, *Poa annua*, (PA) occurs in seven quadrats of which four are on young revegetations and three on old; in the young quadrats it scores 4, 8, 7 and 8, and in the old quadrats, 1, 2 and 5. The summed abundances for the young quadrats are thus 27 and, for the old, 8; this gives a difference calculated as old minus young abundances, of  $8 - 27 = -19$  in favour of young occurrences. This measure is, however, biased towards those species with higher abundance scores such that a rare species with a strong age preference will not generate a high score.

All quadrats					North-facing quadrats					South-facing quadrats				
Spp	Total	O - Y	A <sub>p</sub>	Freq	SppN	TotN	ON-YN	A <sub>p</sub> N	FreqN	SppS	TotS	OS-YS	A <sub>p</sub> S	FreqS
LN	70	-70	-1.00	22	LN	27	-27	-1.00	10	LN	43	-43	-1.00	12
TR	16	-16	-1.00	9	TR	10	-10	-1.00	6	PI L	134	-134	-1.00	7
EpM	22	-22	-1.00	6	LtL	5	-5	-1.00	4	CH	259	-259	-1.00	6
SM	39	-39	-1.00	6	VSp	12	-12	-1.00	4	StG	27	-27	-1.00	4
StP	9	-9	-1.00	5	BeP	9	-9	-1.00	4	Rag	5	-5	-1.00	4
Ep4	6	-6	-1.00	5	EpM	5	-5	-1.00	3	SM	29	-29	-1.00	4
GR	11	-11	-1.00	4	GM	6	-6	-1.00	3	Ep1	26	-26	-1.00	3
VSp	12	-12	-1.00	4	StP	5	-5	-1.00	3	EpM	17	-17	-1.00	3
Rag	5	-5	-1.00	4	PA	12	-12	-1.00	2	TR	6	-6	-1.00	3
CD	3	-3	-1.00	3	H61C	2	-2	-1.00	2	Ep4	4	-4	-1.00	3
MM	7	-7	-1.00	3	GR	9	-9	-1.00	2	MM	7	-7	-1.00	3
HM	7	-7	-1.00	2	Ep4	2	-2	-1.00	2	CD	2	-2	-1.00	2
H61C	2	-2	-1.00	2	SM	10	-10	-1.00	2	HL	3	-3	-1.00	2
T1	2	-2	-1.00	2	T1	2	-2	-1.00	2	HM	7	-7	-1.00	2
PI L	243	-241	-0.99	19	PI L	109	-107	-0.98	12	GR	2	-2	-1.00	2
StG	131	-125	-0.95	8	HR	37	-36	-0.97	3	StP	4	-4	-1.00	2
ViC	60	-56	-0.93	9	StG	104	-98	-0.94	4	HR	221	-189	-0.86	13
HR	257	-225	-0.88	16	ViC	51	-47	-0.92	8	HyH	25	-19	-0.76	6
EqA	85	-67	-0.79	6	EqA	80	-72	-0.90	4	VSt	277	-209	-0.75	31
VSt	524	-400	-0.76	53	VSt	247	-191	-0.77	22	BH	708	-486	-0.68	25
HyH	30	-22	-0.73	9	H61	78	-56	-0.72	20	PsP	239	-159	-0.67	19
CH	399	-281	-0.70	13	HyH	5	-3	-0.60	3	TO	21	-13	-0.62	5
BH	735	-513	-0.70	29	RR	203	-121	-0.60	19	EpH	26	-16	-0.62	3
LtL	6	-4	-0.67	5	PP	92	-51	-0.55	12	EgA	5	-3	-0.60	2
HS	6	-4	-0.67	3	HyM	63	-33	-0.52	7					
TO	22	-14	-0.64	6						PO	54	30	0.56	7
H61	134	-82	-0.61	34	CeF	6	4	0.67	3	RR	53	33	0.62	7
EgA	5	-3	-0.60	2	RF	61	44	0.72	8	BeP	88	58	0.66	7
PA	35	-19	-0.54	7	FE	100	77	0.77	18	BS	304	222	0.73	13
PP	193	-103	-0.53	29	CF	94	73	0.78	4	FE	31	23	0.74	9
Ep1	49	-25	-0.51	8	EpH	15	13	0.87	2	CA	9	7	0.78	2
BP	8	-4	-0.50	6	GH	393	383	0.97	8	TF	49	39	0.80	7
					BS	188	186	0.99	7	AgC	58	48	0.83	9
BeP	97	49	0.51	11	GV	5	5	1.00	2	S8	34	30	0.88	3
QR	10	6	0.60	9	AgC	3	3	1.00	3	PVe	41	39	0.95	3
GH	822	550	0.67	22	PVe	34	34	1.00	3	CF	28	28	1.00	2
CeF	7	5	0.71	4	VR	72	72	1.00	4	LzC	5	5	1.00	2
H1F	15	11	0.73	3	DFm	50	50	1.00	5	EqA	5	5	1.00	2
FE	128	100	0.78	27						H57B	2	2	1.00	2
BS	492	408	0.83	20						VT	8	8	1.00	2
AgC	61	51	0.84	12						RC	15	15	1.00	3
S8	34	30	0.88	3						VR	65	65	1.00	4
PVe	75	73	0.97	6						UD	34	34	1.00	4
AiC	20	20	1.00	2						QR	4	4	1.00	4
LzC	5	5	1.00	2						H8	14	14	1.00	5
H57B	2	2	1.00	2										
GV	5	5	1.00	2										
VT	8	8	1.00	2										
RC	15	15	1.00	3										
UD	34	34	1.00	4										
DFm	50	50	1.00	5										
CF	101	101	1.00	6										
H8	18	18	1.00	6										
VR	137	137	1.00	8										

Table 5.2 Species age preference scores.

To correct for this bias the difference in abundance between groups is divided by the total summed abundances for that species to give a proportional age preference score ( $A_p$ ). In the example of *Poa annua* this would be calculated as  $-19/35 = -0.543$ . This measure tends to produce an opposite bias in the case of species with very low abundances where, for example, the occurrence of only one or two plants in sites of the same age group will generate a maximum score on this scale of preference. For this reason those species which occur in only a single quadrat are excluded from the analysis.

In addition it is important to take note of the species frequencies when interpreting the preference score. Species with low frequencies are still more likely to have a biased preference score because of sampling error. Species with high frequencies may therefore offer a more reliable indication of age preference than do species which have a lower frequency but a higher preference score. Thus, for example, *Plantago lanceolata* ( $A_p = -0.99$ ; Freq = 19) may be considered to typify young sites better than, say, *Holcus mollis* ( $A_p = -1.0$ ; Freq = 2).

Of the remaining species those with an absolute proportional difference score greater than 0.50 are listed by preferred age group in Table 5.2. Species are identified by their abbreviated names. As preference scores ( $A_p$ ) are calculated as old minus young, negative scores indicate a preference for young sites. In addition to the preference scores the total summed abundances (Total), the difference between summed old and young abundances (O-Y), and the species frequencies (Freq) are listed for each species. The calculations are repeated for sub-sets of the data containing, respectively, north- and south-facing quadrats. References to abundance measures and preference scores for these subsets are given a suffix (N, S) to denote the aspect of the data-set. The age preference scores for all species are listed in Appendix D.

It may be seen (Table 5.2) that a number of species show strong preferences for one or other of the two age-groups. *Lathyrus nissolia* (LN) is outstanding in its preference for young sites regardless of aspect. Of the species with relatively high frequencies *Trifolium repens* (TR) and *Plantago lanceolata* (PIL) also show strong preferences for the younger group; these two species also show some differential preference for north- and south-facing slopes respectively.

Preference for old sites is shown by *Viola riviniana* (VR), H8, *Carex flacca* (CF), *Dryopteris felix-mas* (DFm), *Primula veris* (PVe), *Agrostis capillaris* (AgC), *Brachypodium sylvaticum* (BS) and *Fraxinus excelsior* (FE). Reference to Appendix D shows that, with the exception of *Carex flacca*, which is typical of calcareous grassland, these species are associated with woodland habitats.

#### 5.1.2.3. CCA age scores

A comparison may be made between the 26 species shown to have significant changes in abundance over time (Table 5.1) and those ordinated by the factor age and given age scores by the CCA program (Table 4.34) as an indication of the level of consistency between the two methods. This shows that 17 species have the same age bias, eight have the same age preference but do not meet the criterion for inclusion in Table 4.34 (absolute age score > 0.5) and one, *Bellis perennis*, has an age preference different from that shown in Table 5.1.

#### 5.1.2.4 Indicator species

The classification procedures described above (Section 4.4) identified those species which showed an ability to discriminate consistently between groups of old and young quadrats (Tables 4.16 and 4.17). Furthermore, CCA generated species age scores (Section 4.5.4.3) in an ordination constrained by the single factor age and in Section 5.1.2 species' age preference scores ( $A_p$ ) were calculated directly from differences in abundance values between old and young sites. The extent to which species may be used as indicators of successional age has thus been approached by three different methods.

The TWINSpan and Age Preference methods explicitly separated samples from different aspects whereas the CCA method used data from both aspects for all species. Therefore, age scores ( $A_{CCA}$ ) for species which show different preferences on different aspects may confound the derived age score measure.

A comparison of those species used as TWINSpan indicators with those which had high  $A_p$  scores may be made. Eleven TWINSpan indicator species are noted which distinguish between young and old groups on south-facing slopes (Table 4.16). Five of these also have

high Age Preference scores for south-facing slopes (Table 5.2). For each of the five the age preference is consistent between the two methods. On north facing slopes eight species are used as TWINSpan indicators (Table 4.17) of which four also appear with high ( $A_p$ ) scores. Three of these four are indicative of young slopes in both methods whereas *Plantago lanceolata* shows a preference for old quadrats in the TWINSpan classification of north-facing slopes but is shown to be typical of young quadrats by its high negative ( $A_p$ ) score. Examination of Figure 4.19 shows that, in the D2 division the left-hand (-ve) group (D2/A) is predominantly young but the right-hand (+ve) group (D2/B) is made up of equal numbers of young and old samples. The interpretation of the species *Plantago lanceolata* as having a preference for old sites is therefore questionable. Furthermore, in the subsequent division of D2/B into, predominantly young D3/C, and entirely old D3/D, groups, this species is indicative of the young group. Age preferences derived for this group of species would therefore seem to be consistent across both methods of analysis.

## 5.2 Species traits

### 5.2.1 Life history attributes

The approach to succession based on assigning species to functional types has been developed by Grime (Grime, 1979; Grime *et al.*, 1989) who proposed a classification of vegetation based on plant traits or strategies which promote a species survival in the face of three limiting factors; disturbance, competition and stress (Section 1.6.1.1). Competition is defined by Grime as the tendency for neighbouring plants to use the same resources and stress refers to environments where conditions are not conducive to plant growth because of physical, chemical or nutrient-related factors. Species are classified in this scheme according to their abilities to survive one or other of these factors. The classification procedure has been codified (Grime *et al.*, 1989) in the form of a dichotomous key in which species are grouped into functional types by features of their life history, growth-form and phenology.

Vegetation succession following disturbance is characterized, in Grime's scheme, by a change in the dominant strategy from one that is tolerant of disturbance (i.e. ruderal) to one of stress tolerance. In productive habitats a middle stage is suggested in which a competitive strategy is displayed whereas in low fertility habitats the sequence moves

Species	A <sub>p</sub>	Freq.	Strategy	LH	A <sub>GB</sub>
LN	-1.00	22	(R)	A	-
TR	-1.00	9	C-S-R/C-R	P	Y
EpM	-1.00	6	C-S-R	P	(Y)
SM	-1.00	6	(S-R)	P	M
Ep4	-1.00	5	?	?	-
StP	-1.00	5	(S-R)	A	-
GR	-1.00	4	(R)	A	-
Rag	-1.00	4	(C-R)	P	-
VSp	-1.00	4	C-S-R/C	P	(M)
CD	-1.00	3	(S-R)	P	-
MM	-1.00	3	(S-C)	P	(M)
H61C	-1.00	2	O	?	-
HM	-1.00	2	C	P	-
T1	-1.00	2	(S-C)	P	-
PIL	-0.99	19	C-S-R	P	M
StG	-0.95	8	(S)	P	-
VIC	-0.93	9	C/C-S-R	P	M
HR	-0.88	16	C-S-R	P	M
EqA	-0.79	6	C-R	P	-
VSt	-0.76	53	(R)	A	(M)
HyH	-0.73	9	(S-C)	P	-
CH	-0.70	13	(S-C)	P	-
BH	-0.70	29	R	A	(Y)
LtL	-0.67	5	(S-R)	P	-
HS	-0.67	3	(C-R)	B/P	(M)
TO	-0.64	6	R/C-S-R	P	M
H61	-0.61	34	O	?	-
EgA	-0.60	2	S-R	A/B	(Y)
PA	-0.54	7	(S-R)	A/(P)	Y
PP	-0.53	29	C-S-R	P	Y
Ep1	-0.51	8	?	?	-
BP	-0.50	6	(S-R)	A	O
BeP	0.51	11	R/C-S-R	P	M
QR	0.60	9	(S-C)	P	-
GH	0.67	22	C-S-R	A	M
CeF	0.71	4	R/C-S-R	P	Y
H1F	0.73	3	O	?	-
FE	0.78	27	C	P	-
BS	0.83	20	S/SC	P	M
AgC	0.84	12	C-S-R	P	(Y)
S8	0.88	3	(S-R)	P	-
PVe	0.97	6	?	P	M
AiC	1.00	2	(S-R)	A	-
GV	1.00	2	(S-R)	P	O
H57B	1.00	2	?	?	-
LzC	1.00	2	(S-R)	P	-
VT	1.00	2	(C-R)	B	(Y)
RC	1.00	3	C-R/R	P	(Y)
UD	1.00	4	C	P	Y
DFm	1.00	5	S-C	P	-
CF	1.00	6	S	P	Y
H8	1.00	6	?	?	-
VR	1.00	8	S	P	(O)

**Table 5.3 Species strategy, life history type and successional age group.**

Strategy	A <sub>p</sub> Y > 0.50		A <sub>p</sub> O > 0.50		χ <sup>2</sup>
	No.	%	No.	%	
C	2	6	2	10	
S	1	3	2.5	12	
R	4.5	14	1.5	7	
C-R	3.5	11	1.5	7	
S-R	7	22	4	19	
S-C	4	12	2.5	12	
C-S-R	6	19	3	14	
nd	4		4		χ <sup>2</sup> = 2.57
No. Spp.	32		21		p = 0.860

**Table 5.4 Species strategies and age preferences**



directly from ruderal to stress tolerance. The prediction arising from this hypothesis (Table 1.1) is that older sites will display fewer ruderal species and more stress tolerant plants. In a productive site there may be greater numbers of competitors in older samples. However since the time scale of the successional processes cannot be clearly defined (Section 1.6.4), and since the young sites in this study are already 27 years old, an increase in the numbers of competitor species over time cannot be taken as evidence of the operation of succession as defined by this model. Furthermore the management history of the site (Section 1.4) suggests that the revetments have been maintained in a low nutrient condition giving rise to the expectation that competitive strategists are unlikely to have occurred.

Table 5.3 shows those species having age preference scores (Section 5.1.2.2) greater than 0.5 and frequencies higher than one, listed together with their recorded frequencies and strategies, defined by Grime, where this is available. Species are classified into one of seven groups using a dichotomous key relating to features of life history and phenology. Where species are not included in Grime *et al.* (1989) their strategy is inferred from known or published characters using the key. These latter species are indicated by a bracketed symbol denoting their strategy. Also included in the table are the life cycle category (annual, biennial or perennial) and the successional age of communities in which the species is typically found as determined by Gibson and Brown (1991).

32 species are shown in Table 5.3 which have a preference for young sites and an absolute  $A_p$  score greater than 0.50. Of these, four species (12.5%) belong to the ruderal category. Within the 21 species having a preference for old sites ( $A_pO$ ) there are no ruderals, though three species (14%) are categorized as being midway between the ruderal and one other group. The numbers of species in each of the seven strategies is related to age preference class and shown in Table 5.4. Where a species has been categorized as being midway between two strategies then it is counted as having a score of 0.5 for each strategy. The proportion of species displaying each of the strategies is also shown and the result of a  $\chi^2$  test of the degree of association between age preference and strategy is reported. A number of species were recorded which were either of indeterminate identity, or for which information relating to their functional type was not available; these are designated as "nd".

There are fewer species with  $A_p$  scores greater than 0.50 in the old group than in the young. Inspection of the proportional differences between age groups for each strategy (Table 5.4) shows a decrease in ruderal and competitive-ruderal strategies over time and an increase in

SppN	A <sub>p</sub> (N)	FreqN	Strategy	LH	A <sub>GB</sub>
LN	-1.00	10	R	A	-
TR	-1.00	6	C-S-R/C-R	P	Y
LtL	-1.00	4	S-R	P	-
VSp	-1.00	4	C-S-R/C	P	(P)
BeP	-1.00	4	R/C-S-R	P	M
EpM	-1.00	3	C-S-R	P	(Y)
GM	-1.00	3	R/S-R	A	(M)
StP	-1.00	3	(S-R)	A	-
PA	-1.00	2	(S-R)	A/P	Y
H61C	-1.00	2	-	?	-
GR	-1.00	2	(R)	A	-
Ep4	-1.00	2	-	?	-
SM	-1.00	2	(S-R)	P	M
T1	-1.00	2	(S-C)	P	-
PI L	-0.98	12	C-S-R	P	M
HR	-0.97	3	C-S-R	P	M
StG	-0.94	4	(S)	P	-
ViC	-0.92	8	C/C-S-R	P	M
EqA	-0.90	4	C-R	P	-
VSt	-0.77	22	(R)	A	(M)
H61	-0.72	20	-	?	-
HyH	-0.60	3	S-R	A/B	(Y)
RR	-0.60	19	C-R	P	M
PP	-0.55	12	C-S-R	P	Y
HyM	-0.52	7	S-C	P	-
CeF	0.67	3	R/C-S-R	P	Y
RF	0.72	8	S-C	P	-
FE	0.77	18	C	P	-
CF	0.78	4	S	P	Y
EpH	0.87	2	C	P	(Y)
GH	0.97	8	C-S-R	A	M
BS	0.99	7	S/S-C	P	M
GV	1.00	2	(S-R)	P	O
AgC	1.00	3	C-S-R	P	(Y)
PVe	1.00	3	-	P	M
VR	1.00	4	S	P	-
DFm	1.00	5	S-C	P	-

**Table 5.5 Species preferences on north-facing slopes**

Strategy	A <sub>p</sub> Y (N) > 0.50		A <sub>p</sub> O (N) > 0.50		$\chi^2$
	No	%	No.	%	
C	1	4	2	17	
S	1	4	2.5	21	
R	4	16	0.5	4	
C-R	2.5	10	0	-	
S-R	5.5	22	1	8	
S-C	2	8	2.5	21	
C-S-R	6	24	2.5	21	
nd	3		1		$\chi^2 = 8.04$
No. Spp.	25		12		$p = 0.235$

**Table 5.6 Species strategies and age preferences on north-facing slopes**

stress tolerant species. Overall the association between strategy and age group is not significant as judged by a  $\chi^2$  test ( $p > 0.50$ ).

The same analysis is performed using species data partitioned by aspect and results are shown in, Tables 5.5 and 5.6 for north-facing, and Tables 5.7 and 5.8 for south-facing, slopes. On north-facing slopes there is a decrease in the numbers and proportions of ruderal, competitive-ruderal and stress-tolerant-ruderal species over time. There is, conversely, an increase in the proportions of competitive, stress-tolerant and stress-tolerant-competitive species. The result of a  $\chi^2$  test for association is not significant. On south-facing slopes there is an increase in stress-tolerant and competitive-ruderal species and a decrease in the proportions of ruderal and stress-tolerant-ruderal species strategies though, again, the association is not statistically significant.

In each of the three sets of tables there is evidence of a decrease in the proportion of ruderal strategists in the group of species showing a preference for old sites although none of the tests for association between strategy and age generate a significant relation when species are classified into one of seven strategies. However, as some of the  $\chi^2$  tests reported expected values of less than 5, rendering the result less reliable, it is appropriate to combine some of the strategy groups in order to produce fewer classes containing larger numbers of species. Three classes were therefore defined corresponding to the C, S and R strategies. Species previously defined as C-S each contributed 0.5 to the respective classes C and S and classes C-R and S-R were similarly divided. In like manner each species in the C-S-R strategy contributed 0.33 to each of the three classes. The results of this re-classification are shown for, all quadrats, for north-facing quadrats and for south-facing quadrats (Tables 5.9, 5.10 and 5.11 respectively).

When all quadrats are considered together there is a fall in the numbers of competitors but a relatively constant proportion within each age group. For stress tolerators there is an increase in their proportional presence on old slopes whilst ruderal species show a decline in both numbers and proportions over time. For species on north-facing slopes there is a decrease over time in the numbers and proportions of ruderals and an increase in the proportions (but not the numbers) of competitors and stress-tolerators. On south-facing slopes there is a similar decrease in the numbers and proportions of ruderals and a small increase in the proportions of competitors and stress-tolerators. Tests for association

SppS	A <sub>p</sub> (S)	FreqS	Strategy	LH	A <sub>GB</sub>
LN	-1.00	12	R	A	-
PIL	-1.00	7	C-S-R	P	M
CH	-1.00	6	(S-R)	P	-
StG	-1.00	4	(S)	P	-
Rag	-1.00	4	(C-R)	P	-
SM	-1.00	4	(S-R)	P	M
Ep1	-1.00	3	?	?	-
EpM	-1.00	3	C-S-R	P	(Y)
TR	-1.00	3	C-S-R/C-R	P	Y
Ep4	-1.00	3	?	?	-
MM	-1.00	3	(S-C)	P	(M)
CD	-1.00	2	(S-R)	P	-
HL	-1.00	2	C-S-R	P	M
HM	-1.00	2	C	P	-
GR	-1.00	2	(R)	A	-
StP	-1.00	2	(S-R)	A	-
HR	-0.86	13	C-S-R	P	M
HyH	-0.76	6	(S-C)	P	-
VSt	-0.75	31	(R)	A	(M)
BH	-0.68	25	R	A	(Y)
PsP	-0.67	19	-	(P)	-
TO	-0.62	5	R/C-S-R	P	M
EpH	-0.62	3	C	P	(Y)
EgA	-0.60	2	S-R	A/B	(Y)
PO	0.56	7	S/C-S-R	P	M
RR	0.62	7	C-R	P	M
BeP	0.66	7	R/C-S-R	P	M
BS	0.73	13	S/S-C	P	M
FE	0.74	9	C	P	-
CA	0.78	2	C-R	P	Y
TF	0.80	7	C-S-R	P	Y
AgC	0.83	9	C-S-R	P	(Y)
S8	0.88	3	(S-R)	P	-
PVe	0.95	3	?	P	M
CF	1.00	2	S	P	Y
LzC	1.00	2	(S-R)	P	-
EgA	1.00	2	C-R	P	-
H57B	1.00	2	?	?	?
VT	1.00	2	(C-R)	B	(Y)
RC	1.00	3	C-R/R	P	(Y)
VR	1.00	4	S	P	(O)
UD	1.00	4	C	P	Y
QR	1.00	4	(S-C)	P	-
H8	1.00	5	?	?	?

**Table 5.7 Species preferences on south-facing slopes**

Strategy	A <sub>p</sub> Y (S) > 0.50		A <sub>p</sub> O (S) > 0.50		χ <sup>2</sup>
	No.	%	No.	%	
C	2	8	2	10	
S	1	4	3	15	
R	4.5	19	1	5	
C-R	1.5	6	4.5	22	
S-R	5	21	2	10	
S-C	2	8	1.5	7	
C-S-R	5	21	3	15	
nd	3		3		χ <sup>2</sup> = 6.23
No. Spp.	24		20		p = 0.398

**Table 5.8 Species strategies and age preferences on south-facing slopes**

between age-group and strategy were again performed on these groups; none was found to be significant.

### **5.2.2 Species life cycle types**

Species have been classified according to their type of life-cycle; this is related, through measures of longevity, to the species strategy on the r-K life-history spectrum (Section 1.6.1). Tables 5.3 - 5.7 include, for each species, the life cycle type defined according to whether the species follows an annual (A), biennial (B) or perennial (P) cycle. From Table 5.3 it may be seen that, for those species with an absolute age preference greater than 0.50, there are six annuals which have a preference for young sites and two having a preference for old sites. A further two species have life cycles which may be annual/biennial or annual/perennial: these species have been allotted scores of 0.5 for each life cycle category. The numbers of species in each age preference group is shown for each life cycle type, both in total and separately, for each aspect (Table 5.12). In each of the three data sets a comparison of young and old groups shows a decrease in both the number and the proportion of annuals with age. Perennial plants show an increase in their proportional importance with age though this is not reflected in their absolute numbers. Biennials are too few in number to show any trend with age.

### **5.2.3 Species as indicators of successional age**

Gibson and Brown (1991) collated data from a number of studies of limestone grassland successions and have attempted to identify species which typify young, middle and old stages of succession. The successional age category of those species described by Gibson and Brown and included in this study ( $A_{GB}$ ), is printed in Appendix D. Of the 113 species in this study 65 were described by Gibson and Brown as being characteristic of a particular successional stage.

Table 5.3 includes the age category ( $A_{GB}$ ) for those 53 species which had frequencies greater than 1 and age preference scores ( $A_P$ ) greater than 0.5. Of these, 32 have a preference for young, and 21 for old sites. Of the 32 with preference for young sites, 16 were described by Gibson and Brown and of these, six were associated with young, nine

Strategy	PrefY >0.50		PrefO > 0.50		$\chi^2$
	No	%	No.	%	
C	8.75	30.0	5	29.4	$\chi^2 = 0.62$ p = 0.733
S	8.5	29.3	6.75	39.7	
R	11.75	40.5	5.25	30.9	
No. Spp.	29		17		

**Table 5.9 Species strategies (3 classes) and age preferences (all quadrats)**

Strategy	PrefY (N) >0.50		PrefO (N) > 0.50		$\chi^2$
	No	%	No.	%	
C	5.25	23.9	4.083	38.9	$\chi^2 = 2.43$ p = 0.296
S	6.75	30.7	4.583	43.7	
R	10.0	45.5	1.833	17.5	
No. Spp.	22		10.5		

**Table 5.10 Species strategies (3 classes) and age preferences (north-facing quadrats)**

Strategy	PrefY (S) >0.50		PrefO (S) > 0.50		$\chi^2$
	No	%	No.	%	
C	5.417	25.8	6.0	35.3	$\chi^2 = 0.82$ p = 0.665
S	6.167	29.4	5.75	33.8	
R	9.417	44.8	5.25	30.9	
No. Spp.	21		17		

**Table 5.11 Species strategies (3 classes) and age preferences (south-facing quadrats)**

LH	Y		O		YN		ON		YS		OS	
	No.	%	No	%	No	%	No	%	No	%	No	%
A	7	22	2	10	6	24	1	8	5.5	23	0	-
B	1	3	1	5	0.5	2	0	-	0.5	2	1	5
P	20	62	15	71	15.5	62	11	92	16	67	17	85
nd	4		3		3		0		2		2	
Total	32		21		25		12		24		20	

**Table 5.12 Life cycle type and age preferences**

with medium-aged, and one with old successional stages. There were 21 species from this study showing preference for old sites of which nine were not recorded by Gibson and Brown. The remaining 12 were classed as being, six from young, four from medium-aged and two from old, successional stages.

Although a large proportion of species from this study are not included in the data of Gibson and Brown and the ages of the two groups in this study both fall within the medium-aged group (defined as 11-100 years) there is no evidence from this comparison of a progression of species types from young to old at Caerwent.

### 5.3 Community structure: changes over time

A number of measures of community structure are presented below; these are species richness, Simpsons diversity index, dominance and evenness. For each one a comparison is made between values and distributions from old and young communities in order to gauge the change in structure over successional time and to relate this change to that predicted or indicated by successional models. The comparisons are presented in two ways; first the data are analysed as a whole, then subsets of the data representing north- and south-facing slopes are analysed separately. Further subdivision into upper slope and lower slope communities is not indicated by the analyses in Section 4.3.

For each measure the mean value and the variance associated with each community is given below in Table 5.13. In addition the results of a Mann-Whitney U test of difference between median values are reported. A probability (MW/p) of 0.05 or less is taken to be evidence of a significant difference and indicated in bold type.

	Y	O	MW/p	YN	ON	MW/p	YS	OS	MW/p
Species No.	20.97	16.02	<b>&lt;0.001</b>	19.30	13.10	<b>&lt;0.001</b>	22.65	18.95	0.30
variance	23.72	48.90		29.17	23.25		13.61	59.10	
Diversity	7.297	6.083	<b>0.03</b>	5.810	5.108	0.37	8.785	7.057	0.14
variance	6.099	11.34		4.839	5.405		3.025	15.87	
Dominance	0.2722	0.3562	0.12	0.3252	0.3746	0.67	0.2191	0.3378	0.16
variance	0.0087	0.0378		0.0104	0.0339		0.0014	0.0432	
Evenness	0.3406	0.3652	0.22	0.2975	0.3784	<b>&lt;0.001</b>	0.3838	0.3520	0.29
variance	0.0070	0.0078		0.0055	0.0056		0.0051	0.0100	

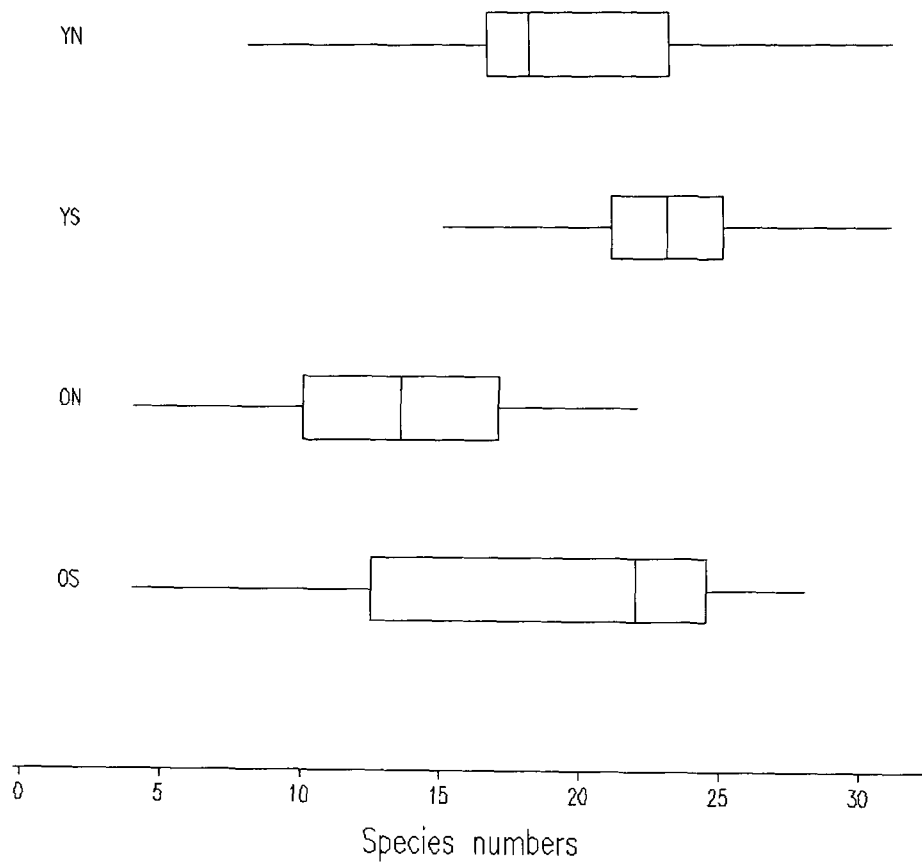
**Table 5.13 Community measures compared between age groups**

#### 5.3.1 Species richness

The simplest measure of community structure is that of species richness (Magurran, 1988). Where a limited area of the community is sampled the measure is more accurately termed species density. Since sampling gives greater weight to the more abundant species the resulting measure necessarily includes a component representing relative abundance in addition to the number of species present in the community .

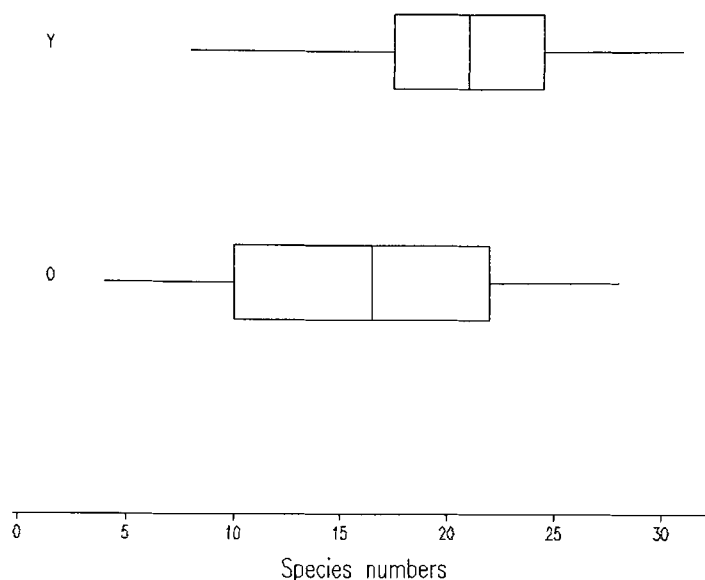
The mean species density from old and young samples (n = 40) is shown in Table 5.13 together with the sample variance (variance). The range of values is illustrated in the





**Figure 5.2** Species numbers in young (Y) and old (O) quadrats grouped by aspect (N/S)

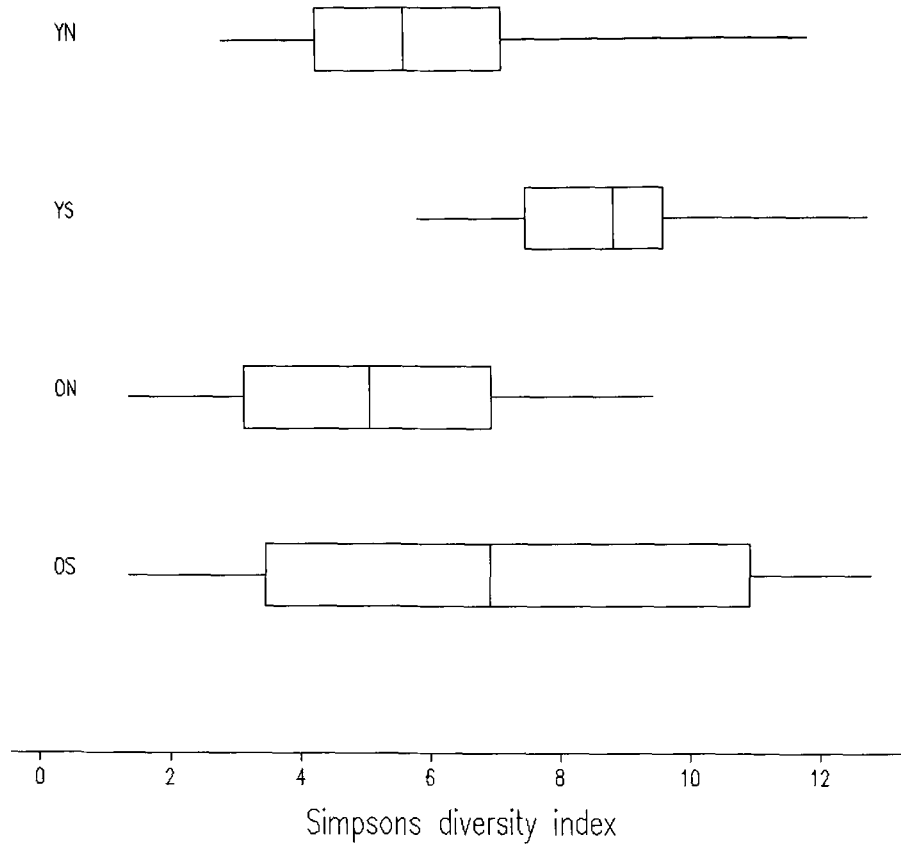
boxplots in Figure 5.1 and the value for each individual quadrat is given in Appendix A. There is a lower mean species density in old samples (16.02) compared with that found in young samples (20.97) and this difference is significant as judged by a Mann-Whitney U test. The probability of this difference arising by chance (MW/p) is less than 0.001.



**Figure 5.1 Species numbers in young and old quadrats**

Table 5.13 also includes a comparison of species densities between age groups from north- and south-facing slopes. These are illustrated in the boxplots in Figure 5.2 where four groups of samples each containing 20 cases are shown. For each aspect group, the quadrats from old slopes have lower mean species densities than those from young slopes. In the case of the north-facing quadrats (YN vs ON) the reduction represents a significant difference ( $p < 0.001$ ) but this is not so for the south-facing quadrats (YS vs OS). It is also apparent (Figure 5.2) that south-facing slopes have higher species densities than north-facing slopes, regardless of age.

There is an overall increase in the range of values of species number (variance) from young to old quadrats (Table 5.13). This is not apparent on north-facing slopes, which show a decrease in variance between age-groups, but is very marked on south-facing slopes.



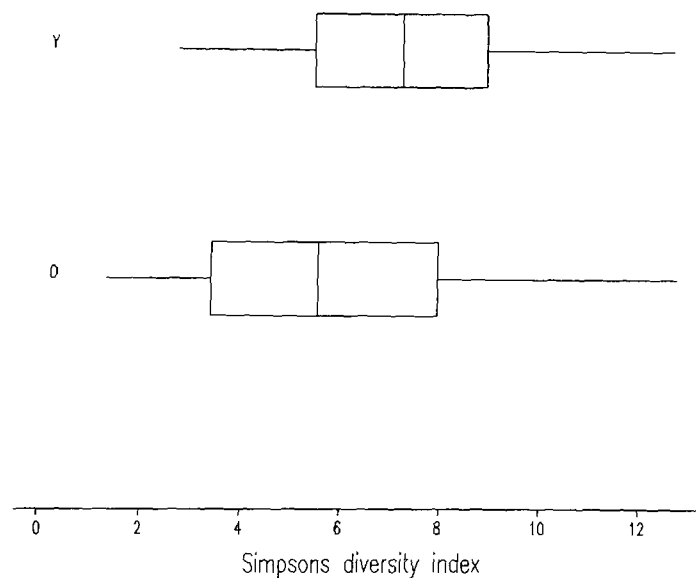
**Figure 5.4 Diversity in young (Y) and old (O) quadrats grouped by aspect (N/S)**

### 5.3.2 Diversity

One of the most widely used measures of diversity is that due to Simpson (Kent and Coker, 1992). Simpson's index ( $D$ ) is a measure of the probability that two individuals chosen at random from a community belong to the same species. Where there are  $n$  individuals in a species and a total number of individuals from all species of  $N$  then the index is calculated as the sum of the proportional abundances of each species,

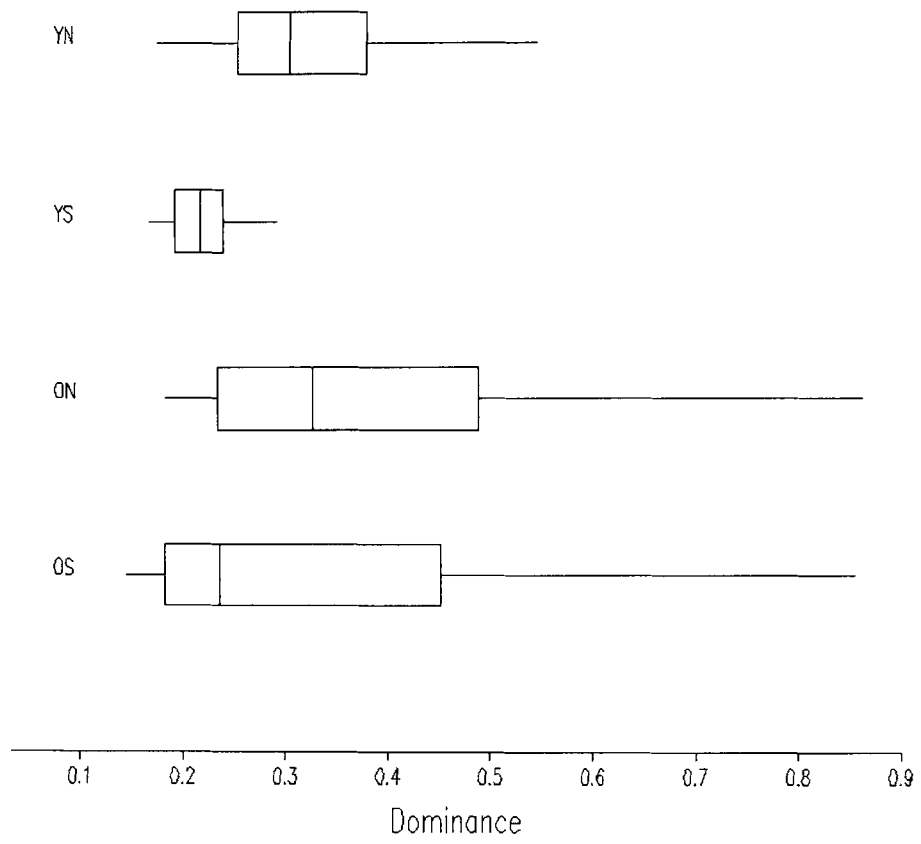
$$D = \sum \left( \frac{n(n-1)}{N(N-1)} \right) \quad \text{Equation 5.1}$$

Following common practice the diversity value reported here (Table 5.13) uses the inverse of this value to give an index which increases with higher levels of diversity (Magurran, 1988). The results for each individual quadrat are included in Appendix A and mean values and sample variances are shown above (Table 5.13). In addition the range of values is illustrated for old and young quadrats (Figure 5.3) and shown separately for each aspect (Figure 5.4).



**Figure 5.3 Diversity measures from young (Y) and old (O) quadrats**

In each case there is a decrease in diversity between young and old samples. From Table 5.13 it can be seen that this difference is significant in the comparison which includes all samples ( $n = 40$ ), but not when comparisons are made between age groups from each aspect category ( $n = 20$ ). The variance of the indices is also seen to increase over time, this being



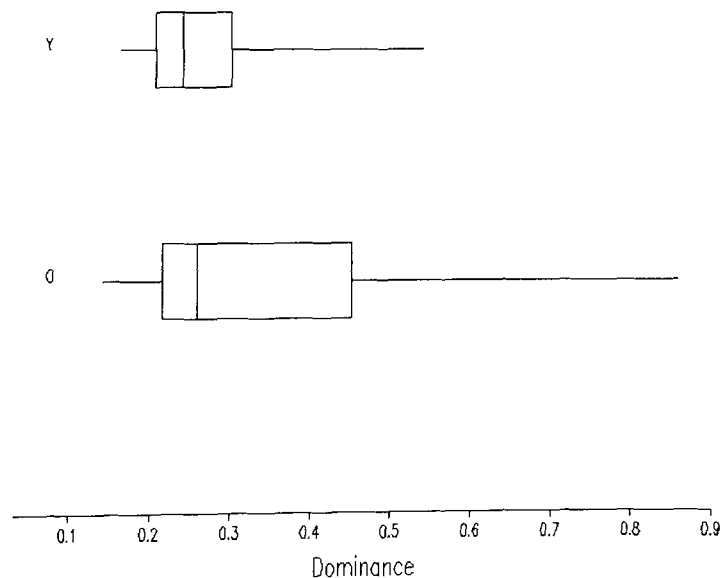
**Figure 5.6 Dominance in young (Y) and old (O) quadrats grouped by aspect (N/S)**

particularly marked on south-facing slopes. Additionally, it may be noted (Figure 5.4) that diversity is higher in quadrats from south-facing slopes regardless of age group.

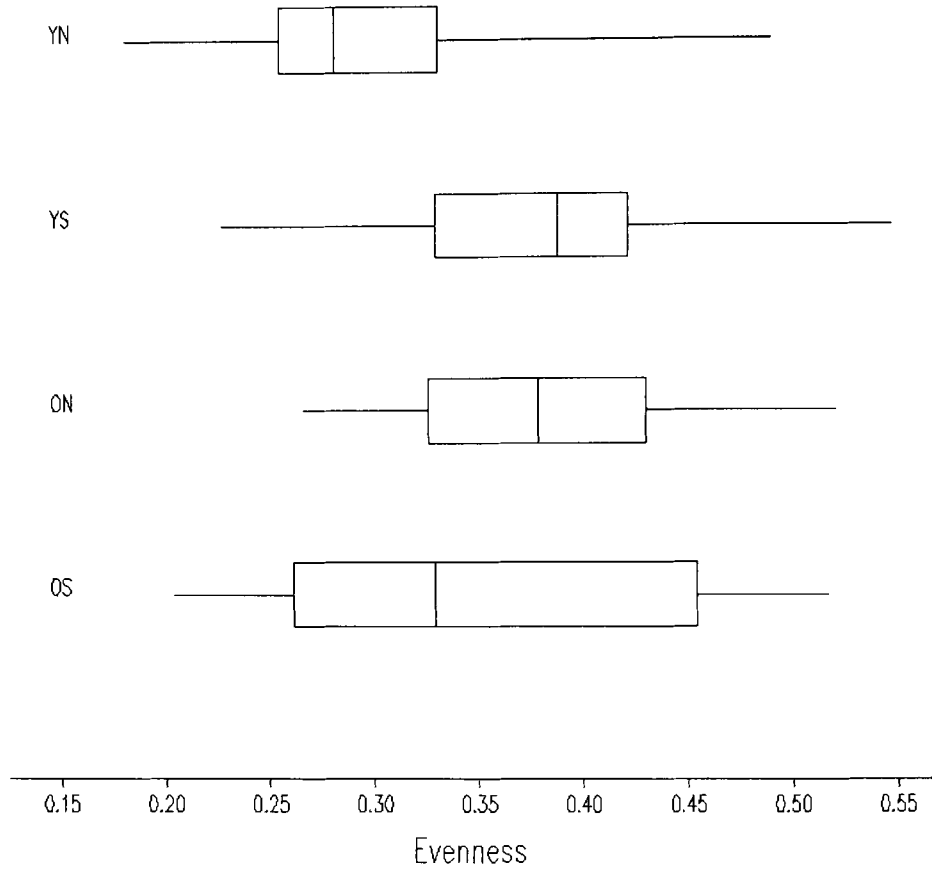
### 5.3.3 Dominance

Dominance is a diversity measure based on the relative proportions of the species in the community (May, 1981; Crawley, 1997). It is calculated as the proportional abundance of the most abundant species in the sample and, as such, has an inverse relation with measures of diversity. Table 5.13 shows the mean dominance and sample variance for old and young quadrats from both the whole data set and separately for north- and south-facing slopes. The measures calculated for each sample are given in Appendix A and the range of the indices is illustrated in Figures 5.5 and 5.6. Dominance is seen to increase with age in each instance though the change is not significant when judged by the Mann-Whitney U test. The variance is markedly higher in the dominance measures from old samples compared with those from young.

For both age groups dominance is also seen to be lower on south-facing slopes (Figure 5.6).



**Figure 5.5 Dominance in young (Y) and old (O) quadrats**

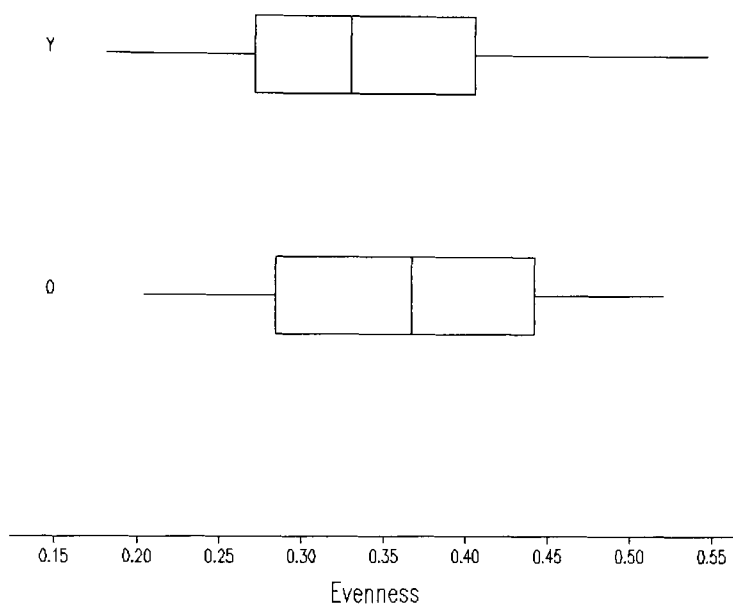


**Figure 5.8 Evenness in young (Y) and old (O) quadrats grouped by aspect (N/S)**

### 5.3.4 Evenness

Evenness is a measure of the similarity of species abundances within a sample (Section 1.6.2.2). It is one component of diversity together with species richness. A measure of evenness may be derived from the Simpson index by calculating the ratio of the measured diversity ( $1/D$ ) to the maximum diversity possible ( $D_{\max}$ ) within the sample. The maximum diversity is equal to the number of species ( $S$ ) so that evenness can be expressed as,

$$\frac{1/D}{D_{\max}} \quad \text{or} \quad \frac{S}{D}$$



**Figure 5.7 Evenness in young (Y) and old (O) quadrats**

Evenness shows a non-significant ( $p = 0.22$ ) increase over time when all the samples are considered together (Figure 5.7). However, when the two aspects are considered separately (Figure 5.8), the north-facing slopes show a significant ( $p < 0.001$ ) increase, and south-facing slopes a non-significant ( $p = 0.29$ ) decrease, in measures of evenness between age groups (Table 5.13).

This measure of evenness, along with others, has been criticised because the calculated value is not independent of the number of species in the sample (Camargo, 1993; Smith and Wilson, 1996). As a check on the method a second evenness index, Camargo's  $E'$  (Smith and Wilson, 1996), was calculated and the tests described above repeated. The  $E'$  values for each quadrat are reported in Appendix A. The values of the two indices are very similar,





having a correlation coefficient of 0.924, and the results of the analysis of Camargos E' values were essentially the same as those described above.

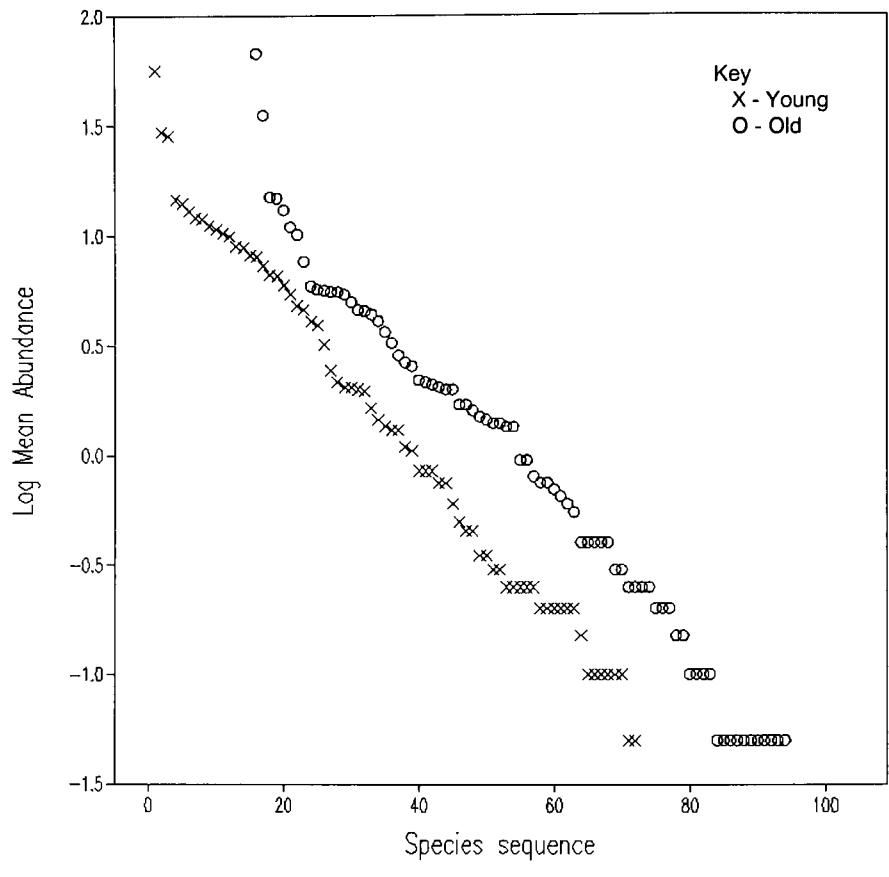
### 5.3.5 Rank abundance distribution

In this section community structure is analysed as a graphical representation in the form of a rank abundance distribution (RAD) of the species abundances (Section 1.6.2.1). Species abundances, averaged for all quadrats in the data subset, are plotted in rank order to form a descending curve whose shape characterizes the composition of the particular community. Figure 5.9 shows RAD plots for the species from young and old quadrats. The two curves are displayed together with the old community curve laterally displaced to aid comparison. Both plots show an initial, steep fall in relative species abundances followed by a gentler gradient in the mid section of the curve with the final tail again becoming steeper. The long mid section appears less steep in the curve depicting abundances from old quadrats.

A numerical analysis of the curves may be applied which tests for a departure from the null model of random distribution of species abundances represented by the lognormal distribution (Gray, 1987). Each curve was fitted to a truncated lognormal distribution (Magurran, 1988; Pielou, 1975), and the degree of fit tested by a  $\chi^2$  test. This test is based on the null hypothesis that the curve under test is not the same as a curve based on the truncated lognormal distribution. A test statistic higher than the critical value (Table 5.14) would suggest that this hypothesis may be rejected. The test statistic is here used to indicate the goodness of fit of the test curve to the truncated lognormal model. A high value of  $\chi^2$  equates with a high probability that the two distributions (the truncated lognormal and the curve under test) are different (Sokal and Rohlf, 1995). Both curves show a significant association with the truncated lognormal distribution (Table 5.14) though the curve representing species from old quadrats has a higher  $\chi^2$  value indicating that the fit was reduced over time.

	Y	O	YN	ON	YS	OS
df	10	10	10	10	10	10
$\chi^2$ crit	18.307	18.307	18.307	18.307	18.307	18.307
$\chi^2$ value	6.898	8.475	5.947	9.137	11.876	9.255
p	0.70	0.50	0.80	0.50	0.20	0.50

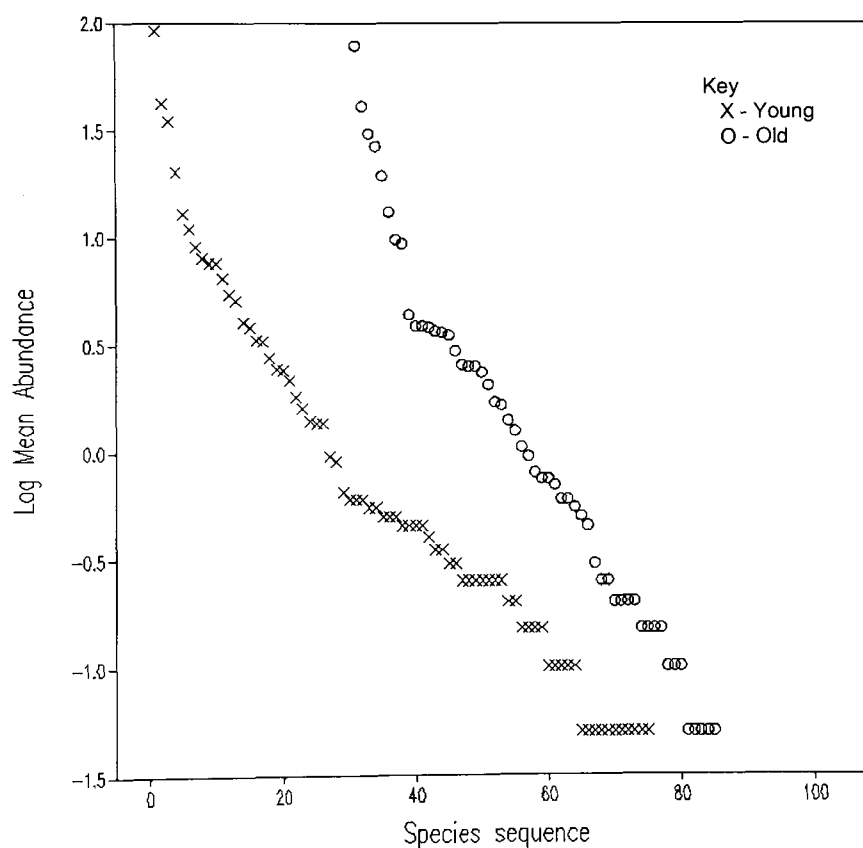
**Table 5.14 Goodness of fit of rank abundance plots**



**Figure 5.11 Rank abundance plots of young and old quadrats from south-facing revetments**

Gray (1987) discusses the problems of interpreting the degree of fit of rank-abundance plots in relation to ecological processes including succession. He concludes that the weight of evidence suggests that successional communities pass through stages which fit firstly, the geometric series when species numbers are low, followed by a mid-stage characterized by the log-series or log-normal model and, finally, a climax stage described again by the geometric series. Within this general framework the plot in Figure 5.9 and the  $\chi^2$  value in Table 5.14 show a reduced level of fit with time.

When the data are partitioned by aspect, north-facing slopes show a reduced level of fit to the null model whilst on the south-facing slopes the fit is improved. Figure 5.10 shows that on north-facing slopes the rank abundance plot becomes steeper with age whereas, in Figure 5.11, the curves for south-facing slopes demonstrate a reduced gradient over time.



**Figure 5.10 Rank abundance plots of young and old quadrats from north-facing revetments**

RAD plots show a complexity of community structure which is not seen in single figure indices of diversity and evenness. All plots show some general features;

- a single dominant species - *Arrhenatherum elatius*
- a small number of dominant species in a steeply falling, initial section of the curve

- a large group of moderately common species forming the bulk of the curve
- a group of rare species is indicated as a steeper tail to the curve

Curves show a relatively consistent pattern between young and old quadrats except that;

- on south facing slopes there is a larger number of rare species in the old group
- on north-facing slopes the old curve is steeper suggesting a decrease in evenness; the steeper curve is probably a result of there being fewer species
- the increase in evenness on north-facing slopes (Section 5.2.4) is due to a reduction in the number of rare species over time
- conversely the decrease in evenness on south facing slopes (Section 5.2.4) may be explained by the increase in numbers of rare species seen at the tail of the curve (Figure 5.11).

In interpreting the RAD plots different parts of the curve may be taken to represent different fractions of the community. It is apparent that changes over time in one fraction are not necessarily mirrored by similar changes in another suggesting that the different community components may not be fully integrated but rather result from the operation of different processes which may function with a degree of independence (Section 6.2.1).

Data set	No of quadrats	Quadrat size		
		Large (2×2m)	Medium (1×1m)	Small (0.6×0.6m)
Young	40	0.5253 (2703)	0.5381 (1422)	0.5967 (1014)
Old	40	0.5529 (2626)	0.5674 (1380)	0.5858 (1040)
		<b>p = 0.71</b>	<b>p = 0.25</b>	<b>p &lt; 0.001</b>
Young/South	20	0.5824 (1838)	0.5489 (965)	0.5954 (712)
Old/South	20	0.5481 (2025)	0.5815 (1017)	0.6336 (770)
		<b>p &lt; 0.001</b>	<b>p = 0.08</b>	<b>p = 0.30</b>
Young/North	20	0.5793 (1842)	0.6582 (908)	0.6423 (416)
Old/North	20	0.6355 (997)	0.6851 (730)	0.7034 (419)
		<b>p &lt; 0.001</b>	<b>p = 0.89</b>	<b>p = 0.06</b>

**Table 5.15 Mean species association indices (C8) compared between old and young slopes at three quadrat sizes: 4.0m<sup>2</sup>, 1.0m<sup>2</sup> and 0.36m<sup>2</sup>**

## 5.4 Interspecific associations over successional time

Section 1.4.5 described how predictions made on the basis of the successional models of Peet (1992) may be used to distinguish between those models. This section describes the results obtained from an analysis of the change in strength of species associations between quadrats from young and old slopes.

As outlined in Section 3.6.7 the method for calculating the index of association follows that described by Hurlbert (1969) and Gitay and Wilson (1995); the index is referred to as C8. The equation for calculating C8 is incorporated into a computer algorithm for use in the Genstat statistical package (Lawes Agricultural Trust, 1995); the program code is shown in Appendix E. The values resulting from the calculation of C8 showed a strongly U-shaped distribution with many values of zero and of unity. Whilst the mean values reported below show an increase in level of association with age in many instances, the application of a statistical test to such differences is problematic because of this distribution. In an attempt to circumvent this difficulty association indices are also calculated using Coles C7 index (Hurlbert, 1969) by applying a modification of the C8 algorithm. In many cases the differences between C7 and C8 may be “small or nonexistent” (Hurlbert, 1969). In this method a minimum value for  $\chi^2$  is not defined with the result that the number of zero values is greatly reduced. Mean values for C7 are reported (Table 5.16) together with the result of a Mann-Whitney U test for differences between median values.

### 5.4.1 Association measures from young and old quadrats

The results of the species association analysis are shown in Table 5.15. As in the analyses reported previously the data are considered both as a whole and as separate groups defined by aspect. In each case the mean level of association is reported at three scales of areal measurement; the 100 cells forming each 2 × 2m quadrat are subdivided to give vegetation samples of 1 × 1m (25 cells) and 0.6 × 0.6m (3 × 3 cells). The number of pairwise comparisons used in each calculation is also reported, bracketed, following the index's value.

It may be seen from the table that for large quadrats the difference in the mean level of association with age in a comparison of all young and all old quadrats is not significant as judged by a Mann-Whitney U test. However, for south-facing slopes there is a significant

decrease in level of association from young to old samples and for north-facing slopes there is a significant increase in association with time. Medium-sized quadrats show a consistent increase in association over time for all data sets though in no case is this statistically significant. Small quadrats show a significant decrease in association when the data are undivided whilst both south-facing and north-facing slopes, considered separately, each show a non-significant increase in species association with time.

#### 5.4.2 Coles C7 index of association

Data set	No of quadrats	Quadrat size		
		Large (2×2m)	Medium (1×1m)	Small (0.6×0.6m)
Young	40	0.5665 (3662)	0.5867 (1893)	0.6258 (1293)
Old	40	0.6365 (3552)	0.6363 (1813)	0.6647 (1296)
		<b>p &lt; 0.001</b>	<b>p &lt; 0.001</b>	<b>p = 0.01</b>
Young/South	20	0.6127 (2369)	0.6002 (1285)	0.6402 (966)
Old/South	20	0.6288 (2634)	0.6417 (1331)	0.6894 (966)
		<b>p = 0.08</b>	<b>p &lt; 0.001</b>	<b>p &lt; 0.001</b>
Young/North	20	0.6443 (2514)	0.6933 (1104)	0.6844 (537)
Old/North	20	0.6823 (1379)	0.7691 (934)	0.7623 (585)
		<b>p &lt; 0.001</b>	<b>p &lt; 0.001</b>	<b>p &lt; 0.001</b>

**Table 5.16 Mean species association indices (C7) compared between old and young slopes at three quadrat sizes: 4.0m<sup>2</sup>, 1.0m<sup>2</sup> and 0.36m<sup>2</sup>**

When associations are calculated using the C7 index all cases show an increase in the mean level of association in old, compared with that found in young, quadrats. With one exception the difference in median values, judged by a Mann-Whitney U test, is significant at a probability of  $p \approx 0.05$ . This result suggests that, except for 4m<sup>2</sup> quadrats on south-facing slopes, there is a tendency for species to segregate over time.

#### 5.5 Predictability

The degree of predictability of species compositions between replicates within a community has been recognized as a means of characterizing successional processes and also of distinguishing between those which are abiotic, and externally driven, and those generated by the internal, ecological processes of species interactions (Section 1.6). Two methods of quantifying vegetation predictability (Section 3.6.8) are used in an attempt to distinguish between the operation of these processes.



### 5.5.1 Spatial rank consistency

Measures of spatial rank abundance consistency (Cr) are calculated for each of the four zones defined by age and aspect and are presented in Table 5.17.

Zone	YN	ON	YS	OS
Cr index	0.8864	0.8385	0.8583	0.8241

**Table 5.17 Spatial rank consistency values for four zones defined by aspect and age**

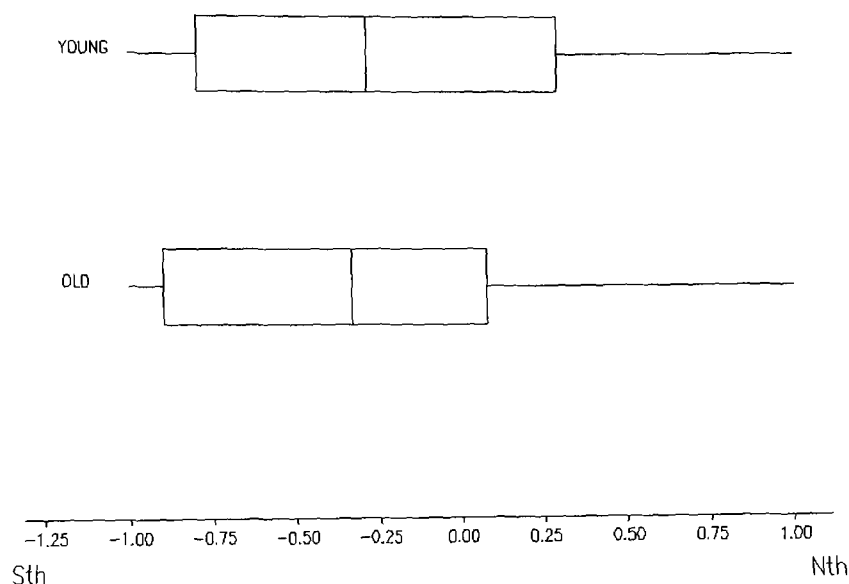
It can be seen from the table that rank consistency values are strongly positive for each group, indicating a high degree of constancy between replicates compared with a random, null model, value of zero (Wilson *et al.*, 1996). Such high values are commonly reported (Grubb *et al.*, 1982; Wilson *et al.*, 1996). Values reported by Watkins and Wilson (1994) for three grassland communities ranged from 0.73 for subalpine tussock, 0.87 for dune tussock and 0.94 in subalpine grassland communities. The values in this study are reduced over time on both aspects. It may also be noted that, for both old and young groups, the Cr index is lower on south-facing, than on north-facing, slopes.

As the data set for each zone generates a single value for the index it is not possible to apply statistical tests to these differences and, since neither the Gradient in Time (GT) nor the Competitive Sorting (CS) models predict a fall in Cr, these results do not serve to distinguish between them and interpretation is problematic. The possible inferences which may be drawn from this exercise are discussed below (Section 6.4.2).

### 5.5.2 Stratification

Predictability may also be measured by the degree of species stratification; that is the strength of the preference which species show for a position along an environmental gradient. In this study species abundances are recorded on north- and south-facing slopes which may be taken to represent a gradient from warm, dry conditions on south-facing slopes, to cool, moist conditions on north-facing slopes. Species may be scored for their preference along this environmental gradient. Preference scores (Ep) are predicted to increase over time under the competitive sorting model whilst remaining unchanged if the gradient in time model operates (Section 1.6.2.5).

Environmental preference scores are calculated in the same manner as that described for age preferences (Section 3.6.8.2). Each of the 49 included species generates a preference score for each of the two age classes with positive values denoting a preference for north-facing, and negative values south-facing, slopes. The range of preference scores is illustrated below (Figure 5.12) and listed for each species in Appendix F.



**Figure 5.12 Environmental preference scores compared between age groups: -ve values represent a preference for south-facing, and +ve values for north-facing, slopes.**

The degree to which preferences change from young to old is analysed by the Wilcoxon signed ranks test (Sokal and Rohlf, 1995). This test shows a small, non-significant ( $p = 0.22$ ), decrease in the strength of species preferences over time.

### 5.5.3 Predictability: summary of results

In summary, predictability, measured by two independent methods, shows a marginal decrease between young and old slopes and is also seen to be lower on south-facing slopes than on north-facing slopes. Neither of Peet's two models predict such a change. The implications of these findings are discussed below (Section 6.4.2).

## CHAPTER SIX: DISCUSSION AND CONCLUSIONS

In this chapter the findings presented in Chapters Three, Four and Five, are discussed. In particular the patterns revealed by multivariate analyses are related to successional processes and the implications, for models of succession, of the tests described in Chapter Five are discussed. The aims and objectives are reviewed, some of the methods used in sampling and analysis are reviewed and suggestions are made for further work in the development of methods and models.

### **6.1 Community structure: vegetation patterns and their relation to the main factors in the study**

A general description of the vegetation samples was obtained using multivariate techniques. In these analyses the overall amount of variation in the data set, reported from CCA and denoted as the total inertia, is equal to 2.700 (Section 4.5.4.1); of this 41.69% is explained by the first four unconstrained ordination axes (DCA run 3, Section 4.3.3); the factors age and aspect are seen to be correlated with axes one and two which together account for 28.68% of the variance. The four canonical factors included in the first CCA run (Section 4.4.4) explain 0.467 or 17.3% of the total. There remains, therefore, a substantial amount of variation not explained by the factors considered in the analyses. This may represent noise in the data or some factor or factors not measured or accounted for in this study.

The major pattern apparent in the species data was that imposed by aspect with the factor age showing a secondary influence. This suggested that the division of the data by aspect would facilitate the analysis of time trends and allow questions relating to differences in successional trajectories on different aspects to be addressed. In addition a number of other factors were considered as part of the general analysis of vegetation pattern; these factors (height, slope angle, disturbance from ants or rabbits and bare ground) were either included explicitly in the design (Section 1.5.1) or came to light as the sampling programme was implemented (Section 3.5.5).

### **6.1.1 Time**

One of the major objectives of the study (Section 1.7.3) was to arrange sites by vegetation composition in an attempt to uncover correlations between time and community structure. The multivariate analyses consistently showed that differences in communities between age groups exist and they support the contention that vegetation change over time is an important structuring force in this herb community. The factor time is, of course, a proxy for a number of processes (colonization, growth and soil development) which operate continuously and whose effects, to the extent that they are cumulative, are increasingly apparent over a temporal interval.

As a newly created bare area of ground offers the opportunity for colonization, there is a marked change in vegetation cover in a relatively short time. First arrivals are likely to include a high proportion of annual species with widely dispersed seeds. These ruderals grow quickly but cannot compete with slower growing competitive species which monopolize space and resources and maintain a presence by vegetative reproduction. Thus the initially plentiful opportunities for colonists rapidly decline as space becomes filled. Further colonization is dependent on the opening up of space resulting from the death of plant shoots. The extent to which new opportunities occur is dependent on the life strategies of the occupants, the nature of the environmental stresses and the continuance of a level of disturbance. Each of these factors may themselves change in relative importance over time.

It is apparent from the DCA analyses (Sections 4.3.5 and 4.3.7) that young sites are more tightly grouped by their similarities of vegetation than are the old sites. This suggests that, as vegetation develops, community compositions have diverged (Section 6.4.2).

### **6.1.2 Bare ground**

The extent of bare ground was shown to be a significant factor associated with community structure by the CCA analysis. It is not correlated with age (Table 4.24) but does have a positive correlation with south-facing sites (Figure 4.20 and Table 4.19).

Bare ground can result from a number of causes. It may be representative of an early stage of succession where plants have yet to colonize; it may result from the inability of

vegetation to colonize or become established. It may also reflect conditions which are unsuitable for plant growth or it may be due to subsequent disturbance within an established community as a consequence of, for example, mechanical interference or slope instability. It is improbable that, over the time scale of this study, vegetation has not had sufficient opportunity to become established in the absence of other limiting factors.

Bare soils have greater temperature extremes than vegetated soils and this effect may also limit colonization on bare areas. This restriction would also tend to be subject to a positive feedback mechanism, maintaining bare areas until they became shaded by lateral spread of tall vegetation from adjacent areas. It is also likely that, on well-drained, south-facing slopes, plants are subject to harsh summer conditions due to heat and moisture stress (Section 1.1.4) and therefore, vegetation cover may be reduced. Since the vegetation in this study had been regularly cut shading is unlikely to have occurred, extreme moisture and temperature regimes would therefore have tended to occur and, as a consequence, bare areas would be maintained.

Substrate instability may also lead to increased levels of soil or root disturbance which would limit vegetation development and result in lower levels of plant cover. The presence of netting, indicating repair work, is taken as evidence of such instability. This might be expected to occur especially on steeper slopes because of the effects of gravity and water on the movement of soil particles (White, 1987). In fact a Spearman rank correlation test gives only a weak correlation between slope angle and the abundance score of bare ground; on south facing slopes the value of the coefficient is 0.2560 with a probability  $p = 0.11$ . The values for north-facing slopes are 0.2176 and  $p = 0.18$ .

Animal activities can be a potent source of vegetation disturbance (Lawton, 1987) and whilst the revetments have not been grazed by domestic livestock (Section 1.1.3), the presence of rabbits and ants has been described. Ant hills showed a strong preference for south-facing slopes; their possible influence in generating alternative successional pathways is discussed below (Section 6.1.3).

In a study of aspect and vegetation, Hutchings (1983) compared the seasonal variation of a number of attributes of calcareous grassland on contrasting aspects having slope angles in the range 16 - 20°. He quotes low values for bare soil (measured by vertical point projection) of less than 5% for slopes on all compass aspects during summer with

increasing, and differential values on different aspects, occurring only during the winter months. Even in winter there is no differentiation between north and south facing slopes, with values of 15 -20% on north- and south-, 20-24% on west-, and 26-30% on east-facing slopes. In this study mean percentage values, taken as estimates of cover at ground level in summer, show 7.4 for south- and 2.0 for north-facing slopes. This comparison suggests the possibility that bare ground may be maintained in this study as a result of steeper slopes and low-nutrient soils.

Although bare ground is a significant correlate in community structure this factor is not related to age in this study and therefore is assumed not to represent a factor in successional change. The association with aspect (Table 4.19) suggests that the reduced coverage on south facing slopes results from an environmental condition which influences a plant's ability to become established. Again, since the amount of bare ground is higher on south facing slopes it is likely that this factor operates directly on plants rather than through competitive interactions. A strong environmental factor would tend to reduce the degree of competitive interactions experienced between individuals in a community. Such a direct effect is likely to be related to water stress resulting from high surface temperatures though this may also be influenced by disturbance to the surface generated by steep slopes and animal activities. Interaction effects between slope angle and aspect (Section 6.1.6) and ant activity and aspect (Section 6.1.3) may also add to this effect.

### **6.1.3 Ant hills**

The CCA analysis shows that the presence of ant hills has a significant regression coefficient (Section 4.5.3) and this may therefore be considered to have a role in structuring the vegetation community present on the revetments. This factor is shown to have a marked positive correlation with south-facing slopes (Section 4.5.4.1). There is no apparent relation between the extent of the ant-hills and the age of the revetment (Figure 4.20; Table 4.19).

Ants have been shown to have a number of ecological impacts in grassland habitats (Wells *et al.*, 1976; King, 1977). Most of the ant hills found in grasslands in the British Isles are constructed by the ant *Lasius flavus* (F) though abandoned mounds may subsequently be occupied by *Lasius niger* or *Myrmica spp.* These ants build underground nests of a spherical design, the uppermost portion protruding above the ground surface to form a mound or ant

hill. The construction involves the movement and sorting of soil particles such that the resulting mound may be composed of a soil different in character from that of the general area. King (1977) describes the soil particles found in ant hills as being smaller and of more uniform size than those of the surrounding soil. It has been suggested that where these activities are found at a high density the effects would be sufficient to influence water penetration, aeration and the chemical status of the soil, rates of organic decomposition and, as a consequence, the composition of the vegetation (Wells *et al.*, 1976). The ants feed on the secretions of roots and root-sucking aphids and it has been suggested that the behavioural characteristics of the ants, in promoting mutualisms with plants and aphids, and in their defensive behaviour against herbivores, generate a selective pressure favouring certain plant combinations (Bronstein, 1994).

King (1977) describes the differences between plant species found on ant hills and those in the surrounding pasture. Whilst the species with a preference for ant hills are almost always present in the adjoining sites their abundances are such as to support the contention that those species on ant hills are more likely to be either short-lived or able to survive burial as soil continues to be heaped on top of them.

The effects of ants on the development of vegetation has been considered by Wells *et al.* (1976) and King (1977); their activities have the potential to alter the conditions for plants and therefore to influence successional change. Ants maintain a presence on the south-facing slopes of the revetments because they have a food source, because it is warm and because they are not excluded by trampling. The vegetational differences between north- and south-facing slopes may therefore be caused, proximately by ant activities, though ultimately it is aspect which is the controlling factor. Nevertheless the influence of ants on the composition of the plant community is likely to be apparent because of the production of microtopographic heterogeneity, mutualistic interactions between ant and plants and edaphic factors resulting from the sorting of soil particles.

Ant hills introduce a degree of soil heterogeneity in that they create patches of soil which are qualitatively different from that of the surrounding areas and they create small-scale (<1m) topographic irregularities in what, on the revetments faces, is a relatively uniform surface; they also generate a small scale but continuous disturbance which would tend to support early successional annual species at a greater level than that found in undisturbed grasslands

of the same age. Thus at the level of the community ant activities might generate greater diversity through the mechanism of disturbance.

Wells *et al.* (1976) suggested that the size of ant hills could be used to assess the time since the last disturbance. If this were the case then the current data set would be expected to show evidence of a difference in ant hill scores between old and young revetments. This was not found to be so in this study. It is possible that the abundance values were recorded at too gross a scale for such an effect to be apparent. Ant hills were not individually measured as in Wells *et al.* (1976), but rather recorded as present/absent in each 20cm × 20cm cell. Whilst a large hill would cover more than one cell this measure of size would likely be averaged out when the cover score for a whole quadrat was considered. A measure of the numbers of ant hills and their mean size may however be calculated where individual ant hills are measured as the number of contiguous cells within a quadrat occupied by each group of occurrences. When this is performed for south-facing slopes then neither the numbers of ant hills, nor their mean size, differ between age groups when tested using a Mann Whitney U test. ( $p = 0.19, 0.72$  respectively). Wells *et al.* (1976) also discuss the likelihood that the size of an ant hill is related to the level of productivity of the site.

Ants are known to prefer warm soils and this has no doubt contributed to their greater abundance on the south-facing slopes. It is also suggested that, when ant hills are shaded by taller or overhanging vegetation, the colonies may be abandoned because temperatures are no longer high enough to support brood production (Wells *et al.*, 1976). It is therefore likely that, in maintaining a vegetation of low stature, the cutting regime in the study area has contributed to the abundance of ant hills. In addition the exclusion of large grazers from the revetments has allowed ant-hills to become large overground structures.

It is clear that on the initially relatively uniform surfaces of the revetment slopes the development of ant hills has contributed to a greater level of heterogeneity in promoting microtopographic variation both at the scale of the revetment face in producing a tussock and between revetment faces. It is likely therefore that the differential development of north and south-facing slopes has been reinforced by the activities of ants.

It therefore seems likely that the ant mounds contribute to a greater floristic diversity by introducing a degree of heterogeneity as a result, either of their activities in disturbing the soil matrix, or their selection pressure in favouring plant species either directly or, mediated



through their role in protecting sap-sucking insects. In the absence of disturbance from grazing animals it may be argued that ants provide an alternative source of moderate, local disturbance and that this generates small scale environmental heterogeneity as well as maintaining a constant source of opportunities for colonization in what would otherwise become a closed cover community.

This reasoning leads to the prediction of a positive correlation between presence of ant hills and species diversity. Increased levels of heterogeneity associated with ant hills may lead to greater number of niches for a greater variety of plants. Again it is difficult in this study to distinguish between the effects of aspect and ants as these two factors are co-related. The hypothesis is, however, tested using a Spearman Rank Correlation test using a measure of diversity and the score for DA (the cover attributed to ant hills). When all 80 quadrats are included the test gives a significant correlation coefficient with  $p < 0.001$ . A similar result is achieved using numbers of ant hills. However when only the south facing data are used the result is no longer significant. This suggests that, since diversity is higher on south-facing slopes (Figure 5.4), the result may be due to the correlation between these two variables rather than a true effect of the ants.

#### **6.1.4 Aspect**

It was anticipated (Section 1.1.4) that the factor aspect would play an important role in determining vegetation structure on the revetments and this was in fact the case as evidenced by the CA, CCA and classification analyses (Sections 4.2- 4.4). In general terms the north- and south-facing slopes are considered to be representative of cool, moist and of warm, dry conditions respectively (Section 1.1.4). As such it was possible to approach the analysis by considering either the whole data set covering a range of conditions or, as two sets of separate conditions, in which differential development of vegetation communities could be matched to the contrasting conditions. In addition the presence of a replicated environmental gradient between north- and south-facing slopes allowed for the analysis of stratification of vegetation over time.

The effects of aspect on the vegetation are thus deemed to be a constant over time. They are predicted to be apparent in the differences in species and species types found which result, directly or indirectly, from differences in conditions. Differences in community structure

between aspects may however be a function of time if there is a process of environmental sorting from an initially random set of species to one in which species become ordered by their abilities to survive the prevailing conditions. The influence of aspect will therefore be considered below in the discussion of community attributes seen to change over time.

### **6.1.5 Height**

The height of a quadrat above the base of the revetment slope was considered as an environmental factor (Section 1.5.1) having the potential for sorting vegetation types along a gradient based on differences in exposure, available soil moisture and differential soil development between upper and lower sections of slopes. This consideration was not supported by the CA, CCA or TWINSpan classification (Sections 4.3-4.5) with the exception of that shown in DCA run 6, axis 1 (Section 4.3.6) which utilizes a reduced data set of south-facing quadrats. This single occurrence suggests the possibility of a factor operating over a vertical gradient on south-facing slopes. However this observation is not supported by other analyses and therefore remains doubtful.

In view of the well-drained nature of the site (Section 1.3) it is probable that differences in height have little impact on the soil moisture conditions experienced by plants within the same slope face. It may also be concluded from the above analyses that any differential exposure to wind and solar radiation (Section 1.1.4) by plants at different heights within a revetment face has little overall effect on the composition of the vegetation.

### **6.1.6 Slope angle**

The angle of slope was used as a factor in the analyses described above (Sections 4.3, 4.4 and 4.5). CA analyses indicate a significant influence of slope angle (Table 4.9) though this finding is not confirmed by CCA. The mechanisms by which slope angle influences vegetation composition may be considered from a number of perspectives. Gravity underlies effects from erosion, disturbance and water runoff whilst surface temperature is partially determined by slope angle as it mediates the effects of direct and indirect solar radiation (Section 1.1.4).

Slope may affect the stability of the soil surface as steeper slopes are more liable to movement due to erosion and gravity (Section 6.1.2); this may make the conditions less favourable to many plant types especially in the early stages of seedling and establishment. Steeper slopes are more likely to show differences between upper and lower zones as there is net removal from upper and net deposition on lower slopes due to gravity.

Steeper slopes on south facing aspects may heat up more quickly as they receive more intense direct solar radiation. They will however receive less indirect radiation since they have a smaller angle of exposure to the sky. Steeper slopes on northern faces are likely to receive less radiation, both direct, since they are more likely to be below the solar horizon, and indirect, since they too have a smaller angle of sky exposure.

Surface runoff of rainwater is likely to be faster on steeper slopes such that the proportion of rain percolating through the surface will be less than on shallower slopes. The net effect will be to reduce the amount of soil moisture on steeper slopes and this effect will tend to be greater at the tops of slopes since lower portions of even steep slopes will receive runoff from above.

It was not practical within the experimental design imposed by the nature of the site (Section 1.4) to control for slope angle. Hence it is difficult to distinguish between the effects of these various mechanisms. It is nevertheless possible to generate likely hypotheses based on what is known from other studies (Perring, 1959; Jastrow *et al.*, 1984). In view of the mechanisms by which slope angle may determine conditions for plant survival described above, the data set containing both north and south-facing slopes is unlikely to show an effect due to solar radiation. Rather, a significant influence of slope angle in the complete data set is likely to result from surface instability. DCA of the whole data shows significant correlations only with the minor axes in runs 1 and 2. However in DCA run 3 (Section 4.3.3), which utilizes options for detrending and downweighting of rare species, there is a significant negative correlation between axis 2 scores and slope angle. This suggests that, when the influence of rare species is reduced, the vegetation is affected by slope angle and, given that this is the case for the both north- and south-facing slopes, it may be inferred that the influence is more likely to be related to slope instability rather than being due to differential irradiation.

When the data are separated by aspect the influence of slope angle is seen to remain. On south-facing slopes, slope angle is positively correlated with axis 1 DCA scores (Section 4.3.5) and negatively correlated with axis 3 scores whilst on north-facing slopes (Section 4.3.7) it is positively correlated with axis 3 scores.

### **6.1.7 Ordination methods: limitations of the CA algorithm**

Whilst the ordination procedures used in CA, TWINSpan and CCA are very widely used in vegetation research they have been criticized because of a technical problem in the coding used to run the ordination algorithm (Oksanen and Minchin, 1997) which is common to all three programs. These authors suggest that the “bug” in the programming generates a fault with the result that the ordination results may be dependent on the order in which the data are input. Whilst this appears, potentially, to be a serious flaw, in practice its influence is likely to be limited to situations in which the eigenvalues of two adjacent axes are of very similar magnitudes. In addition, Oksanen and Minchin, in tests on nine data sets each with 16 different orders of data entry, found that only axes three and four of the ordinations were affected. In the implementation of DCA used in this study (Kovach, 1995) a warning is given when eigenvalues of two successive axes are so similar as to cause instability. No such warnings resulted from any of the seven DCA runs described. The eigenvalues for each run are listed in Tables 4.2-4.8. In addition, when the data for run 3 were rearranged such that species and quadrats were entered in reverse order, both singly and in combination, the output was, in each case, identical to that generated using the unmodified data set. It may be concluded therefore that the DCA runs used in this study are rigorous and the results, and inferences from those results, are valid.

In the case of the classification program TWINSpan, the potential fault is more serious because the program has a more loosely defined convergence criteria which has the effect of increasing instability at the lower divisions. However, the Reciprocal Averaging (RA) sub-routine of the program (Hill, 1979b) includes an instruction to print a warning (“RA Trouble”) if the number of iterations reaches the maximum allowed value of 5 without the residual becoming less than the tolerance value (0.003). It was not possible, in the particular implementation used here (Malloch, 1995), to alter the values of these parameters. Nevertheless, in the analyses presented above (Section 4.4), the number of iterations did not, in any case, exceed 4, and the output from the five program runs did not include any

warnings of “RA Trouble”. The analysis performed in run T1 (Section 4.4.1), was repeated using the reverse data order and the output compared with that generated by the original, unmodified data. It was observed that the sample classification was identical for the groups formed by the first three divisions but that two quadrats were placed in different groups at the fourth division. This finding is consistent with the report of Oksanen and Minchin (1997) which states that the higher divisions are more likely to be affected by instability resulting from non-convergence. Whilst this test is not comprehensive, it does lend weight to the argument that the groups generated by the lower divisions (levels 1-3 in the hierarchy) are stable and consistent under different data order inputs. Inspection of Tables 4.10 - 4.14 indicates that conclusions based on the results of tests of association between TWINSPAN groups and the factors age and aspect are not compromised by the omission of level 4 groups. Whilst it would clearly be desirable for future use of this technique to employ a program which contains a corrected ordination algorithm and stricter convergence criteria, the analyses presented in Section 4.4 remain valid.

The constrained or canonical correspondence analysis (CCA) program employs the same ordination algorithm as that used in DCA and so is subject to the same potential inaccuracies. As was the case for DCA the program output includes a warning in an “iteration report” where convergence is not reached after 17 iterations. Ter Braak (1987-92) suggests that convergence is a problem where subsequent eigenvalues are very close to zero though he ventures that the results from close eigenvalues can still be trusted. For the analyses reported in Section 4.5 convergence was reached after no more than two cycles for each of the four axes and consequently no warnings were generated. It may be stated therefore, that the analysis was not subject to instability or non-convergence and that the results do indeed uncover a significant pattern in the data.

## **6.2 Diversity**

Odum's model of succession (Section 1.6.1.3) makes some general predictions of community change, including those of increasing diversity and evenness, with time. This expectation is based on a holistic, systems paradigm (Odum, 1969) according to which communities are assembled in a manner which maximizes biomass and interconnectedness, so erecting an organized community which achieves maximum control over the physical environment. Within such a systems framework Odum simultaneously accepts that species traits may generate contrary outcomes. Increasing organism size, for instance, will necessarily reduce the number of species in a given area and competitive dominance, leading to exclusion, will also result in reduced diversity. As a scientific hypothesis Odum's model and its predictions relating to change in diversity are thus seen to be poorly formulated to the extent that they are difficult to falsify.

This study has produced evidence of reduced diversity in older communities (Sections 5.3.1 and 5.3.2). Such evidence does not therefore support the expectation of increasing levels of organization over time in grassland communities generated by the systems model of succession. As dominance shows a small increase (Section 5.3.3) Odum's alternative suggestion of an explanatory model based on species traits would seem to be indicated. Furthermore, since there are large differences in diversity between aspects (Figure 5.2) it is likely that physical conditions play a significant role in determining patterns of community assembly.

### **6.2.1 Rank abundance distributions**

Inspection of the RAD plots (Figures 5.9-5.11) gives an overview of community structure not apparent in indices of diversity and evenness. The curves representing relative species abundances may be conveniently divided into an upper, steeply falling section representing the few dominant species, a less steep and longer mid section representing a larger number of species with mid-range abundance values, and a lower tail section, falling more steeply and representing abundance values of rare species. A comparison between plots based on this division of the community is instructive in describing community differences between age groups and aspects.

Since the numbers of species is lower in old quadrats (Table 5.13) the lateral spread of the RAD curve is reduced for older quadrats and so the gradient is necessarily steeper. This apparent reduction in evenness illustrates the possible dependence of diversity and evenness indices on species number. The measures used here (Section 5.3.4) are designed to be independent of species number.

In all three plots there is evidence that the upper section is longer in the old quadrats; this gives the curve the appearance of being steeper but in fact the shorter, young curves are steeper in this upper section. This suggests that there is, consistently, an increasing level of dominance in older sites; however this is poorly represented in the index chosen (Section 5.3.3) which measures the relative abundance of the single most dominant species. Though less steep in the older quadrats, this upper section of the curve contains a greater proportion of the community and therefore suggests a reduction in evenness; the longer drop is more significant because adding more species necessarily makes it less steep in absolute terms.

The mid sections of the curves (Figures 5.10 and 5.11) are shorter in the older quadrats. This reflects the fact that, overall, there are more species in this than in the upper part of the curve and that this number has declined with age. A speculative interpretation might be offered which suggests that, with greater dominance, there are fewer opportunities for species of mid-range abundance to maintain a presence.

The tail of the RAD plot is generally steeper giving the whole curve a sigmoid appearance. It may be seen that in north-facing quadrats (Figure 5.10) there are relatively few species in this lower part of the curve and this is likely to contribute to the increase in evenness over time reported above (Section 5.3.4). In contrast, older quadrats on the south-facing slopes show increased numbers of species in the tail so generating a decrease in evenness.

The RAD curves illustrate the complexities of community structure and some of the difficulties encountered in trying to arrive at an overall description of the community. The tripartite structure revealed in these curves does suggest that this more detailed approach to the analysis of community structure is more likely to yield insights than would attempts to quantify relative abundances in a single index.

The intuitive impression from Figures 5.10 and 5.11, that different structural patterns are shown in north- and south-facing slopes, is supported by the difference in level of fit of the

curves to the truncated log normal model. The curve for north-facing slopes shows a tendency to become less similar to the null random model whilst in south-facing slopes the community structure is more like a randomly generated one. Where communities are predicted to show higher levels of organization (Section 1.6.2.6) the north-facing communities provide supporting evidence whereas those on the south-facing slopes show a tendency to become more of a random assortment. This interpretation is consistent with the observation (Section 1.1.4) that north slopes have conditions which are more amenable to plant establishment and growth so allowing interactions, and a degree of competitive sorting, to occur, whereas on south slopes, subject to stressful conditions related to high rates of insolation, species do not interact to the same degree and consequently are less subject to the organizing influence of interspecific interactions.

### 6.3 Species traits

The predictions derived from Grime's model of succession (Section 1.6.1.1) are only weakly supported by the results of this study (Section 5.2.1) to the extent that numbers and proportions of ruderal species are lower in older quadrats and stress tolerators show a marginal increase. However the numbers of competitors and stress tolerators which meet the criteria for inclusion are small (3.5% and 3.1% respectively) and the association between strategy and age preference is not statistically significant (Table 5.4). These results are consistent across aspects (Tables 5.6 and 5.8).

The species based approach to modeling vegetation development adopted by Grime has been supported by other studies (e.g. Hillier, *et al.*, 1990; Hughes and Fahey, 1991; Smith and Rushton, 1994; Cottrell, 1996; Grime *et al.*, 1997) which show differences in strategy between early and late successional species (Bazzaz, 1996). In this study the weak conclusion may result from the presence of dominant species which do not show strong age preferences. In particular the species *Arrhenatherum elatius* and *Festuca ovina* are widespread (Appendix A) and have low discriminatory powers with respect to age (Appendix D). *Arrhenatherum elatius* is a competitive strategist and *Festuca ovina* a stress tolerator. Given the wide occurrences and high abundances of these species any attempt to model the particular vegetation development in the study area should be capable of explaining such patterns. To that extent Grime's model is of only limited applicability to the communities present in this study.



Insights into the process of community assembly can nevertheless be gained from consideration of a static representation of communities of the two ages by analysis of the relative abundance distribution. The RAD plots (Figures 5.10 and 5.11) show changes in community structure between age groups in terms of the relative proportions of dominance amongst the component species and the analysis describes the degree to which the distributions differ from that of a randomly distributed population.

The division of species into dominance groups suggested above (Section 5.3.5) shows differences between age groups in terms of the species forming the tail of the curves. On south facing slopes there is an increase in the numbers of these rare species on the older slopes whilst on north-facing slopes the opposite trend is displayed. These trends are apparent despite a general trend of decreasing species numbers on both aspects with time (Table 5.13). This difference in pattern between aspects may be interpreted in terms of the Grimian model if the north and south aspects are taken as representing favourable and stressful conditions respectively (Section 1.1.4). On north facing slopes relatively favourable conditions have allowed an increase in the abundance of dominant species (*Arrhenatherum elatius* or *Festuca ovina*) which has tended to exclude the tail species. However, in the stressful conditions found on the south-facing slopes competition is reduced and more species are able to maintain a presence, particularly the stress-tolerators (Table 5.8). This interpretation is consistent with the evidence of a shift in the RAD plots towards a more randomly structured community on south-facing, and a less randomly structured one on north-facing slopes (Table 5.14).

The presence of rare species, though often considered artifactual (Section 3.6.1.4), may thus reveal information useful to an interpretation of the conditions and successional status of a site. In addition, this component of the community has potential conservation value as a local source of colonists for the maintenance of a diverse community in stressed or disturbed habitats (Grime, 1998).

## 6.4 Ecological and evolutionary-based models

Measures of association and predictability enabled a distinction to be made between communities structured by either species interactions or inherent plant traits.

### 6.4.1 Species association

The C7 measure of association between species shows an increase in level between young and old age groups (Table 5.16); this is true for both north- and south-facing quadrats and is consistent across spatial scales. This finding supports Peet's competitive sorting (CS) model of succession suggesting the operation of ecological interactions in generating community structure over time. This effect is less pronounced in large quadrats and less strong on south-facing slopes.

These results provide clear evidence in support of the role of interspecific mechanisms generating pattern in plant communities over successional time. The tendency for differences to be less pronounced in the large quadrats may be suggestive of a scale of operation of the mechanism (Greig-Smith, 1983) of around 1 - 3 m. Given the relative uniformity of the conditions within the revetment slopes (Section 1.1.4) such a mechanism is likely to be biologically driven. It may act directly by propagule dissemination in the immediate vicinity of a competitively superior parent, or indirectly via changes in soil properties driven by, for example, the accumulation of soil organic matter (White, 1987), or by the gradual establishment of a specific decomposer system which favours a particular subset of the earlier species (van der Heijden *et al.*, 1998).

The strength of species associations is less strong on south-facing slopes (Table 5.16). This finding is consistent with, and lends weight to, the explanation of higher levels of diversity (Section 6.3) resulting from reduced rates of competitive exclusion in the harsher conditions experienced on south-facing slopes. Where competitive, or other interspecific, interactions are reduced then the CS model would predict weaker levels of association (Section 1.6.2.4).

## 6.4.2 Predictability

The level of predictability was compared between age groups (Section 5.5) to test for a change in the level of community organization over time. An increase in this effect was a predicted outcome for communities in which species interactions were the predominant structuring force and the comparison served to distinguish between the ecological and evolutionary models of succession (Section 1.6.2.3). Predictability was measured in two ways: the levels of species stratification (Section 5.5.2) and spatial rank consistency (Section 5.5.1) were calculated. Both measures showed a small decrease in predictability in the old quadrats; in the case of stratification this was not statistically significant and for spatial rank consistency no statistical test was applied. These results appear to be directly contrary to the conclusion derived from comparison of levels of species association between age groups (Sections 5.4 and 6.4.1). A number of approaches to this conflict may be considered.

The changes in predictability are small and/or statistically non-significant and they may therefore be considered to represent an outcome of no change between age groups. This approach would therefore accept the result as a confirmation of the prediction made by the gradient in time (GT) model (Section 1.6.1.4), that evolutionary factors are the major structuring forces operating, that species are equally well fitted to their conditions at all stages of succession and so succession itself is driven by external change in environmental conditions.

Alternatively, the results may be interpreted as showing an actual decrease in predictability. A reluctance to reject this conclusion may be tentatively based on the evidence from two different methods of analysis which give consistent results; a line of reasoning may therefore be provisionally followed which explores the implications of such a result with the expectation of new insights and hypotheses being generated. In this case the result does not support either of the two models and therefore indicates the operation of some unanticipated factor or mechanism.

Both of these approaches draw conclusions which run counter to that derived from analysis of species associations which support the CS model (Section 6.4.1). This conflict may be resolved by a consideration of the methods used in the various analyses. Measures of association record the joint presences or absences of any two species within each quadrat (Section 3.6.7) whereas predictability indices record the degree of fidelity of a species

between any two quadrats (Section 3.6.8). Processes which might give rise to differences in species association must therefore operate at the within-quadrat scale of 1-3m whereas processes generating between-quadrat differences may operate over a range between 15 and 1500m. It may therefore be argued that, the conclusion, that competitive sorting acts to structure communities, is valid at the within-quadrat scale but not for scales above 15m where predictability is shown not to increase over time.

At the larger scale of 15-1500m the evidence from this study remains ambiguous with respect to the operation of either, the GT, or some other successional model. The experimental design and the analyses used indicate that the GT model cannot be rejected yet there is evidence of a trend of decreasing predictability on older slopes. The evidence and analyses presented here are not sufficiently detailed to allow a resolution between these options and therefore conclusions about mechanisms other than the GT model remain speculative. Such speculation can however be a source of further hypotheses which are also indicated by other aspects of this study.

Firstly the decrease in spatial rank consistency and levels of stratification suggest a divergence in vegetation development with time. This is also indicated by a general increase in the variance of community measures (Section 5.3.2) and the greater spread of old quadrats in ordination space seen in the DCA results (Section 4.3). An alternative interpretation is that the apparent divergence actually results from the wider spatial distribution of the older revegetations within the study area; this is discussed below.

The suggested influence of aspect in determining levels of community structure is again seen when measures of spatial rank consistency are compared between north- and south-facing slopes (Table 5.17). The lower values of predictability on south-facing slopes are consistent with the contention that these communities are more stressed by environmental conditions (Section 1.1.4) and therefore display less evidence of a structured composition.

## **6.5 Spatial dependence**

The operation of one or more spatially based factors tends to undermine inferences drawn from a comparison of sites to which levels of putative variables have been assigned, or actual variables measured, when those sites are separated in space (Legendre, 1993; Nekola and

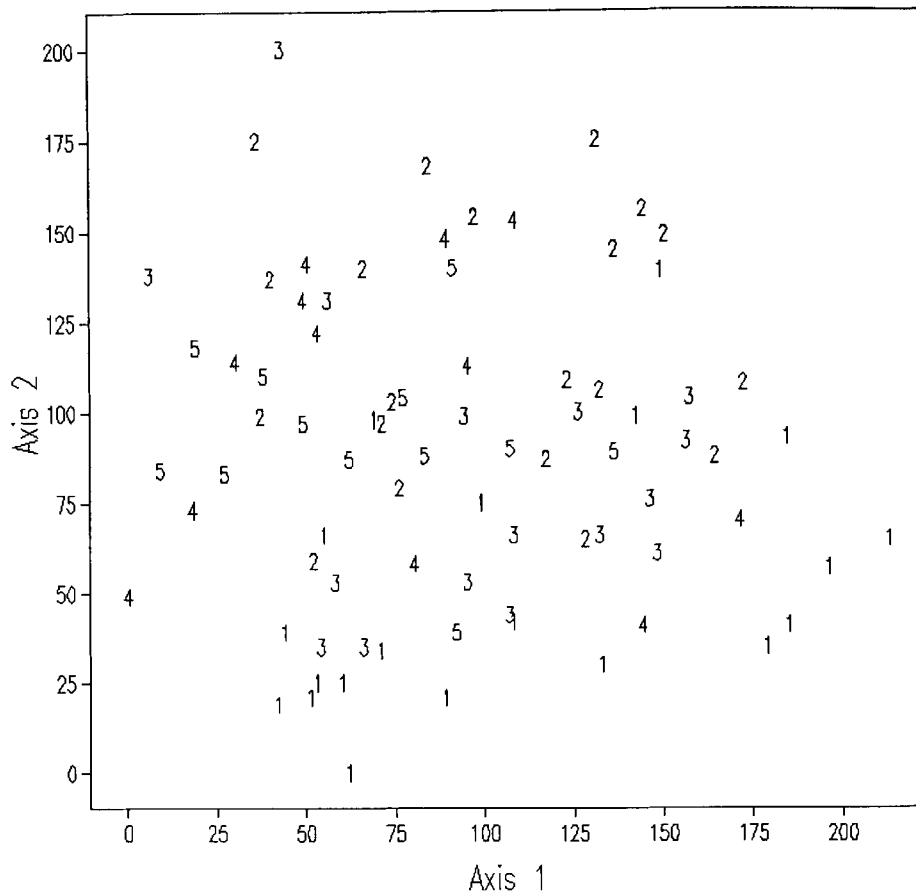
White, 1999). In this study sampling zones are assigned levels of the factors aspect, age and height and differences between sites, based on species compositions, are related to differences in levels of these factors. The extent to which spatial dependence confounds these differences was investigated at the within-revetment scale of 1-20m in the pilot study (Section 3.4), the conclusion being that samples separated by distances greater than 16m were independent of spatial influences. This finding has, however, been questioned by the result of the DCA analyses (Sections 4.3.5 and 4.3.7) where evidence of clustering by geographic location was indicated from an inspection of the sites plotted in ordination space (Figure 4.13).

### **6.5.1 Variance and spatial dependence**

A number of measures derived from quadrat data (e.g. DCA scores and diversity indices) show greater levels of variance in older, than in younger, sites. Levels of diversity (Table 5.13 and Figure 5.8) are seen to have a greater range in older quadrats. A corresponding effect has been noted above in the DCA analyses. This greater variety on older slopes suggests a divergent succession occurring in revetments located over a spatial range of 1.5 km. This variety at the km scale contrasts with the decreased levels of diversity within quadrats (Section 5.3.2).

The high variance in measures of diversity and species richness made at the the 2m quadrat scale between old sites is however largely restricted to south-facing slopes (Table 5.13). This difference suggests that divergence between initially similar sites may be promoted by the harsh conditions generated by high levels of insolation (Section 1.2). Environmental stress is related to low levels of competitive displacement (Section 1.6.1.1) and consequently low levels of dominance (Section 5.3.3).

Increased levels of variance, apparent on older slopes, may, however, reflect the operation of some spatial factor. If vegetation pattern is spatially dependent and similarity between samples is inversely related to their separation distance (Section 3.4) then higher levels of variance may reflect, to some degree, the larger area over which the old revetments are located. Two approaches to this issue are suggested. First an attempt may be made to define the spatial factor and extract its effects from the analysis. Alternatively the factor may itself be the subject for further investigation (Legendre, 1993).



**Figure 6.1 DCA3: all quadrats plotted by spatial group.**  
 1 = N<sub>Y</sub>, 2 = S<sub>Y</sub>, 3 = SW, 4 = SE, 5 = NE

DCA run	Spatial group	Axis 1	Axis 2	Axis 3	Axis 4
3	N <sub>Y</sub>	46.5	20.1	37.9	49.1
	S <sub>Y</sub>	44.7	56.8	34.5	37.2
	SW	43.7	37.2	48.8	25.8
	SE	31.6	48.0	20.5	34.4
	NE	28.2	44.2	63.8	57.3
	p	0.12	< 0.001	<0.001	<0.001
5	N <sub>Y</sub>	30.1	21.1	21.5	26.3
	S <sub>Y</sub>	16.8	18.7	33.3	19.1
	SW	18.5	17.3	16.3	26.8
	SE	20.2	15.0	11.0	9.1
	NE	13.6	32.3	12.6	16.2
	p	0.04	0.08	<0.001	0.02
7	N <sub>Y</sub>	15.6	25.6	33.6	22.5
	S <sub>Y</sub>	21.5	22.0	10.0	26.8
	SW	11.6	15.3	14.1	8.9
	SE	30.0	31.3	21.5	25.7
	NE	29.5	5.7	23.7	17.2
	p	0.01	<0.001	<0.001	0.01

**Table 6.1 Mean rank of spatial groups derived from DCA axis scores by Kruskal-Wallis test.**

If a spatially based factor has an influence in generating variation within the data, and that factor is related to the relative positions of the quadrats, then it may be possible to derive some measure to represent it; for example, it is possible to define a categorical factor associated with groups of quadrats on the basis of their geographical locations (Section 4.3.7). Alternatively, a continuous geographic variable may be defined whereby each quadrat is allocated a value on the basis of its position within a spatial coordinate system. Having defined the spatial factor it may be used to subtract the spatial effect from the analyses described above; for example in CCA it may be entered as a co-variable in the analysis, so allowing any underlying trend related to age to be revealed. Whilst such analyses are beyond the scope of the present work the potential usefulness of the approach is suggested by the following example.

### **6.5.2 Subtraction of spatial influences from the analysis**

The ordinations described above (Sections 4.3.5 and 4.3.7) contain evidence of quadrats organized in a pattern which appears to be related to the spatial layout of the revetments within the study area. This raises the possibility that differences between young and old quadrats relate to spatial separation at a scale of around 100m rather than to temporal effects. The layout of the revetments (Figure 3.5) and the ordination diagrams (Figures 4.9 – 4.14) suggest five, naturally occurring, spatial groups. The young revetments may be divided into northern ( $N_Y$ ) and southern ( $S_Y$ ) groups each containing 20 quadrats and the old revetments into SW, SE and NE groups (Figure 3.5) containing, respectively, 16, 12 and 12 quadrats. To investigate this relation further the plots are displayed below with each quadrat denoted by spatial group (Figures 6.1-6.4).

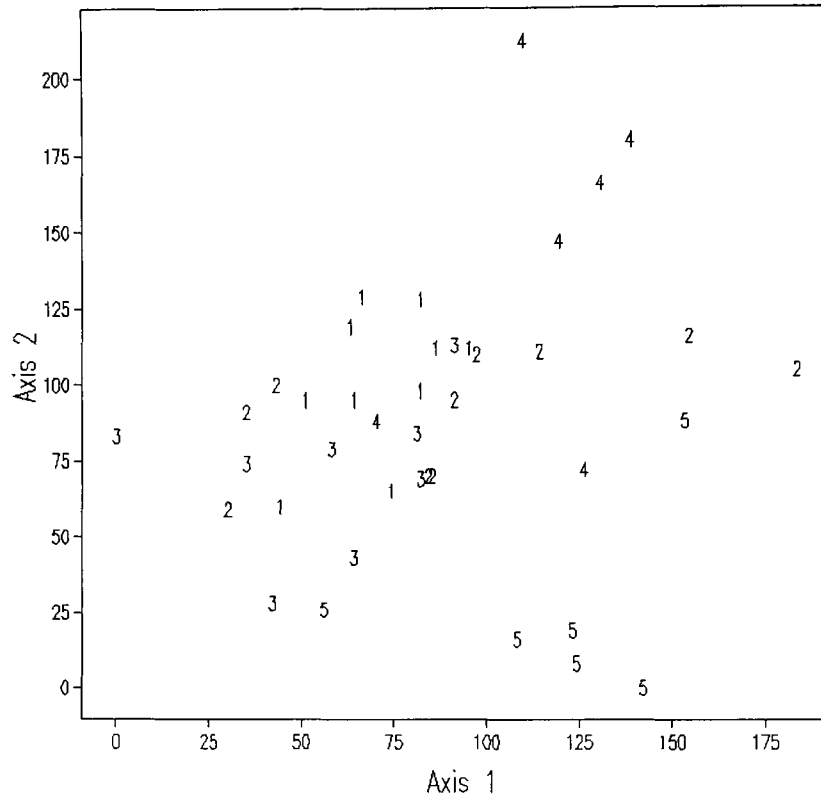
The plot representing DCA run 3 (Figure 6.1) shows evidence of spatial group  $N_Y$  grouped towards the lower end of axis 2 with group  $S_Y$  occupying the remainder of the space. When the data are separated by aspect both south-, and north-facing quadrats show evidence of clustering by spatial group. In the south-facing quadrats group  $S_Y$  is shown to form a compact assemblage on axis 3 (Figure 6.2) and Figure 6.3 shows that, amongst the north-facing quadrats, groups SW, SE and NE are separated on axis 2. Similarly in Figure 6.4, which again shows north-facing quadrats, groups  $N_Y$  and  $S_Y$  are separated along axis 3.

A statistical analysis of these patterns is applied to the data to determine the extent to which spatial patterning accounts for the variation in the DCA scores and, in particular, whether there is a systematic difference between young and old revetments which might confound the analyses of differences based on age. The Kruskal-Wallis test (Sokal and Rolf, 1995) is used for each axis score for the three DCA runs discussed above; the results are shown in Table 6.1.

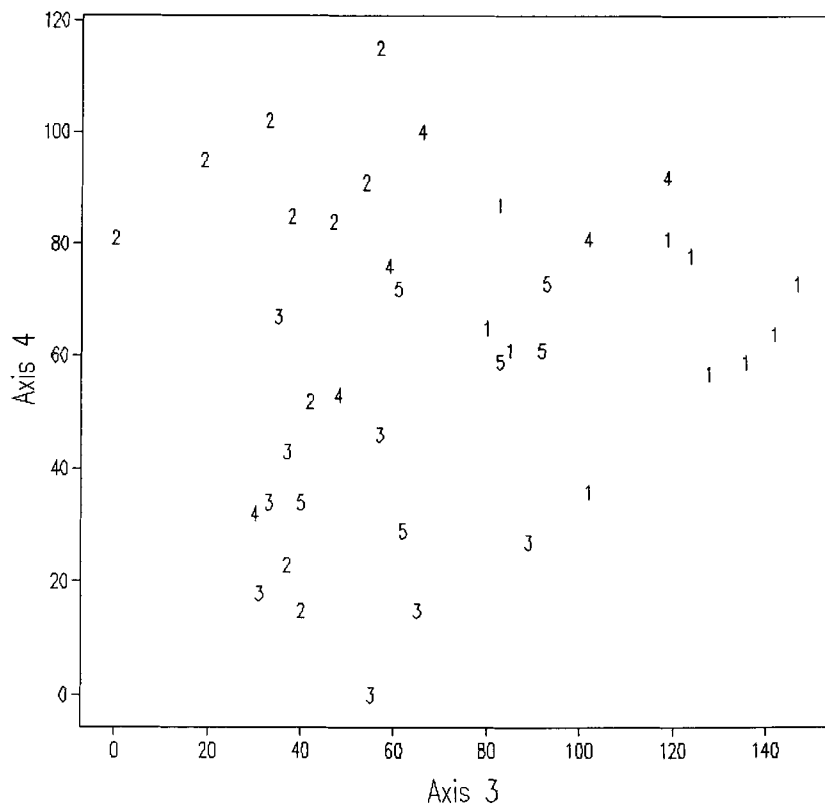
It is apparent that spatial patterning is a significant factor in many of the ordinations. However examination of the differences between mean ranks for the two young groups shows that the pattern is not solely due to the wider dispersion of the old revetments. In addition comparison between Tables 6.1 and 4.9 reveals, for example, that in DCA run 3 axis 1 is significantly related to age but not to spatial group.

The plots shown in Figures 6.1 – 6.4 and the results in Table 6.1 do suggest that a spatial influence contributes to the patterning of the ordinations. However this factor can be seen to operate on and within both age groups and it may therefore be argued that differences due to spatial layout are at least as great within the young group as between the young and old groups or within the old groups. It follows that differences between young and old groups are not systematically affected by spatial patterning and are therefore likely to reflect the operation of the factor time rather than merely separation in space.

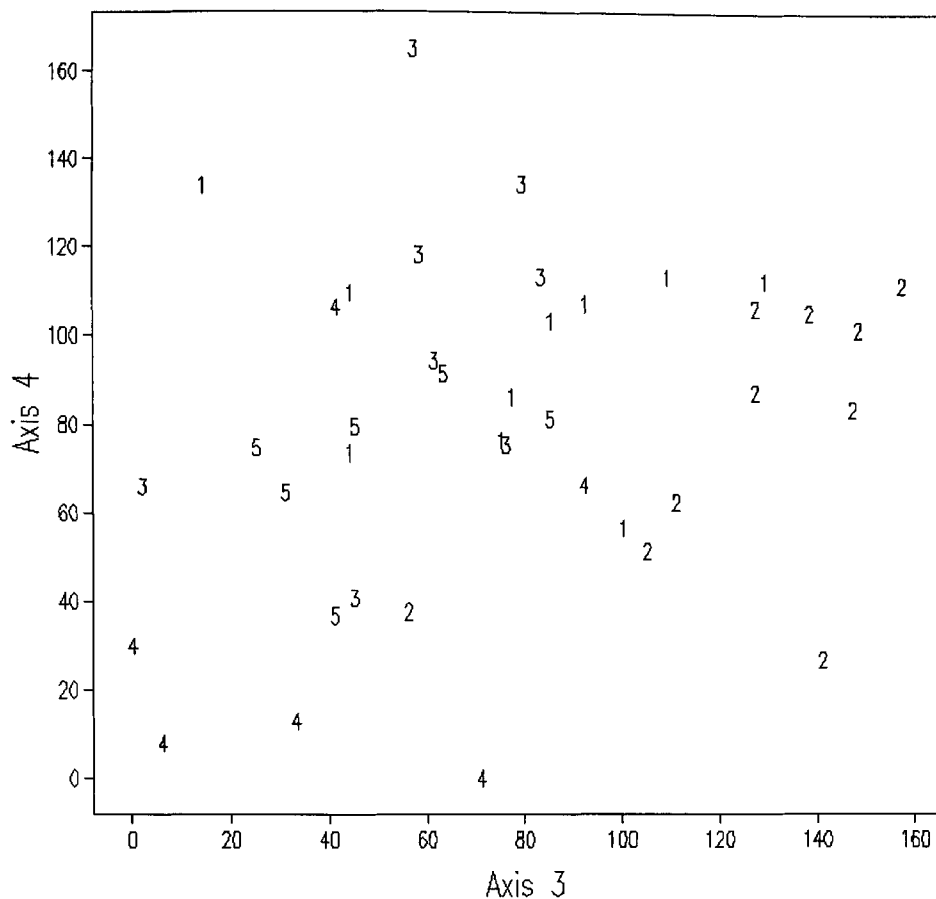




**Figure 6.3 DCA7: N-facing quadrats plotted by spatial group: axes 1 and 2.**  
 1 = N<sub>Y</sub>, 2 = S<sub>Y</sub>, 3 = SW, 4 = SE, 5 = NE



**Figure 6.4 DCA7: N-facing quadrats plotted by spatial group: axes 3 and 4.**  
 1 = N<sub>Y</sub>, 2 = S<sub>Y</sub>, 3 = SW, 4 = SE, 5 = NE



**Figure 6.2 DCA5: S-facing quadrats plotted by spatial group**  
 1 = N<sub>v</sub>, 2 = S<sub>v</sub>, 3 = SW, 4 = SE, 5 = NE.

Although this exercise shows a strong association between geographic groups and species composition those groups do not satisfactorily separate the spatial from the age factor. The association is therefore due, at least, to the combined effects of these two factors. However the increased statistical power gained (Table 6.1) from the explicit inclusion of the spatial factor (*cf.* Table 4.9) indicates that further investigation of spatial effects may yield an improved explanatory model of vegetation community processes.

### 6.5.3 Spatial factors and the development of successional models

It is suggested from the above argument that a successional model is unlikely to generate useful predictions of vegetation development unless the spatial factor uncovered in this study is included. The success of this exercise would depend on the ability to identify the nature of the process, or processes, generating the spatial pattern and, indeed, to fully describe the resulting pattern.

Whilst the data presented thus far indicate the existence of a spatial factor they do not extend to a complete description of that pattern but suggest only that an influence is apparent which has differential effects related to the spatial separation of any two sample points. Whilst much vegetation science is based on an assumed model of species tolerances being distributed in a bell-shaped curve with respect to environmental gradients (Whittaker, 1975; Begon, Harper and Townsend, 1990) a similar assumption of the existence of a causal factor generating landscape scale patterns is not necessarily indicated by the analyses of spatial dependence (Section 6.5.2). In addition to the factors analysed in this study, pattern may be a result of; underlying edaphic or geological factors, or local climatic influences; or it may be an expression of biotic processes such as the mode of vegetation development whereby processes of growth, reproduction, dispersal and colonization result in heterogeneous establishment patterns (Okland and Eilertsen, 1994; Dale, 1999); the outcome of repeated interactions between individuals and species may also generate larger scale patterns over a sufficiently long time interval (Pickett, 1976).

If a process generating spatial structure was expressed as a linear pattern generating a gradient, such as may occur from the presence of a strongly directional wind influencing patterns of pollination, colonization, migration and the appearance of new sites, then it would be useful to identify the direction of that gradient. Alternatively the factor may be of a centrifugal kind (Keddy, 1990), generating radial gradients of influence from a point source, in which case a description of the resulting pattern would require identification of the location of the origin. The possibility of multiple factors, having centrifugal patterns of influence and centred in different locations, suggests the potential for complex spatial patterns which can only be guessed at. If such multiple factors were present together with one or more linear, directional determinants then a mode of vegetation development is suggested which might be described in terms of an epidemiological model (Harper, 1988; Grenfell and Harwood, 1997) incorporating plant propagules as infectious agents, dispersal mechanisms as transmission vectors and environmental conditions, substrate gradients and existing plant cover as conditions conferring immunity or susceptibility. The power of such a model to generate realistic predictions about the course of a succession would be extremely limited without extensive knowledge of available species, soils and environmental factors and constraints, and the ability to integrate such knowledge into a coherent form.

Whilst this approach goes beyond the questions addressed in this study it is suggested as a potentially fruitful area of conjecture and further modeling. The degree to which it may be

justified rests on the amount of extra variation which may be explained by its inclusion in the analyses already described.

## **6.6 Evaluation and contribution**

The findings of this study suggest that succession in this calcareous grassland, following severe soil disturbance, does not lead to a convergent, single climax; that, given similar conditions, vegetation development does not follow the same trajectory in a group of replicates. This conclusion is well supported by the evidence and is therefore valid to an extent which depends on the independence of the replicates (Section 1.5.3), the assumptions of the chronosequence methodology (Section 1.5.2) and the degree of control of factors other than those explicitly included in the study; this being dependent on the history and management of the site (Section 1.4.1).

Analyses of community level processes showed the presence of, at least, two processes operating, independently, at different scales, and tending to produce effects counter to each other. Competitive sorting, operating at the metre scale, was not apparent at the 15-1500 m scale where the effects of a gradient in time mechanism could not be distinguished from an influence related to spatial correlation. A successional model which aims for a realistic predictive capability at a scale greater than 2-3m should be based on the operation of multiple factors incorporated into a structured hierarchy of processes and interactions. It should aim to identify the scale of the patch, within which species interactions occur; to provide a mechanism by which such patches may be integrated into a large landscape and to identify the factor or factors which generate spatial dependence between communities.

Succession as a species replacement process may be described in terms of a change in species strategies. However although Grimes scheme is only weakly supported by this study the data presented contain low numbers of species in some of the strategy categories and it may be further argued that the two time points in the chronosequence do not provide sufficient temporal resolution for a more confident conclusion to be drawn. Notwithstanding these qualifications, the characterization of succession as a species replacement process or as a change in species type where species have been classified into groups based on ecological traits, was shown to be of limited usefulness in this study. Whilst other studies suggest that the period between 27 – 56 years would be expected to show considerable change in grassland

communities (Section 1.6.4) relatively few species in this study showed a significant change between age groups. It is suggested that the degree of disturbance which initiated the succession at the site may have been of a severity more characteristic of primary successions than those seen on abandoned fields and that the rate of succession may have been slower as a consequence (Marrs and Bradshaw, 1993).

Of the species which did show some age class fidelity, change of species type, from ruderal to stress tolerator was only weakly demonstrated. Studies by Grime *et al.* (1997) nevertheless continue to support the contention that plant strategies represent primary ecological types in British herb communities. Such studies, which screen individual species for their characteristics across a range of ecological attributes, have not yet developed to the stage at which community-level behaviours can be predicted (Grime *et al.*, 1997).

In this study it is suggested that impact of individual species may be interpreted in terms of their position within a dominance hierarchy based on the tripartite division of community structure demonstrated by the analysis of the RAD plots. It remains to be seen if such an approach is likely to be successful as a bottom up exercise in which species are assembled according to rules derived from studies of species traits. Rather, as this study indicates, insights may be more likely to arise from the analysis of complete communities whereby species position in a hierarchical community structure may be apparent from their recorded relative abundances. A subsequent correlation between species dominance position and their measured individual traits would indicate the usefulness or otherwise of attempting to formulate assembly rules or bottom-up successional models.

Relatively few species showed strong age preferences and this fact limited the usefulness of the description of this successional series in terms of plant traits based on individual species attributes. Whilst the evidence presented here suggests that this approach is unlikely to produce a predictive model of successional grassland trajectories it is acknowledged that the time scales of this study and the limited temporal resolution of the two point chronosequence used (Section 1.5.2), may conceal finer scale dynamics.

The nature of the spatial factor shown to occur is suggested as an area of potentially useful further research. The description of the pattern exhibited by this factor requires further clarification before an enquiry into its origins may be undertaken. The sampling programme was based on, and to a large extent determined by, the existing layout of replicate revetments.

These conform approximately to that required of an experimental design with the exception that treatments are not randomized amongst the study objects; age groups are located in separate though adjacent geographical spaces.

Sampling quadrats were located in areas deemed to be independent, as shown by analysis of spatial relations of nearby quadrats. Though the results of the pilot study were incorporated into the sampling design, subsequent analysis suggested that spatial correlation may continue to have an impact on the independence of the samples at the landscape scale. This factor is likely to be present in all instances where samples have a spatial relationship unless a disturbance treatment can be applied in a completely controlled, randomized manner. It is difficult to envisage how such control may be achieved in other than small scale microcosms and over a limited temporal interval.

The quadrat sampling method was appropriate to the scale of this rough grassland and the construction ensured objective data collection though a cost was paid in terms of efficiency. The *in situ* assembly of the quadrat was difficult and time consuming particularly on the steeper slopes. However, in view of the detailed analysis of community composition achieved (Section 5.3.5), it is felt that this trade-off was appropriately balanced.

The description of the community variation achieved by the ordinations and classification was in line with the expectations generally recognized from these widely used methods of analysis. The methods produced largely consistent and robust results. The impact of slope angle (Section 6.1.6) was, however, problematic, being indicated as significant in many of the CA analyses but not in the canonical method.

The increase in diversity over time in this low management limestone grassland was shown not to have occurred. The presence of a dominant rank grass demonstrates the importance of an active, moderately intensive management in grasslands where conservation of biodiversity is the aim (Usher, 1993). The successional model based on increasing levels of species richness, diversity and evenness (Odum, 1969) was shown to be inappropriate in this rank grassland.

In this study microtopography was clearly defined by the uniform, plain nature of the slope faces and therefore the effects of aspect in generating topographic heterogeneity could be controlled. Those effects were seen to be powerful and consistent in generating microclimatic

conditions represented respectively by exposed, harsh south-facing, and sheltered, moderate north-facing, slopes. In natural landscapes topographic heterogeneity is likely to occur across a range of scales such that a further powerful influence on community composition must be integrated into any proposed model.

## 6.7 Conclusions

The following inferences have been made as a result of the work described in this study.

- Competitive sorting operates to structure the rough grassland developed on man-made slopes at Caerwent subject to a managed cutting regime.
- The CS mechanism operates over small scales of 1-3 m.
- Larger scale (15-1500m) development of community structure demonstrates divergence over time rather than a move towards a climax.
- Spatial dependence is seen to operate both at the local (1-3m) and larger 15-1500m scales.
- Development pathways are dependent on environmental factors. Where these are strong they over-ride interactions between plants producing a community structure similar to one arising by random allocation of plant individuals.
- Species ecological types do not constitute good descriptors of change in managed grasslands over a timescale of 30-60 years.
- Community structure is not well described in terms of diversity indices. A more useful indicator is given by the overall numbers and relative contributions of the component species.

## 6.8 Future research

Whilst the questions posed by this study (Section 1.7.1) have been addressed within the limitations set by the site and scale of the investigation (Section 1.8) a number of issues remain and others have arisen as a result of the work. These unresolved questions may form the basis for further studies.

A predictive model of community development in grasslands is unlikely to progress beyond the local scale without the explicit inclusion of a spatially based component. The nature of such a model might best be approached by a further analysis of pattern within communities with the aim of further reducing the amount of unexplained variation. The search for an underlying model describing the spatial distribution of plants and plant communities is an active area of research in plant ecology (Gurevitch and Collins, 1994; Dale, 1999). Methods include the use of geostatistics (Rossi *et al.*, 1992; Legendre, 1993), epidemiology (Holmes, 1997) and fractal analysis (Hastings and Sugihara, 1993). Along with this initiative is the recognition that without the integration of phenomena at the small, plant-to-plant scale with landscape scale processes a predictive model having useful applications is unlikely (Bazzaz, 1996; Duarte *et al.*, 1998).

Environmental factors not studied in this work might usefully be included in future studies in order to approach a more complete listing of those geological and edaphic influences on vegetation dynamics. More detailed analysis of micro-climatic influences, as imposed by the topography of the revetments, are also indicated as a means of refining the community descriptions beyond a simple binary classification.

Whilst the conditions at the site have been relatively well controlled the influence of small scale disturbance was apparent. The cumulative impact and differential influence of ant hills provided a disturbance regime which could not be adequately separated from that of aspect. This suggests the need for a study in which the removal of the influence of soil sorting by ants might be used to distinguish between plant diversity generated by environmental and that produced by the ants activities (Section 6.1.3).

This study classed plant traits according to Grime's C-S-R scheme in an attempt to describe successional change in terms of species replacements. Whilst this approach showed little



utility in the categories used a number of other species features may yield an improved description (Thompson *et al.*, 1996; Grime *et al.*, 1997).

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# Appendices

## APPENDIX A

This appendix contains the following data:

Species abundance scores

Numbers of species (Sp. No.)

Diversity measures (Div.)

Dominance measures (Dom.)

Evenness measures:

there are two indices of evenness those of Simpson (EvenS) and Camargo (EvenC)

Attribute scores: abiotic features recorded

Factor levels:

Age:	Young = 1 Old = 2
Aspect:	North-facing = 1 South-facing = 2
Height:	Lower = 1 Upper = 2

Slope: the angle of slope of the revetment face measured in degrees from the horizontal.

Frequency (Frq): the number of quadrats in which each species occurs.

Quad	AA	AE	AgC	AgS	AiC	AO	BeP	B	BP	BS	CA	CC	CD	CE	CeF
1	0	83	0	0	0	0	4	0	1	0	0	1	0	0	0
2	0	100	0	0	0	0	0	0	0	1	0	0	0	0	0
3	0	83	0	7	0	0	0	0	0	0	0	1	0	0	0
4	0	80	0	1	0	0	0	1	0	0	0	1	0	1	0
5	0	99	0	0	0	0	0	0	0	0	0	1	0	6	0
6	0	98	0	0	0	0	0	0	0	0	0	0	0	0	1
7	0	92	0	0	0	0	0	16	0	0	12	0	0	0	0
8	0	87	0	1	0	3	0	0	0	0	0	0	0	0	0
9	0	97	0	0	0	0	1	5	0	0	0	0	0	0	0
10	0	99	0	0	0	0	0	0	0	0	0	1	0	0	0
11	0	85	0	0	0	1	0	0	0	0	0	0	0	0	0
12	0	96	0	0	0	0	2	0	0	0	0	1	0	0	0
13	0	95	0	0	0	0	0	0	0	0	0	1	0	0	0
14	0	93	0	0	0	0	0	0	0	0	0	1	0	0	0
15	0	100	0	0	0	1	0	0	0	0	0	0	0	1	0
16	0	68	0	0	0	0	2	5	0	0	0	11	0	0	0
17	0	93	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	91	0	0	0	4	0	0	0	0	0	0	0	0	0
19	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	100	0	0	0	0	0	0	0	0	0	0	1	0	0
21	0	34	0	54	0	0	0	30	0	0	0	53	0	1	0
22	0	0	0	0	0	0	0	56	2	0	0	51	0	2	0
23	0	72	0	0	0	0	0	0	0	0	0	19	0	0	0
24	0	60	0	0	0	0	14	91	0	0	0	6	1	2	0
25	0	26	0	0	0	0	0	25	1	0	0	40	0	3	0
26	0	75	1	0	0	13	0	20	0	22	0	5	0	0	0
27	0	78	0	0	0	0	0	49	0	0	0	0	0	0	0
28	0	29	3	15	0	0	0	66	0	0	0	6	0	0	0
29	0	59	0	14	0	0	0	16	0	0	0	12	0	0	0
30	0	65	0	0	0	0	0	4	0	0	0	0	0	0	0
31	0	96	0	0	0	0	0	6	0	0	0	2	0	2	0
32	0	68	0	0	0	0	0	29	1	13	1	1	0	2	0
33	0	66	0	0	0	0	0	1	0	0	0	5	0	9	0
34	0	77	0	0	0	0	0	32	0	1	0	3	1	18	0
35	0	7	0	5	0	1	0	71	1	0	0	88	0	1	0
36	0	80	0	1	0	0	0	8	0	0	0	0	0	0	0
37	0	63	0	0	0	3	0	47	0	0	0	1	0	0	0
38	0	47	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	72	1	3	0	0	1	45	0	5	0	0	0	0	0
40	0	48	0	0	0	0	0	1	0	0	0	1	0	0	0
41	0	96	0	0	0	0	0	0	0	0	0	0	0	0	0
42	0	87	0	1	0	5	0	0	0	0	0	3	0	0	0
43	0	66	0	2	1	0	0	0	0	0	0	14	0	0	0
44	0	45	1	0	0	0	0	0	0	0	0	0	0	0	0
45	0	99	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	100	0	0	0	0	0	0	0	0	0	0	0	0	4
47	0	98	0	1	0	0	0	0	0	0	0	0	0	0	0
48	0	85	1	0	0	0	0	0	0	65	0	0	0	0	1
49	0	80	0	0	0	0	0	0	0	2	0	0	0	0	0
50	0	99	0	0	0	0	0	0	0	0	0	0	0	0	0
51	0	99	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	97	0	1	0	0	0	0	0	0	0	3	0	0	0
53	0	39	0	0	0	0	0	0	0	70	0	0	0	0	0
54	0	72	0	3	0	0	0	0	0	0	0	0	0	0	0
55	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	99	1	1	0	0	0	0	0	0	0	0	0	0	0
57	0	95	0	16	0	0	0	0	0	0	0	1	0	0	0
58	0	13	0	0	0	0	0	0	0	12	0	0	0	0	0
59	0	71	0	0	0	7	0	0	0	24	0	0	0	0	0
60	0	29	0	0	0	0	0	0	0	14	0	0	0	0	0
61	0	46	0	3	0	0	0	60	0	0	0	10	0	12	0
62	0	98	0	0	0	0	0	0	0	0	0	2	0	0	0
63	1	15	0	5	0	0	0	0	0	0	0	19	0	0	0
64	0	25	0	2	0	0	0	0	0	0	0	0	0	0	0
65	0	98	0	0	0	0	0	0	0	0	0	6	0	0	0
66	0	99	8	3	0	0	0	7	0	0	0	2	0	0	0
67	0	94	0	1	0	0	0	0	0	0	0	2	0	0	0
68	0	54	7	0	0	0	12	0	0	35	0	0	0	2	0
69	0	95	0	0	0	5	0	6	0	26	0	5	0	0	0
70	0	80	6	8	0	0	0	0	0	66	0	1	0	0	0
71	0	99	0	2	0	0	0	0	0	8	0	0	0	0	0
72	0	92	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	75	0	6	0	0	0	0	0	2	0	7	0	0	0
74	0	30	0	4	0	0	2	6	0	0	0	47	0	0	0
75	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	35	2	17	19	3	0	3	0	17	0	52	0	25	0
77	0	35	0	28	0	0	4	28	0	0	0	45	0	0	0
78	0	47	2	0	0	0	53	0	2	46	0	1	0	1	0
79	0	50	28	3	0	0	0	0	0	9	0	0	0	0	1
80	0	79	0	0	0	0	2	1	0	54	8	4	0	1	0
Frq	1	79	12	28	2	11	11	29	6	20	3	42	3	17	4

Quad	CF	CH	CL	CM	CpV	CS	CSg	CSp	CVg	CVt	DFm	DG	EgA	Ep1	Ep4
1	0	0	0	0	0	0	0	0	0	0	0	4	0	1	0
2	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
4	0	0	0	1	0	0	0	0	0	0	0	18	0	0	1
5	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0
6	0	0	0	1	0	0	0	0	0	1	0	21	0	0	0
7	0	0	0	1	0	0	0	0	2	0	0	18	0	0	0
8	0	0	0	0	0	0	0	0	15	0	0	31	0	0	0
9	0	0	0	1	0	0	0	0	2	0	0	19	0	0	0
10	0	0	0	1	0	0	0	0	47	0	0	4	0	1	0
11	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
12	0	0	0	0	0	0	0	0	4	0	0	3	0	0	0
13	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	6	0	0	1
15	0	0	0	0	0	0	0	0	2	0	0	3	0	0	0
16	0	0	0	0	0	0	0	0	0	2	0	25	0	0	0
17	0	46	0	0	0	0	0	0	17	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	28	0	0	13	0	0	0
19	0	0	0	0	0	0	0	0	32	0	0	0	0	1	0
20	0	34	0	0	0	0	0	0	0	0	0	4	0	8	0
21	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0
24	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0
26	0	0	0	2	0	0	0	0	1	0	0	16	0	0	0
27	0	0	0	0	0	0	0	0	23	0	0	10	4	0	0
28	0	0	0	0	0	0	0	0	0	0	0	40	0	0	0
29	0	0	0	2	0	0	0	0	10	0	0	3	0	0	0
30	0	0	0	0	0	0	0	0	12	2	0	3	0	0	0
31	0	80	0	0	0	0	0	0	0	2	0	0	0	0	1
32	0	0	0	1	0	0	0	0	1	0	0	3	0	0	0
33	0	14	0	0	0	0	0	0	0	0	0	9	0	8	2
34	0	8	0	0	0	0	0	0	5	0	0	6	0	17	1
35	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
36	0	65	0	1	0	0	0	0	36	0	0	2	0	0	0
37	0	51	0	3	0	0	0	0	48	0	0	1	0	0	0
38	0	0	0	0	0	0	0	0	37	0	0	26	0	0	0
39	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0
40	0	41	0	0	0	0	0	0	45	1	0	0	0	0	0
41	54	0	0	0	0	0	0	0	4	0	0	3	0	0	0
42	0	6	0	0	0	0	0	0	0	0	0	15	0	0	0
43	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	1	0	0	0	0	0	0	0	0	12	0	0	0	0
46	0	0	0	0	0	0	0	0	13	0	1	0	0	0	0
47	0	37	0	0	0	0	0	0	0	0	1	0	0	0	0
48	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	33	1	0	1	0	0	0
50	0	0	0	1	0	0	0	0	27	0	0	0	0	12	0
51	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0
52	0	15	0	0	0	0	0	0	4	0	0	1	0	0	0
53	12	0	0	1	0	0	0	0	0	0	0	21	0	0	0
54	5	0	0	0	0	0	0	0	0	0	0	16	0	0	0
55	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0
56	2	0	0	0	0	0	0	0	0	0	0	5	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0
58	0	0	0	0	0	0	1	0	0	1	28	0	0	0	0
59	0	0	0	0	0	0	0	0	20	0	0	4	0	0	0
60	0	0	0	1	0	0	0	0	77	0	0	0	0	0	0
61	21	0	0	0	0	0	0	1	5	1	0	0	0	0	0
62	0	0	0	0	0	0	0	0	59	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	4	0	0	5	0	0	0
64	0	0	0	0	0	0	0	0	13	2	0	4	1	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	7	0	0	0	0	0	0	0	3	0	0	11	0	0	0
67	0	0	0	0	0	0	0	0	32	0	0	35	0	0	0
68	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
69	0	0	0	0	0	1	0	0	24	0	0	3	0	0	0
70	0	0	0	1	0	0	0	0	0	1	0	5	0	0	0
71	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	28	0	0	7	0	0	0
74	0	0	13	0	0	0	0	0	0	0	0	2	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
77	0	0	0	0	0	0	0	1	2	0	0	16	0	0	0
78	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0
79	0	0	0	0	0	0	0	0	8	0	0	3	0	0	0
80	0	0	0	5	0	0	0	0	8	0	0	1	0	0	0
Frg	6	13	1	15	1	1	1	3	46	12	5	54	2	8	5

Quad	Ep5	EpH	EpM	EqA	ER	FE	FO	FR	FV	GD	GH	GM	GR	GV	HHx
1	0	0	0	0	14	1	83	27	0	0	0	0	0	0	0
2	0	1	0	0	8	1	14	3	0	0	0	0	0	0	0
3	0	0	0	0	10	1	42	11	0	0	0	0	0	0	0
4	0	0	0	0	21	0	80	51	0	0	1	0	0	0	0
5	0	0	0	0	5	0	9	3	11	0	0	0	0	0	0
6	0	0	0	0	45	1	51	3	0	0	0	0	0	0	0
7	0	0	0	7	40	0	42	10	0	0	0	0	0	0	0
8	0	0	1	0	20	1	16	0	20	5	0	0	0	0	0
9	0	0	3	0	9	1	14	2	0	0	0	2	0	0	0
10	0	0	0	0	0	0	0	1	1	0	4	0	0	0	0
11	0	0	0	0	4	0	68	13	0	0	0	0	0	0	0
12	0	0	0	0	14	0	29	4	0	0	0	1	0	0	0
13	0	0	1	0	5	0	21	0	0	0	0	0	0	0	0
14	0	0	0	0	2	0	69	6	0	0	0	3	1	0	0
15	0	0	0	0	12	0	3	0	0	0	0	0	0	0	0
16	0	0	0	0	33	0	79	12	0	0	0	0	8	0	0
17	0	0	0	69	0	0	3	0	0	0	0	0	0	0	0
18	0	0	0	0	15	2	20	4	0	0	0	0	0	0	0
19	0	0	0	0	2	0	4	1	0	0	0	0	0	0	0
20	0	0	0	0	1	2	51	1	0	0	0	0	0	0	0
21	0	0	0	0	2	0	91	15	0	0	0	0	0	0	0
22	0	0	0	0	0	0	12	3	2	0	0	0	0	0	0
23	0	0	0	0	0	0	65	5	0	0	0	0	0	0	0
24	0	0	0	0	1	0	38	48	2	0	0	6	0	0	0
25	0	0	0	0	6	0	80	36	3	0	0	0	1	0	0
26	0	0	0	0	7	0	52	19	0	0	0	0	0	0	0
27	0	0	0	0	37	0	1	0	1	3	0	0	0	0	0
28	0	0	0	0	17	1	31	9	0	3	0	0	0	0	0
29	0	0	0	0	10	0	7	2	8	0	0	0	0	0	0
30	0	0	0	0	22	0	1	1	32	0	76	0	0	0	0
31	0	20	0	0	1	1	4	0	0	0	0	1	0	0	49
32	0	1	10	0	26	0	2	2	0	1	0	0	0	0	0
33	6	0	0	0	7	0	31	0	0	0	0	9	0	0	0
34	0	0	0	0	19	0	34	9	0	5	4	23	0	0	0
35	0	0	0	0	4	0	83	27	87	0	0	0	0	0	0
36	0	0	1	0	11	0	1	1	0	15	0	0	0	0	0
37	0	0	0	0	23	1	4	1	0	3	11	0	0	0	0
38	0	0	6	0	64	1	9	0	0	9	3	0	0	0	0
39	0	0	0	0	12	0	21	1	26	0	17	0	0	0	0
40	0	0	0	0	12	0	0	0	17	0	20	25	1	0	0
41	0	0	0	2	0	1	72	5	0	0	0	0	0	0	0
42	0	0	0	0	2	12	52	10	0	0	0	0	0	0	76
43	0	0	0	0	32	17	63	17	0	0	0	0	0	0	0
44	0	0	0	0	100	3	22	0	0	0	0	0	0	2	0
45	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	17	5	45	2	1	0	77	0	0	0	0
49	0	0	0	0	7	0	51	11	39	0	87	0	0	0	0
50	0	0	0	0	0	0	4	0	0	0	35	0	0	0	0
51	0	0	0	0	15	0	52	0	0	0	1	0	0	0	0
52	0	0	0	0	8	17	74	5	10	0	0	0	0	0	0
53	0	0	0	0	31	25	42	6	0	0	0	0	0	3	0
54	0	0	0	2	11	2	99	2	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	0	1	0	6	0	0	0	0	0	0	0	0
57	0	0	0	0	19	0	56	6	0	0	0	0	0	0	0
58	0	14	0	0	2	4	57	0	0	0	0	0	0	0	0
59	0	0	0	0	18	0	30	2	0	0	100	0	0	0	0
60	0	0	0	0	1	1	93	4	0	0	88	0	0	0	0
61	0	0	0	0	15	3	57	5	7	0	0	0	0	0	0
62	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	24	0	64	0	3	0	0	6	0	0	0
64	0	0	0	0	72	2	60	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	18	4	0	17	0	0	0	0	0
67	0	0	0	0	19	0	3	14	0	0	0	0	0	0	0
68	0	0	0	0	41	0	56	20	7	0	8	0	0	0	0
69	0	0	0	0	4	0	8	5	11	0	2	0	0	0	0
70	0	0	0	1	9	0	71	1	1	3	76	0	0	0	0
71	0	0	0	0	3	3	0	0	0	0	100	0	0	0	0
72	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0
73	0	0	0	0	23	13	75	6	0	0	0	18	0	0	0
74	0	0	0	0	30	6	20	1	0	0	12	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	84	20	0	2	1	0	0	0	0
77	0	0	0	0	25	0	21	25	25	1	0	5	0	0	0
78	0	0	0	0	17	0	42	0	0	0	37	0	0	0	0
79	0	0	0	0	8	0	65	4	0	5	62	0	0	0	0
80	0	0	0	4	11	0	56	3	57	0	0	0	0	0	0
Frg	1	5	6	6	64	27	71	54	22	13	22	11	4	2	2

Quad	HL	HM	HR	HS	HvH	HvM	IC	LN	LnC	LP	LtL	LtP	LV	LzC	MA
1	0	0	2	0	0	4	0	0	0	0	0	17	0	0	0
2	0	0	0	0	0	0	0	2	0	0	0	15	0	0	0
3	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
4	4	0	0	0	0	0	0	9	6	0	2	11	0	0	0
5	0	0	0	0	0	0	0	0	0	0	1	4	0	0	8
6	1	0	0	0	0	4	0	0	0	0	0	0	0	0	14
7	5	0	0	3	3	0	0	1	0	0	0	3	0	0	0
8	0	0	0	0	1	5	0	2	0	0	1	1	0	0	5
9	36	0	0	0	0	0	0	3	0	0	0	0	0	0	1
10	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
11	0	0	2	0	0	0	0	0	0	0	0	22	0	0	0
12	0	0	0	0	0	0	0	1	0	0	0	23	0	0	0
13	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	1	30	0	0	0
15	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
16	0	0	32	0	0	28	0	0	5	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
18	0	0	0	0	0	7	0	0	0	0	0	0	6	0	0
19	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	43	0	0	0	0	0	0	0	0	11	0	0	0
22	0	1	26	0	1	0	0	4	0	0	0	0	0	0	13
23	0	0	34	0	0	0	0	1	0	0	0	0	0	0	0
24	0	0	10	0	0	5	0	0	0	0	0	1	2	0	0
25	0	0	33	0	0	1	0	3	0	0	0	0	0	0	13
26	0	0	2	0	5	6	0	0	0	0	0	0	0	0	25
27	0	0	0	0	15	0	0	9	0	0	0	0	0	0	1
28	0	0	0	0	0	24	0	1	0	0	0	0	0	0	8
29	2	0	2	0	0	62	0	8	0	0	0	0	0	0	7
30	0	6	0	0	0	40	0	1	0	0	0	0	2	0	1
31	0	0	0	2	0	0	0	0	0	0	0	15	0	0	10
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24
33	0	0	1	0	0	0	0	0	0	0	0	0	67	0	5
34	0	0	15	0	0	0	0	2	0	0	0	6	0	0	12
35	0	0	39	0	0	4	0	0	0	0	0	0	0	0	2
36	0	0	0	0	1	1	0	3	0	0	0	0	0	0	5
37	0	0	0	0	0	23	0	5	0	0	0	0	4	0	18
38	0	0	0	0	0	0	2	2	0	0	0	0	1	0	12
39	1	0	0	0	0	42	0	4	0	0	0	0	0	0	0
40	0	0	0	0	0	31	0	0	0	0	0	0	2	0	6
41	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
42	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
46	13	0	0	0	0	7	0	0	0	0	0	23	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
48	20	0	0	0	0	0	0	0	0	0	0	0	0	0	20
49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
50	0	0	0	0	1	8	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	8	0	0	9	0	0	0
53	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	32	0	0	0
56	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
58	12	0	0	0	0	0	0	0	0	0	0	9	0	0	10
59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	0	0	1	0	0	0	0	0	0	0	0	0	38	4	16
62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
64	0	0	0	0	0	8	0	0	0	0	0	2	0	0	36
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
68	0	0	0	0	0	14	0	0	0	0	0	0	1	1	22
69	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
74	0	0	10	1	0	0	0	0	0	0	0	0	0	0	10
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
76	0	0	5	0	0	0	0	0	0	0	0	0	49	0	0
77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
78	0	0	0	0	0	66	0	0	0	0	0	0	0	0	6
79	0	0	0	0	0	0	0	0	1	0	1	17	0	0	0
80	0	0	0	0	1	12	0	0	1	0	1	17	0	0	3
Frq	11	2	16	3	9	22	1	22	6	1	5	24	10	2	39

Quad	MM	PA	PE	PgC	PIL	PO	PP	PR	PSP	PV	PVe	QR	RA	Rag	RAt
1	0	4	0	0	3	0	0	0	74	7	0	0	0	0	0
2	0	0	0	0	0	0	1	0	97	0	0	1	0	0	0
3	0	8	0	0	12	0	0	0	71	0	0	1	0	0	0
4	0	0	0	0	1	0	48	0	16	2	0	0	0	0	0
5	0	0	0	0	9	0	1	0	46	0	0	0	0	0	0
6	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	25	0	8	0	1	0	0	0	0	0	0
8	0	0	0	0	9	3	0	0	23	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	30	2	0	0	0	0	0
10	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
11	0	0	0	0	0	0	1	1	96	0	0	0	0	0	0
12	0	0	0	0	0	0	1	0	87	7	0	0	0	0	0
13	0	0	0	0	0	0	0	6	89	4	0	0	0	0	0
14	0	0	0	0	14	0	2	0	38	1	0	0	1	0	0
15	0	0	0	0	2	0	0	0	78	3	0	0	0	0	0
16	0	0	0	0	13	2	4	0	11	15	0	0	0	0	0
17	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0
18	0	0	0	0	14	0	0	0	25	2	0	0	0	0	0
19	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0
21	0	7	0	0	0	0	0	0	20	0	0	0	0	0	0
22	0	0	0	0	0	0	7	0	45	0	0	0	0	2	0
23	0	0	0	0	0	0	12	0	35	0	0	0	0	1	0
24	0	0	0	0	19	9	16	0	5	1	1	0	0	0	0
25	0	0	0	0	1	0	11	0	33	0	0	0	0	0	0
26	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	6	7	0	0	0	0	0
28	0	0	0	0	63	0	0	0	2	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	11	7	0	0	0	1	0
30	3	0	0	0	0	0	1	0	0	6	0	0	0	0	0
31	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
32	0	0	0	0	0	0	1	0	6	1	0	0	0	0	0
33	0	8	0	0	0	0	0	0	9	0	0	0	0	0	0
34	0	0	0	0	10	0	12	0	4	0	0	0	0	0	0
35	0	0	0	0	0	0	19	0	20	0	0	0	0	0	0
36	0	0	0	0	34	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	2	0	0	31	0	0	0	0	0
38	1	0	0	0	6	2	1	0	0	22	0	0	0	0	0
39	0	0	0	0	0	0	0	0	2	41	0	0	0	0	0
40	3	0	0	0	0	0	0	0	0	4	0	0	0	1	0
41	0	0	0	0	0	0	7	0	60	0	0	0	0	0	0
42	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0
43	0	0	0	0	0	0	0	0	20	13	0	0	0	0	0
44	0	0	0	0	1	0	0	0	43	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
47	0	0	0	0	0	0	0	0	2	0	29	0	0	0	0
48	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0
49	0	0	0	0	0	0	2	0	67	2	0	0	0	0	0
50	0	0	0	0	0	0	0	0	47	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
52	0	0	0	0	0	0	0	6	71	2	0	2	0	0	0
53	0	0	0	0	0	0	0	0	29	2	0	0	0	0	0
54	0	0	0	0	0	0	0	0	28	0	0	1	0	0	0
55	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0
56	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0
57	0	0	10	0	0	0	0	0	23	0	2	0	0	0	0
58	0	0	0	0	0	2	0	0	21	0	0	0	0	0	0
59	0	0	0	0	0	0	3	0	59	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	54	0	0	0	0	0	0
61	0	0	0	0	0	0	11	0	11	15	0	1	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	0	1	0	0	0	21	0	0	0	16	0	0	0	0	0
64	0	0	0	0	0	12	0	0	4	0	0	1	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
68	0	0	0	0	0	0	2	11	0	0	2	0	0	0	0
69	0	0	0	0	0	0	2	0	3	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
71	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	1	0	0	0	5	0	0	0	0	0
74	0	0	0	0	0	8	0	0	0	0	0	1	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	1	0	0	9	0	0	0	0	0
77	0	2	0	0	0	0	8	0	0	1	0	0	0	0	0
78	0	0	0	12	0	0	0	0	21	1	38	0	0	0	0
79	0	5	0	0	0	0	2	0	0	0	0	0	0	0	27
80	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0
Frq	3	7	1	1	19	10	29	4	55	30	6	9	1	4	1



Quad	RC	RF	RR	SA	ShA	SJ	SM	SS	StG	SIP	TC	TF	TM	TO	TR
1	0	0	12	0	0	0	0	0	0	0	0	0	0	0	1
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	10	0	0	0	0	0	0	0	0	0	0	0	1
4	0	1	5	0	0	1	0	0	0	0	0	0	0	0	4
5	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	7	0	0	0	0	7	0	0	0	0	0	0	0
8	0	0	0	1	0	0	9	0	0	0	0	0	0	0	0
9	0	0	20	0	0	0	0	0	72	1	0	0	1	0	0
10	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	62	0	0	1	0	0	0	0	0	0	0	0	2
12	0	1	6	0	0	0	0	0	0	0	0	0	0	0	1
13	0	0	27	1	0	0	0	0	0	0	0	0	0	0	1
14	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0
15	0	0	5	0	0	0	0	0	0	3	0	0	0	0	0
16	0	0	0	11	0	0	0	0	0	0	0	18	0	1	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0
20	0	1	0	0	0	0	0	0	7	1	0	0	0	0	0
21	0	0	0	11	0	13	0	0	0	0	0	0	0	0	0
22	0	0	2	12	0	9	0	0	0	0	0	0	0	5	4
23	0	0	3	1	0	4	0	0	0	0	0	0	0	0	0
24	0	0	0	1	0	5	14	0	0	0	0	0	0	0	0
25	0	1	1	14	0	10	0	0	0	0	0	5	0	0	0
26	0	0	0	12	0	2	0	0	0	0	0	0	0	0	0
27	0	8	0	3	0	0	9	0	0	0	0	0	0	0	1
28	0	0	0	1	0	1	5	0	0	0	0	0	0	0	0
29	0	3	0	1	26	26	0	0	14	0	0	0	0	12	0
30	0	16	0	0	0	5	0	0	9	1	0	0	0	0	0
31	0	18	0	0	0	2	0	0	0	3	0	0	0	0	0
32	0	38	0	0	0	17	0	0	0	0	0	0	0	0	0
33	0	72	0	0	0	2	0	0	0	0	0	0	0	0	0
34	0	7	0	8	0	16	0	0	0	0	0	0	0	0	1
35	0	0	4	32	0	19	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
38	0	0	0	9	0	29	1	0	0	0	0	0	0	0	0
39	0	0	0	1	0	29	0	0	1	0	0	0	0	0	0
40	0	0	0	2	0	10	0	0	3	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	15	1	0	0	0	0	0	0	0	2	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0
53	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0
54	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	0	39	6	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	9	0	0	0	0	0	0	0	0	1	0	0	0
60	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0
61	0	11	0	4	0	17	0	0	0	0	0	24	0	2	0
62	0	7	1	0	0	0	0	0	0	0	0	0	0	0	0
63	0	42	0	5	0	12	0	0	0	0	0	0	0	0	0
64	4	5	0	5	0	5	0	5	0	0	0	0	0	0	0
65	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
66	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0
67	0	0	0	6	0	1	0	0	0	0	0	0	0	0	0
68	0	1	0	17	0	15	0	0	0	0	0	6	0	0	0
69	0	0	0	4	0	12	0	0	0	0	0	0	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
71	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0
72	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0
73	0	2	6	2	0	11	0	0	0	0	0	0	0	1	0
74	0	9	36	8	0	6	0	0	0	0	0	0	0	0	0
75	0	0	0	1	0	0	0	0	0	0	2	8	0	0	0
76	10	0	0	0	0	8	0	0	0	0	0	3	0	1	0
77	0	0	0	26	57	0	0	0	0	0	0	0	0	0	0
78	0	0	0	7	0	17	0	0	0	0	0	1	0	0	0
79	0	12	0	1	0	7	0	0	0	0	0	2	0	0	0
80	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0
Frq	3	26	26	35	2	35	6	2	8	5	1	10	2	6	9

Quad	UD	VA	VCh	VIC	VR	VSp	VSt	VT	F1	H14	H14B	H1F	H27	H57B	H61
1	0	0	10	0	0	0	12	0	0	0	0	0	0	0	0
2	0	0	8	0	0	0	28	0	1	0	0	0	0	0	1
3	0	0	85	0	0	0	32	0	0	0	0	0	0	0	7
4	0	0	64	3	0	0	12	0	0	0	2	0	0	0	9
5	0	0	17	0	0	0	0	0	0	0	0	0	0	0	6
6	0	0	2	0	0	0	1	0	0	0	0	0	0	0	3
7	0	0	10	0	0	0	3	0	0	0	0	0	3	0	2
8	0	0	41	0	0	2	2	0	0	0	0	0	0	0	0
9	0	0	40	1	0	0	7	0	0	0	0	0	0	0	1
10	0	0	12	0	0	0	2	0	0	0	0	0	0	0	2
11	0	0	15	1	0	0	17	0	0	0	0	0	0	0	0
12	0	0	1	0	0	0	28	0	0	0	0	0	0	0	4
13	0	0	22	0	0	0	32	0	0	0	0	0	0	0	6
14	0	0	20	0	0	0	9	0	0	0	0	0	0	0	8
15	0	0	15	10	0	3	20	0	0	0	0	0	0	0	10
16	0	0	38	3	0	6	13	0	0	0	0	0	0	0	2
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
18	0	0	1	31	0	0	0	0	0	0	0	0	0	0	5
19	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
20	0	0	6	0	0	1	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	26	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	12	0	0	0	0	0	0	0	3
23	0	0	0	0	0	0	30	0	0	0	0	0	0	0	13
24	0	0	0	0	0	0	5	0	0	0	0	0	0	0	8
25	0	0	0	0	0	0	15	0	0	0	0	0	0	0	1
26	0	0	0	0	0	0	38	0	0	0	0	0	0	0	0
27	0	0	4	0	0	0	8	0	0	0	0	0	0	0	1
28	0	0	21	0	0	0	18	0	0	0	0	0	0	0	0
29	0	0	23	0	0	0	21	0	0	0	0	0	0	0	0
30	0	0	18	9	0	0	4	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	4	0	0	0	0	2	0	0	3
32	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	5	0	0	0	0	0	0	0	7
34	0	0	0	0	0	0	6	0	0	0	0	0	0	0	3
35	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0
36	0	0	5	0	0	0	14	0	0	0	0	0	0	0	0
37	0	0	5	0	0	0	11	0	0	0	0	0	0	0	0
38	0	0	3	0	0	0	5	0	0	0	0	0	0	0	0
39	0	0	13	0	0	0	5	0	0	0	0	0	0	0	0
40	0	0	4	0	0	0	2	0	0	0	0	0	0	0	2
41	0	0	5	0	1	0	0	0	0	0	0	0	0	0	0
42	0	0	55	0	65	0	2	0	0	0	0	0	0	0	2
43	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	6	1	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	49	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	77	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
51	0	0	2	0	0	0	0	0	0	0	0	9	0	0	0
52	0	0	56	0	5	0	4	0	0	0	0	0	0	0	2
53	0	0	30	0	0	0	13	0	0	0	0	0	0	0	4
54	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	89	0	0	0	7	0	0	0	0	0	0	0	0
57	0	0	29	0	0	0	1	0	0	0	0	0	0	0	2
58	0	0	12	0	0	0	0	0	0	0	0	0	0	0	1
59	0	0	88	1	0	0	1	0	0	0	0	0	0	0	0
60	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0
61	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
62	1	0	0	0	1	0	0	0	0	0	0	4	0	0	0
63	21	0	11	0	0	0	0	5	0	0	0	0	0	0	0
64	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
65	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
66	0	0	3	0	0	0	2	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
68	0	1	2	0	0	0	0	0	0	0	0	0	0	0	8
69	0	0	10	0	0	0	0	0	0	0	0	0	0	1	0
70	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
71	0	0	20	0	8	0	1	0	0	0	0	0	0	0	0
72	0	0	2	0	45	0	0	0	0	0	0	0	0	0	0
73	1	0	4	0	11	0	2	0	0	0	0	0	0	0	3
74	11	0	0	0	0	0	1	0	0	0	0	0	0	1	1
75	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0
77	0	0	2	0	0	0	13	0	0	0	0	0	0	0	0
78	0	0	15	0	0	0	0	3	0	0	0	0	0	0	2
79	0	0	29	0	0	0	3	0	0	0	0	0	0	0	0
80	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0
Frq	4	1	58	9	8	4	53	2	1	2	1	3	1	2	34

Quad	H61C	H68	H8	H88	H90	S8	T1	T9	Sp. No.	Div.	Dom.	EvenS	EvenC
1	0	0	0	0	0	0	0	0	21	6.443	0.2274	0.3023	0.3333
2	0	0	0	0	0	0	0	0	19	3.98	0.3497	0.2073	0.2451
3	0	0	0	0	0	0	0	0	18	6.86	0.2174	0.3755	0.3815
4	1	0	0	0	0	0	0	0	31	9.134	0.1747	0.2895	0.3064
5	0	0	0	0	0	0	0	0	17	4.367	0.4231	0.2532	0.3539
6	0	0	0	0	0	0	0	0	16	4.339	0.3874	0.2676	0.2858
7	0	0	0	0	0	0	0	0	24	7.696	0.2866	0.3141	0.3851
8	0	0	0	0	0	0	0	1	26	7.784	0.2843	0.2929	0.3451
9	0	0	0	0	0	0	1	0	26	7.199	0.2608	0.2723	0.2971
10	0	0	0	0	0	0	0	0	15	2.735	0.544	0.1806	0.2315
11	0	0	0	0	0	0	0	0	17	5.961	0.2449	0.3462	0.3325
12	0	0	0	0	0	0	0	0	20	5.18	0.3057	0.2556	0.2895
13	0	0	0	0	0	0	0	0	17	5.121	0.3006	0.2974	0.3165
14	1	0	0	0	0	0	0	0	22	5.882	0.3	0.2832	0.2915
15	0	0	0	0	0	0	0	0	18	4.371	0.3676	0.2399	0.3039
16	0	0	0	0	0	0	0	0	26	11.748	0.1767	0.4412	0.4596
17	0	0	0	0	0	0	0	0	8	3.958	0.369	0.489	0.4514
18	0	0	0	0	0	0	0	0	18	6.393	0.3346	0.3483	0.4126
19	0	0	0	0	0	0	0	0	12	3.025	0.5319	0.2494	0.2881
20	0	0	0	0	0	0	1	0	15	4.024	0.4184	0.2649	0.2887
21	0	0	0	0	0	0	0	0	16	8.912	0.2193	0.5466	0.5197
22	0	0	0	0	0	0	0	0	23	8.607	0.2007	0.3643	0.3978
23	0	0	0	0	0	0	0	0	15	7.185	0.2323	0.4696	0.4477
24	0	0	0	0	0	0	0	0	27	8.349	0.2433	0.3033	0.3506
25	0	0	0	0	0	0	0	0	26	10.081	0.218	0.3784	0.3889
26	0	0	0	0	0	0	0	0	20	8.693	0.2315	0.4246	0.4309
27	0	0	0	0	0	0	0	0	21	7.091	0.2806	0.3304	0.3792
28	0	0	0	0	0	0	0	0	21	9.824	0.1813	0.4567	0.4409
29	0	0	0	0	0	0	0	0	27	12.52	0.168	0.4496	0.4843
30	0	0	0	0	0	0	0	0	25	8.343	0.2235	0.3266	0.3548
31	0	0	0	0	4	0	0	0	25	5.754	0.2909	0.2289	0.2773
32	0	0	0	0	0	0	0	0	23	7.293	0.272	0.3093	0.3283
33	0	0	0	0	0	0	0	0	21	7.561	0.2099	0.3533	0.4105
34	0	0	0	0	0	2	0	0	31	12.681	0.2098	0.3965	0.4654
35	0	0	0	0	0	0	0	0	21	8.892	0.1664	0.4172	0.4014
36	0	0	0	0	0	0	0	0	20	6.496	0.2685	0.319	0.3359
37	0	0	0	0	0	0	0	0	23	9.626	0.175	0.4087	0.3942
38	0	0	0	0	0	0	0	0	23	8.944	0.2148	0.3787	0.3858
39	0	0	0	0	0	0	0	0	22	9.353	0.2063	0.4152	0.401
40	0	0	0	0	0	0	0	0	23	9.486	0.1702	0.4003	0.3898
41	0	0	0	0	0	0	0	0	13	4.679	0.3077	0.3557	0.3481
42	0	0	0	0	0	0	0	0	18	6.896	0.2159	0.3776	0.3682
43	0	0	0	0	0	0	0	0	16	6.413	0.2538	0.3927	0.3976
44	0	0	0	0	0	0	0	0	10	3.521	0.4464	0.3482	0.3429
45	0	0	0	0	0	0	0	0	5	1.333	0.8609	0.2658	0.28
46	0	0	4	0	0	0	0	0	10	2.782	0.5747	0.2754	0.3655
47	0	0	0	0	0	0	0	0	7	2.437	0.5799	0.3451	0.339
48	0	0	0	0	0	0	0	0	17	7.685	0.2014	0.4445	0.4137
49	0	0	0	0	0	0	0	0	18	7.752	0.1816	0.4247	0.39
50	0	0	0	0	0	0	0	0	10	3.94	0.4213	0.3892	0.3843
51	0	0	0	0	0	0	0	0	8	2.744	0.5294	0.3399	0.3483
52	0	0	0	0	0	0	0	0	22	6.951	0.2389	0.3114	0.3477
53	0	0	0	0	0	0	0	0	18	9.408	0.2077	0.5099	0.4812
54	0	0	0	0	0	0	0	0	14	4.015	0.3898	0.2834	0.3166
55	0	0	0	0	0	0	0	0	4	2.094	0.6536	0.52	0.518
56	0	0	0	0	0	0	0	0	12	3.432	0.3764	0.2833	0.2836
57	0	0	0	0	0	0	0	0	14	5.394	0.343	0.3793	0.4036
58	0	0	0	0	0	0	0	0	17	8.183	0.2426	0.4671	0.4693
59	0	0	0	0	0	0	0	0	16	6.79	0.2283	0.4188	0.3955
60	0	0	0	0	0	0	0	0	13	5.717	0.2391	0.4345	0.4
61	0	0	0	0	0	0	0	0	28	12.61	0.1493	0.4379	0.4442
62	0	0	0	0	0	0	0	0	10	2.477	0.5444	0.2457	0.2667
63	0	0	0	0	0	0	0	0	20	9.98	0.2207	0.484	0.5038
64	0	0	0	0	0	0	0	0	22	6.615	0.2667	0.2945	0.3428
65	0	0	0	0	0	0	0	0	6	1.62	0.7717	0.2687	0.2874
66	0	0	4	0	0	0	0	0	17	3.502	0.513	0.2034	0.3441
67	0	0	0	0	0	0	0	0	12	3.89	0.4434	0.3198	0.3451
68	0	0	7	0	0	20	0	0	27	12.661	0.1485	0.4548	0.4544
69	0	0	1	0	0	0	0	0	22	4.988	0.4113	0.2229	0.3508
70	0	0	0	0	0	0	0	0	18	5.151	0.2402	0.2826	0.2905
71	0	0	0	0	0	0	0	0	13	3.262	0.3891	0.2488	0.287
72	0	0	0	1	0	0	0	0	7	3.408	0.46	0.481	0.4614
73	0	0	0	0	0	0	0	0	24	7.735	0.2322	0.3157	0.3838
74	0	0	0	0	0	0	0	0	25	11.841	0.1703	0.4556	0.4571
75	0	0	0	0	0	0	0	0	4	1.354	0.8547	0.3375	0.3568
76	0	0	1	0	0	0	0	0	24	9.499	0.2193	0.3872	0.4048
77	0	0	0	0	0	0	0	0	24	12.779	0.15	0.5163	0.4811
78	0	3	1	0	0	12	0	0	26	12.064	0.1444	0.4531	0.4249
79	0	0	0	0	0	0	0	0	22	8.495	0.1946	0.3777	0.386
80	0	0	0	0	0	0	0	0	28	7.208	0.2324	0.2528	0.2903
Frq	2	1	6	1	1	3	2	1	-	-	-	-	-

Quad	O145	D1	B	BD	DA	DR	N	Age	Aspect	Hgt	Slope
1	0	0	0	0	0	0	0	1	1	2	35.00
2	0	0	0	0	0	0	0	1	1	2	41.00
3	0	0	1	0	1	0	0	1	1	2	37.00
4	0	0	1	0	0	0	0	1	1	2	28.00
5	0	0	19	0	0	0	0	1	1	2	33.50
6	0	0	0	0	0	0	0	1	1	2	28.00
7	0	0	0	0	0	0	0	1	1	2	31.00
8	0	0	0	0	0	0	0	1	1	2	27.50
9	0	0	0	0	0	0	0	1	1	2	28.50
10	0	0	4	0	0	0	0	1	1	2	32.00
11	0	0	1	0	0	0	0	1	1	1	40.50
12	0	0	0	0	0	0	0	1	1	1	40.00
13	0	0	2	0	0	0	0	1	1	1	41.00
14	0	0	0	0	0	0	0	1	1	1	36.50
15	0	0	0	0	0	0	0	1	1	1	34.00
16	0	0	1	0	0	0	0	1	1	1	35.50
17	0	0	1	0	0	0	0	1	1	1	28.00
18	0	0	0	0	0	0	0	1	1	1	22.50
19	0	0	0	0	0	0	0	1	1	1	20.50
20	0	0	0	0	0	0	0	1	1	1	21.00
21	0	0	15	0	0	0	0	1	2	2	34.00
22	0	0	23	0	0	0	0	1	2	2	37.00
23	0	48	14	0	0	0	0	1	2	2	36.00
24	0	0	23	0	4	0	0	1	2	2	30.00
25	0	40	32	0	0	0	0	1	2	2	34.00
26	0	0	0	0	0	0	0	1	2	2	34.00
27	0	0	0	0	3	0	0	1	2	2	26.00
28	0	0	0	0	7	0	0	1	2	2	25.00
29	0	0	0	0	15	0	0	1	2	2	31.00
30	0	0	0	0	9	0	0	1	2	2	28.50
31	0	0	1	0	0	0	0	1	2	1	33.00
32	0	0	5	0	1	0	0	1	2	1	34.50
33	0	0	2	0	2	0	0	1	2	1	32.00
34	0	0	13	0	5	0	0	1	2	1	29.00
35	0	0	26	0	5	0	0	1	2	1	28.50
36	0	0	2	0	6	0	0	1	2	1	31.50
37	0	0	0	0	6	0	0	1	2	1	26.00
38	0	0	1	0	6	0	0	1	2	1	24.50
39	0	0	0	0	12	0	0	1	2	1	26.00
40	0	0	9	0	21	0	0	1	2	1	27.00
41	0	0	0	0	0	0	0	2	1	2	32.00
42	0	0	0	0	0	0	0	2	1	2	29.50
43	0	0	34	0	0	15	0	2	1	2	34.00
44	0	0	0	0	2	0	0	2	1	2	32.50
45	0	0	0	0	0	0	0	2	1	2	34.00
46	0	0	15	0	0	0	0	2	1	2	34.00
47	0	0	0	0	0	0	0	2	1	2	38.50
48	0	0	0	0	0	0	0	2	1	2	36.50
49	2	0	0	0	5	0	0	2	1	2	33.00
50	0	0	1	0	0	0	0	2	1	2	31.00
51	0	0	0	0	6	0	0	2	1	1	29.00
52	0	0	0	0	0	0	0	2	1	1	29.50
53	0	0	0	11	4	0	0	2	1	1	26.00
54	0	0	0	0	0	0	0	2	1	1	32.00
55	0	0	0	0	0	0	0	2	1	1	36.00
56	0	0	1	0	0	0	0	2	1	1	41.00
57	0	0	0	0	0	0	0	2	1	1	41.00
58	0	0	0	0	0	0	0	2	1	1	28.00
59	0	0	0	0	0	0	0	2	1	1	32.50
60	0	0	0	0	0	1	0	2	1	1	35.00
61	0	0	0	0	0	0	0	2	2	2	37.00
62	0	0	5	0	18	0	0	2	2	2	23.00
63	0	0	0	44	0	8	0	2	2	2	32.50
64	0	0	4	0	1	0	4	2	2	2	35.00
65	0	0	5	0	0	2	0	2	2	2	30.00
66	0	0	0	0	0	0	0	2	2	2	36.00
67	0	0	3	0	3	0	0	2	2	2	38.00
68	0	0	2	0	8	0	0	2	2	2	34.00
69	0	0	0	0	8	0	0	2	2	2	28.50
70	0	0	0	0	4	12	0	2	2	2	37.50
71	0	0	0	0	0	0	0	2	2	1	25.50
72	0	0	0	0	10	0	0	2	2	1	28.00
73	0	0	20	0	1	0	0	2	2	1	29.50
74	0	0	31	0	1	27	1	2	2	1	34.50
75	0	0	0	0	5	1	0	2	2	1	31.00
76	0	0	10	7	9	0	0	2	2	1	34.50
77	0	0	18	0	0	7	4	2	2	1	37.00
78	0	0	19	0	2	0	0	2	2	1	31.00
79	0	0	8	0	6	2	0	2	2	1	33.50
80	0	0	4	0	0	0	0	2	2	1	34.00

## APPENDIX B

Quadrat data record sheet

		A	B	C	D	E	F	G	H	J	K		
1 2 3 4 5 6 7 8 9 10	1	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	1	
	2	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	2	
	3	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	3	
	4	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	4	
	5	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	5	
	6	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	6	
	7	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	7	
	8	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	8	
	9	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	9	
	10	G H	G H	G H	G H	G H	G H	G H	G H	G H	G H	10	
		A	B	C	D	E	F	G	H	J	K		

**Quadrat record sheet**

1- Building Number (eg R1028)

R \_\_\_\_\_

2- Quadrant (eg R1028/S)

N  
W E  
S

3- Section

n/a A B C

4- Aspect i (eg R1028/S/N)

N S E W

5- Aspect ii axis = \_\_\_\_\_ +/- 90° = \_\_\_\_\_ degrees from North (0 = N, 180 = S)

6- Zone (eg R1028/S/N/U)

Upper Lower

7- Quadrat number (eg R1028/S/N/U/Q3)

1	5
2	6
3	7
4	8

8- Slope (measured on quadrat frame)

Lt Rt

9- Revetment height

Height = \_\_\_\_\_ m

10- Slope angle

Angle = \_\_\_\_\_ °

11- Age (Young = 27, Old = 56)

Y / O

## APPENDIX C

### DCA ordination axis scores

DCA Run 1

Quadrat	Axis 1	Axis 2	Axis 3	Axis 4	Age	Aspect	Height	Slope
1	1	-25	-58	33	1	1	2	35
2	38	-27	-75	59	1	1	2	41
3	17	-36	-71	32	1	1	2	37
4	-17	-16	-59	21	1	1	2	28
5	25	-15	-43	37	1	1	2	33.5
6	7	-3	-11	12	1	1	2	28
7	3	19	-8	58	1	1	2	31
8	14	-17	-14	25	1	1	2	27.5
9	66	-47	-72	47	1	1	2	28.5
10	73	-12	6	26	1	1	2	32
11	19	-39	-97	53	1	1	1	40.5
12	25	-23	-66	54	1	1	1	40
13	29	-39	-79	53	1	1	1	41
14	21	-12	-61	38	1	1	1	36.5
15	40	-29	-65	54	1	1	1	34
16	-56	-4	-10	12	1	1	1	35.5
17	215	222	187	305	1	1	1	28
18	30	-10	-14	33	1	1	1	22.5
19	84	-21	-24	46	1	1	1	20.5
20	68	46	0	35	1	1	1	21
21	-141	32	-37	16	1	2	2	34
22	-163	42	-21	34	1	2	2	37
23	-58	5	-59	34	1	2	2	36
24	-105	37	18	22	1	2	2	30
25	-119	23	-32	16	1	2	2	34
26	-40	-1	0	4	1	2	2	34
27	-31	28	18	31	1	2	2	26
28	-75	24	14	37	1	2	2	25
29	-71	0	56	17	1	2	2	31
30	24	-74	86	-43	1	2	2	28.5
31	168	247	17	-87	1	2	1	33
32	-28	43	33	-43	1	2	1	34.5
33	-45	132	16	-120	1	2	1	32
34	-53	52	18	2	1	2	1	29
35	-167	30	1	12	1	2	1	28.5
36	65	101	78	58	1	2	1	31.5
37	15	64	91	22	1	2	1	26
38	-18	8	41	7	1	2	1	24.5
39	-47	-12	76	-4	1	2	1	26
40	43	44	123	4	1	2	1	27
41	19	-18	-73	39	2	1	2	32
42	158	160	-123	-209	2	1	2	29.5
43	-19	-4	-30	2	2	1	2	34
44	7	-32	-27	23	2	1	2	32.5
45	84	15	-32	15	2	1	2	34
46	82	-14	-11	31	2	1	2	34
47	122	73	148	31	2	1	2	38.5
48	54	-102	25	-49	2	1	2	36.5
49	39	-86	-1	-11	2	1	2	33
50	69	-51	11	8	2	1	2	31
51	39	-3	-22	12	2	1	1	29
52	39	-17	-55	16	2	1	1	29.5
53	15	-65	-17	-23	2	1	1	26
54	11	-15	-48	23	2	1	1	32
55	79	2	-63	48	2	1	1	36
56	60	-51	-67	26	2	1	1	41
57	12	-21	-45	20	2	1	1	41
58	45	38	-47	-91	2	1	1	28
59	62	-109	4	-28	2	1	1	32.5
60	54	-91	24	-28	2	1	1	35
61	-108	61	9	-35	2	2	2	37
62	84	28	20	3	2	2	2	23
63	-79	51	15	-84	2	2	2	32.5
64	-36	7	18	-19	2	2	2	35
65	32	15	-4	17	2	2	2	30
66	14	1	-1	14	2	2	2	36
67	18	4	-4	28	2	2	2	38
68	-35	-48	80	-40	2	2	2	34
69	13	-23	28	-2	2	2	2	28.5
70	35	-107	59	-62	2	2	2	37.5
71	98	-120	53	-87	2	2	1	25.5
72	122	101	-62	-158	2	2	1	28
73	0	20	-10	-27	2	2	1	29.5
74	-102	16	-25	-24	2	2	1	34.5
75	66	-2	-19	24	2	2	1	31
76	-147	69	0	-76	2	2	1	34.5
77	-170	37	22	17	2	2	1	37
78	0	-105	208	-66	2	2	1	31
79	33	-106	50	-90	2	2	1	33.5
80	-8	-36	47	1	2	2	1	34

Age: 1 = Young, 2 = Old. Aspect: 1 = North, 2 = South.  
Slope is measured in degrees from the horizontal

Height: 1 = Lower, 2 = Upper

Quadrat	Axis 1	Axis 2	Axis 3	Axis 4	Age	Aspect	Height	Slope
1	140	63	90	131	1	1	2	35
2	180	35	66	110	1	1	2	41
3	161	62	84	134	1	1	2	37
4	125	70	83	144	1	1	2	28
5	171	72	76	94	1	1	2	33.5
6	142	111	95	105	1	1	2	28
7	138	88	55	115	1	1	2	31
8	158	108	58	101	1	1	2	27.5
9	215	30	0	185	1	1	2	28.5
10	231	127	70	50	1	1	2	32
11	157	26	84	152	1	1	1	40.5
12	166	43	68	112	1	1	1	40
13	169	41	71	126	1	1	1	41
14	162	56	85	117	1	1	1	36.5
15	182	45	60	95	1	1	1	34
16	90	109	73	117	1	1	1	35.5
17	301	126	65	75	1	1	1	28
18	175	85	52	53	1	1	1	22.5
19	241	82	26	98	1	1	1	20.5
20	203	81	82	76	1	1	1	21
21	25	102	81	157	1	2	2	34
22	7	96	38	134	1	2	2	37
23	91	57	78	139	1	2	2	36
24	50	118	21	96	1	2	2	30
25	37	95	83	146	1	2	2	34
26	101	119	79	128	1	2	2	34
27	118	123	20	63	1	2	2	26
28	69	108	0	78	1	2	2	25
29	86	157	0	96	1	2	2	31
30	175	185	78	81	1	2	2	28.5
31	269	27	70	51	1	2	1	33
32	113	122	108	74	1	2	1	34.5
33	98	31	207	0	1	2	1	32
34	94	100	81	62	1	2	1	29
35	0	137	55	145	1	2	1	28.5
36	200	119	5	5	1	2	1	31.5
37	158	160	26	23	1	2	1	26
38	122	150	57	62	1	2	1	24.5
39	101	185	33	59	1	2	1	26
40	185	176	40	18	1	2	1	27
41	155	48	135	78	2	1	2	32
42	253	0	121	117	2	1	2	29.5
43	123	103	118	123	2	1	2	34
44	139	104	102	119	2	1	2	32.5
45	238	76	99	101	2	1	2	34
46	238	95	53	106	2	1	2	34
47	265	149	39	46	2	1	2	38.5
48	201	159	154	162	2	1	2	36.5
49	192	136	118	127	2	1	2	33
50	221	116	99	65	2	1	2	31
51	182	106	116	88	2	1	1	29
52	179	74	106	131	2	1	1	29.5
53	149	110	147	161	2	1	1	26
54	145	81	123	126	2	1	1	32
55	235	43	72	110	2	1	1	36
56	212	80	94	128	2	1	1	41
57	157	92	106	129	2	1	1	41
58	175	33	194	201	2	1	1	26
59	215	145	140	140	2	1	1	32.5
60	204	156	145	112	2	1	1	35
61	48	109	129	34	2	2	2	37
62	241	124	83	33	2	2	2	23
63	64	125	177	132	2	2	2	32.5
64	97	139	126	123	2	2	2	35
65	187	117	92	79	2	2	2	30
66	161	117	86	74	2	2	2	36
67	167	110	56	78	2	2	2	38
68	102	186	112	143	2	2	2	34
69	166	155	90	95	2	2	2	28.5
70	180	190	177	149	2	2	2	37.5
71	254	185	162	110	2	2	1	25.5
72	246	50	142	46	2	2	1	28
73	138	113	119	100	2	2	1	29.5
74	57	104	134	189	2	2	1	34.5
75	221	109	85	75	2	2	1	31
76	20	100	187	59	2	2	1	34.5
77	3	153	35	151	2	2	1	37
78	141	240	83	132	2	2	1	31
79	181	182	182	153	2	2	1	33.5
80	131	166	99	132	2	2	1	34

Age: 1 = Young, 2 = Old.      Aspect: 1 = North, 2 = South.

Height: 1 = Lower, 2 = Upper

Slope is measured in degrees from the horizontal



Quadrat	Axis 1	Axis 2	Axis 3	Axis 4	Age	Aspect	Height	Slope
1	89	21	138	97	1	1	2	35
2	42	19	106	86	1	1	2	41
3	53	25	155	112	1	1	2	37
4	108	42	148	117	1	1	2	28
5	55	66	99	84	1	1	2	33.5
6	132	106	126	51	1	1	2	28
7	117	87	107	74	1	1	2	31
8	71	97	126	75	1	1	2	27.5
9	52	59	101	79	1	1	2	28.5
10	36	175	113	84	1	1	2	32
11	62	0	129	94	1	1	1	40.5
12	60	25	107	89	1	1	1	40
13	51	21	130	93	1	1	1	41
14	71	34	102	105	1	1	1	36.5
15	44	39	110	80	1	1	1	34
16	128	65	151	104	1	1	1	35.5
17	37	99	42	68	1	1	1	28
18	74	103	106	65	1	1	1	22.5
19	40	137	85	68	1	1	1	20.5
20	76	79	90	92	1	1	1	21
21	179	35	155	139	1	2	2	34
22	196	57	152	143	1	2	2	37
23	133	30	138	111	1	2	2	36
24	184	93	115	156	1	2	2	30
25	185	41	168	125	1	2	2	34
26	164	88	141	110	1	2	2	34
27	136	145	113	98	1	2	2	26
28	172	108	126	129	1	2	2	25
29	123	109	140	146	1	2	2	31
30	66	140	168	145	1	2	2	28.5
31	69	98	28	88	1	2	1	33
32	149	139	121	100	1	2	1	34.5
33	99	75	92	92	1	2	1	32
34	142	99	109	108	1	2	1	29
35	213	65	171	156	1	2	1	28.5
36	97	154	80	96	1	2	1	31.5
37	131	175	127	131	1	2	1	26
38	144	156	160	53	1	2	1	24.5
39	150	149	160	184	1	2	1	26
40	84	168	130	116	1	2	1	27
41	66	35	116	79	2	1	2	32
42	58	53	102	80	2	1	2	29.5
43	132	66	163	82	2	1	2	34
44	108	66	169	0	2	1	2	32.5
45	49	131	31	85	2	1	2	34
46	30	114	35	99	2	1	2	34
47	53	122	24	85	2	1	2	38.5
48	49	97	188	124	2	1	2	36.5
49	27	83	191	126	2	1	2	33
50	19	118	130	99	2	1	2	31
51	94	99	114	78	2	1	1	29
52	54	35	140	97	2	1	1	29.5
53	95	53	176	92	2	1	1	26
54	107	44	147	82	2	1	1	32
55	18	73	0	95	2	1	1	36
56	0	49	140	110	2	1	1	41
57	80	58	128	87	2	1	1	41
58	92	39	146	89	2	1	1	28
59	9	84	201	128	2	1	1	32.5
60	38	110	222	118	2	1	1	35
61	156	92	127	122	2	2	2	37
62	43	200	102	69	2	2	2	23
63	146	76	161	93	2	2	2	32.5
64	157	104	172	25	2	2	2	35
65	89	148	60	76	2	2	2	30
66	95	113	77	88	2	2	2	36
67	108	153	113	53	2	2	2	38
68	136	89	155	85	2	2	2	34
69	91	140	131	112	2	2	2	28.5
70	77	104	190	141	2	2	2	37.5
71	6	138	164	149	2	2	1	25.5
72	56	131	81	80	2	2	1	28
73	126	100	151	79	2	2	1	29.5
74	148	61	149	84	2	2	1	34.5
75	50	141	55	90	2	2	1	31
76	144	41	141	120	2	2	1	34.5
77	171	70	133	100	2	2	1	37
78	83	88	154	122	2	2	1	31
79	62	87	170	121	2	2	1	33.5
80	107	90	137	124	2	2	1	34

Age: 1 = Young, 2 = Old. Aspect: 1 = North, 2 = South.  
Slope is measured in degrees from the horizontal

Height: 1 = Lower, 2 = Upper

Quadrat	Axis 1	Axis 2	Axis 3	Axis 4	Age	Aspect	Height	Slope
1	83	20	141	106	1	1	2	35
2	38	18	110	138	1	1	2	41
3	50	26	157	149	1	1	2	37
4	105	39	152	114	1	1	2	28
5	51	65	102	129	1	1	2	33.5
6	129	104	127	143	1	1	2	28
7	114	84	110	123	1	1	2	31
8	71	95	126	148	1	1	2	27.5
9	50	60	101	108	1	1	2	28.5
10	41	175	107	130	1	1	2	32
11	52	0	131	108	1	1	1	40.5
12	55	21	111	126	1	1	1	40
13	45	22	133	141	1	1	1	41
14	67	30	105	95	1	1	1	36.5
15	41	39	115	152	1	1	1	34
16	125	64	152	102	1	1	1	35.5
17	39	96	41	75	1	1	1	28
18	74	102	107	125	1	1	1	22.5
19	43	137	81	107	1	1	1	20.5
20	75	78	90	88	1	1	1	21
21	163	33	148	37	1	2	2	34
22	183	52	149	72	1	2	2	37
23	125	30	140	89	1	2	2	36
24	181	83	119	74	1	2	2	30
25	174	40	166	64	1	2	2	34
26	162	87	142	80	1	2	2	34
27	138	137	114	141	1	2	2	26
28	172	99	130	125	1	2	2	25
29	121	104	135	71	1	2	2	31
30	64	141	165	47	1	2	2	28.5
31	69	91	26	48	1	2	1	33
32	150	135	122	86	1	2	1	34.5
34	138	93	109	75	1	2	1	29
35	197	61	166	32	1	2	1	28.5
36	102	148	77	109	1	2	1	31.5
37	136	166	123	101	1	2	1	26
38	145	150	158	159	1	2	1	24.5
39	152	141	159	66	1	2	1	26
40	86	163	123	66	1	2	1	27
41	64	37	118	93	2	1	2	32
42	58	54	102	80	2	1	2	29.5
43	125	68	161	109	2	1	2	34
44	102	65	172	215	2	1	2	32.5
45	47	130	29	93	2	1	2	34
46	29	108	33	71	2	1	2	34
47	53	119	21	75	2	1	2	38.5
48	48	107	188	47	2	1	2	36.5
49	24	87	190	90	2	1	2	33
50	18	121	128	94	2	1	2	31
51	92	100	113	102	2	1	1	29
52	51	36	141	114	2	1	1	29.5
53	94	60	181	86	2	1	1	26
54	103	45	148	104	2	1	1	32
55	12	65	0	70	2	1	1	36
56	0	51	142	166	2	1	1	41
57	76	58	128	118	2	1	1	41
58	91	44	148	47	2	1	1	28
59	7	92	201	93	2	1	1	32.5
60	39	117	220	68	2	1	1	35
61	153	87	127	60	2	2	2	37
62	49	199	94	114	2	2	2	23
63	139	75	157	62	2	2	2	32.5
65	85	149	54	100	2	2	2	30
66	93	111	76	99	2	2	2	36
67	108	150	112	158	2	2	2	38
68	133	91	155	61	2	2	2	34
69	91	141	129	73	2	2	2	28.5
70	74	115	191	0	2	2	2	37.5
71	2	147	162	29	2	2	1	25.5
72	59	132	79	73	2	2	1	28
73	122	100	146	91	2	2	1	29.5
75	49	141	53	117	2	2	1	31
76	132	42	136	13	2	2	1	34.5
78	83	92	153	27	2	2	1	31
79	60	92	169	43	2	2	1	33.5
80	104	92	136	17	2	2	1	34

Age: 1 = Young, 2 = Old. Aspect: 1 = North, 2 = South.  
Slope is measured in degrees from the horizontal

Height: 1 = Lower, 2 = Upper

Quadrat	Axis 1	Axis 2	Axis 3	Axis 4	Age	Aspect	Height	Slope
21	271	170	92	108	1	2	2	34
22	296	145	129	113	1	2	2	37
23	243	143	75	77	1	2	2	36
24	206	122	100	57	1	2	2	30
25	270	162	85	104	1	2	2	34
26	170	141	56	38	1	2	2	34
27	127	73	111	63	1	2	2	26
28	164	124	141	27	1	2	2	25
29	131	148	147	84	1	2	2	31
30	48	171	127	107	1	2	2	28.5
31	71	15	44	74	1	2	1	33
32	130	88	44	110	1	2	1	34.5
33	121	55	14	134	1	2	1	32
34	164	100	77	87	1	2	1	29
35	278	182	109	114	1	2	1	28.5
36	81	19	105	52	1	2	1	31.5
37	98	71	148	102	1	2	1	26
38	109	93	127	88	1	2	1	24.5
39	123	172	157	112	1	2	1	26
40	65	80	138	106	1	2	1	27
61	172	119	83	114	2	2	2	37
62	50	0	45	41	2	2	2	23
63	151	122	57	165	2	2	2	32.5
64	142	130	79	135	2	2	2	35
65	100	74	0	30	2	2	2	30
66	109	81	33	13	2	2	2	36
67	114	61	71	0	2	2	2	38
68	128	160	45	80	2	2	2	34
69	103	119	41	37	2	2	2	28.5
70	72	218	25	75	2	2	2	37.5
71	0	180	76	76	2	2	1	25.5
72	61	24	2	66	2	2	1	28
73	134	109	61	95	2	2	1	29.5
74	165	122	58	119	2	2	1	34.5
75	72	79	6	8	2	2	1	31
76	189	150	41	107	2	2	1	34.5
77	202	136	92	67	2	2	1	37
78	83	181	85	82	2	2	1	31
79	70	166	63	92	2	2	1	33.5
80	126	180	31	65	2	2	1	34

Age: 1 = Young, 2 = Old.  
Aspect: 1 = North, 2 = South.  
Height: 1 = Lower, 2 = Upper  
Slope is measured in degrees from the horizontal

DCA: run 6

Quadrat	Axis 1	Axis 2	Axis 3	Axis 4	Age	Aspect	Height	Slope
21	266	169	112	103	1	2	2	34
22	301	149	150	107	1	2	2	37
23	250	149	95	70	1	2	2	36
24	207	123	115	43	1	2	2	30
25	274	166	109	98	1	2	2	34
26	175	140	71	43	1	2	2	34
27	126	74	119	56	1	2	2	26
28	164	123	152	0	1	2	2	25
29	131	144	157	64	1	2	2	31
30	47	172	144	77	1	2	2	28.5
31	73	18	53	81	1	2	1	33
32	128	90	68	118	1	2	1	34.5
34	163	104	90	76	1	2	1	29
35	280	182	130	110	1	2	1	28.5
36	83	21	111	45	1	2	1	31.5
37	100	70	157	99	1	2	1	26
38	106	92	139	81	1	2	1	24.5
39	126	170	168	104	1	2	1	26
40	66	80	147	89	1	2	1	27
61	172	124	100	121	2	2	2	37
62	52	0	49	70	2	2	2	23
63	144	122	88	152	2	2	2	32.5
65	103	73	0	52	2	2	2	30
66	111	85	36	15	2	2	2	36
67	112	62	74	13	2	2	2	38
68	131	161	68	71	2	2	2	34
69	107	118	51	58	2	2	2	28.5
70	77	219	50	73	2	2	2	37.5
71	0	182	89	49	2	2	1	25.5
72	62	27	17	85	2	2	1	28
73	136	109	77	90	2	2	1	29.5
75	75	79	2	24	2	2	1	31
76	191	157	66	118	2	2	1	34.5
78	89	181	106	65	2	2	1	31
79	72	171	83	61	2	2	1	33.5
80	131	176	48	84	2	2	1	34

Age: 1 = Young, 2 = Old.  
 Aspect: 1 = North, 2 = South.  
 Height: 1 = Lower, 2 = Upper  
 Slope is measured in degrees from the horizontal

Quadrat	Axis 1	Axis 2	Axis 3	Axis 4	Age	Aspect	Height	Slope
1	51	95	102	36	1	1	2	35
2	82	128	136	59	1	1	2	41
3	74	65	119	81	1	1	2	37
4	44	60	80	65	1	1	2	28
5	95	112	83	87	1	1	2	33.5
6	43	100	0	81	1	1	2	28
7	35	91	19	95	1	1	2	31
8	85	70	33	102	1	1	2	27.5
9	84	70	57	115	1	1	2	28.5
10	183	105	54	91	1	1	2	32
11	64	95	142	64	1	1	1	40.5
12	66	129	128	57	1	1	1	40
13	82	98	147	73	1	1	1	41
14	63	119	85	61	1	1	1	36.5
15	86	112	124	78	1	1	1	34
16	30	59	42	52	1	1	1	35.5
17	114	111	37	23	1	1	1	28
18	91	95	38	85	1	1	1	22.5
19	154	116	47	84	1	1	1	20.5
20	97	110	40	15	1	1	1	21
41	81	84	65	15	2	1	2	32
42	64	43	37	43	2	1	2	29.5
43	35	74	55	0	2	1	2	34
44	0	83	35	67	2	1	2	32.5
45	138	180	59	76	2	1	2	34
46	130	166	66	100	2	1	2	34
47	119	147	30	32	2	1	2	38.5
48	108	16	61	72	2	1	2	36.5
49	123	19	92	61	2	1	2	33
50	153	88	83	59	2	1	2	31
51	91	113	33	34	2	1	1	29
52	82	69	89	27	2	1	1	29.5
53	42	28	57	46	2	1	1	26
54	58	79	31	18	2	1	1	32
55	109	212	102	81	2	1	1	36
56	126	72	119	92	2	1	1	41
57	70	88	48	53	2	1	1	41
58	56	26	40	34	2	1	1	28
59	124	8	93	73	2	1	1	32.5
60	142	0	62	29	2	1	1	35

Age: 1 = Young, 2 = Old.

Aspect: 1 = North, 2 = South.

Height: 1 = Lower, 2 = Upper

Slope is measured in degrees from the horizontal

## APPENDIX D

### Species attributes

This appendix tabulates the species recorded in this study together with characteristics associated with each species determined from this study and also from other published sources.

Nomenclature follows Stace (1991).

1)- Species are identified by a number 1-98, name and abbreviation (Abrv.). They are listed in the alphabetical order of their abbreviations. Plants which were not identified to species level are listed by number (99-113), abbreviation (*ad hoc* label) and taxonomic level of resolution.

2)- Species frequencies (Freq.) are listed; these denote the number of quadrats in which each species was represented (1-80). Low frequencies are considered to indicate those species in which the age preference calculations are less reliable.

3)- Average abundance (Avg. abund.) for each species was calculated as the abundance value averaged over the number of quadrats in which the species occurs ie its frequency.

4)- Habitats in which each species is typically found (Wade, 1970) are abbreviated as follows.

P - pasture  
CG - calcareous grassland  
G - grassland  
WS - waste ground  
WD - woodland  
R - roadsides  
C - cultivated ground  
B - banks (railway or road)  
DG - dry grassland  
L - limestone  
W - wetlands  
S - sandy places

5)- Species age preference measures

a)- Age preferences ( $A_p$ ) were calculated as described in Section 5.1.2.2. Values are in the range +1.00 to -1.00 with negative values denoting a preference for young slopes.

b)- Age scores ( $A_{CCA}$ ): species scores from CCA run 3 axis 1 (Section 4.5.4.3) which represents the factor old. Positive values denote a preference for old, and negative values for young, slopes.

c)-  $A_{MWU}$  scores are given by the Mann-Whitney U test (Section 5.1.1). MW U scores are calculated separately for each aspect. Smaller values indicate a stronger age preference with significant changes over time denoted by bold type.

6)- Life History (LH) refers to the type of life-cycle of the organism;

A - annual  
B - biennial  
P - perennial

7)- Strategy refers to the classification given by Grime *et al.* (1989). Bracketed entries indicate strategies not given explicitly in Grime *et al.* (1989) but determined from the key given on page 28 of that work (Section 5.2.1).

8)- Successional Age (Succ Age) refers to the successional age of grasslands in which the species typically occurs as determined by Gibson and Brown (1991) (Section 5.2.3). Bracketed entries refer to studies by other authors but collated by Gibson and Brown.

## Appendix D Species attributes

	Species	Abrv.	Freq.	Avg abund	Habitats	A <sub>p</sub>	A <sub>CCA</sub>	A <sub>MWU</sub> (North)	A <sub>MWU</sub> (South)
1	<i>Anagallis arvensis</i>	AA	1	1	C	1.00	106	-	+190.0
2	<i>Arrhenatherum elatius</i>	AE	79	74	WD/P/WS	-0.01	7	-157.5	+148.5
3	<i>Agrostis capillaris</i>	AgC	12	5	P/R/WD	0.84	101	+170.0	+163.0
4	<i>Agrostis stolonifera</i>	AgS	28	7	P/R/WS	0.03	2	+159.5	+148.5
5	<i>Aira caryophyllea</i>	AiC	2	10	DG/WS	1.00	130	+190.0	+190.0
6	<i>Anthoxanthum odoratum</i>	AO	11	4	P/R/WD	-0.13	-7	-184.0	-190.5
7	<i>Bellis perennis</i>	BeP	11	9	P	0.51	72	<b>-160.0*</b>	+169.0
8	<i>Bromus hordeaceus</i>	BH	29	25	P/R/WS	-0.70	-55	<b>-160.0*</b>	<b>-64.0**</b>
9	<i>Blackstonia perfoliata</i>	BP	6	1	P/R/B/WD/L	-0.50	-18	-190.0	-171.5
10	<i>Brachypodium sylvaticum</i>	BS	20	25	WD/P	0.83	96	<b>+147.0*</b>	<b>+140.0*</b>
11	<i>Convolvulus arvensis</i>	CA	3	7	C/R/B/WS	-0.24	-18	-190.0	+199.5
12	<i>Crepis capillaris</i>	CC	42	13	R/C/WS/B/P	-0.16	-14	-161.0	-183.0
13	<i>Carex divulsa</i>	CD	3	1	WD	-1.00	-78	-190.0	-180.0
14	<i>Centaureum erythraea</i>	CE	17	5	R/P/L	-0.08	14	-170.0	-160.5
15	<i>Cerastium fontanum</i>	CeF	4	2	P/R/C	0.71	93	+189.5	+190.0
16	<i>Carex flacca</i>	CF	6	17	R/B/CG	1.00	107	<b>+160.0*</b>	+180.0
17	<i>Carex hirta</i>	CH	13	31	G/WD	-0.70	-63	+191.5	<b>-140.0*</b>
18	<i>Cruciata laevipes</i>	CL	1	13	WD/R/L	1.00	-79	-	+190.0
19	<i>Cratageus monogyna</i>	CM	15	2	WD	-0.22	-15	-180.0	-171.0
20	<i>Clinopodium vulgare</i>	CpV	1	8	WD/P	1.00	106	-	+190.0
21	<i>Carex spicata</i>	CS	1	1	B	1.00	112	-	+190.0
22	<i>Cornus sanguinea</i>	CSg	1	1	WD	1.00	106	+190.0	-
23	<i>Cladonia spp</i>	CSp	3	2	?	-0.33	-30	-	+191.0
24	<i>Cirsium vulgare</i>	CVg	46	17	P/R/WS	0.05	15	+188.0	+174.5
25	<i>Clematis vitalba</i>	CVt	12	1	WD/C	-0.06	-9	-189.0	+191.0
26	<i>Dryopteris felix-mas</i>	DFm	5	10	WD	1.00	107	<b>+150.0*</b>	-
27	<i>Dactylis glomerata</i>	DG	54	9	P/R	-0.32	-29	<b>-102.5*</b>	-151.0
28	<i>Erigonum acer</i>	EgA	2	3	B/L	-0.60	-78	-	-199.5
29	<i>Epilobium ??</i>	Ep1	8	6		-0.51	-38	-172.0	-170.0
30		Ep4	5	1		-1.00	-93	-180.0	-170.0
31		Ep5	1	6		-1.00	-95	-	-190.0
32	<i>Epilobium hirsutum</i>	EpH	5	8	W	-0.07	-1	+199.5	-190.0
33	<i>Epilobium montanum</i>	EpM	6	4	WD/C/WS	-1.00	-93	-170.0	-170.0
34	<i>Equisetum arvense</i>	EqA	6	14	WS/C/R/B	-0.79	-76	-198.0	+180.0
35	<i>Elytrigia repens</i>	ER	64	17	C/WS/R	0.02	-2	-160.0	-193.5
36	<i>Fraxinus excelsior</i>	FE	27	5	WD	0.78	84	+151.0	+180.0
37	<i>Festuca ovina</i>	FO	71	39	DG	0.09	19	+181.0	+181.5
38	<i>Festuca rubra</i>	FR	54	9	P/R/B	-0.30	-16	-153.5	-173.5
39	<i>Fragaria vesca</i>	FV	22	17	WD	-0.13	1	+200.0	-179.5
40	<i>Geranium dissectum</i>	GD	13	6	R/B/C/WS	-0.22	-14	-190.0	-178.0
41	<i>Glechoma hederacea</i>	GH	22	37	WD	0.67	75	+155.5	+177.5
42	<i>Geranium molle</i>	GM	11	9	R/C/P	-0.41	-22	-170.0	-178.0
43	<i>Geranium rotundifolium</i>	GR	4	3	?	-1.00	-91	-180.0	-180.0
44	<i>Galium verum</i>	GV	2	3	P/R/B	1.00	109	+180.0	-
45	<i>Hedera helix</i>	HHx	2	63	WD	0.22	26	+190.0	-190.0
46	<i>Holcus lanatus</i>	HL	11	10	P/R	-0.06	0	-195.0	-180.0
47	<i>Holcus mollis</i>	HM	2	4	WD	-1.00	-88	-	-180.0
48	<i>Hypochaeris radicata</i>	HR	16	16	P/R	-0.88	-66	-170.0	<b>-122.0*</b>
49	<i>Heracleum sphondylium</i>	HS	3	2	R/B/P/WS	-0.67	-96	-190.0	-199.5
50	<i>Hypericum humifusum</i>	HyH	9	3	P/WD	-0.73	-69	-189.5	-179.0
51	<i>Hypericum maculatum</i>	HyM	22	18	R/WD/B	-0.43	-29	-172.5	<b>-134.0*</b>
52	<i>Inula conyzae</i>	IC	1	2	R/B/WD/L	-1.00	-93	-	-190.0
53	<i>Lathyrus nissolia</i>	LN	22	3	P/B	-1.00	-91	<b>-100.0**</b>	<b>-80.0**</b>
54	<i>Linum catharticum</i>	LnC	6	5	P/R/L	0.21	31	+189.5	+190.0
55	<i>Lolium perenne</i>	LP	1	1	P/R/WS	1.00	123	-	+190.0

	Species	Abrv.	Freq.	Avg. abund.	Habitats	Age Pref	Age score (CCA)	MW U (North)	MW U (South)
56	<i>Lathyrus linifolius</i>	LtL	5	1	WD	-0.67	-59	-160.0*	+190.0
57	<i>Lathyrus pratensis</i>	LtP	24	11	P/WD/B	-0.26	-19	-170.5	-181.0
58	<i>Leucanthamum vulgare</i>	LV	10	17	P/B/R	0.02	15	-190.0	-171.5
59	<i>Luzula campestris</i>	LzC	2	3	P/B/R	1.00	108	-	+180.0
60	<i>Myosotis arvensis</i>	MA	39	10	C/B/WD/L	-0.01	-5	+191.5	-180.5
61	<i>Malva moschata</i>	MM	3	2	R/B/WD/P	-1.00	-83	-	-170.0
62	<i>Poa annua</i>	PA	7	5	G/WS/C	-0.54	-49	-180.0	+193.0
63	<i>Potentilla erecta</i>	PE	1	10	B/P/WD	1.00	106	+190.0	-
64	<i>Peltigera canina</i>	PgC	1	12	?	1.00	138	-	+190.0
65	<i>Plantago lanceolata</i>	PI L	19	13	P/R/B/WS	-0.99	-90	-95.0**	-130.0**
66	<i>Pilosella officinarum</i>	PO	10	6	P/B/WD	0.44	10	-189.5	+187.5
67	<i>Poa pratensis</i>	PP	29	7	R/WS/C/P	-0.53	-39	-164.5	-161.5
68	<i>Potentilla reptans</i>	PR	4	6	R/B/P	0.42	51	-190.5	+190.0
69	<i>Pseudoscleropodium purum</i>	PsP	55	31	CG*	-0.23	-14	-164.5	-101.5**
70	<i>Prunella vulgaris</i>	PV	30	8	P/R	-0.40	-29	-147.5	-180.0
71	<i>Primula veris</i>	PVe	6	13	P/WD	0.97	121	+170.0	+189.0
72	<i>Quercus robur</i>	QR	9	1	WD	0.60	36	+189.0	+160.0*
73	<i>Ranunculus acris</i>	RA	1	1	P/R/WD	-1.00	-99	-190.0	-
74	<i>Rosa agg.</i>	Rag	4	1	WD	-1.00	-72	-	-160.0*
75	<i>Rumex acetosella</i>	RAt	1	27	P/B/WS	1.00	123	-	+190.0
76	<i>Rumex crispus</i>	RC	3	5	R/WS/C	1.00	92	-	+170.0
77	<i>Rubus fruticosus</i>	RF	26	13	WD	0.00	2	+174.0	+188.0
78	<i>Ranunculus repens</i>	RR	26	10	C/R	-0.34	-54	-127.5*	-192.5
79	<i>Sonchus asper</i>	SA	35	6	C/WS	-0.12	-11	-199.5	+195.5
80	<i>Sherardia arvensis</i>	ShA	2	42	C	0.37	-15	-	+199.5
81	<i>Senecio jacobaea</i>	SJ	35	9	P/WD/B/WS	-0.31	-17	-170.0	-128.0*
82	<i>Sanguisorba minor</i>	SM	6	7	B/R/CG	-1.00	-84	-180.0	-160.0*
83	<i>Stachys sylvatica</i>	SS	2	6	WD	-0.17	-60	-190.0	+190.0
84	<i>Stellaria graminea</i>	StG	8	16	R/P	-0.95	-92	-178.5	-160.0*
85	<i>Stellaria pallida</i>	StP	5	2	S	-1.00	-98	-170.0	-180.0
86	<i>Trifolium campestre</i>	TC	1	2	R/C	1.00	129	-	+190.0
87	<i>Trisetum flavescens</i>	TF	10	7	P/R	0.34	43	+191.0	+150.0*
88	<i>Trifolium micranthum</i>	TM	2	1	P/WD/S	0.00	5	+200.0	-
89	<i>Taraxacum officinarum</i>	TO	6	4	WS/C/G	-0.64	-50	-190.0	+193.0
90	<i>Trifolium repens</i>	TR	9	2	WS/G	-1.00	-88	-140.0*	-170.0
91	<i>Urtica dioica</i>	UD	4	9	R/WD/WS	1.00	48	-	+160.0*
92	<i>Viola arvensis</i>	VA	1	1	C/WS	1.00	115	-	+190.0
93	<i>Veronica chamaedrys</i>	VCh	58	20	WD/P	0.13	19	+198.0	+168.0
94	<i>Vicia cracca</i>	ViC	9	7	WD/P/B	-0.93	-91	-156.0	-190.0
95	<i>Viola riviniana</i>	VR	8	17	WD	1.00	111	+160.0*	+160.0*
96	<i>Vicia sepium</i>	VSp	4	3	WD	-1.00	-99	-160.0*	-
97	<i>Vicia sativa</i>	VSt	53	10	R/WS/C	-0.76	-69	-77.0**	-30.0**
98	<i>Verbascum thapsus</i>	VT	2	4	R/B/WS	1.00	118	-	+180.0
99	fungus	F1	1	1		-1.00	-99	-190.0	-
100	?	H14	2	1		0.00	6	-190.0	+190.0
101	?	H14B	1	2		-1.00	-98	-190.0	-
102	?	H1F	3	5		0.73	87	+190.0	+199.5
103	?Ranunculaceae	H27D	1	3		-1.00	-99	-190.0	-
104	?Asteraceae	H57B	2	1		1.00	17	-	+180.0
105	?Fabaceae	H61	34	4		-0.61	-50	-85.0**	-154.0
106	?Fabaceae	H61C	2	1		-1.00	-99	-180.0	-
107	?Geraniaceae	H68E	1	3		1.00	138	+190.0	+190.0
108	?	H8	6	3		1.00	118	-	+150.0*
109	?	H88	1	1		1.00	114	-	+190.0
110	?	H90	1	4		-1.00	-98	-	-190.0
111	?Cyperaceae	S8	3	11		0.88	112	-	+189.0
112	?	T1	2	1		-1.00	-99	-180.0	-
113	?	T9	1	1		-1.00	-99	-190.0	-



	Species	Abbrev	Freq	LH	Strategy	Succ Age
1	<i>Anagallis arvensis</i>	AA	1	A	R/S-R	Y
2	<i>Arrhenatherum elatius</i>	AE	79	P	C	M
3	<i>Agrostis capillaris</i>	AgC	12	P	C-S-R	(Y)
4	<i>Agrostis stolonifera</i>	AgS	28	P	C-R	M
5	<i>Aira caryophyllaea</i>	AiC	2	A	(S-R)	-
6	<i>Anthoxanthum odoratum</i>	AO	11	P	S-R/C-S-R	M
7	<i>Bellis perennis</i>	BeP	11	P	R/C-S-R	M
8	<i>Bromus hordeaceus</i>	BH	29	A	R	(Y)
9	<i>Blackstonia perfoliata</i>	BP	6	A	(S-R)	O
10	<i>Brachypodium sylvaticum</i>	BS	20	P	S/S-C	M
11	<i>Convolvulus arvensis</i>	CA	3	P	C-R	Y
12	<i>Crepis capillaris</i>	CC	42	A/B	R/S-R	(M)
13	<i>Carex divulsa</i>	CD	3	P	(S-R)	-
14	<i>Centaureum erythraea</i>	CE	17	B	S-R	M
15	<i>Cerastium fontanum</i>	CeF	4	P	R/C-S-R	Y
16	<i>Carex flacca</i>	CF	6	P	S	Y
17	<i>Carex hirta</i>	CH	13	P	(S-C)	-
18	<i>Cruciata laevipes</i>	CL	1	P	(S-C)	-
19	<i>Cratageus monogyna</i>	CM	15	P	S-C	-
20	<i>Clinopodium vulgare</i>	CpV	1	P	(S-C)	M
21	<i>Carex spicata</i>	CS	1	P	(S)	-
22	<i>Cornus sanguinea</i>	CSg	1	P	(C-R)	-
23	<i>Cladonia spp</i>	CSp	3	(P)	O	-
24	<i>Cirsium vulgare</i>	CVg	46	B	C-R	(M)
25	<i>Clematis vitalba</i>	CVt	12	P	(S-C)	-
26	<i>Dryopteris felix-mas</i>	DFm	5	P	S-C	-
27	<i>Dactylis glomerata</i>	DG	54	P	C-S-R/C	M
28	<i>Erigonum acer</i>	EgA	2	A/B	S-R	(Y)
29	<i>Epilobium ??</i>	Ep1	8	?	-	-
30		Ep4	5	?	-	-
31		Ep5	1	?	-	-
32	<i>Epilobium hirsutum</i>	EpH	5	P	C	(Y)
33	<i>Epilobium montanum</i>	EpM	6	P	C-S-R	(Y)
34	<i>Equisetum arvense</i>	EqA	6	P	C-R	-
35	<i>Elytrigia repens</i>	ER	64	P	(C-R)	Y
36	<i>Fraxinus excelsior</i>	FE	27	P	C	-
37	<i>Festuca ovina</i>	FO	71	P	S	(M)
38	<i>Festuca rubra</i>	FR	54	P	C-S-R	(M)
39	<i>Fragaria vesca</i>	FV	22	P	C-S-R	M
40	<i>Geranium dissectum</i>	GD	13	A	(C-R)	Y
41	<i>Glechoma hederacea</i>	GH	22	A	C-S-R	M
42	<i>Geranium molle</i>	GM	11	A	R/S-R	(M)
43	<i>Geranium rotundifolium</i>	GR	4	A	(R)	-
44	<i>Galium verum</i>	GV	2	P	(S-R)	O
45	<i>Hedera helix</i>	HHx	2	P	S-C	-
46	<i>Holcus lanatus</i>	HL	11	P	C-S-R	M
47	<i>Holcus mollis</i>	HM	2	P	C	-
48	<i>Hypochaeris radicata</i>	HR	16	P	C-S-R	M
49	<i>Heracleum sphondylium</i>	HS	3	B/P	(C-R)	(M)
50	<i>Hypericum humifusum</i>	HyH	9	P	(S-C)	-
51	<i>Hypericum maculatum</i>	HyM	22	P	(S-C)	-
52	<i>Inula conyzae</i>	I C	1	P	S/S-R	(M/Y)
53	<i>Lathyrus nissolia</i>	LN	22	A	(R)	-
54	<i>Linum catharticum</i>	LnC	6	A	S-R	M
55	<i>Lolium perenne</i>	LP	1	P	(S-C)	M
56	<i>Lathyrus linifolius</i>	LtL	5	P	(S-R)	-

	Species	Abbrev	Freq	LH	Strategy	Succ Age
57	<i>Lathyrus pratensis</i>	LtP	24	P	C-S-R	(O)
58	<i>Leucanthamum vulgare</i>	LV	10	P	C-S-R/C-R	M
59	<i>Luzula campestris</i>	LzC	2	P	(S-R)	-
60	<i>Myosotis arvensis</i>	MA	39	A/P	R/S-R	(Y)
61	<i>Malva moschata</i>	MM	3	P	(S-C)	(M)
62	<i>Poa annua</i>	PA	7	A/(P)	(S-R)	Y
63	<i>Potentilla erecta</i>	PE	1	P	(C-R)	O
64	<i>Peltigera canina</i>	PgC	1	(P)	-	?
65	<i>Plantago lanceolata</i>	PI L	19	P	C-S-R	M
66	<i>Pilosella officinarum</i>	PO	10	P	S/C-S-R	M
67	<i>Poa pratensis</i>	PP	29	P	C-S-R	Y
68	<i>Potentilla reptans</i>	PR	4	P	(C-R)	Y
69	<i>Pseudoscleropodium purum</i>	PsP	55	(P)	-	-
70	<i>Prunella vulgaris</i>	PV	30	P	C-S-R	Y
71	<i>Primula veris</i>	PVe	6	P	-	M
72	<i>Quercus robur</i>	QR	9	P	(S-C)	-
73	<i>Ranunculus acris</i>	RA	1	P	C-S-R	?
74	<i>Rosa agg.</i>	Rag	4	P	(C-R)	-
75	<i>Rumex acetosella</i>	RAt	1	P	C-S-R/S-R	?
76	<i>Rumex crispus</i>	RC	3	P	C-R/R	(Y)
77	<i>Rubus fruticosus</i>	RF	26	P	S-C	-
78	<i>Ranunculus repens</i>	RR	26	P	C-R	M
79	<i>Sonchus asper</i>	SA	35	A/B	R/C-R	(Y)
80	<i>Sherardia arvensis</i>	ShA	2	A	(S-R)	Y
81	<i>Senecio jacobaea</i>	SJ	35	P	R/C-R	M
82	<i>Sanguisorba minor</i>	SM	6	P	(S-R)	M
83	<i>Stachys sylvatica</i>	SS	2	P	(C)	(Y)
84	<i>Stellaria graminea</i>	StG	8	P	(S)	-
85	<i>Stellaria pallida</i>	StP	5	A	(S-R)	-
86	<i>Trifolium campestre</i>	TC	1	A	(S-R)	(Y/M)
87	<i>Trisetum flavescens</i>	TF	10	P	C-S-R	Y
88	<i>Trifolium micranthum</i>	TM	2	A	(S-R)	-
89	<i>Taraxacum officinarum</i>	TO	6	P	R/C-S-R	M
-90	<i>Trifolium repens</i>	TR	9	P	C-S-R/C-R	Y
91	<i>Urtica dioica</i>	UD	4	P	C	Y
92	<i>Viola arvensis</i>	VA	1	A	(R/C-R)	(M)
93	<i>Veronica chamaedrys</i>	VCh	58	P	C-S-R/S	Y
94	<i>Vicia cracca</i>	ViC	9	P	C/C-S-R	M
95	<i>Viola riviniana</i>	VR	8	P	S	(O)
96	<i>Vicia sepium</i>	VSp	4	P	C-S-R/C	(M)
97	<i>Vicia sativa</i>	VSt	53	A	(R)	(M)
98	<i>Verbascum thapsus</i>	VT	2	B	(C-R)	(Y)
99	<i>fungus</i>	F1	1	(P)		
100		H14	2	?	-	-
101		H14B	1	?	-	-
102		H1F	3	?	-	-
103		H27D	1	?	-	-
104		H57B	2	?	-	-
105		H61	34	?	-	-
106		H61C	2	?	-	-
107		H68E	1	?	-	-
108		H8	6	?	-	-
109		H88	1	?	-	-
110		H90	1	?	-	-
111		S8	3	P	(S-R)	-
112		T1	2	P	(S-C)	-
113		T9	1	P		-

	Species	Abbrev	Habitats
1	<i>Anagallis arvensis</i>	AA	C
2	<i>Arrhenatherum elatius</i>	AE	WD/P/WS
3	<i>Agrostis capillaris</i>	AgC	P/R/WD
4	<i>Agrostis stolonifera</i>	AgS	P/R/WS
5	<i>Aira caryophyllaea</i>	AiC	DG/WS
6	<i>Anthoxanthum odoratum</i>	AO	P/R/WD
7	<i>Bellis perennis</i>	BeP	P
8	<i>Bromus hordeaceus</i>	BH	P/R/WS
9	<i>Blackstonia perfoliata</i>	BP	P/R/B/WD/L
10	<i>Brachypodium sylvaticum</i>	BS	WD/P
11	<i>Convolvulus arvensis</i>	CA	C/R/B/WS
12	<i>Crepis capillaris</i>	CC	R/C/WS/B/P
13	<i>Carex divulsa</i>	CD	WD
14	<i>Centaurium erythraea</i>	CE	R/P/L
15	<i>Cerastium fontanum</i>	CeF	P/R/C
16	<i>Carex flacca</i>	CF	R/B/CG
17	<i>Carex hirta</i>	CH	G/WD
18	<i>Cruciata laevipes</i>	CL	WD/R/L
19	<i>Cratageus monogyna</i>	CM	WD
20	<i>Clinopodium vulgare</i>	CpV	WD/P
21	<i>Carex spicata</i>	CS	B
22	<i>Cornus sanguinea</i>	CSg	WD
23	<i>Cladonia spp</i>	CSp	?
24	<i>Cirsium vulgare</i>	CVg	P/R/WS
25	<i>Clematis vitalba</i>	CVt	WD/C
26	<i>Dryopteris felix-mas</i>	DFm	WD
27	<i>Dactylis glomerata</i>	DG	P/R
28	<i>Erigonum acer</i>	EgA	B/L
29	<i>Epilobium ??</i>	Ep1	
30		Ep4	
31		Ep5	
32	<i>Epilobium hirsutum</i>	EpH	W
33	<i>Epilobium montanum</i>	EpM	WD/C/WS
34	<i>Equisetum arvense</i>	EqA	WS/C/R/B
35	<i>Elytrigia repens</i>	ER	C/WS/R
36	<i>Fraxinus excelsior</i>	FE	WD
37	<i>Festuca ovina</i>	FO	DG
38	<i>Festuca rubra</i>	FR	P/R/B
39	<i>Fragaria vesca</i>	FV	WD
40	<i>Geranium dissectum</i>	GD	R/B/C/WS
41	<i>Glechoma hederacea</i>	GH	WD
42	<i>Geranium molle</i>	GM	R/C/P
43	<i>Geranium rotundifolium</i>	GR	?
44	<i>Galium verum</i>	GV	P/R/B
45	<i>Hedera helix</i>	HHx	WD
46	<i>Holcus lanatus</i>	HL	P/R
47	<i>Holcus mollis</i>	HM	WD
48	<i>Hypochaeris radicata</i>	HR	P/R
49	<i>Heracleum sphondylium</i>	HS	R/B/P/WS
50	<i>Hypericum humifusum</i>	HyH	P/WD
51	<i>Hypericum maculatum</i>	HyM	R/WD/B
52	<i>Inula conyzae</i>	I C	R/B/WD/L
53	<i>Lathyrus nissolia</i>	LN	P/B
54	<i>Linum catharticum</i>	LnC	P/R/L
55	<i>Lolium perenne</i>	LP	P/R/WS
56	<i>Lathyrus linifolius</i>	LtL	WD

	Species	Abbrev	Habitats
57	<i>Lathyrus pratensis</i>	LtP	P/WD/B
58	<i>Leucanthemum vulgare</i>	LV	P/B/R
59	<i>Luzula campestris</i>	LzC	P/B/R
60	<i>Myosotis arvensis</i>	MA	C/B/WD/L
61	<i>Malva moschata</i>	MM	R/B/WD/P
62	<i>Poa annua</i>	PA	G/WS/C
63	<i>Potentilla erecta</i>	PE	B/P/WD
64	<i>Peltigera canina</i>	PgC	?
65	<i>Plantago lanceolata</i>	PI L	P/R/B/WS
66	<i>Pilosella officinarum</i>	PO	P/B/WD
67	<i>Poa pratensis</i>	PP	R/WS/C/P
68	<i>Potentilla reptans</i>	PR	R/B/P
69	<i>Pseudoscleropodium purum</i>	PsP	CG*
70	<i>Prunella vulgaris</i>	PV	P/R
71	<i>Primula veris</i>	PVe	P/WD
72	<i>Quercus robur</i>	QR	WD
73	<i>Ranunculus acris</i>	RA	P/R/WD
74	<i>Rosa agg.</i>	Rag	WD
75	<i>Rumex acetosella</i>	RAt	P/B/WS
76	<i>Rumex crispus</i>	RC	R/WS/C
77	<i>Rubus fruticosus</i>	RF	WD
78	<i>Ranunculus repens</i>	RR	C/R
79	<i>Sonchus asper</i>	SA	C/WS
80	<i>Sherardia arvensis</i>	ShA	C
81	<i>Senecio jacobaea</i>	SJ	P/WD/B/WS
82	<i>Sanguisorba minor</i>	SM	B/R/CG
83	<i>Stachys sylvatica</i>	SS	WD
84	<i>Stellaria graminea</i>	StG	R/P
85	<i>Stellaria pallida</i>	StP	S
86	<i>Trifolium campestre</i>	TC	R/C
87	<i>Trisetum flavescens</i>	TF	P/R
88	<i>Trifolium micranthum</i>	TM	P/WD/S
89	<i>Taraxacum officinarum</i>	TO	WS/C/G
-90	<i>Trifolium repens</i>	TR	WS/G
91	<i>Urtica dioica</i>	UD	R/WD/WS
92	<i>Viola arvensis</i>	VA	C/WS
93	<i>Veronica chamaedrys</i>	VCh	WD/P
94	<i>Vicia cracca</i>	ViC	WD/P/B
95	<i>Viola riviniana</i>	VR	WD
96	<i>Vicia sepium</i>	VSp	WD
97	<i>Vicia sativa</i>	VSt	R/WS/C
98	<i>Verbascum thapsus</i>	VT	R/B/WS
99	fungus	F1	
100		H14	
101		H14B	
102		H1F	
103		H27D	
104		H57B	
105		H61	
106		H61C	
107		H68E	
108		H8	
109		H88	
110		H90	
111		S8	
112		T1	
113		T9	

## APPENDIX E

Program code for the calculation of the C8 index of species association using the Genstat language version 5.3.2 (Lawes Agricultural Trust, 1995).

"Spassoc1.com. This program calculates an index of association (C8) between species pairs after Hurlbert (1969). The particular implementation shown below uses the Old North (ON) data subset"

```
set [pause=0;diagnostic=faults]
open 'ONassocS.out'; channel=3; filetype=output
copy [print=output] 3

scalar [value=72] s ;decimals=0  "s is the number of species in the
  dataset"
scalar [value=80] q;decimals=0
variate [nvalues=q] species[1...s];decimals=0;minimum=0;maximum=1
symmetricmatrix [rows=s] identifier= ONC8S
scalar [value=0] nospp ;decimals=0
scalar [value=20] n;decimals=0  "n is the number of quadrats in the
  data-set"
scalar [value=0] a,b,c,d ;decimals=0
open 'dat96ms.txt'; channel=2; filetype=input ; width=900
read [print=*; channel=2] species[1...s]

" ` if f(A), ie (a+b), or f(B) ie (a+c) equals zero or unity the 2x2 table
provides no information on association'. For each species first check if
there is more than one occurrence in the current data set."

calc splimit=(s-1)
for i=1...splimit
  if sum(species[i]).gt.1  "for binary data this selects those
    species with more than a single occurrence"
    calc nospp=nospp+1
    calc z=i+1
    for k= z...s
      for j=41...60  "change this range depending on which subset is
        being used: Y=1-40;O=41-80;YN=1-20 etc. See table 3.2"
        if species[i]$[j].gt.0
          if species[k]$[j].gt.0
            calc a=a+1  "both species are present"
          else
            calc b=b+1  "species i present, species j absent"
          endif
        else
          if species[k]$[j].gt.0
            calc c=c+1  "species i absent, species j present"
          else
            calc d=d+1  "both species are absent"
          endif
        endif
      endif
    endif
  endif
endfor
```

"1)- construct a contingency table"

```
if species[i]$[j].gt.0
  if species[k]$[j].gt.0
    calc a=a+1  "both species are present"
  else
    calc b=b+1  "species i present, species j absent"
  endif
else
  if species[k]$[j].gt.0
    calc c=c+1  "species i absent, species j present"
  else
    calc d=d+1  "both species are absent"
  endif
endif
```

endfor

"2)- Calculate the observed  $\chi^2$  value ie obschi."

```
calc obschi = (((a*d)-(b*c))**2)*n)/((a+b)*(a+c)*(b+d)*(c+d))
```

"3)- calculate the maximum possible  $\chi^2$  value; i.e. maxchi"

```

if (a*d).ge.(b*c)
    calc maxchi = ((a+b)*(b+d)*n)/((a+c)*(c+d))
else
    if a.le.d
        calc maxchi= ((a+b)*(a+c))*n/((b+d)*(c+d))
    else
        calc maxchi= ((b+d)*(c+d)*n)/((a+b)*(a+c))
    endif
endif

```

"4)- calculate the minimum  $\chi^2$  value; i.e. minchi"

```
calc ahat= ((a+c)/n)*(a+b)
```

"calculate gahat which can take one of three values;

a- if ahat is an integer then gahat = ahat

b- if (a\*d)<(b\*c) then ahat is rounded down to the next lowest integer to give gahat

c- if (a\*d)>=(b\*c) then ahat is rounded up to the next integer to give gahat"

```

calc remain=modulo(ahat;1)
    if remain.eq.0
        calc gahat=ahat
    else
        if (a*d).lt.(b*c)
            calc gahat = (ahat-remain)    "round down"
        else
            calc gahat = (ahat-remain)+1  "round up"
        endif
    endif

```

```
calculate minchitop= (n**3)*((ahat-gahat)**2)
```

```
calculate minchibot=(a+b)*(a+c)*(c+d)*(b+d)
```

```
calculate minchi=minchitop/minchibot
```

```
calculate c8left= (((a*d)-(b*c))/abs((a*d)-(b*c)))
```

```
calculate c8right= abs(sqrt((obschi-minchi)/(maxchi-minchi)))
```

"5)- calculate the value of Coles C8 index"

```
calculate ONC8S[i;k] = c8left*c8right
```

```
calc a=a-a:& b=b-b:& c=c-c:& d=d-d
```

```
    endfor
```

```
endif
```

```
endfor
```

```
calc nospp=0
```

```
calc AONC8S =abs(ONC8S)
```

```
calc MAONC8S =mean(AONC8S)
```

```
print AONC8S, MAONC8S
```

```
open 'associat'; channel=1; filetype=backingstore
```

```
store [channel=1; subfile=ONC8S;print =catalogue] ONC8S
```

```
stop
```

## APPENDIX F

Stratification; species environmental preference scores grouped by age

Species	PrefY	PrefO
<i>Arrhenatherum elatius</i>	0.24215	0.07650
<i>Agrostis capillaris</i>	-1.00000	-0.89286
<i>Agrostis stolonifera</i>	-0.82178	-0.53271
<i>Anthoxanthum odoratum</i>	-0.30769	0.20000
<i>Bellis perennis</i>	-0.25000	-1.00000
<i>Bromus hordeaceus</i>	-0.91346	-1.00000
<i>Brachypodium sylvaticum</i>	-0.95238	-0.16889
<i>Crepis capillaris</i>	-0.87821	-0.81250
<i>Centaureum erythraea</i>	-0.66667	-1.00000
<i>Carex hirta</i>	-0.52353	1.00000
<i>Cratageus monogyna</i>	-0.28571	-0.33333
<i>Cirsium vulgare</i>	-0.19149	-0.05769
<i>Clematis vitalba</i>	-0.11111	-0.50000
<i>Dactylis glomerata</i>	0.10638	-0.08876
<i>Epilobium hirsutum</i>	-0.90909	0.47368
<i>Equisetum arvense</i>	1.00000	-0.11111
<i>Elytrigia repens</i>	-0.03882	-0.06549
<i>Fraxinus excelsior</i>	0.42857	0.52632
<i>Festuca ovina</i>	0.10356	0.07260
<i>Festuca rubra</i>	-0.08157	-0.21348
<i>Fragaria vesca</i>	-0.69524	-0.37888
<i>Geranium dissectum</i>	-0.77273	-1.00000
<i>Glechoma hederacea</i>	-0.92647	0.13120
<i>Geranium molle</i>	-0.82857	-1.00000
H61	0.24074	-0.15385
<i>Holcus lanatus</i>	0.89655	1.00000
<i>Hypochaeris radicata</i>	-0.70124	-1.00000
<i>Hypericum humifusum</i>	-0.69231	-0.50000
<i>Hypericum maculatum</i>	-0.66551	-0.73913
<i>Linum catharticum</i>	1.00000	0.88235
<i>Lathyrus pratensis</i>	0.59259	0.60417
<i>Leucanthamum vulgare</i>	-0.85714	-1.00000
<i>Myosotis arvensis</i>	-0.70526	-0.64516
<i>Poa annua</i>	-0.11111	-1.00000
<i>Pilosella officinarum</i>	-0.41176	-0.90909
<i>Poa pratensis</i>	-0.10811	-0.33333
<i>Potentilla repens</i>	1.00000	-0.29412
<i>Pseudoscleropodium purum</i>	0.61768	0.87768
<i>Prunella vulgaris</i>	-0.47239	-0.45714
<i>Quercus robur</i>	1.00000	0.00000
<i>Rubus fruticosus</i>	-0.96386	-0.43030
<i>Ranunculus repens</i>	0.88372	-0.02381
<i>Sonchus asper</i>	-0.78512	-0.91579
<i>Senecio jacobaea</i>	-0.97222	-1.00000
<i>Trisetum flavescens</i>	0.56522	-0.87234
<i>Taraxacum officinarum</i>	-0.88889	-1.00000
<i>Veronica chamaedrys</i>	0.61829	0.65123
<i>Vicia cracca</i>	0.68966	1.00000
<i>Vicia sativa</i>	-0.05195	-0.09677