ALTITUDINAL DISTRIBUTION OF VEGETATION IN THE HEADWATERS OF THE WONGUNGARRA RIVER, VICTORIA

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Snow Gums beneath a thunderstorm over the Wongungarra Valley.

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Table of contents

Abstract

Changes in vegetation composition with respect to altitude were investigated in the sclerophyllous forests of the Australian mountain region. Vegetation was surveyed at 148 sites along two transects which were located to maximise variation in altitude and minimise the influence of environmental factors not directly related to altitude. The measurement, simulation, and estimation of environmental variables revealed that this aim was met except at the end-points of the transects where secondary influences are present. The dominant pattern of species compositional change along the transects correlates with altitude. Distinct vegetation types observed near valley-bottoms and ridge-tops are (informally) explained in terms of secondary environmental influences. The main body of vegetation, *i.e.* that which is not proximate to watercourses or ridges, generally exhibits a continuum of compositional change with respect to altitude. However, a discontinuity occurs near the subalpine/montane interface (*c.* 1300-1450 m above sea level). The discontinuity is apparently not related to boundaries of canopy composition but possibly to dominant understorey species - in particular the dense, low shrub *Oxylobium alpestre* which provides an insulated microclimate for many alpine herb species. This, and other suspected associations imply that a degree of natural community formation overlies the continuum. Whilst absolute compositional differences exist between the vegetation of north and south facing slopes, a very similar pattern of compositional change was observed at both these climatic extremes.

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Glossary

Technical terms used in this thesis are explained as follows, as are many common English terms which have specific meanings in vegetation science.

- **Abundance:** An arbitrary quantitative measure of the amount of a species present in an area - e.g. dry mass, percentage cover, density.
- **Allelopathy:** Chemical inhibition of one plant by another (through *edaphic* mechanisms).
- **Alpine:** Those areas lying above the natural tree-line (*c.f.* McDougall 1982, p.12).
- **Aspect:** The direction (relative to true north) in which a *slope* faces.
- **Biota:** Biological organisms.
- **Community:** *1:* A perceived or established *vegetation* type of a given *composition. 2:* A group of species which have naturally coincident distributions.
- **Composition:** The *composition* of the vegetation in an area refers to the plant species occurring in that area. Numerically, a vector of species *abundances* for a given location.
- **Continuum:** A distribution of species (with respect to an *environmental* gradient) where each species is distributed independently of other species. The 'opposite' of a community.
- **Ecotone:** A narrow region of rapid *compositional* change.
- **Edaphic:** Pertaining to soil.
- **Environment:** The climatic, geological, historical, biological, and edaphic framework within which a plant is located.
- **Epiphyte:** A plant which is rooted upon another plant (e.g. mistletoe).
- **Katabatic wind:** A wind system associated with drainage of cool air down mountain slopes and valleys.
- **Lignotuber:** A woody swelling (usually underground) at the base of the stem/s of certain plants.
- **Montane:** All mountainous areas which are not *subalpine*, *alpine*, or *riparian.*
- **Riparian:** Areas where the vegetation is apparently influenced by close proximity to watercourses.
- **Sclerophyll:** A plant with hard, stiff, or leathery leaves (e.g. eucalypts).
- **Slope:** *1:* A hillside. *2:* The angle of inclination of a *slope*.
- **Structure:** Refers to the physical distribution of plants in space - *e.g.* whether they are shrubs or trees.
- **Subalpine:** Areas where *Eucalyptus pauciflora* (Snow Gum) typically dominates the canopy.
- **Transect:** An imaginary geographic line along which vegetation is systematically sampled.

Chapter 1. Introduction

1.1. Introduction

In broad terms, the aim of this work is to contribute to the understanding of plant distribution patterns in the Australian Alps and the factors that influence those patterns. The gradient analysis approach of Whittaker (1967) views vegetation within a framework of environmental gradients. In a given region, the researcher may chose to study vegetation with respect to as many environmental gradients as are present or, conversely, a single environmental gradient may be considered in detail and isolation. I have chosen to consider vegetation patterns along the altitudinal gradient - a complex gradient which reflects the influence of a number of environmental factors.

There is no direct connection between vegetation patterns and altitude for altitude is simply a measure of height above sea level. However, physical factors such as air temperature are very closely related to altitude and it is thus appropriate to say that altitude is an *indirect* environmental influence on vegetation. The altitudinal gradient encountered as one walks up a steep mountainside is a convenient compression of a number of climatic factors. On such a slope, temperature and rainfall variations that might otherwise be exhibited over large distances occur within only a few kilometres. This enables the researcher to study vegetation within large environmental amplitudes and within a contained and otherwise relatively homogeneous study area.

It is asked whether or not natural plant community formation occurs in the study area. If it were the case that mechanisms existed whereby certain groups of species required similar growing conditions, or that certain species were able to ameliorate growing conditions for other species, then those species might be expected to grow together as a natural community. The resulting coincidence of species distributions might be observable along the altitudinal gradient. This concept lies at the heart of the study of plant communities as explained in Section 1.3.

To provide additional scope, the work described here is repeated at two extremes of the radiation gradient. Two transects are sampled along the full height of long, steep, and constant slopes - one facing north (high radiation) and one facing south (low radiation). The vegetation present along these transects is the subject of this study. The transects are located so as to minimise any environmental influences not directly related to altitude.

1.2. Aims and hypotheses

The specific aims of this study are stated as hypotheses below. In each case, both the null (H_0) and alternative (H_1) hypotheses are presented.

Aim One. Examination of community patterns:

H_0: Compositional change of vegetation along the altitudinal gradient is continuous and no 'communities' are recognisable.

H_1: Species composition is arranged along the altitudinal gradient such that 'communities' are recognisable (due to correlated distributions of species), each being separated by short zones of rapid change (ecotones).

Aim Two. Explanation of community patterns:

H_0: There is no clear relationship between changing species composition and environmental factors.

H_1: Vegetation changes along the altitudinal gradient correlate with measurable changes in environmental conditions which are likely to be causal.

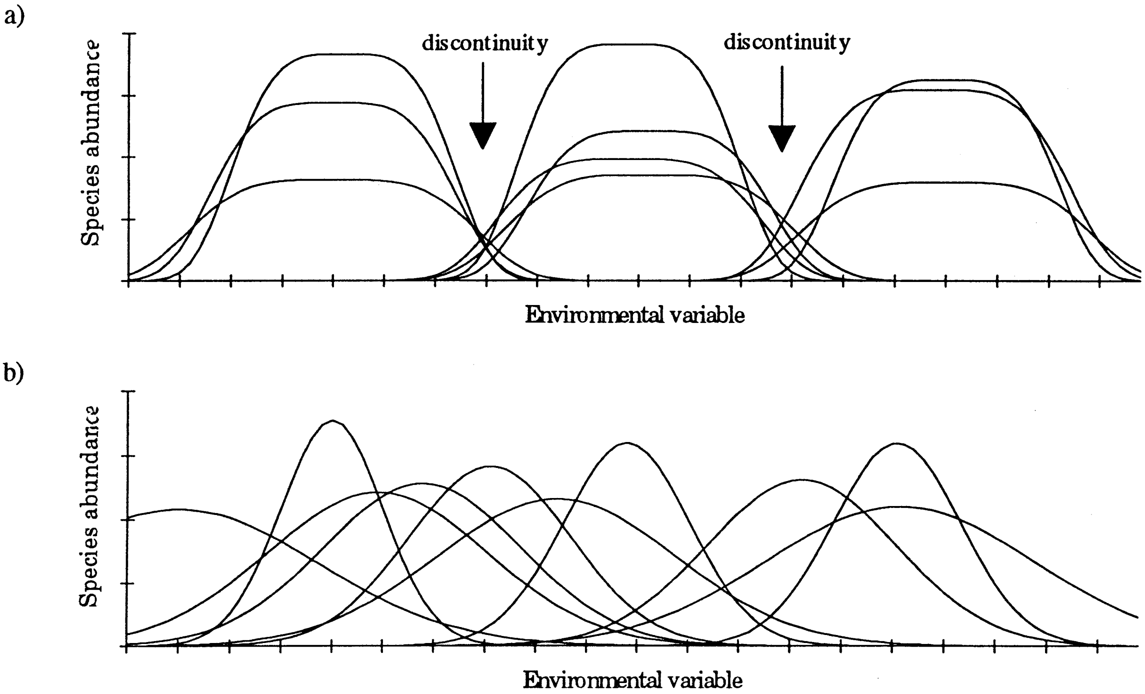
In this study the 'environment' of a plant refers to the climatic, geological, historical, biological, and edaphic situation within which it is located. The 'biological environment' of a plant refers to the presence of other biota - including other plants. The environmental components listed above are inter-related. Of particular note is that the edaphic environment of a plant may be influenced by both itself and other plants - thus, circular influences are acknowledged. Note that as this is an observational and not an experimental study, the establishment of causality is not possible in determining the influence of these factors *vis-à-vis* the second hypothesis (Shipley & Keddy 1987) - hence the reference to 'likely' causality.

1.3. Communities and continua

Earlier this century, in what has been termed the 'community *versus* continuum debate', an extensive literature attempted to clarify the nature of plant communities. Two authors are commonly accredited with originating two opposing hypotheses that explain the dynamic behaviour of vegetation. Clements (1916, 1920, Clements *et al* 1929) asserted that a community is a super-organism which has evolved and adapted over time (like other organisms) and that a community is a natural unit (i.e. it has boundaries beyond which we can recognise other communities). Gleason (1926, 1939) claimed that a community is 'merely a coincidence' of species, each acting as an individual with its own particular requirements for survival and growth; and that recognition of communities is artificial *i.e.* for our convenience only.

Discontinuities in floristic composition as shown in Figure 1.1a are generally considered to be evidence for the organismic-community hypothesis (Pielou 1975, p. 105). No such discontinuities occur in Figure 1.1b which displays a *continuum* (Curtis & McIntosh 1951) or individualistic pattern.

Figure 1.1. Expected patterns of species abundance along an arbitrary environmental gradient given (a) the organismic-community hypothesis; and (b) the individualistic-hypothesis (after Austin 1985). In (a), species abundances are aligned into communities with discontinuities between them. In (b), each species responds independently to the environmental gradient - thus forming a continuum of vegetation change.



The modern position takes a middle ground in the debate. Most authors now acknowledge the existence of both discontinuities and continua in vegetation (Mueller-Dombois & Ellenberg 1974, p. 29) although discontinuities are seen as the exception rather than the rule (Ricklefs 1990, pp. 659 & 675). Such discontinuities may be taken in the appropriate environmental context as evidence that natural formation of plant communities can occur to some extent (Brewer, 1988, p. 374). It is left to contemporary workers to place each instance of vegetation at an appropriate point within the individualistic/organismic framework.

The study of communities and continua in the vegetation of the Australian Alps is incomplete. Inventory and descriptive publications describing plant communities have emerged from government authorities (e.g. McDougall 1982; Walsh *et al* 1984; Schulz *et al* 1987; Cherry *et* *al* 1987; Gullan *et al* 1981) but, no theoretical consideration is made in these works as to the nature of the communities. A handful of publications has examined vegetation along altitudinal gradients in Australia. Often, only trees are considered (Austin & Cunningham 1981; Austin *et al* 1983; Williams 1990; Turner 1976) and where understorey vegetation is included, compositional discontinuities may be explained in terms of non-biological factors such as geological boundaries and fire regime (Ogden & Powell 1979), and climatic discontinuities and migrations during the Holocene (Kirkpatrick & Brown 1987). Continua are often suggested or implied but rarely verified explicitly in the absence of non-biological influences (e.g. Ashton 1976; Kirkpatrick 1984). The neglect of detailed theoretical work in the Australian Alps is of note given the unique situation within the Australian Alps whereby sharp discontinuities in canopy composition are observed in the absence of distinct environmental change (e.g. between *E. pauciflora* (Snow Gum) and montane species such as *E. dives* (Broad-leaved Peppermint) and *E. delegatensis* (Alpine Ash); Williams 1989, Abstract; McDougall 1982, p.15). An aim of the present work is to determine whether such discontinuities are also reflected in the understorey composition. It is quite possible that differences in canopy composition may affect the understorey through mechanisms such as shading, wind protection, or soil nutrient exchange and allelopathy (chemical inhibition of the growth of one plant by another).

1.4. Methods

The methods used to achieve the two main aims (Section 1.2.) of this thesis employ an 'accepted paradigm' for the analysis of community data which first 'allows the biota to tell their own story before deducing links to specific environmental variables' (Clarke & Ainsworth 1993). The 'story' of the biota is told here through the surveying of vegetation composition at many sites along the altitudinal gradient and the subsequent analysis of this data using multivariate pattern recognition techniques. Three techniques are used in combination to effectively reveal the key features of vegetation distribution with respect to altitude. 'Links to specific environmental variables' are deduced by measuring, simulating, and estimating candidate variables and then manually and numerically correlating them with the vegetation data using a multivariate correlation technique specifically designed for this type of work.

1.5. Summary

This study seeks to provide a contribution to Australian mountain ecology by investigating plant distribution patterns with respect to altitude. The methods used centre on numerical analysis of vegetation and environmental data obtained along two transects which are located to sample the altitudinal gradient evenly. The aim of the work is to describe the patterns of plant distribution with respect to altitude in typical vegetation of the Australian Alps and to explain the influences that determine these patterns. It is asked whether only climatic and geological factors account for vegetation change or whether historical, biological, and edaphic factors are also significant. In particular, attention is paid to the possibility that some degree of organisation into natural communities through biological mechanisms may be present. This consideration is significant in plant community theory - especially given the sparsity of Australian work on the matter.

1.6. Thesis organisation

The body of the thesis commences in Chapter Two which provides background information on the chosen study area. The methodology and details of data collection and analysis are explained in Chapter Three and results are presented in Chapters Four and Five. In response to Aim One (Section 1.2.), Chapter Four moves from a general prosaic description of the vegetation of the study area through to detailed numerical examination of the altitudinal sequence of compositional change. The results of environmental analyses and their correlation with vegetation results appears in the fifth chapter. A discussion of vegetation/environment correlations appears in the final chapter which includes an explicit response to the principal aims of the work before the conclusion of the thesis.

Chapter 2. The study area

2.1. Introduction

This chapter introduces the field study area and provides relevant background information on its character, environment, history, and suitability for study. Information obtained through personal inquiry and research is supplemented by that taken from environmental and ecological surveys undertaken by government authorities.

2.2. Selection criteria

In selecting the site for this research, it was necessary that a number of criteria be fulfilled:

1. The site should exhibit an altitudinal range in the order of one kilometre. Through this range, it is likely that at least one major change in canopy species would be clearly observable.
2. The site should lie on a uniform and representative geological substrate.
3. The site should be undisturbed by logging and civil operations and be relatively undisturbed by recreational and agricultural operations.
4. The site should be representative of Australian mountain vegetation. A schematic map of Victorian forests (Forests Commission Victoria 1984) assisted in this judgement.
5. The site should enable a transect to be extended up a steep slope in the study area with minimal variation in topography apart from that occurring over the length of the transect itself.
6. The site should have a known recent fire history.
7. The site should be not so steep as to include rocky outcrops which might result in sharp and unusual discontinuities on the environmental gradient.

2.3. Location and access

The area chosen is in the headwaters of the Wongungarra River approximately 10 km southwest of Mount Hotham (Figures 2.1 and 2.2) in the Alpine National Park. For the sake of clarity, 'the study area' herein refers to the catchment of the east branch of the Wongungarra River above its confluence with Mount Selwyn Creek. Access is possible via the Alpine Road and the Dargo Road. From these, two four wheel drive tracks extend west along the ridges either side of the valley. The northern track, Twins Road, is navigable by light four wheel drive vehicles. The southern track is only accessible by conventional four wheel drive vehicles which were not available to the author - necessitating a half-day walk for access to the area. There are no established tracks within the valley itself.

2.4. General description

Plates 2.1 and 2.2 show typical views of the study area which is partly within the Alpine National Park (Bogong Unit) (Survey & Mapping, Victoria 1991) and partly Public Land (Land Conservation Council 1982b, Map A). The terrain, whilst devoid of large rocky outcrops, is rugged and steep. A vertical difference of 1143 metres separates the top of the Blue Rag Range (south of the valley) from the Wongungarra River at its confluence with Mount Selwyn Creek. The area is completely forested with the exception of a few high-points.

Figure 2.1. Location of the study area in Victoria, Australia.

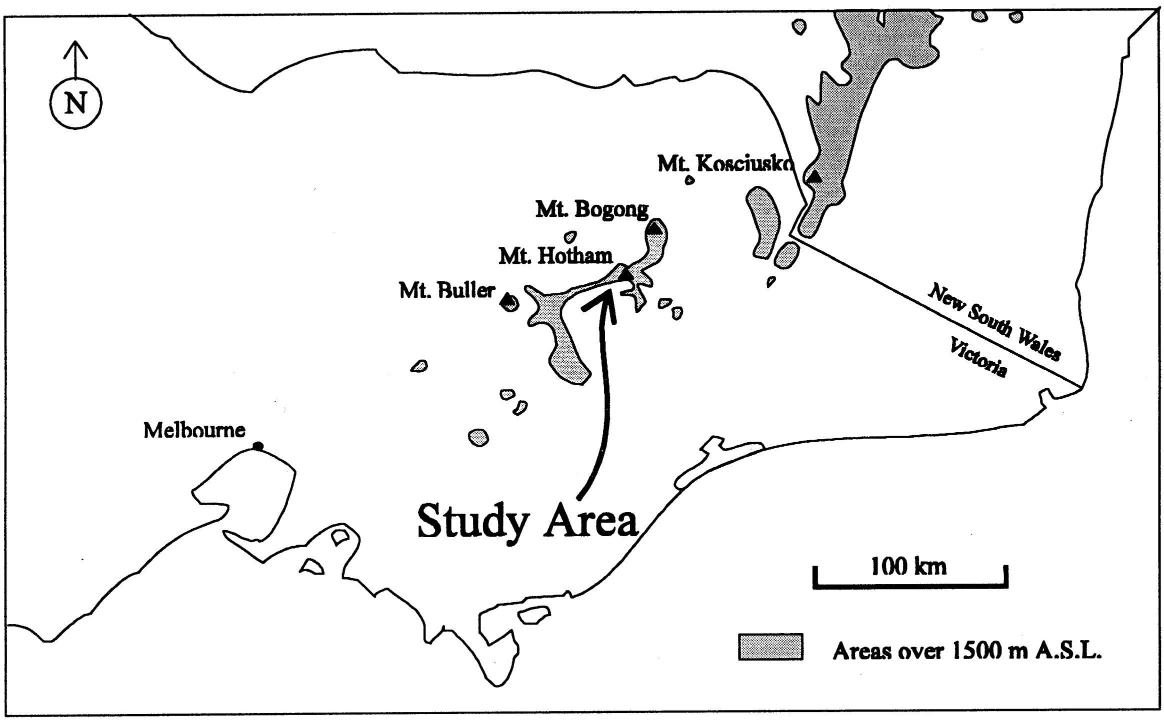


Plate 2.1. View of the Wongungarra valley looking south towards the Blue Rag Range (including Transect A) from The Twins.

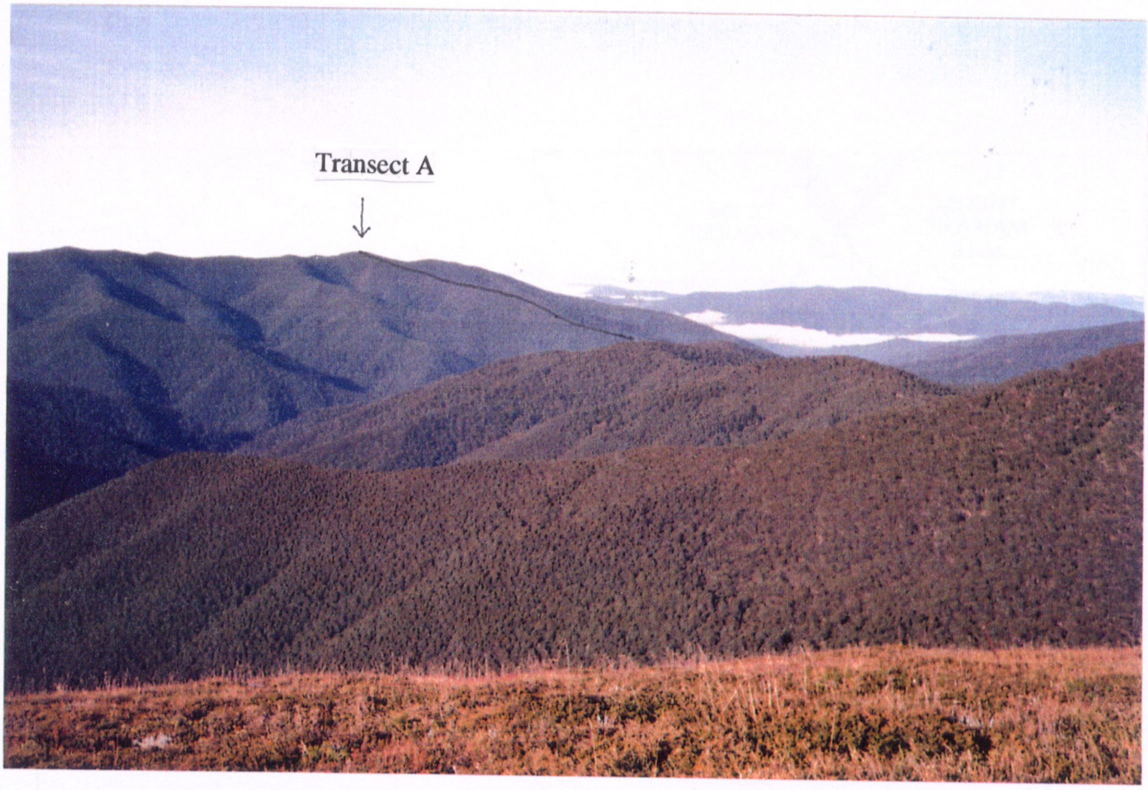


Plate 2.2. View of the Wongungarra valley looking north towards the Barry Ranges (including Transect B) from the Blue Rag Range.

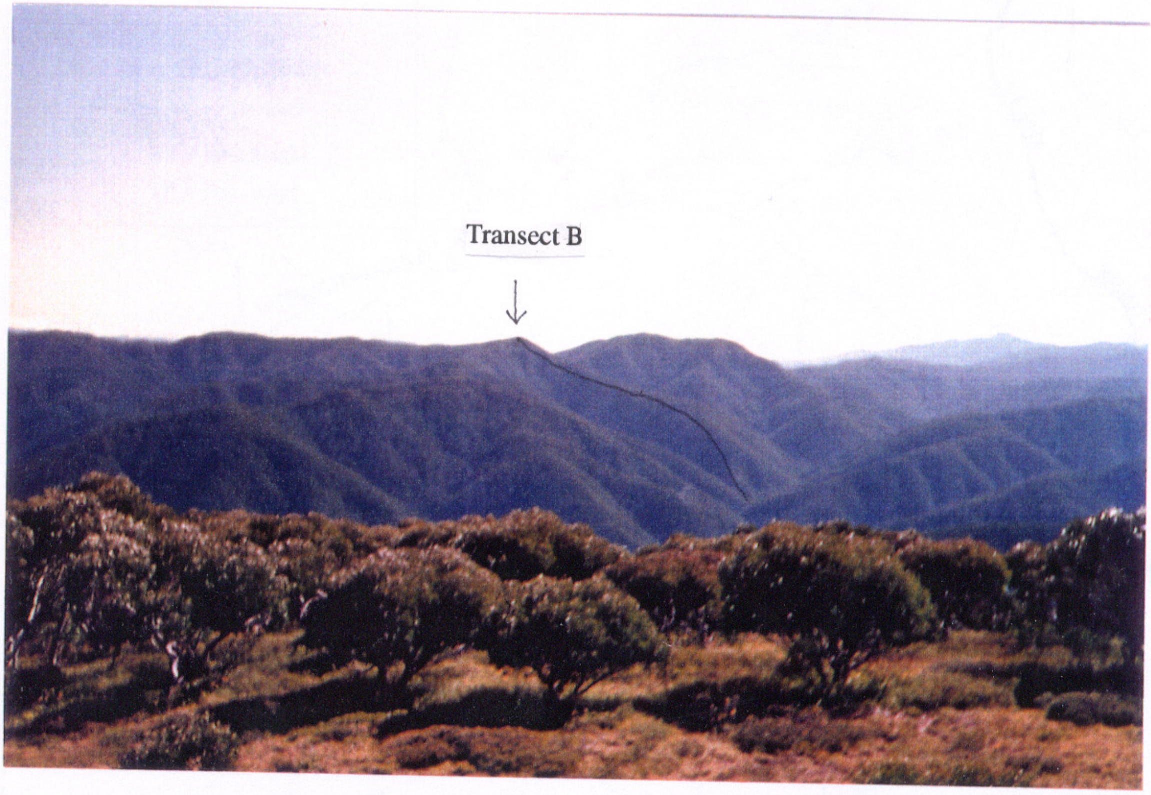
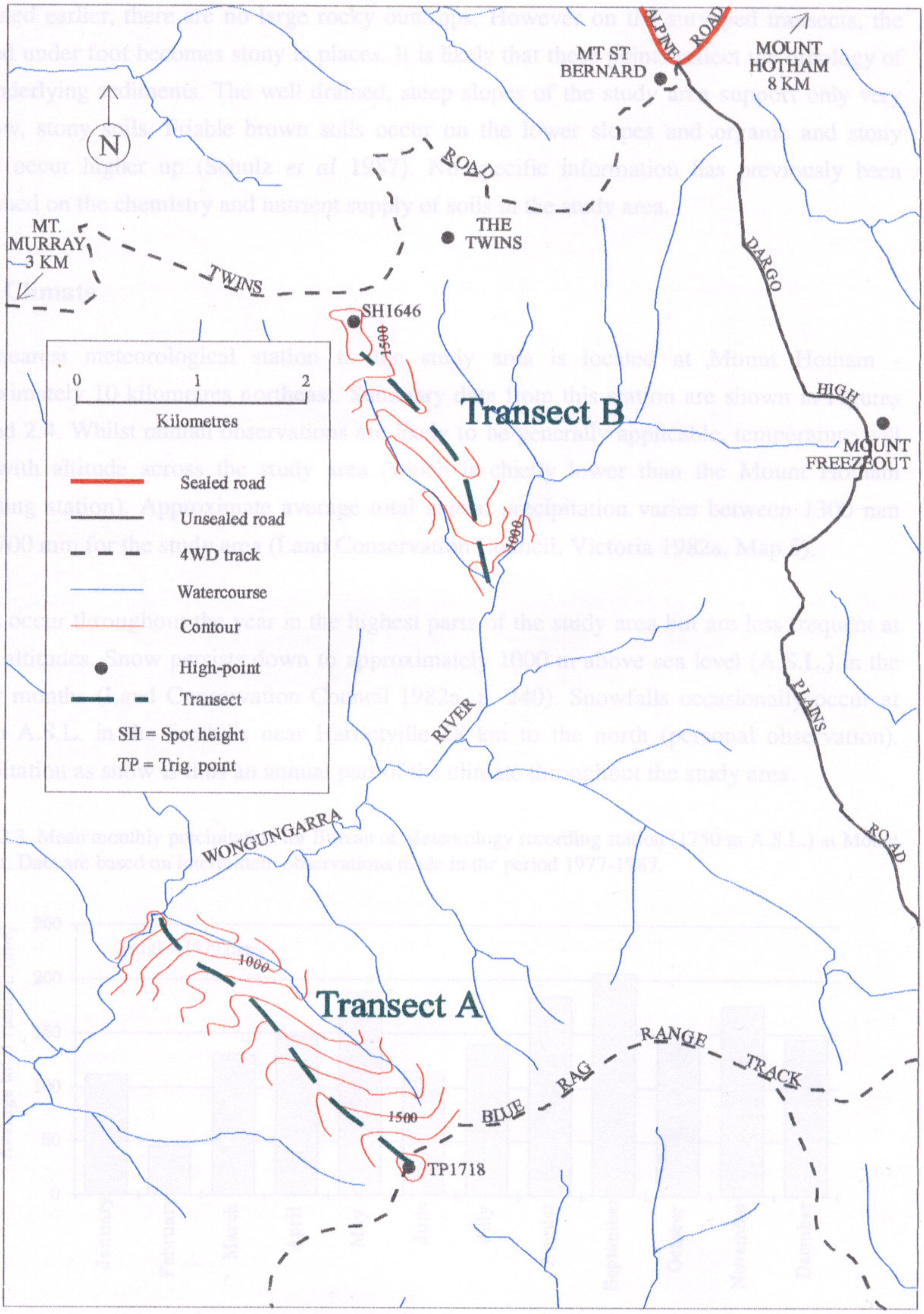


Figure 2.2. Map of the headwaters of the Wongungarra River showing the location of the two study transects.



2.5. Geology and soils

The study area is underlain by Ordovician sediments. These include siltstones, sandstones, carbonaceous shales, and marine cherts (Land Conservation Council, Victoria 1982a, Map 4). As noted earlier, there are no large rocky outcrops. However on the surveyed transects, the ground under foot becomes stony in places. It is likely that these points reflect the lithology of the underlying sediments. The well drained, steep slopes of the study area support only very shallow, stony soils. Friable brown soils occur on the lower slopes and organic and stony loams occur higher up (Schulz *et al* 1987). No specific information has previously been published on the chemistry and nutrient supply of soils in the study area.

2.6. Climate

The nearest meteorological station to the study area is located at Mount Hotham - approximately 10 kilometres northeast. Summary data from this station are shown in Figures 2.3 and 2.4. Whilst rainfall observations are likely to be generally applicable, temperature will vary with altitude across the study area (which is chiefly lower than the Mount Hotham recording station). Approximate average total annual precipitation varies between 1300 mm and 1700 mm for the study area (Land Conservation Council, Victoria 1982a, Map 5).

Frosts occur throughout the year in the highest parts of the study area but are less frequent at lower altitudes. Snow persists down to approximately 1000 m above sea level (A.S.L.) in the winter months (Land Conservation Council 1982a, p. 240). Snowfalls occasionally occur at 600 m A.S.L. in the foothills near Harrietville 18 km to the north (personal observation). Precipitation as snow is thus an annual part of the climate throughout the study area.

Figure 2.3. Mean monthly precipitation for Bureau of Meteorology recording station (1750 m A.S.L.) at Mount Hotham. Data are based on intermittent observations made in the period 1977-1987.

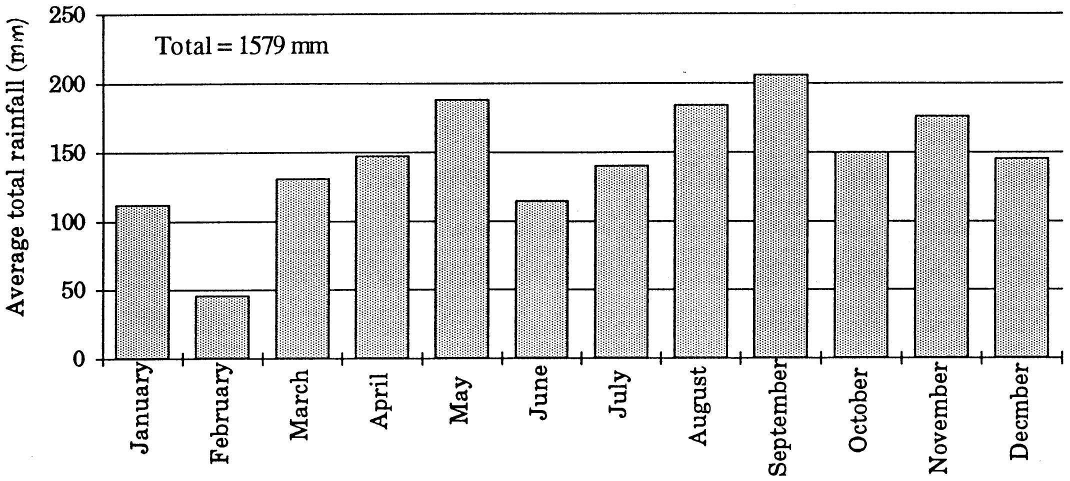
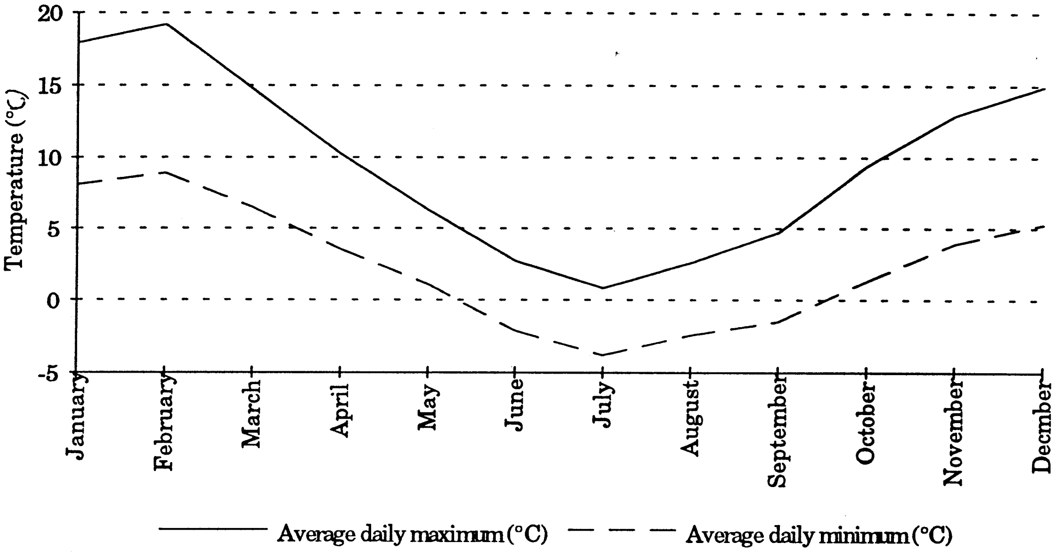


Figure 2.4. Average temperatures for Bureau of Meteorology recording station (1750 m A.S.L.) at Mount Hotham. Data are based on intermittent observations made in the period 1977-1987.



2.7. Vegetation[1]

The vegetation of the Wongungarra valley has been surveyed in part by Schulz *et al* (1987) and Cherry *et al* (1987). These publications employ the terminology of Gullan *et al* (1981) and Forbes *et al* (1981) whereby 'communities' are defined with respect to 'character' species. The communities of the study area described by these authors are titled Alpine Heathland, Snow Gum Woodland, Montane Forest, Montane Riparian Forest, and Riparian Forest.

2.8. Fire history

Fire history in the general area of the Wongungarra valley is not well documented (McDougall 1982, p. 20). The great bushfires of 1939 were widespread across most of the Victorian Alps (Paine 1982) however inspection of early aerial photographs suggests that burning was patchy in the vicinity of the study area. Photographs taken in 1954 (Survey and Mapping, Victoria 1954a, b), 15 years after the 1939 fires, show heavy scars (presumably due to fire) near Mount Freezeout to the east of the study area, less severe fire evidence near the Twins to the north and no fire evidence to the south. Earlier photographs would be required to assess the situation further as forests may show substantial regeneration after fire as viewed from the air after 15 years. Aerial photography of the area is listed by VicImage (Survey and Mapping

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[1] Taxonomic nomenclature in this thesis follows Ross (1993).

Victoria) catalogues as being undertaken in 1944 by the military, however this photography was reportedly destroyed in a fire on R.A.A.F. premises in 1963 (pers. comm. Flt. Sgt. B. Andrews[2]). In conclusion, it is possible that the 1939 fires affected Transect B but, not Transect A. The extent of previous fires is not known.

2.9. Human influence

Aborigines are known to have ventured into Victoria's higher mountains for food (Land Conservation Council, Victoria 1982a, p. 12) and it is possible that the Wongungarra valley was included in these excursions. The first European visitations were probably associated with grazing on the nearby Bogong High Plains which began as early as 1851 (Land Conservation Council, Victoria 1982a, p. 14) and continue to the present. The Victorian mining boom of the late 1800's saw the cutting of a single exploration track through the study area which probably provided only foot access along the Wongungarra River (Ferguson c. 1900). Very little evidence remains of this track and some associated diggings. It is likely that only minor exploratory operations were conducted in the area. The study area has never been logged (Pittock 1991) although logging was due to commence nearby on the western slopes of Mt. Murray in 1993 (Mr. R. Rossington[3], pers. comm.). The area is not a traditional attraction for bushwalkers although the publication of an article emphasising the Wongungarra's pristine environment (Pittock 1991) has apparently encouraged visits by nature enthusiasts. In the two years I have been visiting the area, I have noticed incipient walking tracks forming on some of the major spurs.

In comparison with other parts of the Victorian Alps, the Wongungarra valley has been subject to minimal human disturbance. Grazing is likely to have been the only major human influence on the vegetation since European discovery of the area although the intensity of current grazing activities is not clear. Grazing Licences apply to portions of the Blue Rag Range (excepting reference areas) and the eastern Barry Ranges (Doug Hooley[4] pers. comm.) but cattle have only been seen by this author in the eastern Barry Ranges. No cattle or cattle faeces were found on either of the two transects surveyed in this work. However this fact does not exclude the possibility of significant past impact. The mountain environment is highly sensitive to grazing pressure (Carr & Turner 1959; Land Conservation Council, Victoria 1982a, p. 14; McDougall 1982, Summary; Dickinson & Kirkpatrick 1986; Ashton & Williams 1989). Fragile elements of alpine vegetation such as rosette herbs occur within both subalpine and alpine areas in the Wongungarra valley and it is likely that the abundance of these is

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[2] Master Index, CPE, RAAF Williams, Laverton, Melbourne

[3] Office Manager, Department of Conservation and Natural Resources, Bright Regional Office.

[4] Statewide Planning Officer, National Parks, Department of Conservation and Natural Resources.

heavily influenced by the presence of cattle. Grazing by domestic livestock has been found to result in significant changes to all elements of vegetation including even *Eucalyptus pauciflora* (Snow Gum) (Barker 1988, Carr & Turner 1959).

Chapter 3. Data collection and analysis[5]

3.1. Introduction

This chapter details the methodology employed in the collection and analysis of vegetation and environmental data. Satisfaction of Aim One (Section 1.2.) requires firstly that numerical vegetation data must be obtained for the study area; and secondly that the data are analysed using techniques designed to reveal patterns within multivariate data. After a discussion of the sampling strategy employed in data collection, the three main types of multivariate analysis used to examine distribution and composition patterns within the data are described. As prescribed by Aim Two (Section 1.2.), the 'explanation phase' of the study attempts to explain observed vegetation patterns in terms of environmental factors. Thus, relevant environmental variables are measured, estimated, and simulated and the means by which this is done is described in the latter sections of this chapter. In the final section, a numerical method for linking environmental and vegetation data is described. This method is augmented with original ideas.

3.2. Vegetation data collection and analysis

3.2.1. Sampling pattern

Discrete sample sites are spaced along steep transects with roughly constant slope and aspect. This minimises environmental influences other than those related to altitude but does not exclude historical influences (Pielou 1977, Ch. 14.2) such as fires which may have affected only certain parts of a given transect. Historical influence could be reduced by averaging data from a number of separate but environmentally similar transects. All 1:100 000 maps of the Victorian Alps were examined in search of suitable sites but no two candidate sites were found to be sufficiently similar. Almost every high mountain spur varies considerably in slope and aspect. An alternative strategy that reduces historical influence is to take a random sample from amongst any set of points with similar environmental parameters excepting those associated with altitude. Such a set of points would be difficult to determine for the Wongungarra valley and also difficult to reach in the field. In southern New South Wales, Austin *et al* (1983) obtained a pseudo-random sampling pattern from existing quadrat data compiled by various sources. A similar data set is maintained in Victoria by the Flora Section of the Department of Conservation and Natural Resources from which data from the 71

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[5] Fieldwork was conducted throughout 1992 and 1993. Removal of minimal plant and soil material in early 1993 was authorised by Amended Research Permit 923/093 issued under the provisions of the National Parks Act by the Department of Conservation and Natural Resources.

surveyed points falling within a 400 km^2 region overlapping the study area were obtained. For the purposes of the present work, these data did not provide an adequate distribution of sites with respect to environmental parameters. A better data set may be obtained by considering an area larger than 400 km^2 but it is considered that such data would be adversely subject to floristic and environmental heterogeneity across the area. Thus, whilst theoretically inferior, the method of single transects emerges from those suggested as the most appropriate approach to detailed consideration of vegetation along the altitudinal gradient.

3.2.2. Transect location

In order to provide additional scope, two transects are surveyed. One faces predominantly north (Transect A); the other, south (Transect B). Their locations are shown in Figure 2.2. The sites are carefully chosen to exhibit very little topographic variation other than that which varies over the full extent of the site. A transect extending along the site should have constant slope and aspect and should be kept away from zones of rapid environmental change such as watercourses and spur-tops. Thus, each transect runs along a spur-flank just below the spur-top which is used as a reference line to facilitate accurate location. A Global Positioning System (G.P.S.) receiver (satellite navigation) was trialed to aid site location but was found to be unsuitable due to limited battery life and interference from trees and surrounding topography.

3.2.3. Sample site location within transects

The sample sites are evenly distributed along the transects with respect to altitude, and a single quadrat is surveyed at each site. Evenness ensures approximately equal representation of sites along the gradient which helps prevent bias in analysis techniques such as ordination (see Section 4.3.4.). This statement is partly dependent upon the assumption that the biological significance of any factor related to altitude (such as temperature) is linear with respect to altitude as measured in metres above sea level - a fact which is by no means assured. Taking the case of temperature for example, it may be that the physical response of any given plant (as expressed by abundance) to variations in temperature may not only be non-linear but discontinuous and subtly dependent upon other environmental variables. However, if only for the sake of analytical simplicity, I suggest that it is intuitively wise to maintain a roughly even distribution of sample sites along the altitudinal gradient.

Regular spacing of sample sites implicitly leads to an even distribution along the altitudinal gradient. An altitudinal spacing of ten metres was selected as a compromise between detail and available time in the field. In order to minimise the effect of variations in barometric pressure, two altimeters are used to implement the desired spacing. Readings taken from an altimeter over the course of a day were found to be subject to seemingly random fluctuations which are difficult to correct. A correction system was developed by defining a set of landmark objects such as large ant-hills and unusual trees. Average landmark altitudes were calculated from independent measurements using separate, corrected calibrations of the altimeter. The resultant altitude of sample sites is then derived from a further system of interpolation between landmarks with temporal corrections.

3.2.4. Quadrat design and survey

At each sample site, a 10 m x 10 m quadrat is defined within which the abundance of all non-epiphytic vascular plant species is recorded. The abundance of understorey species is recorded using a visually assessed cover index (Table 3.1). The ideal quadrat size for a given area of vegetation should be large enough to contain a representative portion of the vegetation but not so large as to allow intra-quadrat variation associated with environmental gradients. An appropriate size can be determined by construction of a species-area curve. However, because the vegetation along the transects varies significantly, the size determined by this method would be ideal only at the place of determination. In this study a commonly used and convenient size of 100 m^2 was chosen and subjectively evaluated over 11 trial quadrats. There was no indication that this size would be inadequate.

Table 3.1. The Braun-Blanquet foliage cover index of plant abundance (Mueller-Dombois & Ellenberg 1974, p. 59). Note that a cover index of '+' is converted to 0.5 in all numerical analyses.

+	cover < 5%, few individuals
1	cover < 5%, any no. of individuals
2	cover 5-25%, any no. of individuals
3	cover 25-50%, any no. of individuals
4	cover 50-75%, any no. of individuals
5	cover 75-100% any no. of individuals

A tree is defined here as an individual of a species which comprises part of the vegetation canopy at some point in the study area and whose trunk diameter at breast height is at least 5 cm. Accordingly, some commonly recognised 'trees' such as *Acacia kettlewelliae* (Buffalo Wattle) are considered part of the understorey. The motivation for this formal distinction is the obvious structural distinction between the tall canopy and any other vegetation. Where multiple stems are exhibited by *Eucalyptus pauciflora* (Snow Gum), an individual tree is judged as those stems which appear to originate from a single lignotuber.

Abundance of trees is measured using the Point Centred Quarter (P.C.Q.) method (Mueller-Dombois & Ellenberg 1974, p. 109). At each sample point, four compass quarters were defined. Diameter at breast height (D.B.H.) and distance from the sample point was recorded for the nearest tree in each quarter. The mean basal area (m^2) for individuals of each species was estimated from D.B.H. values. Absolute density (ha^{-1}) of trees was estimated using the inverse of the mean nearest-tree distance. Relative density (ha^{-1}) for each species was then derived as the product of absolute density and each species' relative frequency in the sample. The final abundance value, termed 'dominance', was calculated as the product of relative density and mean basal area.

A large degree of undesirable local variation is evident in the P.C.Q. data, even after using a running average of results. This is due to the statistical basis of the P.C.Q. method which requires a large number of P.C.Q. measurements for any given result. An alternative sampling strategy which counted and measured the trunk diameters of all trees in a given area was trialed in the latter stages of field work. This method resulted in reduced local variation in the data. However, it could not be included in the analysis because the data obtained using the method were incomplete.

Understorey and canopy data were not combined for analysis because the relationships between the two may be unique within the vegetation as a whole and therefore should not be concealed by merging. Connections between the canopy and the understorey are able to be determined by direct examination of the respective analyses for each.

3.2.5. Plant identification

Significant taxonomic revision has occurred since the publication of Willis's (1970, 1972) complete treatment of the Victorian flora. Thus, in the current absence of more recent guides, a number of references have been used for plant identification in this study. These are Willis *(op cit),* Cochrane *et al* (1973), Costermans (1983), Costin *et al* (1979), Norton (1979), Cronin (1989), Elliot and Jones (1982, 1984, 1986, 1990), McCann (1987), Duigan (1991), and Scarlett *et al* (1992). Species lists for the area compiled by other workers have also aided identification (McDougall 1982, Walsh *et al* 1984, Cherry *et al* 1987, Schulz et al (1987), Forbes *et al* 1981, Gullan *et al* 1981). Nomenclature follows that of Ross (1993).

Individuals of the grass genus *Poa* are particularly difficult to identify at the species level (Vickery 1970). Identification by published keys (Willis *op cit*, Vickery 1970, Norton 1979) is largely based on reproductive material which is usually not present in each quadrat. In the field however, one observes certain distinguishing characteristics of general appearance and these have served here as a crude basis for classification in an attempt to prevent information loss resulting from identifying individuals only to genus level. I have chosen to aggregate sample observations into six 'species'. *Poa sp. 1* is distinguished by flat blades and may be *P. ensiformis*, *P. labillardieri*, or *P. hothamensis*. *Poa sp. 2* is distinguished by rolled blades. Some samples of this 'species' have in fact been later identified as *Chionochloa pallida* and not *Poa*. *Poa sp. 3* only occurs at the top of Transect A and has inrolled blades with a bluish appearance. *Poa sp. 4* only occurs at the top of Transect B and has very thin, green inrolled blades. It may in fact be *Agrostis sp.* Individuals of *Poa sp. 5* occur near the river and are thinner and more wiry than those of other species. Only one individual of *Poa sp. 6* was observed. It has a distinctive bushy head and is probably *P. sieberana var. hirtella.*

3.2.6. Analysis

3.2.6.1. Standardisation

In the multivariate analyses to follow, it is not always sufficient to analyse the data in the form in which is was originally obtained - analysis of standardised data is also necessary. Abundant species are found to have more influence on analytical results than less abundant species (Clarke 1993) but it is not immediately clear whether this is a desirable phenomenon. It is an open question as to whether or not a plant species may be considered more important if it is more abundant. Hence, each analysis (described below) is performed on both raw and standardised data. Bray-Curtis standardisation is used whereby all species are first standardised to have unit maxima and then all sites are standardised to have unit totals (Bray & Curtis 1957, p. 328).

3.2.6.2. Distance measures

Raw vegetation composition data is usually represented as a 'species-in-site' matrix (see Table 4.1). Such a matrix can be thought of as specifying a set of 'site-vectors' in 'species-space' - the axes of species-space being defined by species abundances. The multivariate analysis, or pattern recognition, techniques used in this study employ this model of 'vectors in a hyper-dimensional space' in their methodology. The simplest instance of this is in the concept of a 'distance measure' which numerically represents the compositional dissimilarity between two sites. Cosine distance, and Bray-Curtis distance (Equations 3.1 and 3.2) are the two distance measures which have been used in this study. Bray-Curtis distance (Bray & Curtis, 1957) is widely used in ecology and has performed well in comparison with other distance measures (Faith *et al* 1987; Clarke 1993). It is used here in shade diagrams and ordinations but was not available for classification (see Section 3.2.6.5.) where cosine distance was used. This compromise is justified by the fact that shade diagrams constructed using cosine distance and Bray-Curtis distance showed that the two distance measures behaved very similarly.

Equation 3.1. Cosine distance between sites *X* and *Y* with species abundances a_{iX} and a_{iY} where $i=1, 2, \ldots, S$ and *S* species are present in the species-in-site matrix. The equation gives the cosine of the angle between two vectors in Euclidean space. A value of 1 represents identical vectors; zero represents orthogonal vectors.

$$CD_{XY} = \frac{\sum_{i=1}^{S}(a_{iX} \times a_{iY})}{\sqrt{\sum_{i=1}^{S} a_{iX}^{2}} \times \sqrt{\sum_{i=1}^{S} a_{iY}^{2}}}$$

Equation 3.2. Bray-Curtis distance between sites *X* and *Y* with species abundances a_{iX} and a_{iY} where $i=1, 2, \ldots, S$ and *S* species are present in the species-in-site matrix. The equation is arbitrarily defined for the purposes of ecology and has no direct geometrical analogue.

$$BC_{XY} = \frac{1}{S} \frac{\sum_{i=1}^{S}|a_{iX} - a_{iY}|}{\sum_{i=1}^{S}(a_{iX} + a_{iY})}$$

3.2.6.3. Shade diagrams

Shade diagrams are direct, graphical representations of the compositional relationship between all the sites in a species-in-site matrix (Digby & Kempton 1987, p. 140). They are useful in facilitating an understanding of the behaviour of different distance measures and standardisation procedures as well as in representing data in an easily interpretable manner. A shade diagram appears as a matrix of shaded squares whose columns and rows represent sites. Each square in the matrix is shaded according to the 'distance' between the corresponding site vectors. Shade diagrams were constructed for both unstandardised and standardised data using cosine, and Bray-Curtis distance measures. Bray-Curtis distance yielded the most interpretable diagrams so the others were considered no further.

3.2.6.4. Ordination

The dimensionality of species-space is large (equal to the number of species present in the data set). It is useful to be able to think of relationships between sites in a data set in terms of the spatial relationships between their locations in species-space. However, the large dimensionality prohibits such mental niceties. Ordination techniques attempt to derive a low-dimensional image of site-vectors in species-space that preserves as much spatial structure as possible. In this way, the major patterns of the compositional relationship amongst sites can more easily be observed.

Multidimensional scaling (M.D.S.) was selected as the most appropriate ordination technique for the present work (Minchin 1987). M.D.S. selects a dimensionality for the 'image' data set and attempts to arrange a set of points (sample sites) with that dimensionality such that the distances between points in image-space correlate with the respective distances in species-space. A 'stress' measure is defined as an indicator of the suitability of any given solution. A number of forms of M.D.S. have been developed. The combined use of global nonmetric M.D.S. (G.N.M.D.S.) and hybrid M.D.S. (H.M.D.S.) operating with Bray-Curtis distance is recommended (Minchin 1991, Faith *et al* 1987). Data from each transect were ordinated separately using H.M.D.S. as well as in combined form using G.N.M.D.S. Ordination procedure[6] followed that suggested by Minchin (1991). One and two dimensional solutions are presented.

3.2.6.5. Classification

Classification, when applied to species-in-site data, finds classes of similar sites (*i.e.* separated by low 'distance') within the data. The virtue of classification is that it produces discrete, and hence easily interpretable, results. The vice of classification is that it produces these results whether or not distinct classes of similar sites actually occur in the data. Prior, exploratory analysis using ordination can help to identify and validate doubtful classification boundaries.

Cluster analysis or agglomerative, hierarchical classification (Digby & Kempton 1987, p. 125) was performed on both unstandardised and standardised data using average and single linkage combined with Euclidean and cosine distance measures[7]. Average linkage considers the distance between two groups of sites as being the average between-group site-pair distance. Single linkage considers only the shortest between-group site-pair distance (nearest-neighbour). Cosine distance and average linkage were found to be most suitable (Bray-Curtis distance was not supported by the software).

3.3. Environmental data collection and analysis

In order to explain patterns of vegetation distribution in terms of environmental variables, all candidate variables must first be investigated. The essential requirement in quantification of environmental variables is not to determine their absolute value, but to determine the existence or otherwise of environmental *discontinuities*. Complex models of mountain microclimates have been developed which accurately estimate a number of biologically significant parameters

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[6] All ordinations in this work have been performed using the DECODA software package (V2.04, ANUTECH, A.N.U. Canberra).

[7] Analysis was performed using the SPSS software package (V5.01 for Windows, SPSS Inc., Chicago).

(Moore *et al* 1993) and it is possible that the present work would be enhanced by the consideration of these at a later date. Currently, basic indirect and direct indicators of climate have been considered.

3.3.1. Climate

A number of climatic (and edaphic) influences are related to slope and aspect which are recorded at each site.

Temperature is almost inverse linearly correlated with altitude. Temperature decreases by about 6° C for every kilometre ascended (Linacre 1992, p. 73; Slatyer 1978), leading to mean temperature range over the study area of approximately 7° C. It is likely that katabatic winds induce temperature inversions in the valley-bottoms, where colder than normal temperatures may be expected (Linacre 1992, p. 318; Colls & Whitaker 1990, p. 114), and that exposed ridge tops also experience altered temperature regimes as a result of higher winds (Linacre 1992, p. 80).

Rainfall variation along each transect would be difficult to quantify accurately. The Report on the Alpine Study Area (Land Conservation Council 1982a, Map 5) suggests higher rainfall at higher altitudes in line with common meteorological observations but the scale at which this relationship is valid is unclear. Rainfall variation across the study area may be minimal.

Radiation (e.g. light) incident on a slope is dependent upon many factors, one of which is view factor: the proportion of the sky unobstructed by surrounding topography. View factor is a significant, locally variable factor in the calculation of surface energy budgets in mountainous terrain (Moore *et al* 1993) and has been simulated across the study area by computer (Watson in prep., see Appendix 1).

3.3.2. Lithology

Whilst there is no major change in geological substrate within the study area, lithological variation is evidenced by stratigraphically aligned rocky patches which are likely to affect vegetation (Myers, 1979). Throughout the course of field work, indices of rock cover and estimated 'rockiness' were trialed in an attempt to provide some numerical reflection of changing lithology.

3.3.3. Soil

The nature of the soil-plant relationship in forest ecosystems is complex. Of key importance is that the relationship between soil and plant is bi-directional. Thus any vegetational changes that are found to correspond to edaphic changes cannot immediately be explained by the edaphic changes. However, this does not arrest the need to investigate soil changes along the transects. Nutrient cycling between plant and soil provides a hypothetical mechanism for interaction between plant species and subsequent formation of natural associations and communities - both of which may be reflected in distribution patterns. Basic soil analysis may provide some clues regarding this.

A total of 33 soil samples was collected along the transects at approximately 50 metre altitudinal intervals. At each sample site, a small amount of top-layer soil was combined from three randomly located points. This was often difficult due to the rockiness of the substrate. After collection, samples were stored in air tight bags for one week then weighed, air dried for one month, and weighed again. The dried samples were ground to pass a 2 mm sieve whilst twigs, roots, charcoal, and stones larger than 2 mm were removed and weighed. The sieved fraction (termed 'fine-earth') was used for chemical analysis. Fine-earth sub-samples were obtained using a 'splitting' device which enabled true sub-sampling without bias toward particular grain sizes or weights.

3.3.3.1. Moisture

Soil moisture is estimated from weight loss after air-drying by the (original) index described in Equation 3.3.

Equation 3.3. An original index of soil moisture - all values are weights.

$$moisture = \frac{water}{water + fine\ earth}$$

...where...

$$water = undried\ sample - dried\ sample$$

...and...

$$fine\ earth = dried\ sample - stones$$

3.3.3.2. pH

Soil pH is an easily quantified variable which is correlated with the solubility and other chemical properties of the soil (Leeper & Uren 1993, p. 192). Geographic variation in soil pH may thus indicate the presence of significant variation in more direct soil properties such as dissolved aluminium concentration which responds to low pH (Attiwill & Leeper 1987, p. 25). To determine the pH of each soil sample, 20g of fine earth was mixed with 100 ml H_2O, then shaken manually for one minute, and shaken using an orbiter for one hour. A digital pH meter was used to measure the pH of the resulting 1:5 soil slurry.

3.3.3.3. Exchangeable cations and cation exchange capacity

Certain soil nutrients occur as 'exchangeable cations' adsorbed onto colloids (e.g. clay particles) within the soil. The major exchangeable cations[8] Na^+, K^+, Mg^{2+}, and Ca^{2+} are of significant interest in the study of soil chemistry with all but Na^+ being important plant macro-nutrients (Attiwill & Leeper 1987, p. 15). The ability of the soil to provide 'exchange sites' for exchangeable cations is termed its 'cation exchange capacity' (C.E.C.) and is a measure of its potential total fertility - *i.e.* its long-term ability to supply nutrients to plants (Jones 1982, p. 12).

Both the concentration of major exchangeable cations and the C.E.C. of soils along the transects was determined using a barium chloride / ammonium chloride extractant method which is well suited to acid soils[9]. The procedure is summarised in appendix 1. Both exchange acidity and concentrations of the major exchangeable cations are determined first and then C.E.C. is estimated as the sum of these values.

3.3.3.4. Litter

Litter from canopy species may affect understorey vegetation through either the physical or chemical (*i.e.* allelopathic) inhibition of germination and seedling growth. It is also the major path way of nutrient return to the soil system and so contributes to the nutrient pool measured as major exchangeable cations and C.E.C. Litter cover was recorded for each vegetation survey quadrat using the index described in Table 3.1.

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[8] Leeper & Uren (1993, p. 202) recommend against the use of the more common terms 'exchangeable bases' and 'basic exchangeable cations'.

[9] The 'ammonium acetate method' (Hefferman 1985, p. 113) was initially used (with modification) but later discarded because of unsatisfactory results caused by the strong acidity of the soils.

3.4. Correlation of environmental and vegetation data

Clarke and Ainsworth (1993) outline a new method for describing links between community structure and environmental variables *i.e.* for finding informal correlations between environmental variables and distribution patterns. The method is superior to previous methods (such as Canonical Correlation, e.g. Mardia *et al* 1979) because it enforces few constraints on a) the respective representation of distances within both vegetation data and environmental data; and b) the nature of the link between the vegetation and the environment. However, it does not currently allow for statistical statements to be made regarding derived correlation coefficients.

In a similar fashion to nonmetric multidimensional scaling (N.M.D.S.), the method operates with distance matrices. The harmonic rank correlation (H.R.C.) coefficient, which uses only ranks of distances, is used as a measure of similarity between two distance matrices: one defined on the vegetation data and the other defined on some subset of the environmental data. Clarke and Ainsworth's method (1993) simply finds the subset of normalised, transformed environmental variables whose distance matrix is best 'correlated' with that of the vegetation data. I have employed a modification of the method whereby the environmental variables are able to contribute in varying amounts - not equally, as global normalisation dictates. Under this modification the 'best correlation' is obtained iteratively by repeatedly varying the standard deviation of the environmental variables in turn until the optimal solution is found. Thus, an indication of the extent to which each environmental variable is correlated with vegetation patterns is determined.

Chapter 4. Vegetation results

4.1. Introduction and general description

In response to Aim One (Section 1.2.), this chapter presents the results of vegetation survey and analysis along with preliminary interpretation of the findings. Basic observations which can be made directly from the raw data are discussed prior to the presentation of multivariate analyses (shade diagrams, ordination, and classification). Each successive analysis adds to the understanding of the compositional patterns present within the data. A general description of the vegetation of the study area appears first.

A large portion of the study area is montane forest which is distinguished by a number of tall eucalypts. *Eucalyptus delegatensis* (Alpine Ash) is widely distributed - often forming pure stands on south facing slopes (Plate 4.4). On the drier, north facing slopes (Plate 4.2) it is common to find mixed stands of *E. dives/radiata* (Broad/Narrow Leaved Peppermint), *E. rubida* (Candlebark), and *E. viminalis* (Manna Gum) with occasional individuals of *E. delegatensis*. The understorey of the montane forest exhibits considerable variation. In some places, dense thickets of *Daviesia latifolia* (Hop Bitter Pea) dominate whereas, in other areas, the understorey layer is almost absent. In the immediate vicinity of watercourses, the forest takes on a riparian character. Here, tall individuals of *Eucalyptus viminalis* tower above a mid-storey of *Acacia dealbata* (Silver Wattle). The riparian understorey is typical of Australian wet sclerophyll forests being dominated by a variety of ground and tree-fern species nearest the watercourse and supporting a rich ground layer of herbs beneath small trees of the genera *Cassinia* (Cassinia), *Leptospermum* (Tea-tree), *Pomaderris* (Pomaderris), and *Pittosporum* (Banyalla).

At its upper limits around 1200-1400 m, montane forest borders with Snow Gum woodland which is the sole form of subalpine forest in the study area. In the canopy the boundary between the two may be either sharp or gradual. The existence of an associated change in the understorey is not obvious and is indeed partly the subject of the current work. In general, the understorey of subalpine areas contains a stronger herb and grass element than lower areas although many places are dominated by dense, low shrubs - particularly *Oxylobium alpestre* (Alpine Oxylobium). North facing slopes (Plate 4.1) are more open than south facing slopes (Plate 4.3). On the upper Snow Gum woodland slopes, characteristically alpine species gradually appear - most visibly indicated by species of the family *Asteraceae* (Daisies). Occasionally, in areas of high exposure to wind, high altitude, and southerly aspect, complete alpine heathland vegetation is found above a local treeline.

Plate 4.1. Typical subalpine vegetation on north facing slopes (Transect A, 1545 m).

Plate 4.2. Typical montane vegetation on north facing slopes (Transect A, 902 m).

Plate 4.3. Typical subalpine vegetation on south facing slopes (Transect B, 1480 m).

Plate 4.4. Typical montane vegetation on south facing slopes (Transect B, 1065 m).

4.2. The understorey

4.2.1. Raw data

The understorey data (Table 4.1.) comprise abundance recordings for 134 plant species. Of these, 34 occur only along Transect A, 36 occur only along Transect B, and 64 are common to both transects.

Smoothed abundance curves[10] are shown in Figures 4.1 and 4.2. Whilst is not intended that specific species distributions be discernible from these graphs, they provide a good indication of some important features of the data. Firstly, it is clear that a small number of species dominate most of the vegetation. Secondly, the composition of the vegetation constantly changes as one moves along the transects. Thirdly, there are no *obvious* alignments of abundance curves into groups of similarly distributed species. Finally, we note that geographically neighbouring sites tend to have similar species composition and that geographically separate sites tend to markedly differ in species composition. In other words, it appears from the raw data, that compositional similarity is proportional to geographic proximity. These preliminary observations are borne out in detail in following sections.

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[10] Each plotted value is the weighted average of five (fewer at ends of transects) raw values. Weights are [0.1, 0.2, 0.4, 0.2, 0.1].

Table 4.1. Raw understorey data for both transects.

	Transect A																																																																																				
Altitude	1718	1710	1700	1690	1680	1670	1660	1650	1640	1630	1620	1610	1599	1588	1577	1566	1555	1545	1534	1523	1512	1501	1490	1479	1468	1457	1446	1435	1425	1414	1403	1392	1381	1370	1360	1350	1342	1325	1322	1307	1300	1290	1272	1270	1256	1240	1239	1222	1205	1200	1188	1180	1172	1155	1150	1137	1122	1120	1104	1093	1087	1070	1063	1053	1045	1025	1015	1000	986	976	967	951	938	927	909	902	889	877	870	853	851	832	828	813	804
Site number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Acacia dealbata																																							+																																																+
Acacia kettlewelliae																																																																+	+		1	+	+	+	1	+		+		+	1	+	1		1	1	+		
Acacia obliquinervia																																				+			+		+			+	+		+		+				+	+			+	+			+				+																								
Acaena novae-zelandiae																																																																																							
Acetosella vulgaris	+	+																																																																																					
Aciphylla glacialis	+	+				+		+																																																																														
Aphanes microcarpa	+																																																																																							
Arthropodium milleflorum			+	+	+		+	1	+	+	+	+	+	+	+	+		+	+	+	+		+	+	+	+	+	+	+																																																									
Asperula gunnii	+	+	+	+	+	1	+	1	+	+	+	+	+	+								+	+					+	+																																																			+						
Asplenium bulbiferum																																																																																							+
Asplenium flabellifolium																																																																																					+	+	+
Asteraceae sp. 1																																																																																							+	
Australina pusilla ssp. muelleri																																																																																							
Blechnum cartilagineum																																																																																							2
Blechnum nudum																																																																																							2
Brachyscome rigidula	+	+																																																																																					
Brachyscome sp. 1																																																																																							
Brachyscome spathulata	+	+	1	+	1	+	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+																																										
Bracteantha subundulata	+	+									+																																																																													
Cardamine gunnii											+													+																																																													+	
Carex breviculmis	+																																																																																						
Cassinia aculeata																																+			+		+	+	+		+					+	+			+				+																							+								
Cassinia longifolia																																																		+					+								+			+	+		+			+		+			+		1	1	1	2	+	1	+
Celmisia spp.	+	+	+	+	+	+	+	+	+	+	+	+	+	1	+	+	+		+	+						+																																																												
Chrysocephalum semipapposum																																																																																		+	+	1	
Clematis aristata																					+		+	+		+											+																																													+	1	1	+	+	
Comesperma ericinum																																																													+			+	+		+					+	+	+			+		+						
Coprosma hirtella											+				+		+			+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	1	+	+	1	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+	+	+		+	+	+	+	+	+	+	+				+	+			+			
Coprosma quadrifida																																																																																		+				1	1
Correa lawrenciana																																																																																							
Cotula alpina	+																																																																																							
Craspedia spp.	+	+	+	+	+	+		+	+		+	+	+										+			+																																																													
Danthonia racemosa	1																																																																																							
Danthonia sp. 1		+			1	1	1	1	+	+	+	+	+	+	+	1	+	+	+	+	1	+	+	+	+	+	+	1	+	+	+	1	+	+				+		+																																													
Danthonia tenuior																																																																																								
Daviesia latifolia																									3			2	1	2	+	1	2	2	1	2	1	2	3	3	2	1	2	1	1	1	3	2	3	3	2	+	+	2	1	1	2	1	+	2	+	+	1	1	+	1	1		2	2			+	+	1	+	1	+	1						
Daviesia ulicifolia								1		+	+	+	+	+	1	1	1	1		1	+	1	+	+	+	1	+	1							+		+							1	+			+	1								1		+			1			+							+	1												
Derwentia derwentiana																																																																																							
Deyeuxia brachyathera																																																																																							
Deyeuxia microseta																																																																																							
Deyeuxia monticola																				+															+																																																					
Deyeuxia quadriseta																																																																																							
Dianella tasmanica																								1										+		+		+		+		+	+	+	+	+	+	+		+											+	+		+					+			+	+	+	+	+	+	+	1		+			+	+
Dicksonia antarctica																																																																																						3
Echinopogon ovatus																																																																																							+
Epilobium billardierianum																																																																																							
Epilobium ciliatum																																																																																							
Erigeron pappochromus	+	+																																																																																						
Eucalyptus delegatensis																																																															+																							
Eucalyptus pauciflora		+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+		+		+																																																						
Eucalyptus radiata																																														+				+		+			+										+		+		+		+	+					+		+						
Eucalyptus rubida																																		+			+							+								+																																		
Eucalyptus spp.																																										+	+					+	+				+	+		+		+	+																										
Euphrasia collina																																																																																							
Exocarpos cupressiformis																																																																					+																
Exocarpos strictus																																																									+											+								+				1	1	+			
Gahnia spp.																																																																																							
Galium gaudichaudii																														+																																																				+				1	+
Gaultheria appressa																																																																																							
Gentianella spp.																																																																																								
Geranium potentilloides																																																																																						+	+
Geranium sp. 1																																																																																								
Gnaphalium spp.																																																																																							+
Gonocarpus montanus											+	+							+		+							+					+	+	+	+	+		+		+	+	+	+				+	+										+		+	+	+	+	+	+	+	1	+	+	+	+	+				+	+	+			+			
Goodenia hederacea		+	1	1	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	1		+	1		+																																																				
Grevillea australis	+	2																																																																																					
Grevillea victoriae																																																																																							
Gynatrix pulchella																																																																																							
Helichrysum scorpioides	+	+	+		+		+	+	+	+	+	+	+	+	+													+				+				+																																																		
Herb 1																																																																																							
Hydrocotyle spp.																																																																																							
Hypochoeris radicata	+	+	+	+				+	+		+							+					+		+	+																																																													
Kunzea ericoides																																																																															2					
Lagenifera stipitata																																																																																							
Leptinella filicula																																																																																							
Leptorhynchos squamatus	+	+																																		+			+																																																	
Leptospermum grandifolium																																																																																							
Leucochrysum albicans ssp. albicans	+	+																																																																																						
Leucopogon gelidus																																																																																							
Leucopogon hookeri	+	+	1	+	+	1	+	+	+	1	1	+	1	1	+	1		+	+	+	+	+	+	+	1	+	+																																																													
Lobelia gibbosa																																														+																		+					+					+														
Lomatia fraseri																																																																																				+	1	
Luzula spp.																																																																																	+		+	+	+	+
Microseris aff. lanceolata (Alps)		+	+	+	+								+																																																																											
Monotoca scoparia																																									+	+										+	+		+		+		1	+	+	1	1	+	2	+	1	+		+	1	+	2	1	1	+	1	+	1		+				

Transect B																																																															
1639	1628	1617	1606	1596	1586	1577	1567	1557	1548	1538	1528	1518	1509	1499	1489	1480	1470	1460	1451	1441	1431	1422	1409	1398	1386	1375	1364	1353	1342	1331	1320	1309	1297	1287	1276	1265	1254	1242	1231	1222	1209	1196	1183	1170	1157	1143	1130	1117	1104	1091	1078	1065	1055	1045	1035	1025	1015	1005	995	985	975	965	Altitude
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	Site number
																																																										+	+	+		+	Acacia dealbata
																																																															Acacia kettlewelliae
																	+	+	+		+	+			+	+	+		+	+	+	+	+		+	+	+	+	+																								Acacia obliquinervia
			1		+																																																					+	+	+	+	+	Acaena novae-zelandiae
+	+	1	+	+	+	+	+							+																																																	Acetosella vulgaris
	+	1	1	+	+	+	+	+		+				+																																																	Aciphylla glacialis
																																																															Aphanes microcarpa
		+	+	+	+																																																										Arthropodium milleflorum
+	+	+	+		1	+	1	+			+																																																				Asperula gunnii
																																																															Asplenium bulbiferum
														+																																						+							+	+	+	+	Asplenium flabellifolium
																																																															Asteraceae sp. 1
																																																														+	Australina pusilla ssp. muelleri
																																																														+	Blechnum cartilagineum
																																																															Blechnum nudum
+	1	1																																																													Brachyscome rigidula
			2	1	1	+	1	1																																																								Brachyscome sp. 1
+		+	+	+	+	+	1	+	+	+	+		+	+																																																	Brachyscome spathulata
																																																															Bracteantha subundulata
																																																															Cardamine gunnii
1																																																															Carex breviculmis
																																																															Cassinia aculeata
																																																															Cassinia longifolia
	+	+	+	+	+	+	+	+	+	1	+		+	+	+	+	+	+	1		+		+	+	+	1	+		+		1	2	1	1	1			1	+			+																					Celmisia spp.
																																																		+			+					+	+	1			Chrysocephalum semipapposum
																																													+	+	+	+		+	+	+	+		+	+	+	+		1			Clematis aristata
																																																															Comesperma ericinum
																								+		+	+		+	1	1	1	+	1	1	1	+	+	+	+	+	1	+	1	1	1	1	1	1	1	1	1	+	1	+	+	+	+	+			Coprosma hirtella
																																																				+					1	+	1			+	Coprosma quadrifida
																																																											+			2	Correa lawrenciana
																																																															Cotula alpina
		+	1	+	+	+	+	+		+				+																																																	Craspedia spp.
+	+																																																														Danthonia racemosa
																																																															Danthonia sp. 1
+	+																																																														Danthonia tenuior
																														+				2	1	+	1	1	1	1	1	3	1	3	2	2	1	2	3	3	1	1	2	2	2	2	1						Daviesia latifolia
																					+								+	1	+																																Daviesia ulicifolia
																																																+				+							+	+			Derwentia derwentiana
	1																																																														Deyeuxia brachyathera
	+																																																														Deyeuxia microseta
+	+	+	+																																																												Deyeuxia monticola
+	+	+	+																																																												Deyeuxia quadriseta
									+	1	1	1	1	1	1					1			+		+					+	+	+		1			1						2	2	1	1		+		+	+	+	+		1	1			+	+			Dianella tasmanica
																																																														+	Dicksonia antarctica
																																																															Echinopogon ovatus
		+	+																																																												Epilobium billardierianum
																																																														+	Epilobium ciliatum
+	2	1	+	+	+		+																																																									Erigeron pappochromus
																																																															Eucalyptus delegatensis
+			+	1		+	+	+	+	+	+	+	+	+	+	+	+		+	+																																											Eucalyptus pauciflora
																																																																Eucalyptus radiata
																																																																Eucalyptus rubida
																																																																Eucalyptus spp.
				+	+		1	+																																																								Euphrasia collina
																																																															Exocarpos cupressiformis
																																																															Exocarpos strictus
																																																														+	Gahnia spp.
																																																								+				+			Galium gaudichaudii
																								1			+																					+														Gaultheria appressa
		+	1	+	+	+	+																																																								Gentianella spp.
																																																											+		+	+	Geranium potentilloides
	+	1	+		1																																																										Geranium sp. 1
																																																															Gnaphalium spp.
	+	+		+	+	+	+	+	+	+	+		+								+			+	+					+											+		+	+	+	+		+							+								Gonocarpus montanus
+			+	1	1					+			1		+	+	1	1	+	+	+	+																				+	1																				Goodenia hederacea
2	2	3	2	2	1	+	+																																																								Grevillea australis
																						1																																									Grevillea victoriae
																																																													2	+	Gynatrix pulchella
																									+								+	1																				+				+	+	+			Helichrysum scorpioides
																																								+																							Herb 1
																																																														+	Hydrocotyle spp.
			+																																																												Hypochoeris radicata
																																																															Kunzea ericoides
+	+		+																																																								+				Lagenifera stipitata
	+	+	+																																																												Leptinella filicula
+	+	+																																																													Leptorhynchos squamatus
																																																														2	Leptospermum grandifolium
+	1	+	+	+	+																																																										Leucochrysum albicans ssp. albicans
							+				+	+	1	+	+	1	1	+	1	1	1	+	2	2	1	1	+	1			1						+					1			1	1																	Leucopogon gelidus
1	2	2	1	+	1	+	1	1	+	+			+	+		+	+	+				+			+																																						Leucopogon hookeri
																																																															Lobelia gibbosa
																																																						+	+	+	2	2	1	2	2	1	Lomatia fraseri
+	+	+	+	+			+	+	+				+	+																																											+					+	Luzula spp.
+	+																																																														Microseris aff. lanceolata (Alps)
																																																															Monotoca scoparia

(Table 4.1 continued)

	Transect A																																																																																				
Altitude	1718	1710	1700	1690	1680	1670	1660	1650	1640	1630	1620	1610	1599	1588	1577	1566	1555	1545	1534	1523	1512	1501	1490	1479	1468	1457	1446	1435	1425	1414	1403	1392	1381	1370	1360	1350	1342	1325	1322	1307	1300	1290	1272	1270	1256	1240	1239	1222	1205	1200	1188	1180	1172	1155	1150	1137	1122	1120	1104	1093	1087	1070	1063	1053	1045	1025	1015	1000	986	976	967	951	938	927	909	902	889	877	870	853	851	832	828	813	804
Site number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Olearia alpicola																																																																																					
Olearia erubescens											+							+	+	+														+	+		+	+	+	+			+		+	+		+																																					
Olearia megalophylla																																																																																					
Olearia phlogopappa																																								+			+																			+												+				+	+	+	+	+	+	1	+
Olearia rugosa											+																																																																										
Oreomyrrhis eriopoda			+	+				+		+	+		+								+																																																																
Orites lancifolia																																																																																					
Oxalis spp.																																																																																					1
Oxylobium alpestre	+	2	2	3	3	3	4	4	5	4	2	2	1	2	2	2	3	2	2	+	2	1	2	1	2	1	2	+																																																									
Ozothamnus stirlingii																																																																																					
Persoonia confertiflora																																			+		+				+	+		+	+	+			+			+	+	+	1	+	+	+		+	+	+	+		+	+		+	+	+		+	1				+		+			+			
Picris sp. (Eastern Highlands)				+																																																																																	
Pimelea alpina						+												+		+			+	+	+	+	+	+		+	+		+		+	+			+		+	+		+			+										+				+	+	+	+			+				+				+				+						
Pimelea axiflora																																																																																					
Pittosporum bicolor																																																																																					1
Plantago euryphylla																																																																																					
Poa sp. 1		3	+	+	1	+	+	+	+	+	+	1	+	+	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	2	+	+	1	+	1	+	+			+	+				+																	+												+					2
Poa sp. 2			+	+					+	+	1	+	1	1	+	2	2	2	1	1	1	2	2	2	2	3	2	2	+	+	1	+	1	1	1	1	+	+	1	+	1	2	1	1	+	1	+	+	+	+	+	1	+	+	1	+	1	+	+		+	+	+	+	1	+		1	+	+			+		+	+		1	+	2	1	1	1	2	
Poa sp. 3	3																																																																																				
Poa sp. 4																																																																																					
Poa sp. 5																																																																																					+
Poa sp. 6																																						+																																															
Poaceae sp. 1																																																																																					+
Poaceae sp. 2																																																																																					
Podolepis robusta	+	2	+																																																																																		
Polyscias sambucifolia																													+		+	+	+	1		+	+	+	+	+		+		+	+		+	+		+		+	+	+	+		1				+	+		+		+		+		+	+		+			+	+	+	+		+			+	+
Polystichum proliferum																																																																																					+
Pomaderris aspera																																																																																					2
Poranthera microphylla							+									+				+					+	+	+				+			+		+		+	+	+				+	+	+				+					+																							+		+	+				
Prostanthera rotundifolia																																																																																		1	4	1	
Pteridium esculentum																																															+																			+		1		+	2	1	2	1	1	+	1	+	1	+	1	+			+
Pterostylis spp.																																																																																					
Ranunculus spp.																																																																																					
Rhodanthe anthemoides	+																																																																																				
Rubus parvifolius																																																																																		+			1
Scleranthus biflorus	+	+																																																																																			
Senecio gunnii	+	+				+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+		+			+	+	+	+			+	+	+	+	+			+																																											+		
Senecio lautus		+	+	+							+			+						+			+																																																												+		+
Senecio linearifolius																																																																																		+		+	+
Sigesbeckia spp.?																																																																																					
Stellaria flaccida																																																																																					3
Stellaria pungens	+	+	+	+	+	+	+	+	+	+	+		+	+				+	+	+			+	+	+	+	+	+	+	+		+																																																+		+	+	1	+
Stylidium graminifolium	+	+	+				1	1	+	+		+							+	+				+			+															+	+																						+																				
Tasmannia xerophila																																																																																					
Urtica incisa																																																																																					+
Veronica serpyllifolia																												+																																																									
Viola betonicifolia	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		+		+		+		+		+	+	+	+	+			+							+																																														
Wahlenbergia gloriosa																						+	+	+	+	+	+	+	+			+																																																					
Wahlenbergia sp. 1																																																												+																						+			+

	Transect B																																																														
Altitude	1639	1628	1617	1606	1596	1586	1577	1567	1557	1548	1538	1528	1518	1509	1499	1489	1480	1470	1460	1451	1441	1431	1422	1409	1398	1386	1375	1364	1353	1342	1331	1320	1309	1297	1287	1276	1265	1254	1242	1231	1222	1209	1196	1183	1170	1157	1143	1130	1117	1104	1091	1078	1065	1055	1045	1035	1025	1015	1005	995	985	975	965	Altitude
Site number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	Site number
Olearia alpicola																																																													1			Olearia alpicola
Olearia erubescens																																													+																			Olearia erubescens
Olearia megalophylla																										+	+	1	+	+	+		1	1	1	1	1																											Olearia megalophylla
Olearia phlogopappa																																									+			+	+			2	+		1	1	1	1	+		+	+	+	+	1	1		Olearia phlogopappa
Olearia rugosa							1		+	+	1	+		+	1	+	+		+																																													Olearia rugosa
Oreomyrrhis eriopoda	+	1		+		+	+	+	+						1																																												+	+				Oreomyrrhis eriopoda
Orites lancifolia												+	1		1																																																	Orites lancifolia
Oxalis spp.																																																												+	+	1	+	Oxalis spp.
Oxylobium alpestre	2	3		2	1	1	3	2	1	4	3	3	3	3	1	3	4	3	3	3	3	3	3	2	2	2	3	4	3	3																																		Oxylobium alpestre
Ozothamnus stirlingii																																																	+		+													Ozothamnus stirlingii
Persoonia confertiflora																																																																Persoonia confertiflora
Picris sp. (Eastern Highlands)																																																																Picris sp. (Eastern Highlands)
Pimelea alpina		1	+	1	+	1	1	1	+	+																																																						Pimelea alpina
Pimelea axiflora																																																											1	+				Pimelea axiflora
Pittosporum bicolor																																																								+	1	1	1				1	Pittosporum bicolor
Plantago euryphylla			+	+																																																												Plantago euryphylla
Poa sp. 1	2	1	2	2	2	2	4	3	3	3	2	2	1	2	1	1	2	3	4	3	2	1	2	1	1	2	1	1	1	+	1	1	1	1	+	1	1	1	+	+	+	1	1	1	1	2	3	2	3	3	3	3	1	1	1	2	1	2	2	1	2	1	1	Poa sp. 1
Poa sp. 2	2	1	3	2																																																												Poa sp. 2
Poa sp. 3																																																																Poa sp. 3
Poa sp. 4	+	1	+	+		+		+																																																								Poa sp. 4
Poa sp. 5																																																					1		+	1				1	1			Poa sp. 5
Poa sp. 6																																																																Poa sp. 6
Poaceae sp. 1																																																																Poaceae sp. 1
Poaceae sp. 2				+	+			+																																																								Poaceae sp. 2
Podolepis robusta																																																																Podolepis robusta
Polyscias sambucifolia																																+	+	1	+		+	+	+				+	+	+	+	+	+	1		+	+	1	1	+	1	+	+	1	+	1			Polyscias sambucifolia
Polystichum proliferum		+	+	2	+	+	+		+			+	+		+																				+														+		+	+	+	+		+	1	2	1	2	1	3	3	Polystichum proliferum
Pomaderris aspera																																																																Pomaderris aspera
Poranthera microphylla																																															+																	Poranthera microphylla
Prostanthera rotundifolia																																																																Prostanthera rotundifolia
Pteridium esculentum																																																												+				Pteridium esculentum
Pterostylis spp.																																																												+	+			Pterostylis spp.
Ranunculus spp.																																																												+	+			Ranunculus spp.
Rhodanthe anthemoides																																																																Rhodanthe anthemoides
Rubus parvifolius																																																										+		+	+	1	+	Rubus parvifolius
Scleranthus biflorus		1	+	+																																																												Scleranthus biflorus
Senecio gunnii		+	+	+	+	+																																																										Senecio gunnii
Senecio lautus						+																																																										Senecio lautus
Senecio linearifolius																																					+																								+	+		Senecio linearifolius
Sigesbeckia spp.?																																																															+	Sigesbeckia spp.?
Stellaria flaccida																																																														3	1	Stellaria flaccida
Stellaria pungens	+	+	+	2	+	1	1	+	+	+	+	1			1																																					+	+					+	+	1	+			Stellaria pungens
Stylidium graminifolium	+			+	1	+	1	1	1	1	1	1	1	+	1	+	+		+	+	+	+	+	+		+	+	+	+	+	1	1	1	+	+	+		+	+	+	+	+	+	+	+		+			+	+										1			Stylidium graminifolium
Tasmannia xerophila				+			1		+		+	+	2	1	+		+				+		+	1										+																														Tasmannia xerophila
Urtica incisa																																																															+	Urtica incisa
Veronica serpyllifolia																																																																Veronica serpyllifolia
Viola betonicifolia	+	+	+	+	+	1		+																							+			1															+											+	+			Viola betonicifolia
Wahlenbergia gloriosa			+	+		1	+	+	+			+																																									+	+			+	+	+		+	+	+	Wahlenbergia gloriosa
Wahlenbergia sp. 1																																																																Wahlenbergia sp. 1

Figure 4.1. Smoothed plant species abundances along Transect A showing the abundance of dominant species in relation to the majority of species.

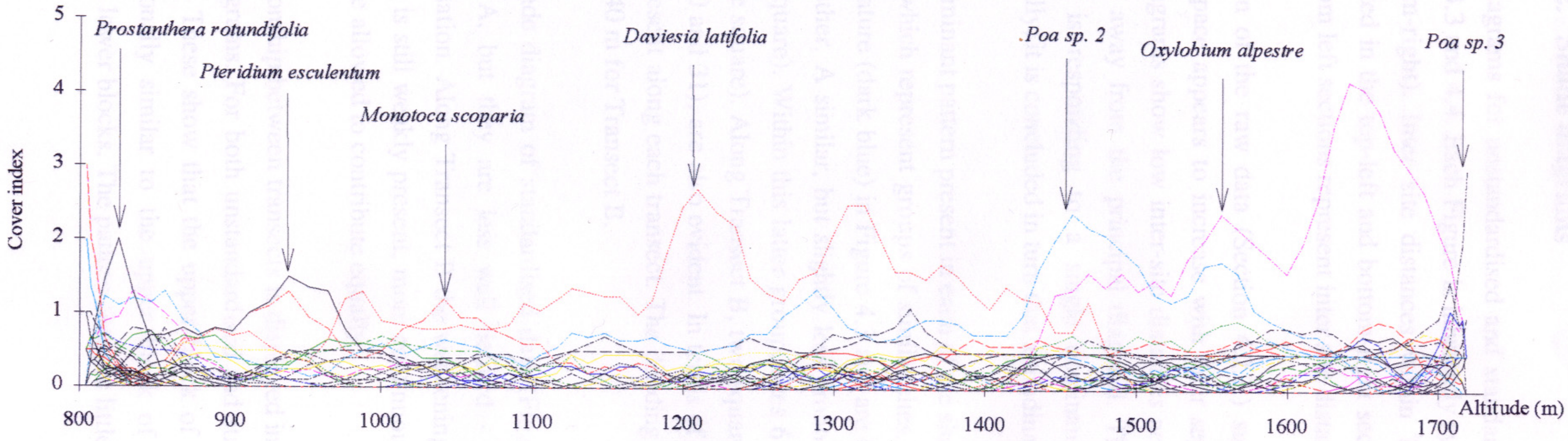
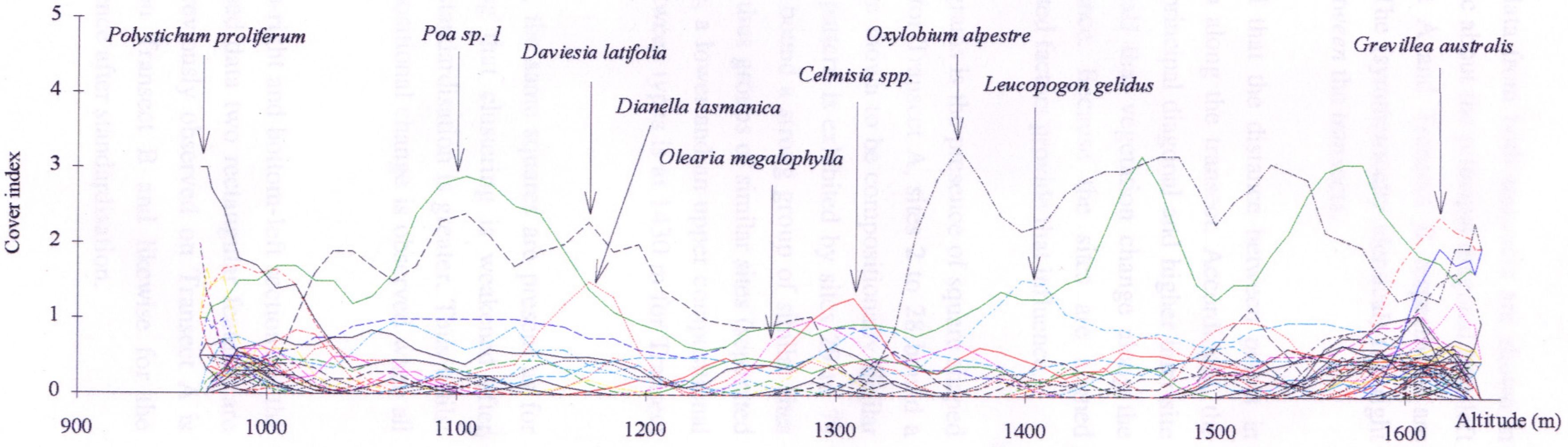


Figure 4.2. Smoothed plant species abundances along Transect B showing the abundance of dominant species in relation to the majority of species.



4.2.2. Shade diagrams

Shade diagrams for unstandardised and standardised data from both transects are shown in Figures 4.3 and 4.4. Each Figure is inherently symmetric about the principal diagonal (top-left to bottom-right). Inter site distances within Transect A and Transect B respectively are represented in the top-left and bottom-right sections. The (symmetrically identical) top right and bottom left sections represent inter site distances *between* the transects.

Inspection of the raw data (Section 4.2.1.) suggested that the distance between points in species space appears to increase with their separation along the transect. Accordingly, the shade diagrams show low inter-site distances near the principal diagonal and higher inter-site distances away from the principal diagonal. This reveals that vegetation change along the transects is responding to a single dominant influence. Because the sites are aligned altitudinally, it is concluded in turn that altitudinally-related factors provide that influence.

A less dominant pattern present in each of the shade diagrams is the presence of square shaped features which represent groups of similar sites. Thus, for Transect A, sites 2 to 28 bound a square feature (dark blue) in Figure 4.3 and are therefore shown to be compositionally similar to each other. A similar, but slightly less pronounced, pattern is exhibited by sites 29 to 79 (yellow square). Within this latter group, sites 61 to 79 bound a strong group of similar sites (dark blue square). Along Transect B, two squares, and thus groups of similar sites (separated at sites 30 and 31), are also evident. In terms of altitude, a lower and an upper compositional type is present along each transect. The dividing line between types is at 1430 m for Transect A and 1340 m for Transect B.

In the shade diagram of standardised data (Figure 4.4), the same squares are present as for Transect A, but they are less well defined - implying that clustering is weakened after standardisation. Along Transect B the weakening after standardisation is greater. Thus whilst clustering is still weakly present, more continuous compositional change is observed when all species are allowed to contribute equally.

The relationship between transects is displayed in the top-right and bottom-left sections of the shade diagrams. For both unstandardised and standardised data two rectangular features are displayed. These show that the upper block of sites previously observed on Transect A is compositionally similar to the upper block of sites on Transect B and likewise for the respective lower blocks. The pattern changes little in essence after standardisation.

Figure 4.3. Shade diagram showing compositional distance relationships between all sites from both transects without standardisation. The Bray-Curtis distance measure is used.

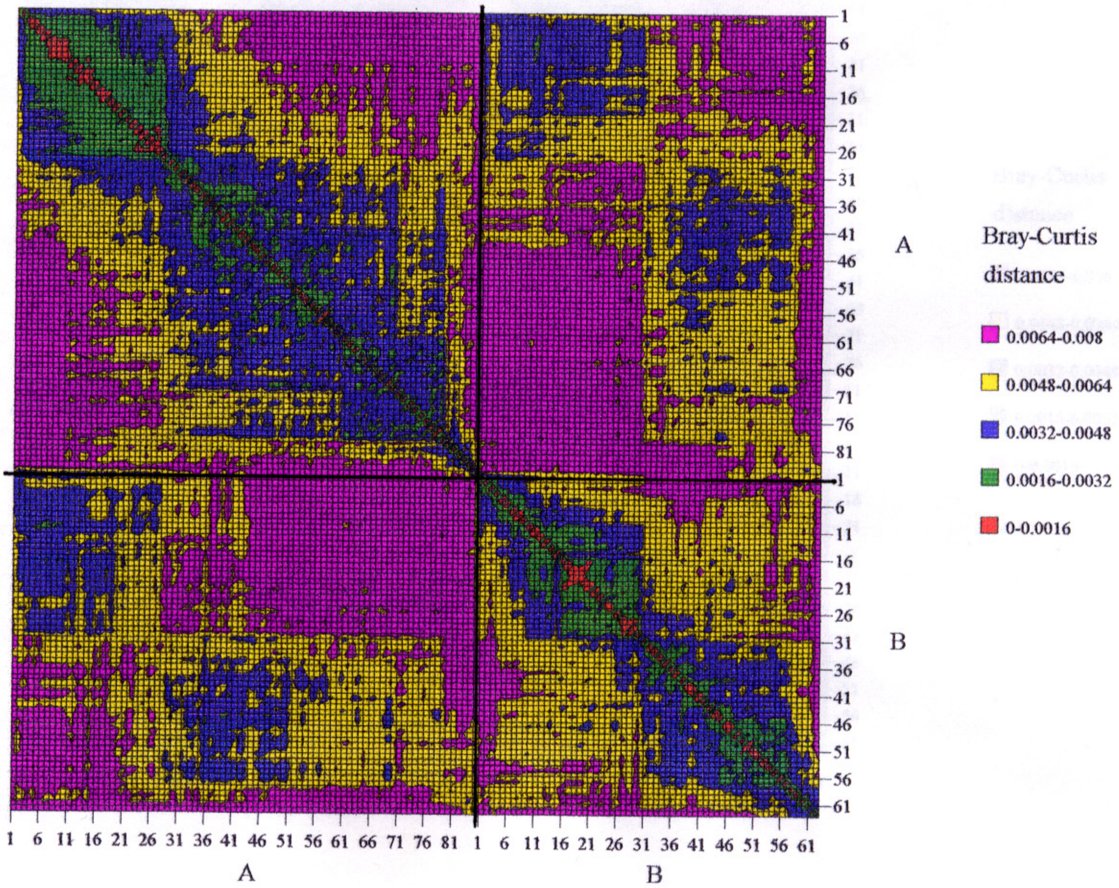
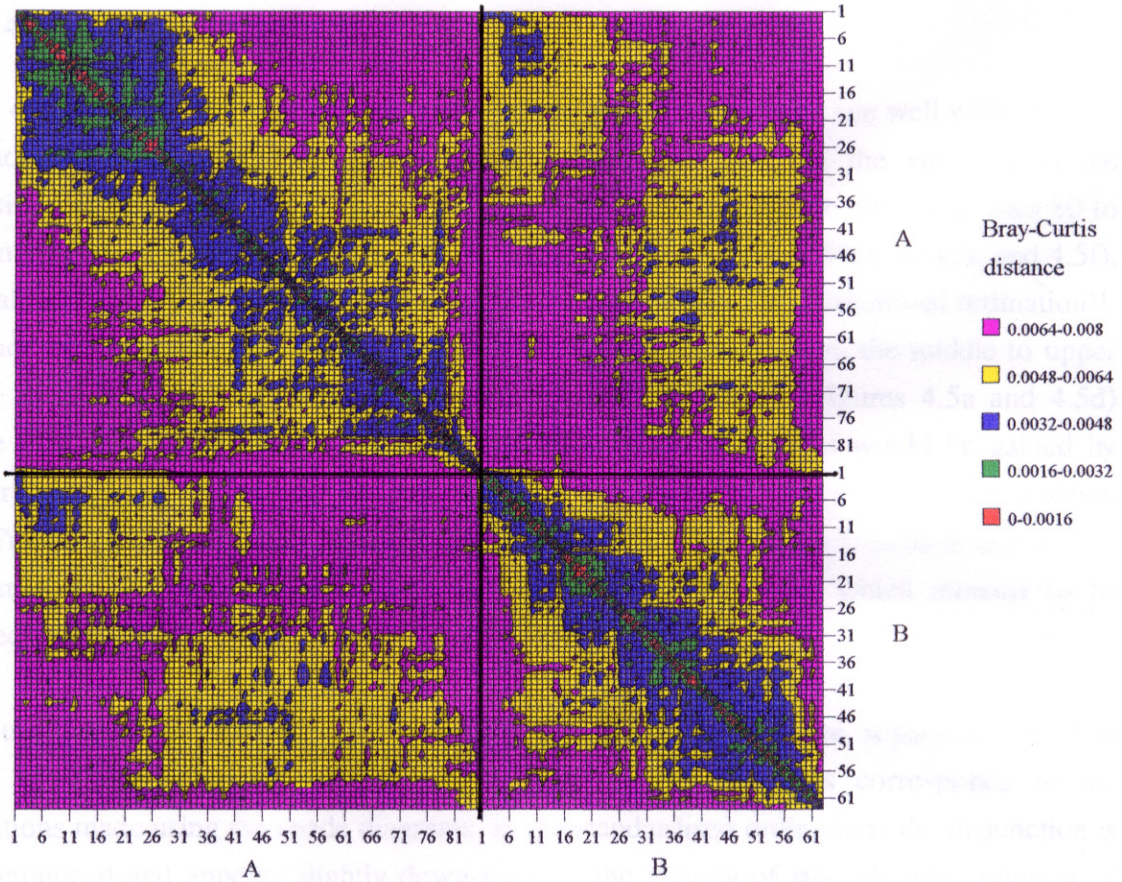


Figure 4.4. Shade diagram showing compositional distance relationships between all sites from both transects after standardisation. The Bray-Curtis distance measure is used.



4.2.3. Ordination

Ordination results are shown in Figures 4.5, 4.6, and 4.7. Each figure contains results from ordinations of raw data and from matching ordinations of standardised data. One and two dimensional ordinations are presented in each case with an accompanying plot of achieved stress versus dimensionality to act as a guide as to which of the ordinations is most suitable. Note that in two dimensional ordinations, each dimension is of equal importance - there is no 'first dimension' and 'second dimension' as is the case with other ordination techniques.

4.2.3.1. Transect A

Figures 4.5b and 4.5e show that one dimensional ordination scores correlate well with altitude. This indicates that altitudinally-related factors account for most of the variation in the composition of vegetation along Transect A. A number of lower altitude sites (e.g. sites 80 to 85) do not conform to this pattern. In the two dimensional ordinations (Figures 4.5c and 4.5f), scores along the horizontal axis correlate well with those of the one dimensional ordination[11]. The other axis separates the lower altitude sites (noted previously) from the middle to upper altitude sites. The graphs of achieved stress versus dimensionality (Figures 4.5a and 4.5d) indicate that little improvement in the representation of these patterns would be gained by considering a three dimensional ordination. Thus, the variation in vegetation composition along Transect A is explained primarily by the influence of altitudinally-related factors but secondarily by the influence of at least one other significant factor which remains to be identified.

In the unstandardised ordinations, the middle and upper sites can be separated into two clusters by a disjunction in the 'vicinity' of sites 25 and 28. This corresponds to the observations made using the shade diagrams. In the standardised ordinations the disjunction is less pronounced and appears slightly down-slope in the vicinity of site 30. Interpretation of these patterns is deferred until the final section of the chapter.

4.2.3.2. Transect B

Ordinations of Transect B data (Figure 4.6) reveal slight differences in the major patterns of composition between the two transects. The influence of altitude is again observed in the one dimensional ordination of unstandardised data but less so in the ordination of standardised data. Figure 4.6d shows that this latter ordination was achieved at a greater stress than

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[11] A plot of the scores with respect to each other clearly shows this. For brevity this plot is not presented here.

previous ordinations and thus it is probable that the curve of scores shown in Figure 4.6e has resulted from an untenable attempt to reduce the dimensionality of standardised data from Transect B to one. The two dimensional ordination of unstandardised data from Transect B (Figure 4.6c) presents more distinct clustering than its counterpart from Transect A, although the same basic structure is observed. Two large clusters clearly separate most of the lower sites from the upper sites and two smaller, more dispersed clusters further separate the extreme lower and upper sites. The major separation is made between clusters above and below sites 30 and 31. This agrees with the results of shade diagrams. The standardised analogue of the pattern is similar in overall structure but the clusters are less pronounced. Once again, interpretation of these patterns is given in the final section of this chapter and in Chapter 6.

4.2.3.3. Both transects combined

The most notable feature of the ordinations of combined data (Figure 4.7) is that when the sites of a single transect are considered in isolation, the spatial organisation observed is very similar to that derived from the ordination of those sites only. Because *intra*-transect site relationships have been discussed in the previous two sections and have not changed significantly in an ordination of combined data, they are not considered in the present discussion of *inter*-transect site relationships. In the one dimensional ordinations of both standardised and unstandardised data, sites from Transect A appear slightly to the right of sites from Transect B. Thus the site in Transect A which is most similar to a site in Transect B is usually found approximately 100m higher above sea level. This agrees with the common observation that the altitudinal sequence of vegetation types is shifted downward on south facing slopes (Transect B) relative to north facing slopes (Transect B).

Figure 4.5. Ordinations of all data from Transect A: a, b, c show ordinations of unstandardized data; d, c, e show ordinations of Bray-Curtis standardised data; a, d show achieved stress in each dimensionality; b, e show one dimensional ordinations; c, f show two dimensional ordinations.

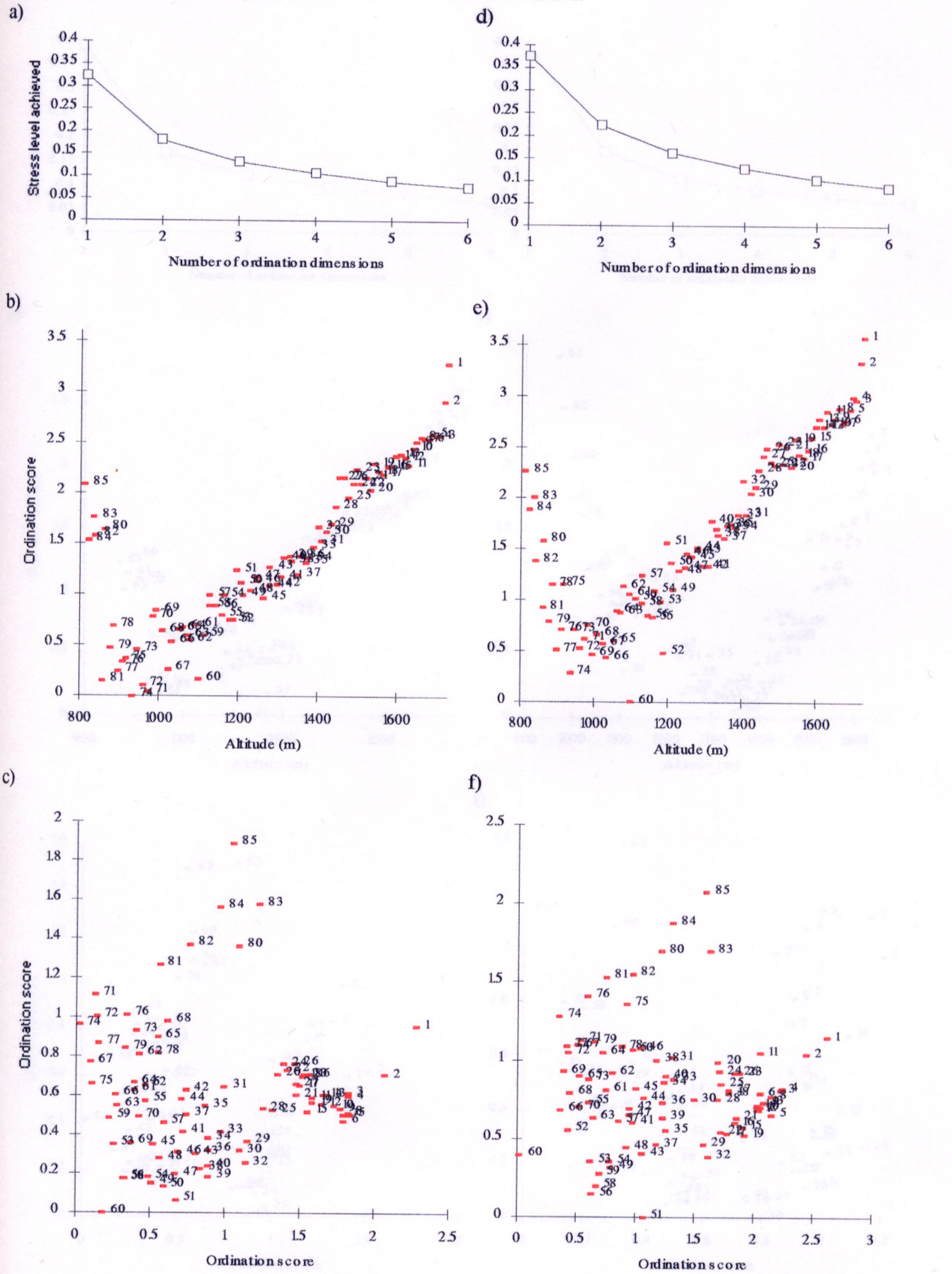


Figure 4.6. Ordinations of all data from Transect B: a, b, c show ordinations of unstandardized data; d, c, e show ordinations of Bray-Curtis standardised data; a, d show achieved stress in each dimensionality; b, e show one dimensional ordinations; c, f show two dimensional ordinations.

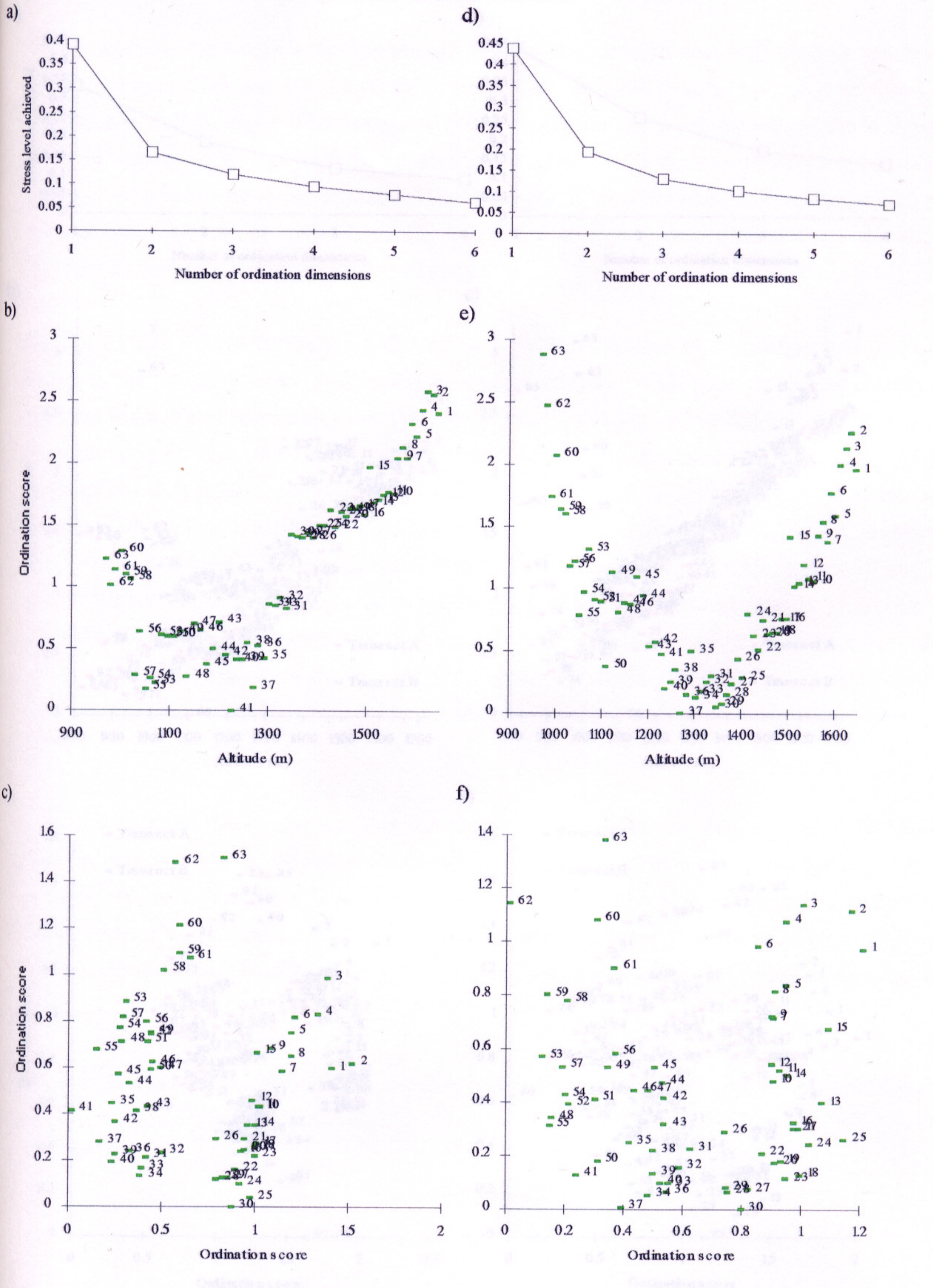
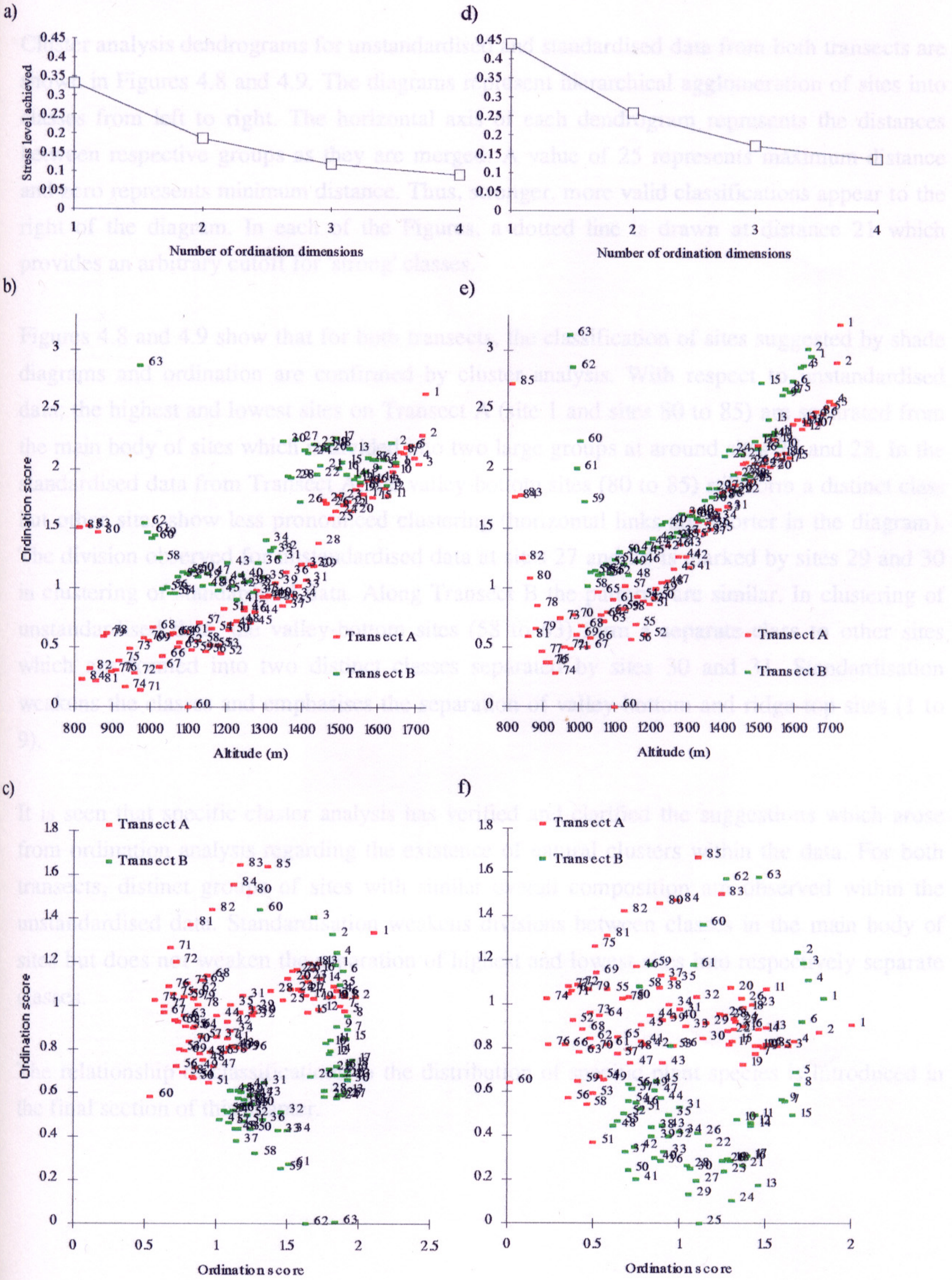


Figure 4.7. Ordinations of all data from both transects: a, b, c show ordinations of unstandardized data; d, c, e show ordinations of Bray-Curtis standardised data; a, d show achieved stress in each dimensionality; b, e show one dimensional ordinations; c, f show two dimensional ordinations.



4.2.4. Classification

Cluster analysis dendrograms for unstandardised and standardised data from both transects are shown in Figures 4.8 and 4.9. The diagrams represent hierarchical agglomeration of sites into classes from left to right. The horizontal axis of each dendrogram represents the distances between respective groups as they are merged. A value of 25 represents maximum distance and zero represents minimum distance. Thus, stronger, more valid classifications appear to the right of the diagram. In each of the Figures, a dotted line is drawn at distance 21 which provides an arbitrary cutoff for 'strong' classes.

Figures 4.8 and 4.9 show that for both transects, the classification of sites suggested by shade diagrams and ordination are confirmed by cluster analysis. With respect to unstandardised data, the highest and lowest sites on Transect A (site 1 and sites 80 to 85) are separated from the main body of sites which is divided into two large groups at around sites 27 and 28. In the standardised data from Transect A, the valley-bottom sites (80 to 85) still form a distinct class but other sites show less pronounced clustering (horizontal links are shorter in the diagram). The division observed for unstandardised data at sites 27 and 28 is marked by sites 29 and 30 in clustering of standardised data. Along Transect B the patterns are similar. In clustering of unstandardised data, the valley-bottom sites (58 to 63) form a separate class to other sites which are formed into two distinct classes separated by sites 30 and 31. Standardisation weakens the classes and emphasises the separation of valley-bottom and ridge-top sites (1 to 9).

It is seen that specific cluster analysis has verified and clarified the suggestions which arose from ordination analysis regarding the existence of natural clusters within the data. For both transects, distinct groups of sites with similar overall composition are observed within the unstandardised data. Standardisation weakens divisions between classes in the main body of sites but does not weaken the separation of highest and lowest sites into respectively separate classes.

The relationship of classifications to the distribution of specific plant species is introduced in the final section of this chapter.

Figure 4.8. Cluster analysis dendrograms of unstandardised (left) and standardised (right) species-in-site data from Transect A using average (between groups) linkage operating with a cosine distance measure.

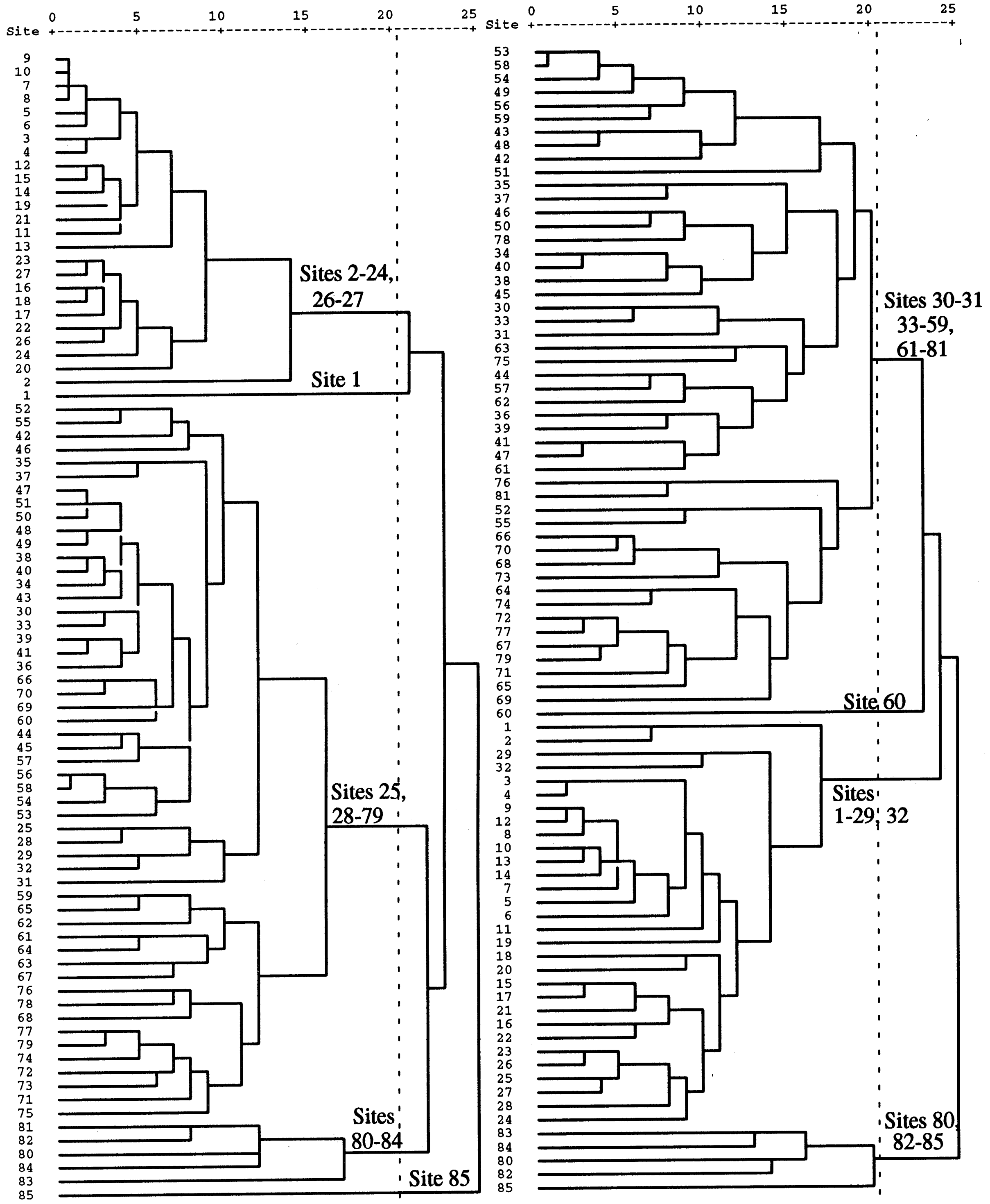
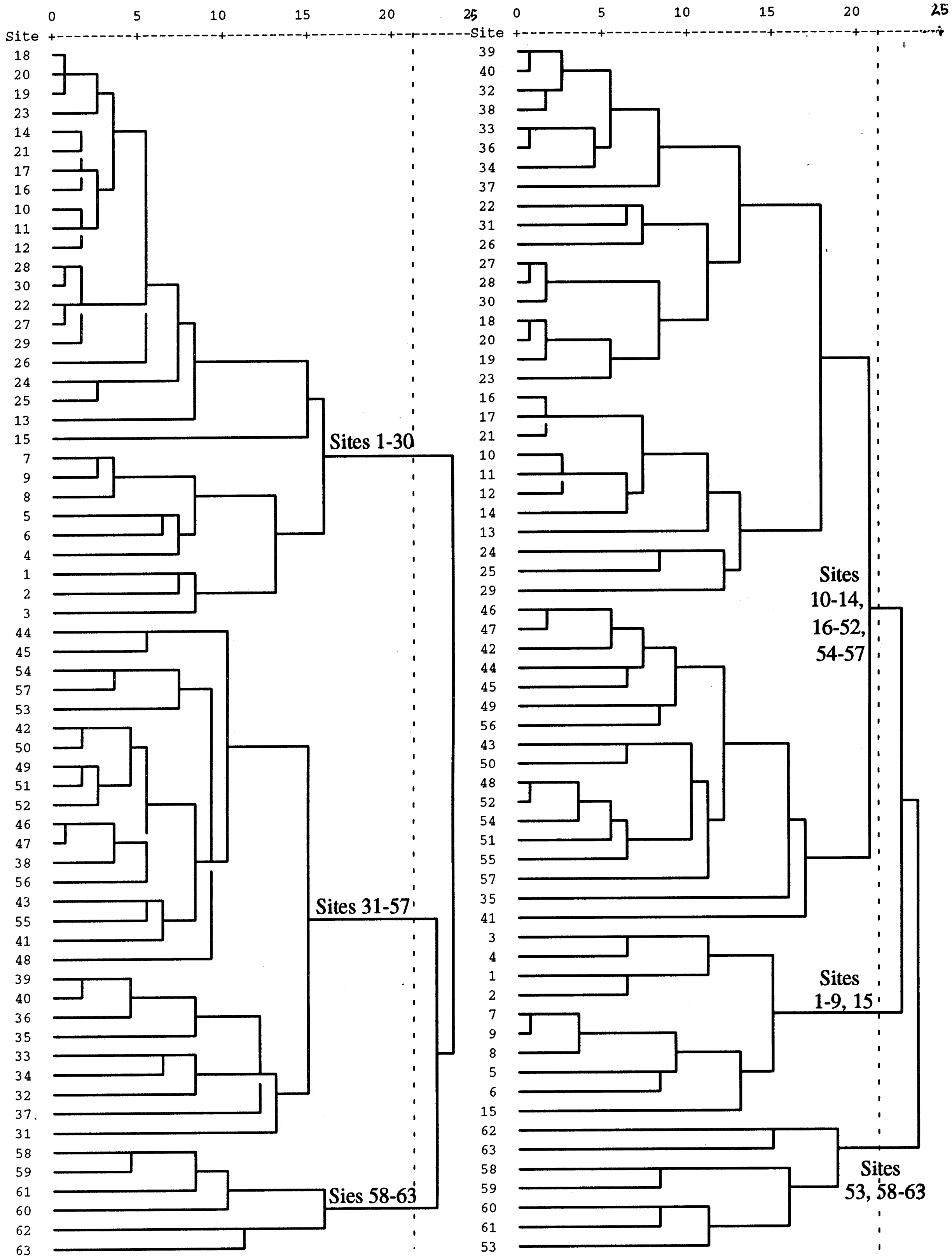


Figure 4.9. Cluster analysis dendrograms of unstandardised (left) and standardised (right) species-in-site data from Transect B using average (between groups) linkage operating with a cosine distance measure.



4.3. The canopy

The major distributional patterns of canopy composition are shown in Figures 4.10 and 4.11. In both transects, *Eucalyptus pauciflora* exclusively dominates the higher altitude canopy but decreases in abundance with increasing altitude. In the lower, montane reaches, the transects differ markedly. The montane forest of Transect A is comprised of mixed stands chiefly of *E. rubida*, *E. radiata*, *E. delegatensis*, and *E. viminalis*. *E. rubida* occurs between 1100m and 1400m, *E. viminalis* occurs lower down between 800m and 1050m, and *E. radiata* and *E. delegatensis* are more generally distributed. Along Transect B, the montane forest is a pure, even aged stand of *E. delegatensis*. A riparian forest common to both transects is exhibited at the valley bottom. In these sites *E. viminalis* dominates a mid-storey of *Acacia dealbata*.

The differences in tree composition between the transects probably reflect not only environmental differences (e.g. aspect) but also historical differences. The montane forest of Transect A is mature, with many large individuals present whilst the Alpine Ash (*E. delegatensis)* of Transect B is dense and roughly even aged (as judged by diameter, see Bowman & Kirkpatrick 1984). The southern slopes of Mount Murray to the west support a less dense stand of much larger Alpine Ash (pers. obs. 1992) which is indicative of more mature forest. The comparison shows that the dense Alpine Ash of Transect B are probably regrowth from severe fire in 1939. This explanation is reinforced by aerial photography (Section 2.8.) which suggests that the 1939 fires may have affected Transect B, but did not reach as far west as Mount Murray. Thus it is probable that the two transects surveyed in this work have different recent fire histories.

Figure 4.10. Five-site averaged dominance of trees along Transect A.

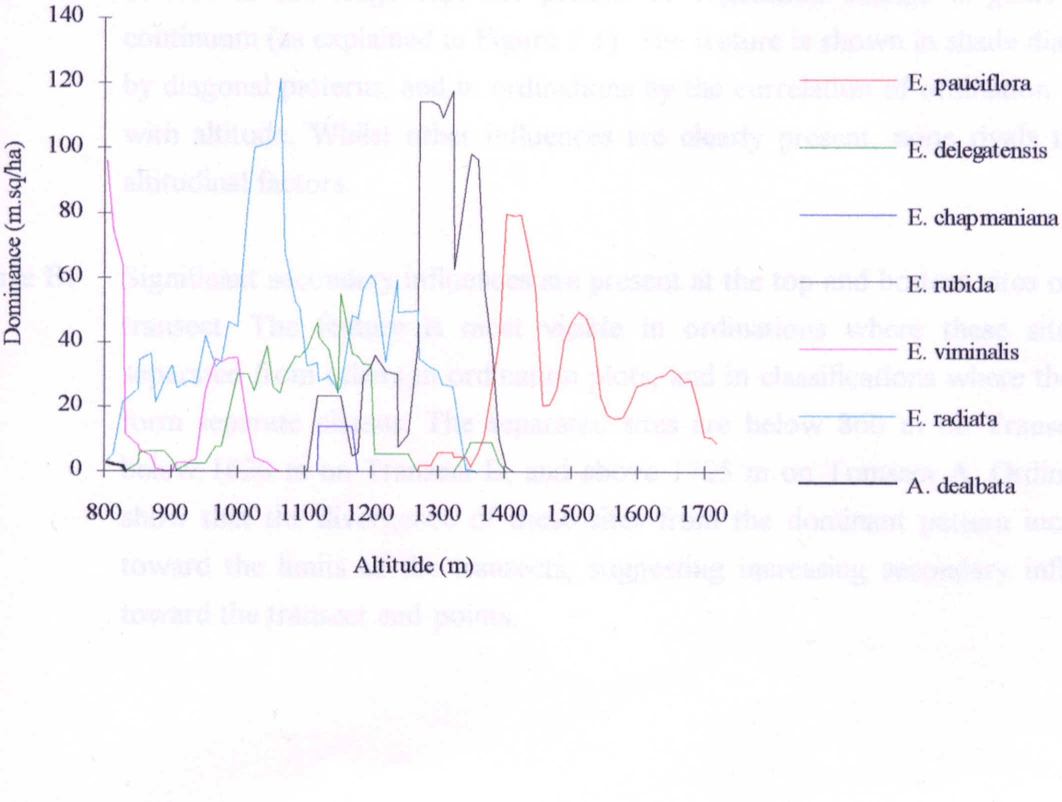
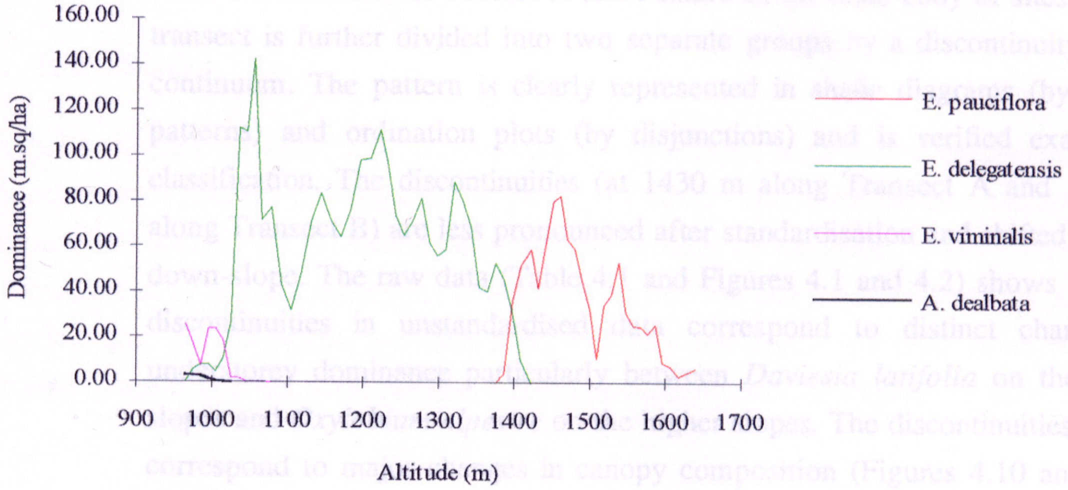


Figure 4.11. Three-site averaged dominance of trees along Transect B.



4.4. Summary

The results of a number of analyses of raw and standardised species-in-site data have been presented in this chapter. Each analysis has contributed a unique element to the understanding of the patterns of species composition present within the data and how these relate to plant distribution. The patterns of vegetation composition and distribution with respect to altitude within the study area can be explained as follows in terms of three key features, denoted Feature A, Feature B, and Feature C.

Feature A. *On the whole*, factors directly related to altitude are the leading influence on the vegetation along the transects. As we move up a transect from the valley-bottom to the ridge top, the pattern of vegetation change is *generally* a continuum (as explained in Figure 1.1). The feature is shown in shade diagrams by diagonal patterns, and in ordinations by the correlation of ordination scores with altitude. Whilst other influences are clearly present, none rivals that of altitudinal factors.

Feature B. Significant secondary influences are present at the top and bottom sites of each transect. The feature is most visible in ordinations where these sites are separated from others in ordination plots, and in classifications where the sites form separate classes. The separated sites are below 860 m on Transect A, below 1020 m on Transect B, and above 1705 m on Transect A. Ordinations show that the divergence of these sites from the dominant pattern increases toward the limits of the transects, suggesting increasing secondary influence toward the transect end-points.

Feature C. After consideration of Feature A and Feature B, the main body of sites in each transect is further divided into two separate groups by a discontinuity in the continuum. The pattern is clearly represented in shade diagrams (by square patterns) and ordination plots (by disjunctions) and is verified exactly by classification. The discontinuities (at 1430 m along Transect A and 1340 m along Transect B) are less pronounced after standardisation and shifted slightly down-slope. The raw data (Table 4.1 and Figures 4.1 and 4.2) shows that the discontinuities in unstandardised data correspond to distinct changes in understorey dominance particularly between *Daviesia latifolia* on the lower slopes and *Oxylobium alpestre* on the higher slopes. The discontinuities do *not* correspond to major changes in canopy composition (Figures 4.10 and 4.11) nearby between *E. pauciflora* and montane species (at 1375 m for Transect A and 1400 m for Transect B). The weakening of the discontinuities after standardisation implies that whilst the pattern is primarily related to dominant species, clustering is still present in the composition of the vegetation as a whole.

Ordination shows that the patterns of vegetation composition change exhibited along the two transects are alike in many ways despite the fact that shade diagrams show that no single site on Transect A is very similar to any site on Transect B. Ordination of combined data from the two transects shows that the compositional similarities between the transects are misaligned by approximately 100 vertical metres *i.e.* Transect B is like a lower version of Transect A - presumably because of the different microclimate experienced on the shady (south facing) side of the valley.

Chapter 5. Environmental results

5.1. Introduction

In response to Aim Two (Section 1.2.), this chapter provides a basis for the explanation of the plant community patterns described in the previous chapter. The results of environmental data collection and analysis are presented and comment is made on the major trends observed and on the success of the measurement and simulation of environmental factors as a whole. Following this, the measured and simulated variables are combined with those implicitly estimated in terms of altitude for the analysis of correlations with the vegetation data.

5.2. Topography

As shown in Figure 5.1, the aim to survey transects of uniform aspect and slope has been satisfied. Quadrats on Transect A face north ($\mu = 9°$, $\sigma = 17°$) and those of Transect B face south ($\mu = 205°$, $\sigma = 26°$). The slope of Transect A is consistently steep although more so toward the bottom of the valley. Transect B is steep at either end and more level in its middle third.

5.3. Radiation.

Figure 5.2 shows the results of view factor simulation by computer for both transects. At the top of each transect 100% of the sky is visible (excepting obstruction by trees). For the upper two thirds of each transect, at least 85% of the sky remains unobstructed by surrounding topography. In the lower third of each transect, the view factor drops rapidly to just over 60%. In summary, view factor is high throughout most of the transects but near the valley-bottom the terrain becomes steeper and view factor diminishes accordingly. Whilst this observation does not refer to the variation in absolute radiation levels, and it does not account for the increased shade experienced on south-facing slopes, it gives a good indication of *intra-transect* variation of a factor which significantly influences incident radiation on a local scale (Moore *et al* 1993).

Figure 5.1. Aspect and slope along transects A and B.

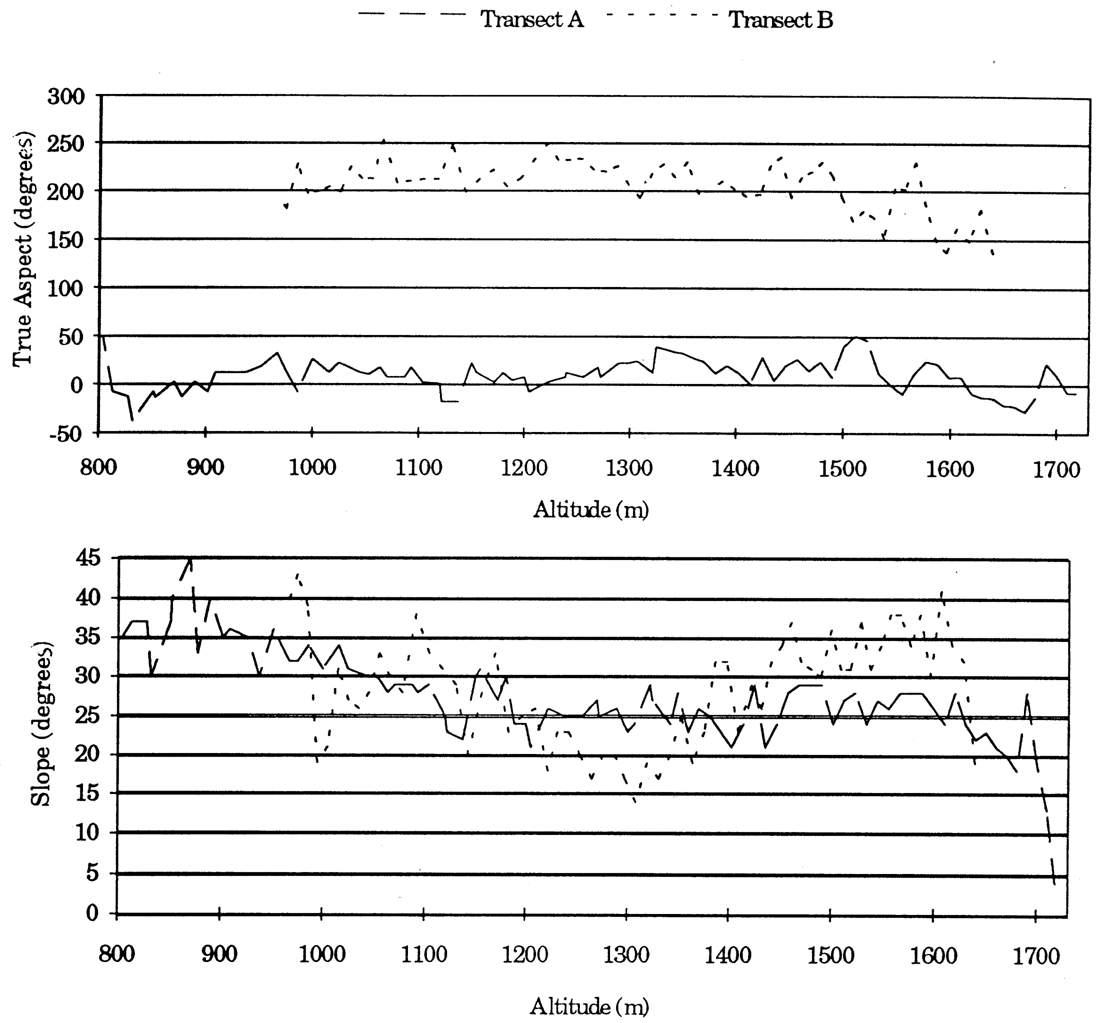
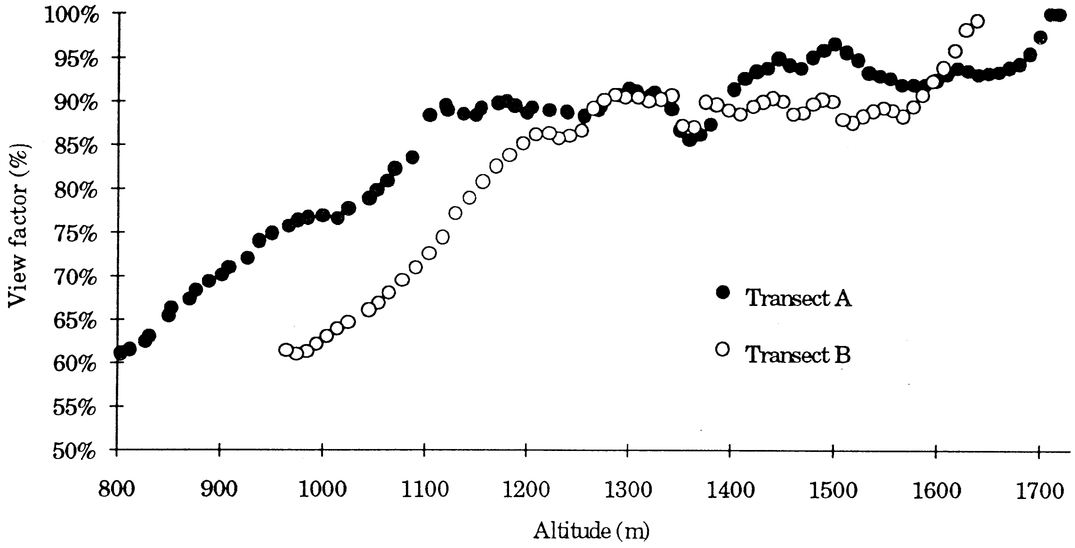


Figure 5.2. View factor (proportion of the sky hemisphere unobstructed by topography) estimated by computer simulation for both transects.



5.4. Lithology

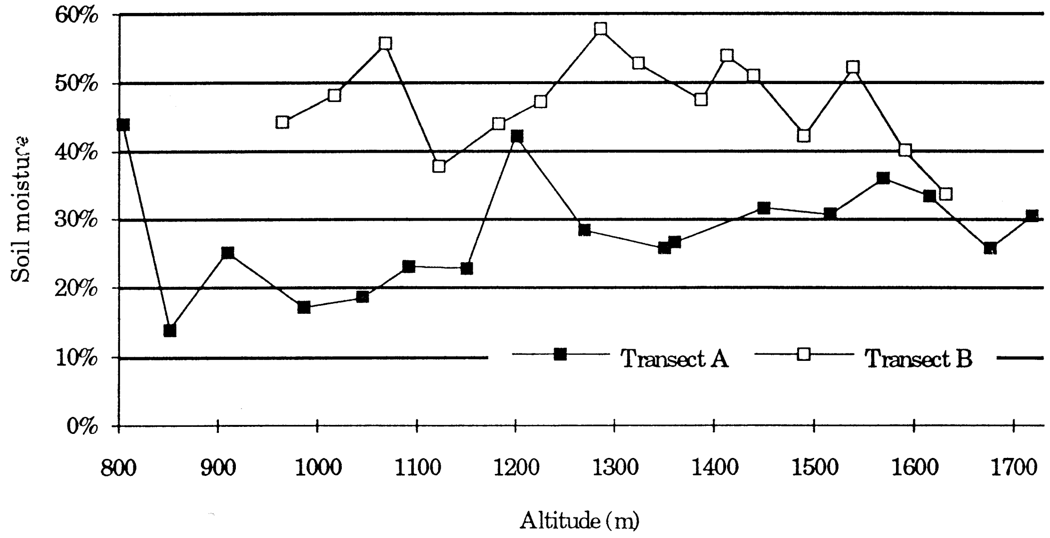
Subjective measures of 'rock cover' and 'rockiness' were recorded for most quadrats. The rock cover index was found to be inadequate for this purpose because of the effects of litter which may completely cover otherwise rocky areas. Rockiness was arbitrarily quantified on a five point scale. The results showed only broad scale variation apparently associated with slope angle and thus were considered no further. Future work may benefit from more appropriate measures of lithology.

5.5. Soil[12]

5.5.1. Moisture

As expected, Transect B (south facing) is more moist than Transect A (north facing) (Figure 5.3). Samples from Transect A were taken one day after uniform, heavy rain. Samples from Transect B were taken the following day. The different sampling times do not affect the above conclusion because they favour more pronounced evaporation of recent precipitation, and thus drier samples, to be exhibited on Transect B. The moistness of Transect B could be related to the physical water holding ability of the soil on that transect but is more easily explained by lower radiation experienced on south facing slopes, and hence lower evaporation. No clear, within-transect trends are evident (except for high moisture in the valley-bottom site for Transect A).

Figure 5.3. Soil moisture along each transect.



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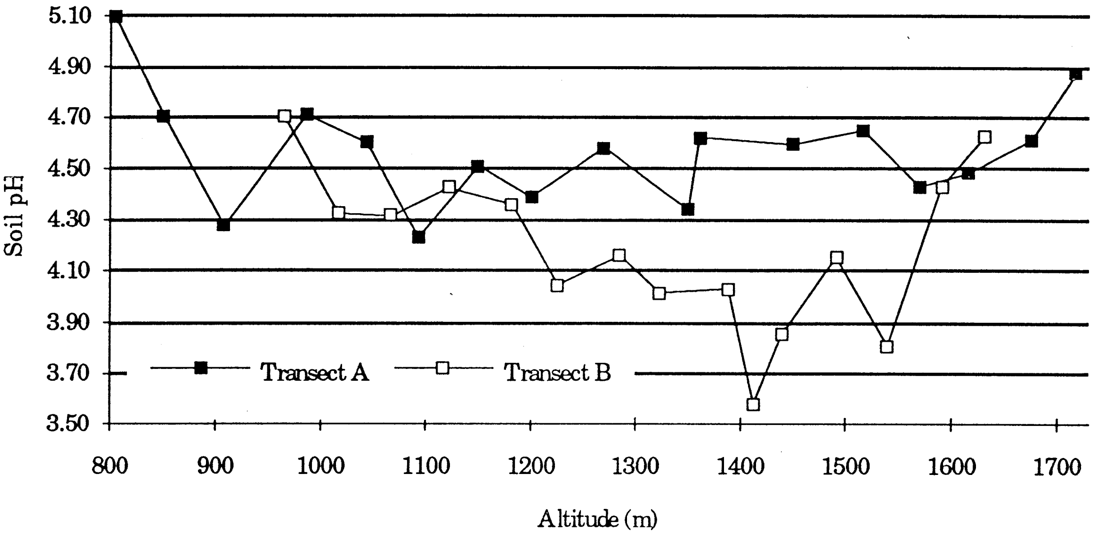
[12] Tabulated results corresponding to the graphs presented in this section appear in Appendix 3.

5.5.2. pH

The results of soil pH analysis (Figure 5.4) reveal that all the soils of the two transects may be regarded as 'strongly acidic' (Leeper & Uren 1993, p. 191); generally more so than has been found in previous studies of similar southeast Australian subalpine and montane forest soils[13] (Adams 1984, Adams & Attiwill 1986, Ellis & Graley 1987, Feller 1980). The soils of Transect B are generally more acidic than those of Transect A and within both transects there is a trend towards greater pH at the higher and lower extremes.

Figure 5.4. 1:5 soil slurry pH along each transect.



5.5.3. Major exchangeable cations

Concentrations of major exchangeable cations along the transects (Figures 5.5 and 5.6) agree in range with results obtained for similar southeast Australian subalpine and montane forests (Adams 1984, Adams & Attiwill 1986, Ellis & Graley 1987, Feller 1980) with the exception of exchangeable potassium which is higher in the present study. The results are highly variable between sampling sites. Limited, duplicate analyses suggest that whilst some of the variation can be attributed to random analytical error, most is inherent in the samples. Some sites (e.g. at 1539m on Transect B) exhibit anomalously high values for all four cations. It is likely that too few sub-samples were collected at each site to eliminate the effects of local heterogeneity of surface soils.

Almost no difference in general nutrient status is observed between the transects. In Transect A, Na^+ and Mg^{2+} are much more concentrated near the valley bottom than elsewhere.

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[13] Ellis and Graley (1986) used a 1:2 soil slurry in H_2O, Feller (1980) used 1:1 in H_2O and 1:2.5 in $CaCl_2$ (lower values), whereas a ratio of 1:5 in H_2O was used in the present study.

A similar pattern is present in Transect B for Ca^{2+} and Mg^{2+}. Above the valley bottom, Ca^{2+} maintains roughly constant concentration with increasing altitude whilst K^+ and Mg^{2+} decrease slightly and Na^+ increases slightly.

Figure 5.5. Major exchangeable cations adsorbed onto exchange sites in samples from Transect A.

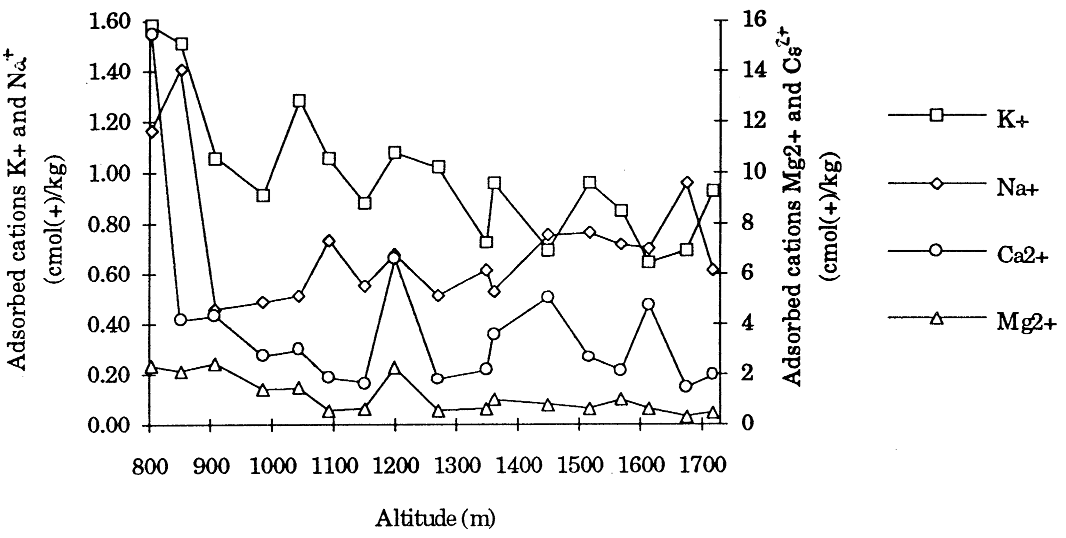
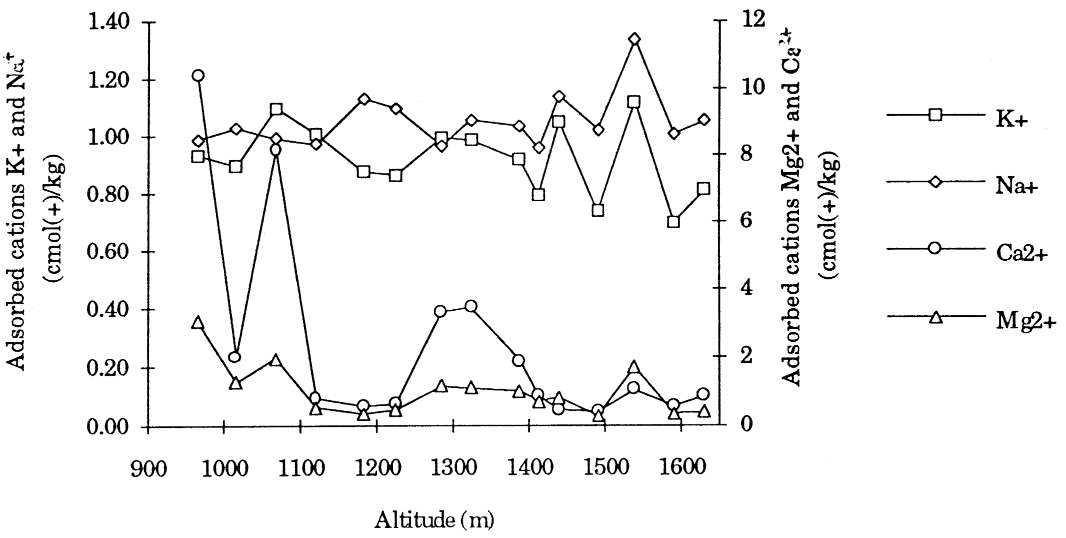


Figure 5.6. Major exchangeable cations adsorbed onto exchange sites in samples from Transect B.



5.5.4. Cation exchange capacity

As expected for acid soils, C.E.C on both transects (Figures 5.7 and 5.8) is largely comprised of exchange acidity. All values are in the range 20-45 cmol(+)kg^{-1} and agree with the studies cited in Section 5.5.3.[14]. There are no major differences in C.E.C. between the two transects and no major trends observed within each transect. The fact that at least slight trends have been observed in other soil variables but that C.E.C. is roughly constant suggests that C.E.C. may not be an appropriate summary variable to incorporate into a discussion of the soils of the study area. The soils in question display generally lower pH than has been reported previously in the literature (*op cit*) so the question is raised as to whether measurement of C.E.C. is of any use when dealing with strongly acidic soils because of the inherently increased saturation of exchange complexes with H^+ ions.

Figure 5.7. Cation exchange capacity (C.E.C.) of soil samples along Transect A derived as the sum of major exchangeable cations (total major exchangeable cations, T.M.E.C.) and exchange acidity.

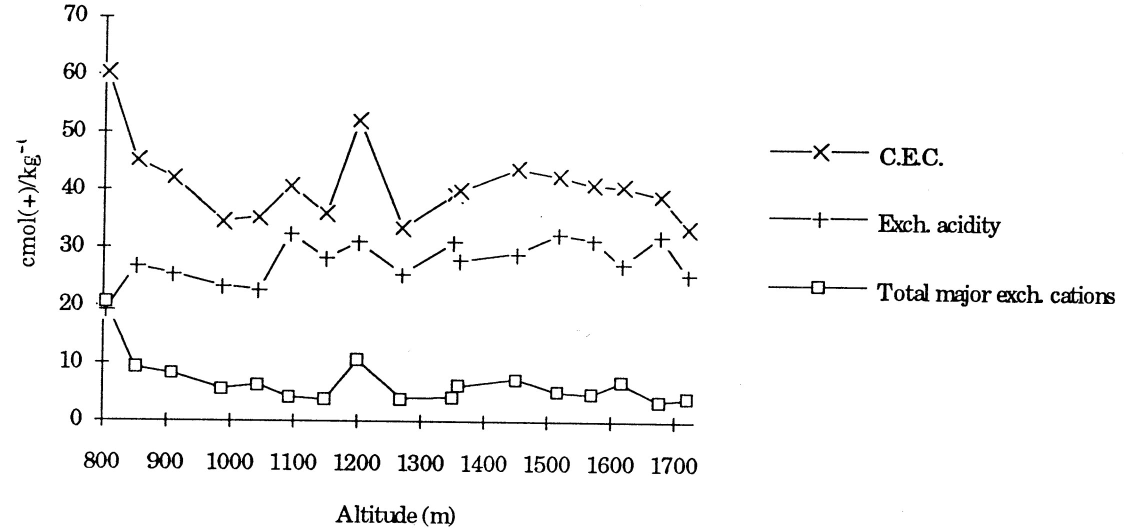
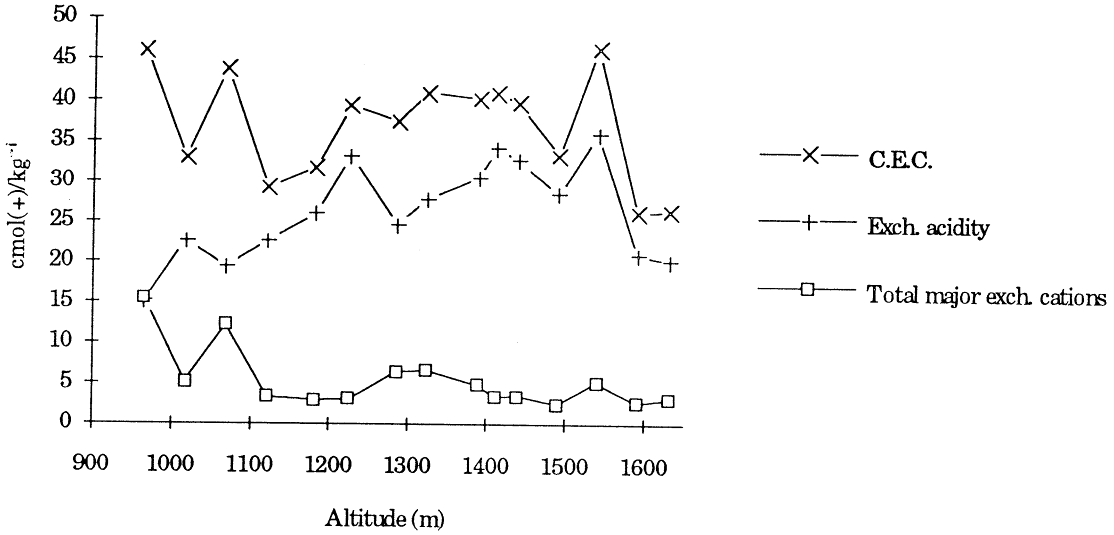


Figure 5.8. Cation exchange capacity (C.E.C.) of soil samples along Transect B derived as the sum of basic cations and exchange acidity.



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[14] *Detailed* comparisons with these other results are invalidated by differences of method (Gillman *et al* 1983).

5.6. Correlation of environmental and vegetation data

Environmental variables were numerically analysed for correlation with vegetation patterns in two ways: 1) where individual soil variables were submitted for analysis; and 2) where soil summary variables were submitted (along with non-soil variables). In each of the four analyses (Table 5.1), a harmonic rank correlation (H.R.C.) coefficient of 0.78 was obtained (where a maximum of 1.0 represents perfect rank correlation). This value is comparable to the values (0.79, 0.80, and 0.86) achieved by the originators of the method (Clarke & Ainsworth 1993) using environmental variables which correlated well with biotic data. The relative contributions of each variable toward obtaining the stated coefficient appear in the columns of Table 5.1. These values indicate *the extent to which each variable accounts for variation in vegetation composition* (given the achieved H.R.C.). Note that whilst this modification of Clarke and Ainsworth's method (1993) allows for the contribution of each variable to differ, it retains the constraint that each variable is assumed to have constant influence across all sites. For example, the method could not specifically reveal the influence of a variable that is only biologically significant at the valley-bottom (unless of course that variable only varied at the valley-bottom and was constant elsewhere). Thus, the results of correlation analysis are presented only as a guide to better-informed, manual interpretation.

In each analysis, altitude accounts for the greatest proportion of the achieved correlation, especially in Transect A. Soil pH is consistently the next most significant factor accounting for between a third and half the variation which is accounted for by altitude. In the analyses using individual soil variables, Ca^{2+} is significant along Transect A and Mg^{2+} is significant along Transect B. In analyses using soil summary variables, total major exchangeable cations (T.M.E.C.) accounts for more of the achieved correlation than cation exchange capacity (C.E.C.) which, as suggested in Section 5.5.4., is not considered to be useful here. Slope is significant along Transect B.

Table 5.1. Harmonic rank correlation between environmental and standardised vegetation data. Each column contains the proportions (*i.e.* relative standard deviations) of each environmental variable which were combined to achieve the maximum correlation coefficient shown at the bottom of the column. Note that soil variables were linearly interpolated between soil sampling sites to obtain a value for each vegetation sampling site.

	Using 10 variables		Using 7 variables	
Environmental variables	Transect A	Transect B	Transect A	Transect B
Altitude	65 %	42 %	57 %	44 %
View factor	0 %	0 %	4 %	1 %
Slope	3 %	12 %	4 %	13 %
Aspect	0 %	7 %	0 %	8 %
Soil pH	19 %	20 %	17 %	22 %
Soil K^+	5 %	1 %	-	-
Soil Na^+	11 %	0 %	-	-
Soil Mg^{2+}	11 %	14 %	-	-
Soil Ca^{2+}	17 %	3 %	-	-
Soil exch. acidity	9 %	3 %	-	-
Soil T.M.E.C.	-	-	15 %	12 %
Soil C.E.C.	-	-	10 %	0 %
H.R.C. coefficient	.78	.78	.78	.78

Whilst the observed correlations do not imply causality; they suggest which environmental factors directly influence vegetation distribution, and are used in the next chapter to support an informal explanation of the three key features of vegetation distribution noted in the previous chapter (Section 4.4.).

5.7. Summary

It is re-iterated from sections 3.2.1. and 3.2.2. that the two transects surveyed in this study were chosen to exhibit little environmental variation other than that directly related to altitude. In general, this aim has been met. Exceptions lie within 100 m of the bottom of the transects and within a few tens of metres of the ridge-tops. This leaves 830 m on Transect A and 615 m on Transect B within which few secondary influences are suspected. Soil acidity varies unimodally along Transect B with a peak at the interface between *Eucalyptus pauciflora* and *E. delegatensis* in the canopy. Given the correlation between pH and vegetation distribution, this pattern deserves investigation in future work.

Between the transects, significant differences were recorded in aspect (hence radiation), soil moisture, and soil pH. These differences as well as the probable difference in recent fire history between the transects may explain the general compositional dissimilarity observed between the transects (*c.f.* Gill 1993, p. 214). In spite of this, a structurally similar pattern of vegetation change is exhibited along the altitudinal gradient of both north and south facing slopes.

Numerical correlation of environmental variables with plant community patterns was undertaken as an aid to manual inspection of the data. Altitude 'accounts' for most of the variation in vegetation but soil pH, and certain exchangeable cations are also significant. It is acknowledged that these results do not imply causality.

Chapter 6. Discussion and conclusion

6.1. Introduction

This chapter centres on a discussion and response to the principal aims of the work stated in Section 1.2. The results of the previous two chapters are interpreted and related to the literature and the chapter closes with a conclusion on the findings of the thesis and their applicability to the understanding of Australian mountain vegetation as a whole.

6.2. Findings of Aim One. Examination of community patterns

Three key features are observed in the distribution of vegetation in the study area with respect to altitude. 'Feature A' is a general, unidirectional correlation of compositional change with altitude - a continuum. 'Feature B' is the existence of compositionally distinct communities near the valley-bottoms and ridge-tops. 'Feature C' is the existence of a discontinuity (at 1430 m on north facing slopes and 1340 m on south facing slopes) in the otherwise continuous altitudinal sequence of compositional change exhibited within the main body of vegetation.

Whilst Feature A and Feature B are accepted characteristics of vegetation distribution in mountainous areas, Feature C has rarely been reported in the literature on the Australian Alps. This is possibly due to the limited range of environmental variation studied by other workers. For example, Hogg and Kirkpatrick (1974) found a continuum of change over an altitudinal range of 545 m in southeast Tasmania. Continua were also found over small environmental ranges by Gullan (1978) at Cranbourne in Victoria and Ashton (1976) at Mount Piper in Victoria. The 'discontinuity in a continuum' found in the present work is not at variance with the continua presented in the literature but is an expansion of the findings of these workers.

Moderate similarities in composition exist between north and south facing slopes, and these are most pronounced between sites separated by approximately 100 vertical metres. This pattern is identified in the mid-latitudes of both North America and Europe by Holland and Steyn (1975) who cite altitudinal shifts in the order of 300 m between opposing aspects. In Australia, a 200 m shift is reported for treelines in the mainland Alps (Slatyer 1989) and a shift of similar magnitude is inferred from Kirkpatrick and Brown (1987) for alpine vegetation in southwest Tasmania.

The hypotheses of Aim One are re-stated from Chapter 1.:

H_0: Compositional change of vegetation along the altitudinal gradient is continuous and no 'communities' are recognisable.

H_1: Species composition is arranged along the altitudinal gradient such that 'communities' are recognisable (due to correlated distributions of species), each being separated by short zones of rapid change (ecotones).

Feature A lends support to H_0 as a general statement but this is largely countered by Feature B and Feature C which support H_1. H_0 is true only to the extent that a general, unidirectional trend of compositional variation with respect to altitude is the dominant regime of vegetation change along the transects. Support for H_1 depends on the consideration of an important, if semantic, issue. The term 'altitudinal gradient' may refer to altitude in the geographic sense or in the sense of environmental variables which correlate with altitude irrespective of local geography. In the geographic sense, the distinctly separate community formation shown near the valley-bottoms and ridge-tops of the study area (Feature B) is valid evidence in support of H_1. If the second, environmental, interpretation is taken, these communities do not strictly occur with respect to the 'altitudinal gradient' because non-altitudinally related environmental influences are present in these locations. Immediately, this is of little consequence because of the presence of Feature C where community formation is observed with respect to both forms of 'altitudinal gradient' and non-altitudinal variation is absent across the ecotone between the communities. The pattern is weakened but still present when dominant species are considered to be equally important to less abundant species. To conclude, this research has shown that the alternative hypothesis (H_1) of Aim One is favoured.

6.3. Findings of Aim Two. Explanation of community patterns

The first key feature of vegetation distribution (Feature A), a correlation of vegetation change with altitude, was observed in shade diagrams, ordinations, and correlation analysis. An explanation for this correlation rests simply with the biologically significant environmental variables which vary with altitude, particularly temperature.

A number of environmental variables offer explanations of Feature B (the separation of the valley-bottom and ridge-top sites from the main body of sites). View factor decreases significantly within approximately 300 m of the valley-bottom but this range does not align with the compositional separation of valley-bottom sites (within about 60 m of the river) and very little significance was attributed to view factor in correlation analysis. Soil pH is high in valley-bottom and ridge-top sites, a pattern which matches Feature B and is supported by the correlation analysis. Thus a probable link exists between vegetation composition and the complex chemistry of soil acidity. The two major exchangeable cations which best accounted for correlation with vegetation data (Ca^{2+} along Transect A and Mg^{2+} along Transect B) were those which most clearly exhibited a distinct peak in the lowest soil sampling site. Thus, they too present a possible link with Feature B, as does the associated summary variable, 'total major exchangeable cations' (T.M.E.C.). Valley-bottom sites may also experience temperature inversions (in the order of whole degrees Celsius in magnitude) as a result of orographically related winds (Linacre 1992, p. 318; Barry 1992, pp. 158-89) which thereby provide a further explanation for the distinct valley-bottom vegetation type. Variation in soil drainage conditions can not provide a complete explanation for the pattern because soils are well drained on all sites but the lowest and riparian (valley-bottom) vegetation is observed a number of sites higher than this. To conclude, variations in soil pH, soil nutrient status, and temperature all provide possible explanations for the distinct composition of vegetation near the valley-bottom but drainage conditions, if at all, are only significant in the immediate vicinity of the river.

The characteristic vegetation of the ridge-top sites is undoubtedly influenced by high exposure to the elements. Strong winds structurally inhibit the growth of trees (Snow Gum) so an ameliorated climate for shrubs and herbs is therefore lacking (McDougall 1982, p. 12). An altered temperature regime also occurs (Linacre 1992, p. 80).

An explanation for Feature C, the discontinuity within the main body of sites, is not offered by any of the environmental variables quantified in Chapter 5. All these variables are roughly constant or vary only slightly across the discontinuity (at 1430 m along Transect A and 1340 m along Transect B). Other variables remain to be considered. It is unlikely that geological variation can be called to account for the discontinuity because the same pattern occurs at similar altitudes on both transects (as shown by shade diagrams and ordination of combined vegetation data) and it is improbable that *identical* geological influences are present in these two locations. The biological influence of canopy species is also unlikely because boundaries in canopy composition (determined by climate and intra-canopy competition -Williams 1990; Ashton 1981) do not coincide with the discontinuity in the understorey (Feature C). Possible explanations are offered in terms of climatic history, fire history, and biological influence from within the understorey as follows.

Climatic history offers a possible explanation for the discontinuity *via* the downward migration of vegetation during periods of glaciation. During the glacial oscillations of the Pleistocene, plant species extinction is hypothesised to have occurred as lower adapted species were 'forced' into the sea by global cooling. In the intervening warmer periods (*i.e.* the present) lower regions are vegetated by species which are adapted to the extinction/speciation regime and higher regions maintain the original and separate flora. The (hypothetical) resulting altitudinal division of vegetation types is suggested to explain diversity patterns in central

Tasmania (Ogden & Powell 1979) and community patterns in southwestern Tasmania (Kirkpatrick & Brown 1987) and New Zealand (*c.f.* Druitt *et al* 1990). Both these patterns are found in the present study area[15]. The present Victorian distribution of 'relic' stands of *Eucalyptus pauciflora* (Snow Gum) at low altitudes, over a vertical kilometre from the current lower limit of subalpine *E. pauciflora* (Williams & Ladiges 1985), indicates that glacial oscillations of the temperature regime have been severe enough for patterns described above to be evidenced in present day Victorian subalpine vegetation (*c.* 1400 m A.S.L.). The possible relationship between changing Pleistocene climate regimes and the presently observed discontinuity (Feature C) requires further investigation.

Possible explanations for the discontinuity are offered in terms of fire history and biological factors, both of which involve the influence of dominant species. In Chapter 4 it was observed that clustering into 'upper' and 'lower' sites on each transect, whilst weakened, was still present after the data were standardised to equalise the influence of all species on the observed patterns. Thus the two clusters of composition in the altitudinal sequence, with a discontinuity between them, are a feature of the entire composition of vegetation and not just that of the dominant species (e.g. *Daviesia latifolia*, *Oxylobium alpestre*). However, the pattern is most clearly observed in the distributions of the dominant species and thus it is possible the discontinuity in overall species composition is a response by smaller species to differential influences associated with the dominant species. These influences may involve a difference in susceptibility to fire between a sparse understorey (beneath *Daviesia latifolia*) and a dense, fuel rich understorey (dominated by *Oxylobium alpestre* and various grasses) (*c.f.* Ashton & Williams 1989, p. 145). Fire disturbance may also be related to other environmental gradients (Harmon *et al* 1983). Alternatively a biological influence may be possible through microclimatic and edaphic mechanisms. Structurally, *Daviesia latifolia* is a tall, open shrub which may affect the microclimate (e.g. wind, light) of smaller species in a different way to *Oxylobium alpestre* which is a low, dense shrub. Many rosette herbs grow in the insulated environment amongst the branches of *O. alpestre* (*c.f.* McDougall 1982, p. 7). Edaphic influences could occur through differences in nutrition from leaf litter between the dominant species although, at least with respect to litter from canopy species, although the work of Wilson and Zammit (1992) shows this to be unlikely. Some doubt is thrown on all forms of biological association by the work of Austin and Nicholls (1988) who found no evidence for inter-specific competition or co-adaptation in a eucalypt forest of southern New South Wales.

In summary, two of the three key features of vegetation distribution noted in Chapter 4 can be explained by environmental variation. Feature A, a correlation with altitude, is explained by

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[15] Diversity patterns were analysed by this author but, for brevity, are not presented here.

climatic phenomena which relate directly to altitude. In the study area, the most notable of these is the difference in mean temperature between the upper and lower altitudes in the order of 7° C. Feature B correlates well with observed increases in soil nutrient status and pH, as well as possible temperature inversions near the valley-bottom. Explanation of the pattern thus rests with the obvious differential influence of these factors on the survival of plant species. The reasons for the observed differences in fertility in lower sites are unclear: leaching of nutrients to lower sites may occur or, alternatively, a biological influence may be enforced by dominant species. Feature C, that most relevant to the theory of plant communities, is not explained by any of the variables considered in Chapter 5. A number of suggestions are made as to the reason for a discontinuity in the altitudinal sequence of vegetation composition. Climatic oscillations associated with periods of glaciation have been implicated by a number of authors in explanations of similar patterns. Also, differences in fire regime caused by structural differences in dominant understorey species may be significant as may biological/microclimatic influences and biological/edaphic influences, although previous work finds against these latter two mechanisms. The matter is one for speculation which necessitates further study directed specifically at this problem.

The hypotheses of Aim Two are re-stated from Chapter 1.:

H_0: There is no clear relationship between changing species composition and environmental factors.

H_1: Vegetation changes along the altitudinal gradient correlate with measurable changes in environmental conditions which are likely to be causal.

It has been shown that measurable changes in environmental conditions (H_1) such as temperature and soil fertility account for most of the variation in vegetation composition along the altitudinal gradient - specifically, Feature A and Feature B. The likely causality of these factors is inferred from established ecological knowledge regarding the influence of factors such as temperature and soil fertility on plant survival. At this stage, H_0 is also valid to the extent that Feature C remains unexplained. It would be beneficial in further research to examine the factors which control the environmental variation which has been brought into play in this discussion. The current work only seeks to acknowledge the presence of (likely) causal environmental influences and not to explain their existence in turn.

6.4. Conclusion

The aims of the work have been met successfully. In practical terms, a number of areas involved novel methods. View factor was simulated successfully and results show distinct trends (although correlation analysis does not show view factor to be important). A modification to a developing method of nonmetric correlation analysis was conceived with the result that significantly greater use could be made of correlation analyses than would be possible with published methods. Most importantly, the decision to survey a large number of vegetation sites within a narrow range of environmental variation has enabled more detailed investigation of the altitudinal gradient than has previously been published in Australia.

Theoretical success has come with the satisfaction of the two main aims of the work. The findings are pertinent to the greater knowledge of Australian plant biogeography. Whilst the work was conducted within the confines of a single valley, it applies to a flora, climate, and geology which are found throughout the Victorian mountain region (Costermans 1983). There is every reason to expect that the findings will thus be applicable throughout this region.

With respect to geographic variation in altitude, the composition of Victorian mountain vegetation is predominantly determined by altitudinally-related factors. Exceptions to this rule occur near valley-bottoms where other climatic and edaphic factors are significant, and near ridge-tops where climatic factors are significant. Within the remaining, main body of vegetation, historical or biological influences appear to be active near the interface between the subalpine and montane regions (*c.* 1300-1450 m A.S.L.). The evidence for this is the observation of a discontinuity in the sequence of compositional change in the absence of external environmental influence.

This thesis presents some of the only work that has examined the theoretical nature of plant communities along the altitudinal gradient in Australian mountain vegetation. As stated in the introduction, the existence of both communities and continua is acknowledged globally by modern plant community theoreticians. The present work contributes to the Australian element of this understanding in finding that altitudinal distribution of vegetation in the Victorian montane and subalpine region exhibits a 'community within continuum' pattern.

Recommendations

Throughout the course of the current work, certain presently untenable requirements arose which should be considered by those undertaking future research of a similar nature:

- An effort should be made to survey the vegetation during spring when many species of the genus *Poa* exhibit reproductive material which is necessary for their identification.
- Significant improvement to the assessment of climatic influences could be made by use of modern bioclimatological modelling techniques (Moore *et al* 1993).
- Soil survey and analysis requires great effort but should be undertaken as thoroughly as possible to alleviate the effects of local heterogeneity which may have influenced the results of the present work. An assessment of inter-specific biological influence would benefit from analysis of nitrogen and phosphorus in addition to the elements covered here.
- Once a 'main body' of sites unaffected by secondary influences has been isolated, these sites should be submitted separately for multivariate analysis. This would enable a much more accurate understanding of distribution patterns solely with respect to the primary gradient (in this case altitude).
- A full understanding of the processes affecting plant distribution should include an explanation of the distribution of environmental heterogeneity, not just an acknowledgment of its existence as an explanation for vegetational heterogeneity (as was presented here).

Appendix 1. Computer simulation of view factor

View factor (proportion of the sky hemisphere unobstructed by topography) was simulated by calculation of the horizon visible from each point on a grid of 125 m x 125 m cells overlain on the study area as follows:

A 20 km x 20 km digital terrain model (D.T.M.) of the topography was manually entered at 1 km resolution and then smoothed using bi-quadratic interpolation to yield a D.T.M. at 500 m resolution. Terrain data was manually updated in the new model only for (critical) cells in the vicinity of the transects. The process was repeated to yield a 125 m x 125 m D.T.M.

The visible horizon was calculated for each cell in the D.T.M. as follows. For each subject cell, the elevation and azimuth to every other cell was calculated and recorded if no other cell subtended a greater elevation at that azimuth. Thus the elevation of the highest point on each azimuth (quantised to 1° intervals) was determined. Considering these horizon points as lying on a hemisphere centred on the subject cell, the surface area above the horizon points was summed relative to the total hemispherical surface area thus yielding the view factor.

To derive view factor values at each site along both transects, the location of the transects was overlain on the D.T.M. and the view factor at each site (located by altitude) was determined by bi-quadratic interpolation of view factors from the nine surrounding D.T.M. cells. The interpolation process removed most but not all of the quantisation error inherent in the coarse sampling grid.

The software used for this simulation was written by the author in the C++ programming language running under Microsoft Windows 3.1 on an Intel 80486 machine.

Appendix 2. Laboratory procedure for soil chemical analysis

The method of soil cation analysis employed in the present work yields an estimate of cation exchange capacity (C.E.C.) via the sum of the basic exchangeable cations and exchange acidity. The method is based on those of Gillman and Sumpter (1986) and Hart *et al* (1986).

100 ml 0.1N $BaCl_2/NH_4Cl$ solution is mixed with 10g fine-earth. The resulting slurry is shaken, orbited, and washed with the above solution through Whatman's 541 filter paper. At this stage, all previously adsorbed cations should be in solution in the leachate which is diluted to 250 ml with H_2O. Standard Na^+, K^+, Ca^{2+}, and Mg^{2+} solutions are made in H_2O at the appropriate concentrations. After constructing calibration curves, Na^+ and K^+ concentrations in the leachate are determined using a Flame Spectrophotometer and Ca^{2+} and Mg^{2+} concentrations are determined using an Atomic-absorption Spectrophotometer (A.A.). Dilutions of the leachate is required for some analyses. Exchange acidity is determined by titration of the leachate with 0.01N NaOH solution to a given pH - in this case pH 8.5.

All basic cation, exchange acidity, and C.E.C. results are given in the S.I. unit $cmol(+)kg^{-1}$ (Attiwill and Leeper 1987, p. 16). Values for Na^+, K^+, Ca^{2+}, and Mg^{2+} are calculated from the determined ionic concentrations by accounting for dilution factors, fine-earth sample weight, and the atomic weight and valency of the cation in question. Values for exchange acidity are similarly calculated as the number of cmol OH^- required to bring the leachate to pH 8.5 (by addition of a 0.01N solution). The total C.E.C. of the soil is estimated as the sum of the basic cations and the exchange acidity.

As well as H^+, Al^{3+} ions comprise a large portion of exchange acidity in acid soils. A number of attempts were made to analyse for Al^{3+} using both an A.A and a Flow Injection Analyser (F.I.A.). These were unsuccessful due to difficulties with the method and the instrumentation.

Appendix 3. Numerical soil analysis results.

Table A3.1. Numerical results of soil analyses (refer to Section 5.5.). Units of all cation results are cmol(+)kg^{-1}.

Altitude (m)	pH	Moisture (% weight)	K^+	Na^+	Mg^{2+}	Ca^{2+}	T.M.E.C.	Exch. acidity	C.E.C.
965	4.7	44%	0.9	1.0	3.0	10.4	15.4	15.2	45.9
1017	4.3	48%	0.9	1.0	1.3	2.0	5.2	22.7	33.0
1068	4.3	56%	1.1	1.0	2.0	8.1	12.2	19.4	43.8
1121	4.4	38%	1.0	1.0	0.5	0.8	3.3	22.6	29.2
1182	4.4	44%	0.9	1.1	0.3	0.6	2.9	26.0	31.8
1225	4.0	47%	0.9	1.1	0.5	0.6	3.1	33.3	39.4
1285	4.2	58%	1.0	1.0	1.1	3.3	6.4	24.6	37.4
1323	4.0	53%	1.0	1.1	1.1	3.5	6.6	27.8	40.9
1388	4.0	47%	0.9	1.0	1.0	1.9	4.9	30.5	40.2
1413	3.6	54%	0.8	1.0	0.7	0.9	3.4	34.2	40.9
1439	3.9	51%	1.0	1.1	0.8	0.5	3.5	32.6	39.6
1491	4.2	42%	0.7	1.0	0.3	0.4	2.5	28.4	33.3
1539	3.8	52%	1.1	1.3	1.7	1.0	5.2	36.0	46.3
1590	4.4	40%	0.7	1.0	0.4	0.6	2.7	20.8	26.1
1631	4.6	34%	0.8	1.1	0.4	0.9	3.1	20.1	26.2
804	5.1	44%	1.6	1.2	2.3	15.5	20.6	19.3	60.4
851	4.7	14%	1.5	1.4	2.1	4.1	9.2	26.8	45.2
909	4.3	25%	1.1	0.5	2.4	4.3	8.2	25.6	42.0
986	4.7	17%	0.9	0.5	1.4	2.7	5.5	23.5	34.6
1045	4.6	18%	1.3	0.5	1.5	3.0	6.2	22.8	35.2
1093	4.2	23%	1.1	0.7	0.6	1.8	4.2	32.3	40.7
1150	4.5	23%	0.9	0.5	0.6	1.7	3.7	28.3	35.7
1200	4.4	42%	1.1	0.7	2.3	6.6	10.6	30.9	52.1
1270	4.6	28%	1.0	0.5	0.6	1.8	3.9	25.6	33.3
1350	4.3	26%	0.7	0.6	0.6	2.2	4.1	30.9	39.2
1360	4.6	27%	1.0	0.5	1.0	3.6	6.1	27.8	39.9
1450	4.6	32%	0.7	0.8	0.8	5.0	7.3	29.1	43.6
1516	4.7	31%	1.0	0.8	0.6	2.7	5.0	32.3	42.4
1570	4.4	36%	0.9	0.7	1.0	2.2	4.7	31.5	40.9
1615	4.5	33%	0.6	0.7	0.6	4.7	6.7	27.2	40.6
1675	4.6	26%	0.7	1.0	0.3	1.5	3.5	32.0	38.9
1718	4.9	30%	0.9	0.6	0.5	1.9	4.0	25.6	33.5

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Vegetational continuity or discontinuity along altitudinal gradients?
A review of international theory and Australian practice.

Fred Watson

Introduction

Within community ecology, a lively debate has been in progress since the turn of the century on the question of whether vegetation communities are real, or simply abstractions of our observation. This debate is often referred to as the 'community versus continuum' debate (hereafter - CVC). In the first section of this review, the fundamental concepts of CVC are introduced and key publications involved in its development are dealt with chronologically. In the second section, experimental work on patterns of altitudinal variation in vegetation is discussed with an emphasis on the Australian situation.

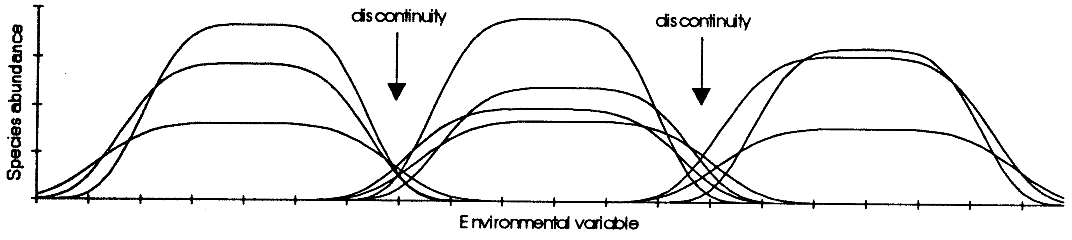
The community versus continuum debate

The CVC debate centres around the common observation that 'types' of vegetation can be recognised on the basis of their characteristic floristic composition (i.e. that one can say the vegetation throughout a given area is of *type* X). In North America, the ideas of Clements set out in three lengthy monographs (Clements 1916, 1920; Clements *et al* 1929) are usually cited as the origin of the debate. Clements asserted that a community is a super-organism which has evolved and adapted over time (like other organisms) and that a community is a natural unit (i.e. it has boundaries beyond which we can recognise other communities). These assertions represent one extreme of the debate. The other extreme was independently provided by both Gleason (1926, 1939) in the United States and Ramensky (1926, 1930) in the Soviet Union. These authors claimed that a community is 'merely a *coincidence*' (Gleason p. 16) of species - each acting as individuals with their own particular requirements for survival and growth. The ideas of this time are often aligned within a dichotomous framework defined by the 'community-organism hypothesis of Clements' and the 'individualistic hypothesis of Gleason'.

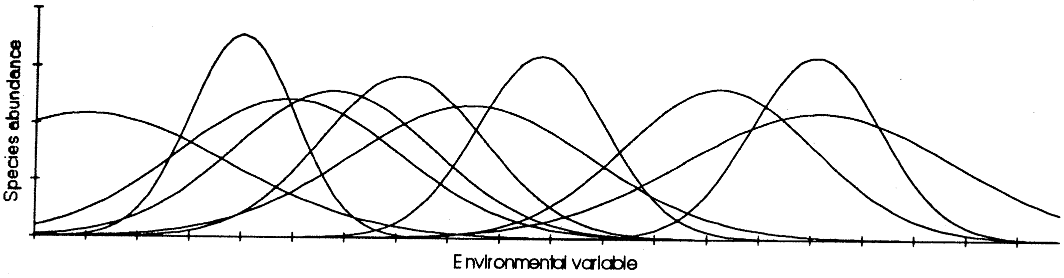
Given each of the hypotheses above, expected patterns of species abundance (response curves) along an arbitrary environmental gradient can be graphed as in Figure 1. (after Austin 1985). Of key relevance to this review is that *discontinuities* in floristic composition as shown in Figure 1 a) are generally considered to be evidence for the organismic-community hypothesis. No such discontinuities occur in Figure 1 b) which displays a *continuum* pattern.

Figure 1. Expected patterns of species abundance along an arbitrary environmental gradient given a) the organismic-community hypothesis; and b) the individualistic-hypothesis (after Austin 1985). In a), species abundances are aligned into communities. In b), each species responds independently to the environmental gradient.

a) Expected species responses according to organismic hypothesis - discontinuities between communities



b) Expected species responses according to individualistic hypothesis - a continuum



Across the atlantic the seminal statements of Ramensky were joined by those of Braun-Blanquet (1928, 1932, 1951, 1964) amongst many others. The Braun-Blanquet approach to vegetation science dealt predominantly with 'associations' as a unit of study (Westhoff & Van der Maarel 1973). 'Associations' were recognised on the basis of character species of high environmental 'fidelity'. Recognition of the heterogeneity of associations, whilst acknowledged, was implicitly a secondary issue and was never tested.

A more experimental phase in the CVC debate began with the work of Curtis and his colleagues in Wisconsin. The word 'continuum' was introduced as the expression of individualistic phenomena along environmental gradients (Curtis and McIntosh 1951). Subsequent work on montane vegetation sequences in the United States by Whittaker (1956, 1960), Bray and Curtis (1957), and Curtis (1959) is fashionably used as definitive evidence of the existence of continua (c.f. textbooks cited below). Daubemire (1966) has argued against such use. Nevertheless, these works have stimulated plant community theory more than any others.

By the 1960's, an extensive literature relating to CVC had been published and synthesis was required. Odum (1959) provided a limited summary in the second edition of his textbook. Major (1961a, b) exposed the parallel expansion of European literature to the English speaking world with a translation of a review by Ponyatovskaya (1959). Three large reviews followed which remain prominent today (Whitttaker 1962, 1967; McIntosh 1967). These specifically summarize classification, gradient analysis, and evidence for the continuum hypthesis respectively. No author was prepared at the time to integrate these concepts at a large scale in a review of the CVC debate *as a whole*.

In modern reviews of 1960's community theory, Daubenmire (1966, 1968) is consistently cited as a relatively solitary advocate of organismic-community ideas. Daubenmire (1966) criticised the loose sampling methods and site selection of the Wisconsin school (Curtis, McIntosh *et al*) in favour of his own; whereby he found discontinuity along a gradual environmental gradient and hence evidence supporting the organismic-community hypothesis. He suggested that ignorance of vegetation dynamics may lead the researcher to prematurely conclude the existence of continua. This position was also stressed by Langford and Buell (1969).

Settlement of the CVC debate has involved some form of compromise between Clementsian and Gleasonian extremes. Statements to this effect have gradually emerged throughout the life of the debate. A range of these (selected from ecology textbooks) appears below:

> '...a continuum does not continue indefinitely; sooner or later... a natural discontinuity is produced.' Odum, 1959, p. 255.
>
> 'It is apparent to many ecologists that under some conditions vegetation forms a continuum, under other conditions it forms discrete communities, and that most vegetation is somewhere between.' McNaughton & Wolf, 1973, p. 563 (Quoting Beals, 1969).
>
> 'Familiar assemblages occur because many plants physically affect the places in which other plants must live,... but the environment, acting on individuals, is the decisive factor in constructing a community' Colinvaux, 1973, p. 70.
>
> '...there seems to be general agreement now that a concrete, regional vegetation cover may show both, discontinua or sharp boundaries and gradually changing patterns or continua.' Mueller-Dombois & Ellenberg, 1974, p. 29.
>
> 'The information available leans toward the individualistic interpretation of the community.' Krebs, 1985, p. 458.
>
> 'The safest statement we can make about community boundaries is probably that they do not exist, but that some community boundaries are more sharply defined than others.' Begon *et al*, 1986, p. 597.
>
> '...there is a marriage to be achieved between the realistic aspects of the climax notion... and the experimental approach of the individualists.' Crawley, 1986, p. 5.

> 'The nature of vegetational variation, however, hovers tantalisingly between these two extreme points of view.' Goldsmith, 1986, p. 501.

> 'The assemblage of species is not a natural unit in the sense that they are bound together by some obligatory relationship. But the assemblage does operate as a functional unit in [certain ways] just as the organismic advocates propose.' Smith, 1986, p. 446.

> 'I forecast that we will find that within both questions neither alternative provides the whole answer, for ecology deals with a mixture of pattern and probabilism.' Southwood, 1987, p. 21.

> 'There is enough evidence on both sides of this question to indicate that the individualistic/continuum and integrated/classification views are not alternatives, one of which must be wrong, but rather complementary, equally valid ways of viewing communities.' Brewer, 1988, p. 374.

> 'The separate concepts of both open and closed communities have some validity in nature.' ...but... 'Generally speaking, communities are not discrete units separated by abrupt transitions in species composition.' Ricklefs, 1990, p. 659 & 675.

In conjunction with the development of community theory, an extensive literature has recorded the theoretical development of ordination and classification techniques (Minchin 1987; Gauch *et al* 1981; Whittaker and Gauch 1978; Fasham 1977; Austin 1985). Kent and Ballard (1988) found that 27.5% of 734 surveyed articles relating to ordination or classification were devoted to the 'philosophy and method' of these techniques. Of key relevance to this review is that classification procedures force groupings within a data set to appear - even if they do not actually exist - whereas ordination procedures do not. The numerical corollary of a hypothetical organismic-community is a group, or cluster, of species in environment-space. Because classification techniques find groups regardless of the degree to which they occur, they are unsuited for the specific task of establishing the validity of either hypothesis in the CVC debate. Braun-Blanquet (*op cit*) exclusively used classification techniques and thus, his findings and those of his students are of no bearing in the CVC debate. It must be noted that ordination techniques are subject to certain assumptions which invalidate their use also as *conclusive* tools in the CVC debate (Minchin 1987, 1989).

By 1973, the CVC debate as originally described lay in the past (Whittaker 1973 p. 326, 1978 p. 4). 'Most plant ecologists now accept the continuum as an appropriate description of vegetation' (Austin 1990). Current research attempts to find statistically valid models for the study of continua (Austin, 1980). Gauch and Whittaker (1972) provided a statement of the underlying 'bell-shaped' response curve model perceived from Whittaker's earlier experimental work (1956, 1960). 'Few other papers on vegetation analysis can be said to have addressed vegetation theory in recent years' (Austin, 1987). Austin (Austin & Smith 1989) showed that the model of Gauch and Whittaker was inappropriate and produced a new model which awaits scrutiny by Academia.

Austin (1985, 1989) concludes that 'community is a spatial concept dependent on landscape pattern while the continuum is an environmental concept referring to an abstract space'. Thus, whilst continua are now accepted, no literature opposes the possibility that communities may manifest themselves in transects through real space. It is the nature of these communities, with respect to altitude, which is reviewed in the following section.

Expressions of the community versus continuum debate along altitudinal gradients

'Mountains are ideal places for the description and causal study of environmental responses of plant communities because short lineal distances cause large environmental changes' (Baruch, 1984). An ideal method with which this phenomenon may be studied is to observe plant communities as they change along altitudinal gradients in mountainous areas. Table 1 summarises selected work employing this method:

Table 1. A brief selection of literature specifically examining altitudinally based vegetation patterns. Localities are grouped by continent. Key to standardised species groups: *A = all vascular; E = Eucalypts; T = trees and canopy spp.; S = shrubs and/or ferns; H = herbs; V = vines and/or epiphytes; B = bryophytes; F = families.*

Author/s	Year	Region	Location	Species included	Range (approx)
Whittaker	1956	Temperate	East USA	A	550-2100m
Whittaker	1960	Temperate	West USA	A	450=1700m
Mark & Sanderson	1962	Temperate	New Zealand	?	?
Mark	1963	Temperate	New Zealand	T, S, H	0-1000m
Scott *et al*	1964	Temperate	New Zealand	A	150-1000m
Wells and Mark	1966	Temperate	New Zealand	T, S, H	0-1000m
Scott and Armstrong	1966	Temperate	New Zealand	H, V	0-1000m
Wilson *et al*	1990	Temperate	New Zealand	A	0-1400m
Druitt *et al*	1990	Temperate	New Zealand	T, S	750-1200m
Breckle	1974	Temperate	Afghanistan	A	0-5000m
Tewari	1985	Temperate	India	T	600-2600m
Hogg & Kirkpatrick	1974	Temperate	Tasmania	A	0-500m
Ogden & Powell	1979	Temperate	Tasmania	T, S, H	150-1200m
Kirkpatrick	1984	Temperate	Tasmania	A	400-1200m
Kirkpatrick & Brown	1987	Temperate	Tasmania	A	0-1000m
Minchin	1989	Temperate	Tasmania	A	900-1350m
Turner	1976	Temperate	N.S.W. Aust.	T, S, V	800-1050m
Austin & Cunningham	1981	Temperate	N.S.W. Aust.	E	0-1250m
Austin *et al*	1983	Temperate	N.S.W. Aust.	E	0-2200m
Austin *et al*	1985	Temperate	N.S.W. Aust.	E	0-2200m
Austin	1987	Temperate	N.S.W. Aust.	E	
Hall	1971	Tropical	Nigeria	A	900-?m
Hall	1973	Tropical	Cameroon	A	0-4100m
Hamilton	1975	Tropical	Uganda	T	900-4500m
Hamilton & Perott	1981	Tropical	Kenya/Uganda	A	2000-3300
Grubb & Whitmore	1966	Tropical	Ecuador	T, S	N/A
Baruch	1984	Tropical	Venezuela	A	2900-4100m
Oshawa	1991	Tropical	SE Asia	F	0-3800m
Kitayama	1992	Tropical	Borneo	T	600-3400m
Frahm & Gradstein	1991	Tropical	Multiple	B	0-3500m
Beals	1969	Arid	Ethiopia	T, S	800-2050m
Woldu *et al*	1989	Arid	Ethiopia	T, S, H, V	1450-3300m
Villagran	1981	Arid	Chile	S, H	3100-4350m

The most notable characteristic of tropical work listed in Table 1. is the use of the word 'zone'. 'A zone is a belt of homogeneous vegetation bounded by relatively narrow boundaries' (ecotones) (Kitayama 1992). By omission of any qualification to the contrary, some authors appear to assume that *naturally defined* zones exist (e.g. Hall 1971, 1973). Other authors speak in zonational terms but briefly acknowledge that the change between zones may be continuous (i.e. that boundaries are artificial constructs) (e.g. Hamilton & Perott 1981; Oshawa 1991) or sharp (e.g. Baruch 1984; Grubb and Whitmore 1966).

Few authors specifically test for the existence of continuity or discontinuity between altitudinally patterned areas of vegetation in the tropics - and fewer still make any reference to publications involved in the CVC debate. Serious criticism can be levelled against the work of some of these authors. Hamilton (1975) has been cited (e.g. in Druitt *et al* 1990) as establishing the existence of continua in African forests. However, this conclusion is premature. Using only a single sketchy analysis of altitudinal range data on a biased selection of tree species compiled exclusively from secondary sources which in turn related to three geographically separate mountain ranges, Hamilton drew the broad conclusion that 'when the country is considered as a whole, forest vegetation in Uganda forms an altitudinal continuum'. Such a conclusion is invalidated by clearly insufficient methodological standards.

Kitayama (1992) described three discontinuities defining four distinct zones on Mt Kinabalu, Borneo by means of classification and cluster analysis of fourteen sample plots. The existence of relative discontinuity between zones was determined with the following logic: 'Classified sample groups are well correlated with altitude. Accordingly, they are considered altitudinally defined vegetation zones.' Kitayama's conclusions are mathematical artefacts of the classification method.

Most discussion of tropical vegetation 'zones' centres around the search for appropriate classification and nomenclature for local and global patterns. Frahm and Gradstein (1991) reviewed some of this work on a worldwide scale in an attempt to rationalise the variety of named zones described by other authors. Five global altitudinal vegetation zones are described using bryophytes as indicators. The definition of these zones took no account of the sharpness of boundaries described in the source publications.

In the few instances where descriptions were given of the nature of altitudinal vegetation boundaries in the tropics, environmental factors were often held responsible (e.g. the Massenerhebung effect: Grubb & Whitmore 1966; Grubb 1971) This author was not able to find any work on altitudinal patterns of vegetation in the tropics that is able to contribute evidence to the CVC debate.

Arid areas have been studied also. On two transects in Ethiopia along otherwise similar slopes, Beals (1969) found 'more discontinuity in the vegetational change caused by altitude along the steep slope than along the gentle slope.' He suggested inter-specific competitive exclusion as the likely cause of greater community affinities on steeper slopes in general. Villagrán (1981) used the methods of Braun-Blanquet (1964), which ignore the possibility of continuous change, to define four vegetation zones in the Chilean Andes. Woldu *et al* (1989) used a suite of new methods to separately recognise 'stratocoena' in Ethiopian vegetation. Within these, 'points of discontinuity' appear to be recognised subjectively. It is not clear whether these results can be soundly related to the CVC debate.

The brief survey detailed in Table 1. (above) revealed studies of temperate vegetation along altitudinal gradients predominantly in North America, New Zealand, and Australia. Whittaker's work in North America (1956, 1960, 1975) explored altitudinal gradients and, as noted earlier, has been used as general evidence supporting the individualistic hypothesis. In New Zealand, a comprehensive picture of altitudinal vegetation patterns was established initially by Mark and his colleagues (Mark & Sanderson 1962; Mark 1963; Scott *et al* 1964; Wells & Mark 1966; Scott & Armstrong 1966) and more recently by others (e.g. Wilson *et al* 1990; Druitt *et al* 1990). '...it appears that most descriptions of altitudinal gradients in New Zealand recognise a break in the continuum between the upper forests.... and the lower, more diverse forests' (Druitt *et al* 1990).

Studies from other parts of the temperate world (excluding Australia) are not abundant. Breckle (1974) assumed zonation in a biogeographical discussion of Central Asian flora. Tewari *et al* (1989) appear to have found two distinct zones of forest trees. However their report lacks certain details and few conclusions may be drawn from this observation.

Within Australia, the greater body of work on altitudinal gradients has been conducted in Tasmania - one of the few areas where the altitudinal gradient is not dominated wholly by *Eucalyptus*. At Mount Field near Hobart, Ogden and Powell (1979) found 'two *Eucalyptus* dominated zones separated by a relatively narrow, but distinct, rainforest zone. However, the authors rightfully do not purport to have described a transect along a continuous *direct* environmental gradient. Significant variation in topography, geological substrate, and fire history occurred along the transect. Hence, the paper cannot contribute any greater conclusion to the CVC debate than that which vaguely suggests some form of *continuum within community* pattern.

Much of Kirkpatrick's work (Hogg & Kirkpatrick 1974; Kirkpatrick 1984; Kirkpatrick & Brown 1987) involves altitudinal gradients in Tasmania . In a study, of altitudinal and successional variation on the West Coast Range, a general continuum was tentatively suggested (Kirkpatrick 1984). A more detailed study in the far south-west, revealed a sharp discontinuity at one point in the altitudinal sequence. An environmental and an historical explanation were cautiously proposed to explain this - mechanisms such as inter-specific competition that may lead to the formation of natural communities were ruled out.

In the rainforests of northern New South Wales, Turner (1976) found elements of both continuity and discontinuity. Topographic variations influenced these patterns to a certain extent but it is implied from Turner's writing that species interaction relating to the dominance of *Nothofagus* is also involved. Thus, *continuum within community* is once again shown.

The gradient analysis work of Austin and his colleagues (Austin and Cunningham 1981; Austin *et al* 1983; Austin *et al* 1985; Austin 1987; Minchin 1989) often incorporates altitudinal factors. However, the primary aim of this work is to analyse statistically the response curves of (e.g.) *Eucalyptus* species to various environmental gradients by generating predictive models of their behaviour. One might say that, whilst clearly aware of the organismic-community hypothesis, Austin and his colleagues prefer to temporarily assume the universal existence of continua in their work. Competitive community style interactions are referred to as 'problems' in the formulation of appropriate response models.

Other work on vegetation boundaries in Australia forests relates to this review. Ashton (1976) describes a vegetational continuum influenced by several environmental factors on a small, forested mountain in Central Victoria. Although inter-specific competition was deemed 'likely' as a distributional control, its influence was not revealed in the analysis. The small environmental ranges in the study area appear to preclude the formation of any *continuum within community* patterns as have been observed elsewhere in Australia. Two altitudinal boundaries were examined by Ashton (1981 - *E. regnans* above *E. obliqua*) and Williams (1989 - *E. pauciflora* above *E. dives*). In both discussions, competition emerged as playing a key role in determining the position of the boundary between the two species.

Conclusion

In the first half of this century, plant community theorists were motivated by a desire to elucidate the inherent nature of plant communities. Two alternative propositions were postulated, and many researchers attempted to show that one of these was essentially valid whereas the other was not. Synthesis occurred in the 1960's and it became apparent that a compromise must be sought. To this day, a universal model of vegetation theory incorporating such a compromise has not been found. Perhaps the most dominant pattern that has emerged is not *community versus continuum* but *continuum within community*. Current work has set aside these traditional themes in an attempt to satisfy the need for statistically valid conclusions regarding fundamental species responses to environmental gradients.

A theoretical understanding of global patterns of vegetation at different altitudes would be an important contribution to science. Unfortunately, biogeography has not progressed much further than basic description in this regard. Tropical studies, whilst comprehensive in a descriptive sense, are currently of little theoretical value. Temperate regions have been the arena for theoretical development itself and are thus better understood. Vegetation change with altitude in Australia is not well covered in the literature. Australian studies on altitudinal gradients have proceeded with incompatible aims than are necessary for an understanding of the floristic and compositional community patterns in Australia's unique mountain forests.

Epilogue

The study of altitudinal change in vegetation relates to many facets of ecology and biogeography. The CVC debate is just one of these. The author is currently involved in a study of altitudinal vegetation patterns in the Wongungarra River, Victoria, Australia. Abundances of all vascular species have been recorded from around 160 quadrats on two transects spanning nearly 1000 vertical metres. An effort has been made to exclude all environmental influences other than those directly related to altitude. It is likely that this work will be able to contribute to an understanding of community theory in mountainous *Eucalyptus* forests - particularly with respect to links between canopy and understorey species.

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