# VEGETATIONAL CHANGE ALONG AN ALTITUDINAL GRADIENT, MOUNT EGMONT, NEW ZEALAND

by

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# ABSTRACT

A direct gradient analysis was conducted on Mt Egmont, New Zealand, firstly to examine quantitatively changes in composition, physiognomy and structure of the vegetation along the altitudinal gradient in order to investigate the accepted notions of vegetation zonation, and secondly to relate such an analysis to other New Zealand gradient analyses and to the two views on vegetation description and analysis, the continuum view and the discrete community (association) view.

Vegetation data was collected at altitudinally defined sites on five major ridges on Mt.Egmont; North Egmont (Blundell's Track, Ngatoro Track and the Razorback), York Road Track Ridge, Stratford (Summit Road), Dawson Falls (Summit Track), and Lake Dive Track Ridge. The data collected on the York Road Track Ridge provided the basis for describing altitudinal change while the remainder was used to examine in detail the tree-shrub and shrub-tussock interfaces.

Sample size (quadrat and line transect) was determined after minimal area checks to ensure that a representative combination of species was sampled at each site. Data from a total of sixty plots was collected and preliminary analysis, including graphing of the major species distributions and calculation of similarity matrices to compare quadrats, revealed a tendency toward discontinuity in species distributions. This allowed a classificatory rather than ordinatory strategy of data analysis to be followed. Cluster analyses based on statistical tests of species association were used to determine "natural" groupings of positively associated species and qualitative and quantitative classifications of samples were used to define vegetation zones or groupings at specific similarity index levels.

Tree-shrub interfaces and tussock-shrub interfaces were compared on the basis of species complement, the degree of floristic, physiognomic and structural discontinuity in the vegetation, and differences in species interaction at each of the locations.

The effects of data amalgamation, altitudinal interval employed, altitudinal range encountered, and classificatory versus ordinatory techniques, on the conclusions drawn were examined.

Graphing of species distributions, cluster analyses, and classifications supported in part previously described zonation patterns but enabled a refinement of the generally accepted notions of vegetation zonation on Mt Egmont. In contrast to previous research the vegetation zones identified have a quantitative and objective basis.

Comparison of the results with those of other New Zealand gradient analyses enabled elucidation of several major species distributions and species interactions because of the unique species complement found on Mt Egmont.

Comparison of different data collection and manipulation techniques indicated that decisions made may cause data to conform to one or other of the two major approaches (continuum or discrete community types) to vegetation description and analysis.

The study of the tree-shrub interfaces and shrub-tussock interfaces showed that the vegetation on Mt Egmont exhibits a spectrum of species distributions ranging from continua through to discontinuities at different locations and specific examples of each are described. Possible explanations advanced include differences in species complement and species interaction, the non-equivalence of the altitudinal gradient at different locations, and differences in environmental factors including slope and aspect.

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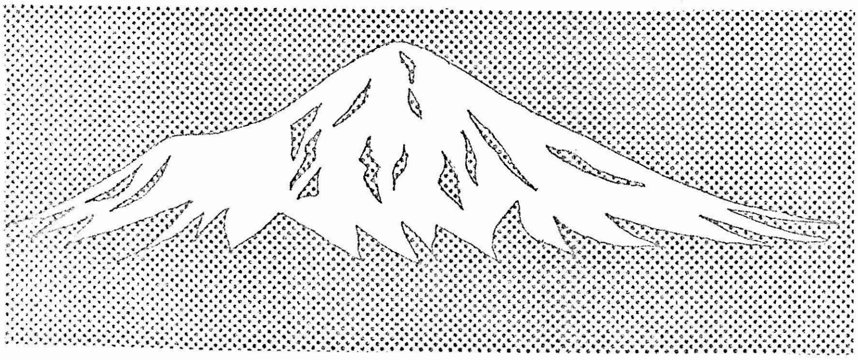
I have a love, scented of musk Cassinia.
She is constant in presence yet everchanging in state.
On her green braid limbs sculpted by tinkling crystal,
there is an upthrust of life.
Smooth and simple pointed shell becomes diverse,
textured, slotted amongst relatives, computer controlled?
Her oscillating cape covers, freezes, thaws but gives
a purity of colour, shape to contrast with the
clouded sky...

(1964)



# TABLE OF CONTENTS

Chapter 6. (continued)

Page

APPENDICES

APPENDICES (Continued)

# LIST OF TABLES

## LIST OF FIGURES

# Chapter 1

## INTRODUCTION

The aim of this research is two-fold:- firstly an attempt has been made to examine quantitatively the changes in composition, physiognomy, and structure of the vegetation between 2,600ft (792m) and 6,100ft (1,858m) in order to confirm or refute the accepted notions of zonation pattern on Mt Egmont of Buchanan (1869), Cockayne (1928), Mason (1951), Schweinfurth (1962), Wilson (1961), Druce (1964, 1966, 1974), and George (1967); secondly an attempt has been made to examine the much wider implications of such an analysis in relation to the two major schools of thought with regard to vegetation analysis: the continuum school and the discrete community (association) school. Whittaker (1970) presents four distinct hypotheses which may be applied to the second part of this research.

1. Competing species, including dominant plants, exclude one another along sharp boundaries. Other species evolve toward close association with the dominants and toward adaptation for living with one another, and giving way at a sharp boundary to another assemblage of species adapted to one another.
2. Competing species exclude one another along sharp boundaries, but do not become organised into groups with parallel distributions.
3. Competition does not, for the most part, result in sharp boundaries between species populations. Evolution of species towards adaptation to one another will, however, result in the

appearance of groups of species with similar distributions.

4. Competition does not usually produce sharp boundaries between species populations, and evolution of species in relation to one another does not produce well defined groups of species with similar distributions. Centres and boundaries of species populations are scattered along the environmental gradient.

These four hypotheses represent the range of possibilities from individualistic species distribution through to distinct species assemblages or communities so that an analysis of the data in order to test these hypotheses should provide further evidence for or against the major schools of thought in vegetation analysis.

## Thesis organisation

The literature relevant to this study of vegetational change along an altitudinal gradient on Mt Egmont can be subdivided into four main categories. First, there are the studies of Mt Egmont's vegetation listed above which are reviewed in Chapter 2. Second, there are the original gradient analyses and particularly the work of Whittaker (1956, 1967) which played a major role in the development of the more recent continuum school of thought in vegetation description and analysis. Third, there are the more recent altitudinal gradient analyses which add new dimensions and directions to Whittaker's original work notably Beals (1969), and Reeder and Reichert (1975). Finally, there are the New-Zealand based altitudinal gradient analyses in the main carried out in the south of the South Island and which provide useful comparisons with the results described in the present study. All of these direct gradient analyses are reviewed in Chapter 3. Chapter 4 describes and justifies the methods of data collection employed in the present study. Chapter 5 consists of the site description for the York Road Track Ridge the major sampling location. Chapter 6 describes, discusses, and compares the results and analyses of the vegetation data collected at York Road Track Ridge, Stratford, North Egmont, Lake Dive Track Ridge, and Dawson Falls. Chapter 7, the final chapter, is a discussion and conclusion based on the results and analyses of the present study, their comparison with the literature reviewed in Chapters 2 and 3, which attempts to relate directly back to the research aims described in Chapter 1.

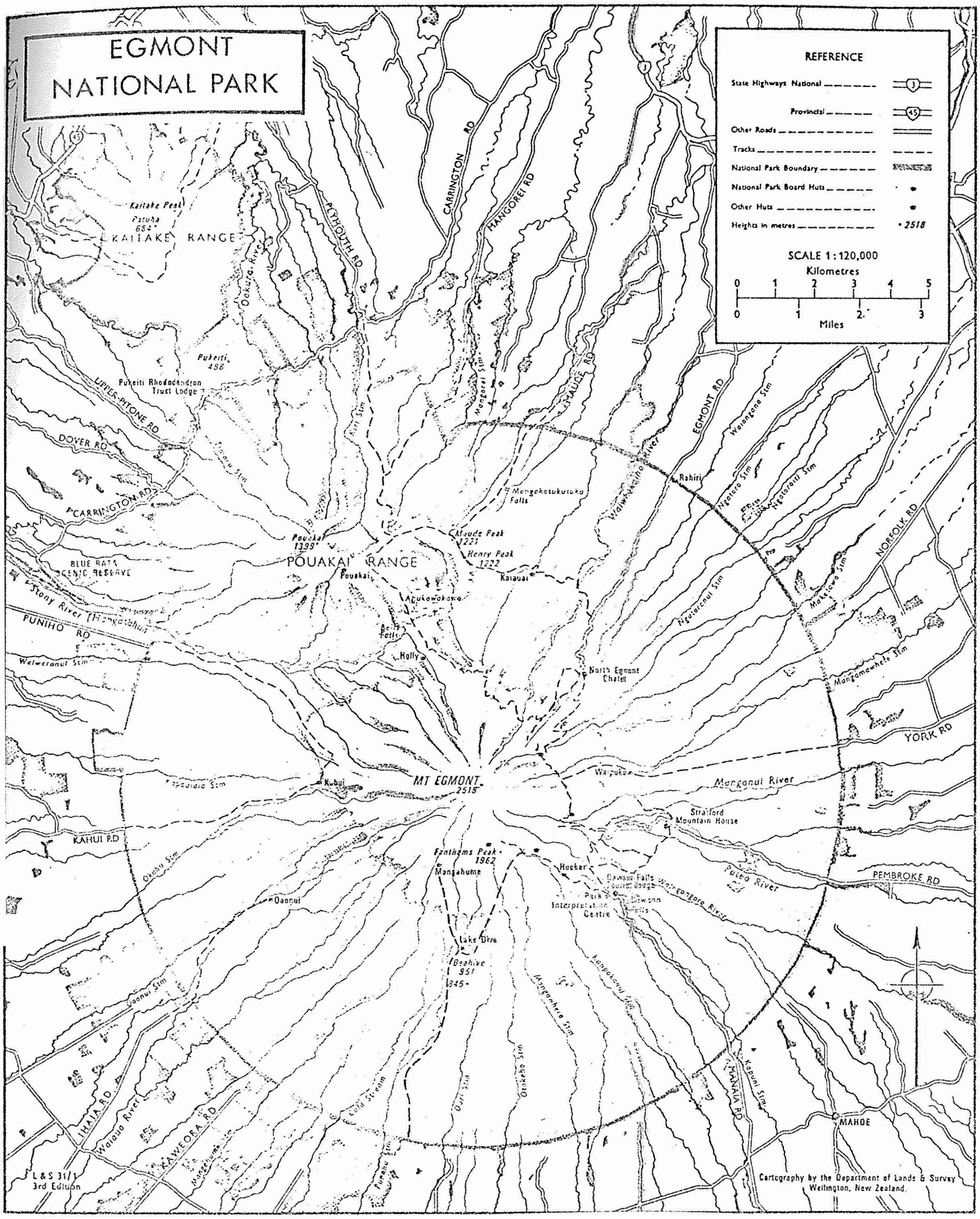


Figure 1
LOCATION OF SAMPLE SITES

York Road Track Ridge - Track following ridge above Waipuku(York Rd)Hut.

North Egmont - Tracks above North Egmont Chalet.

Dawson Falls - Summit Track between Park Interpretation Centre and Hooker Hut.

Lake Dive Track Ridge - Track from Lake Dive Hut to Kapuni Lodge.

Stratford - Alongside road leading to Stratford Mountain House.

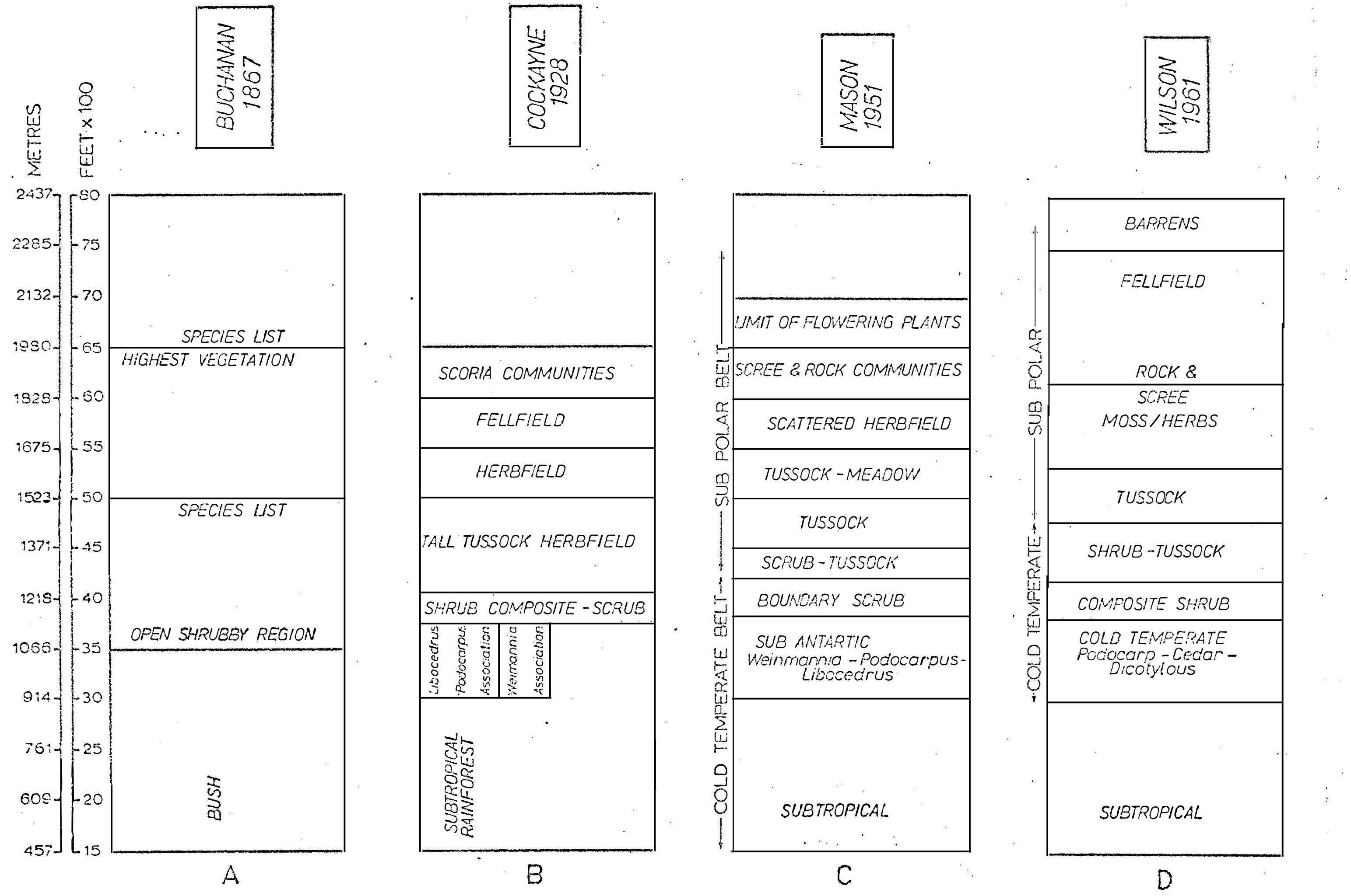


Figure 2 MOUNT EGMONT VEGETATION ZONES PROPOSED 1867 - 1965

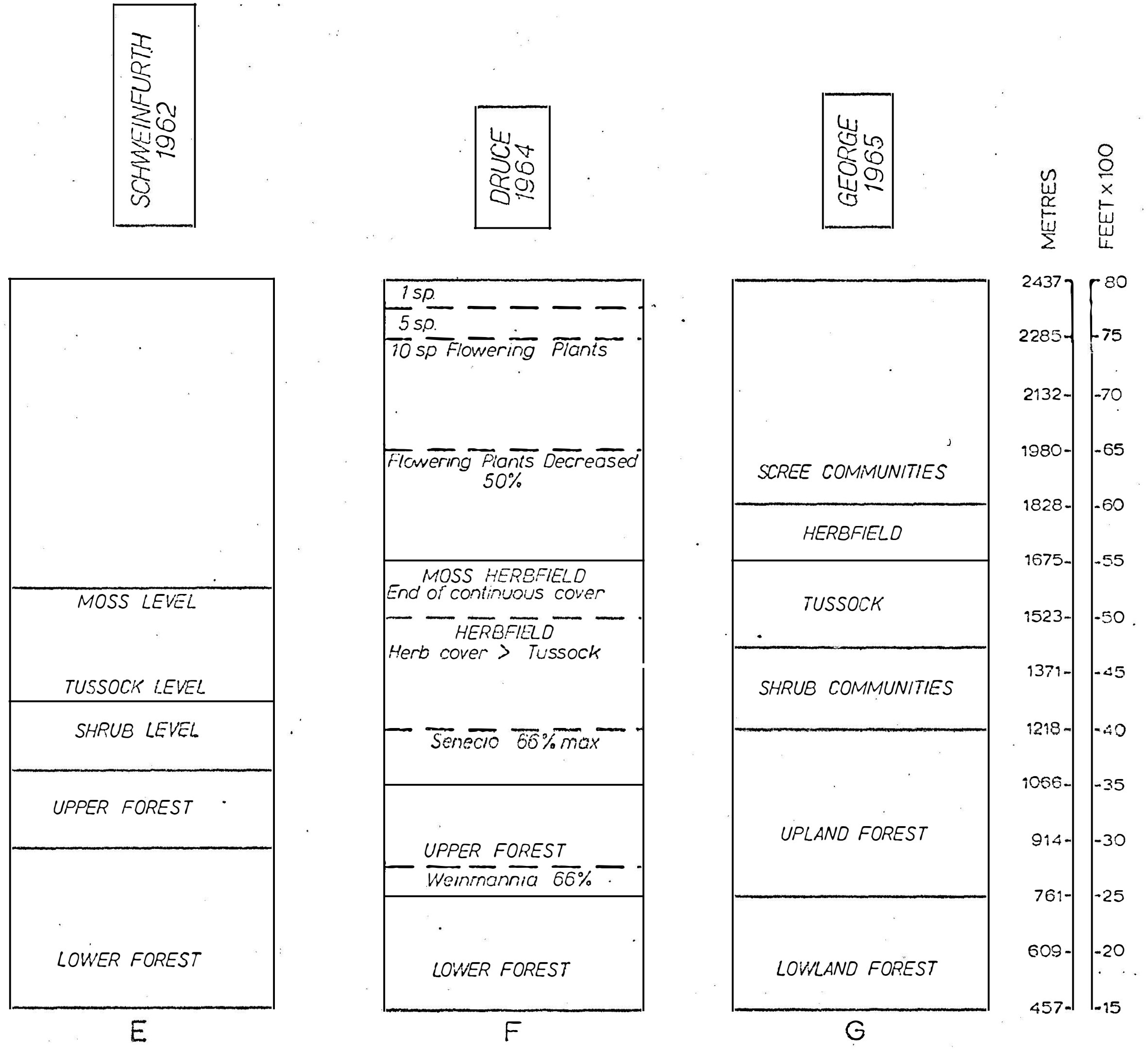


Figure 2 contd.

## Chapter 2

## THE VEGETATION OF MOUNT EGMONT: REVIEW OF THE LITERATURE

Zones or belts of vegetation have long been recognised on Mt Egmont although their delimitation in terms of altitude and species composition has varied from author to author. In the majority of cases the difference can be attributed to the length of time available to each for field study and the fact that many explored small sections of the mountain only. The various delimitations of zones or belts of vegetation on Mt Egmont are summarised in historical sequence on Figures 2a - 2g along with altitudinal limits and major canopy species where possible. As is to be expected some of the species identification of the earlier researchers on Mt Egmont have subsequently proved inaccurate. For simplicity the known inaccuracies have been corrected in this review with either the correct species name or left with the genus name only where necessary. A.P. Druce's unpublished checklist of the higher plants of Mt Egmont and in particular the section entitled "Doubtful and Erroneous Records not included in the Main List" p.50-54 forms the basis for these corrections. Metric altitudinal equivalents have also been included where necessary.

Buchanan (1869) concentrated mainly on providing a list of species collected on Mt Egmont with particular reference to the altitude at which the species were found. He did however describe two major vegetation categories: the bush (up to 3,500ft (1,066m)), and an open shrubby region (at 3,500ft (1,066m)). The tree species listed as being most common included *Weinmannia racemosa*, Metrosideros robusta Podocarpus totara, Knightia excelsa, Dysoxylum spectabile, Podocarpus ferrugineus, Melicytus ramiflorus, Aristotelia serrata, Pseudowintera colorata, and Schefflera digitata. In the open shrubby area Buchanan listed the most prominent plants as being Libocedrus bidwillii, Senecio elaeagnifolius, and Olearia arborescens while other common species included Pseudopanax simplex var.sinclairii, Coprosma spp., Coriaria spp., Pittosporum tenuifolium, and Dracophyllum filifolium. Although not emphasising zonation Buchanan listed the species common above the shrubby region and up to 5,000' (1,523m) as Ranunculus nivicola, Ourisia macrophylla, Epilobium glabellum, Epilobium nummularifolium, Euphrasia cuneata, Celmisia glandulosa var. latifolia, Celmisia gracilenta, Forstera bidwillii var. densifolia, and Drapetes dieffenbachii. Finally, came the highest vegetation 6,500' (1,980m), consisting of a few scattered plants of Claytonia australasica, Anisotome aromatica, Helichrysum sp., Wahlenbergia pygmaea, and Poa spp. Buchanan's description resulted from an approach via the Pouakai Ranges, Ahukakawa Swamp, and then an ascent to approximately 6,500' (1,980m) on the west face of Egmont. The reason for this route of ascent "by the side facing West, as offering a more varied vegetation" (Buchanan 1869, 57) is interesting in light of the present day knowledge of geological history that is the effect of recent debris flows on the vegetation composition.

Cockayne (1928) in Section 111. "The Vegetation of the High Mountains" describes several aspects of Egmont's vegetation in terms of a classification of plant communities. Chapter 1 General Remarks includes a section on Vertical Distribution (the belts of vegetation) in which Cockayne describes what he considered to be the major causal factors for zonation.

"All important is the average winter snow-line above which the ground for some months is covered continuously with snow. Below this line the covering is not continuous, though at intervals more or less snow lies on the ground throughout winter." (Cockayne, 1928, 226.)

Given this as the major causal factor Cockayne recognised how edaphic conditions, change of latitude, and moisture availability complicates the vertical distribution in such a way as to make it impossible to supply definite heights for the belts of vegetation. A general classification in terms of length of time of snow cover is however provided by Cockayne and is summarised in Table 1 below:

Table 1.

Average length of time of snow cover and corresponding vegetation belts (after Cockayne 1928)

| VEGETATION BELT | LENGTH OF SNOW COVER |
|---|---|
| Alpine Belt | Max. winter snow cover to perpetual snow-fields |
| Upper Subalpine | lesser period than above |
| Lower Subalpine | no continuous cover greater than 1-2 weeks |
| Montane | snow 2-3 days/year |
| Lowland | 0-2 days/year |

Before actually proceeding to describe and classify the plant communities in relation to the broad vegetation belts already summarised, and with respect to major species, physiognomy and climatic and edaphic factors Cockayne stated an important reservation: "the distinction between lowland (in some localities) montane and subalpine forest is arbitrary, all grading into one another and possessing many species in common." (Cockayne, 1928, 254.)

This statement seems very important in light of the more recent approaches to vegetation description and analysis however, Cockayne went on to say:

> "Nevertheless in proceeding from the lowlands to the timber line, well marked belts of vegetation are encountered, the true lowland species according to latitude and aspect, going out at certain altitudes and being replaced by those of the high mountains; also there are purely high mountain associations". (Cockayne, 1928, 254.)

Vegetation communities are then defined and described including several from Mt Egmont under the categories Subtropical Rain Forest and allied communities, Shrub-composite Scrub, Mixed communities:- Rock, Scoria, Fellfield of the wet mountains, North Island Dry Herbfield and Tall Tussock Herbfield.

In the category Subtropical Rain Forest Cockayne described two groups of associations found on Egmont the first a (Kamahi) W. racemosa group and the second a (Southern Kaikawaka - totara) L. bidwillii - P. hallii group. A W. racemosa (Goblin Forest) association was described as occurring as a distinct belt from the neighbourhood of Dawson Falls to the North Egmont House and probably extending right around the mountain. The main species included at first some comparatively low statured trees of Dacrydium cupressinum giving way to W. racemosa decreased in stature and much branched. Important small trees and shrubs listed were Griselinia littoralis, Fuchsia excorticata, Pseudowintera colorata, Carpodetus serratus, Coprosma parviflora, and Coprosma tenuifolia. Important ground cover species listed were Blechnum capense, B. fluviatile, Polystichum vestitum, Uncinia banksii, and Astelia nervosa. Podocarpus hallii entered the association at higher altitudes becoming equivalent to that in which Libocedrus was present and gave way to subalpine scrub.

A *Libocedrus* - *Podocarpus* association was described with reference to an area in the vicinity of the North mountain-house not extending to the Stratford house. Cockayne described the dominant species at approximately 900m as *P. hallii* (in abundance) giving way to *L. bidwillii* (soon becoming dominant) with *W. racemosa* and *G. littoralis* also abundant. Common shrubs listed include *P. colorata*, *C. serratus*, *A. serrata*, *Melicytus lanceolatus*, *F. excorticata*, *P. simplex var. sinclairii*, *Pseudopanax colensoi*, *Myrsine divaricata*, *Hebe stricta*, *Coprosma australis*, *C. tenuifolia*, *C. parviflora*, *C. pseudocuneata*, and *S. elaeagnifolius*. *P. colorata* and *A. nervosa* were listed as important in the undergrowth and forest floor respectively.

The Shrub-composite Scrub community was described as commencing at about 1,140m and giving out at about 1,240m. The dominant species included *S. elaeagnifolius* and/or *D. filifolium* with other principal species being *P. hallii*, *Carmichaelia sp.*, *P. colensoi*, *P. simplex var. sinclairii*, *G. littoralis*, *M. divaricata*, *H. stricta*, *C. tenuifolia*, *C. pseudocuneata*, *C. parviflora*, *O. arborescens*, and *Cassinia vauvilliersii*.

Under the heading Mixed communities Cockayne described the major species for Herbfield, Fellfield, Scoria slopes and Rock communities. The Herbfield communities included the Tall Tussock-herbfield and the Dry Herbfield, the former dominated by *Chionochloa rubra* and interspersed with *Hymenophyllum multifidium*, *Lycopodium fastigiatum*, *Notodanthonia setifolia*, *A. aromatica*, *Gaultheria depressa*, *F. bidwillii var. densifolia*, *C. major*, *C. glandulosa var. latifolia*, *Rauolia glabra*, *Helichrysum sp.*, *Cotula squalida*, *O. macrophylla*, and *R. nivicola*. Shrubs of low stature listed were *D. filifolium*, *C. vauvilliersii*, and *Hebe odora*. Tall Tussock-herbfield was described as "occupying the slopes whereas the herbfield proper was confined to the gullies, the controlling factor as to which kind of herbfield shall occupy the ground being the length of time this is covered by the winter snow, the tall tussock-herbfield being for longer free from snow." (Cockayne, 1928, 317.) Cockayne also noted the usage of the term Moss association by the settlers because of the large white hummocks of Rhacomitrium spp. Similar species were designated as important for both fellfield and scoria communities the former occurring at lower altitudes and with altitudinal increase becoming more open until the scoria slopes were only dotted with plants. Included were Luzula colensoi, C. australasica, Gentiana bellidifolia, A. aromatica, Poa colensoi, and Gaultheria sp. for scoria communities and with the addition of Epilobium glabellum var. erubescens for fellfield communities. Rock community species of importance listed were N. setifolia, P. colensoi, A. aromatica, Gaultheria sp., Helichrysum sp., Coprosma pumila, Pentachondra pumila, D. dieffenbachii, F. bidwillii, and C. glandulosa var. latifolia.

Mason (1951) began by stating that Mt Egmont offers the most perfect example in New Zealand of an altitudinal zonation of vegetation. His opening paragraph confirms a discrete community standpoint.

"The following belts, governed primarily by temperature are often remarkably sharply separated from one another - often the transition from one to another is effected within the distance of less than fifty yards. Within a square mile may be seen a dozen distinct and very interesting plant communities." (Mason, 1951, 23.)

The altitudinal zonation then adopted by Mason is summarized on Fig. 2c and is essentially the same as Cockayne's although several of the titles applied differ as do the altitudinal limits listed.

Mason termed the forest between 3,000ft (914m) and 3,800ft (1,157m) subantarctic in direct contradiction to Cockayne's original classification of New Zealand forests. The Shrub-composite Scrub of Cockayne is termed Boundary scrub and Zotov's (1938) major categories Cold Temperate Belt and Warm Subpolar Belt are used. No species additional to those cited by Cockayne are included by Mason in fact the species lists are less detailed.

Wilson (1961) in an unpublished thesis titled "The Vegetation of Mount Egmont: an ecological study of the subpolar vegetation" repeated Mason's (1951) claim of Egmont providing a near perfect example of altitudinal zonation but adapted Cockayne's (1928) and Druce's (1961) classification of mountain vegetation to name the altitudinal zones. This classification is summarised on Fig. 2d. The Forest Zone between 3,000ft (914m) and 3,800ft (1,157m) thus becomes the Cold Temperate Podocarp-cedar-dicotylous Forest with Cold Temperate Composite Scrub between 3,800ft (1,157m) and 4,200ft (1,279m) and Cold Temperate Shrub-tussock between 4,200ft (1,279m) and 4,800ft (1,462m). All the other titles are recognisable in the previously mentioned classifications. Wilson's species lists for altitudinal zones are for the most part less detailed than even Mason's however the purpose of the thesis was a more detailed study of the subpolar vegetation and it is in this section that Wilson's work covered some new ground. Under the headings Subpolar Scree Fields, Subpolar Fellfield, Rock and Scree, Subpolar Tussock Field and Alpine Bog the important species were discussed. Field work was based on the Eastern slopes of Egmont for the first three categories and the Pouakai Ranges for the last two. Relative importance of species was indicated using a rating system and descriptions of scree colonisation and species adaptations included. The species lists are essentially the same as Cockayne's with the addition of Colobanthus sp. in rock and scree communities and Bryum sp., in Moss and herbfields. Wilson's work on the colonisation of the scree fields on Mt Egmont is unique. The sequence of terrace formation described from N.E. Egmont (Tahurangi) is summarised on Table 2.

Table 2

Sequence of Terrace Formation N.E. Egmont after Wilson (1961)

1. Initial obstruction or slowing down of moving scree.
2. Establishment in greater numbers of E. glabellum and C.australasica.
3. Changing substrate conditions leading to establishment of Colobanthus, Luzula, and Poa in the shelter of established plants.
4. Accumulation of moving fine scoria behind clumps of Colobanthus - the first semblance of a terrace.
5. Establishment of further clumps of Colobanthus and associated plants 4-6" lower down and in angle ± 30° and their eventual coalescence at the tongue of the scree slope.
6. Colonisation by Helichrysum sp., and Drapetes dieffenbachii together with terrace forming plants of the stabilized areas in and between the advancing line of terraces, and the edge of the former moving scree slope.
7. Establishment of further terraces as the marginal terraces coalesce and scree stabilizes higher up.
8. Colonisation by plants of the moss-herbfield - Gaultheria sp., and Coprosma pumila and Rhacomitrium spp. with a corresponding drop in Colobanthus and Luzula representation.

Along with the sequence of scree colonisation Wilson described the growth forms of the sub polar species noting their adaptations to the extreme environmental conditions and the way the community was stratified both above and below ground in terms of aerial parts and root systems enabling what he termed a communal sharing of the available environmental conditions.

Schweinfurth (1962) writing in a paper entitled "Mt Egmont Taranaki and a contribution to the study of the vertical arrangement of the vegetation" concentrated on describing the change in species composition and physiognomy on the Stratford and Dawson Falls approaches to Egmont. Proceeding in terms of an ascent from the forest edge to higher altitudes he identified zones of vegetation summarised on Fig. 2c along with their altitudinal limits. Overall the boundaries recognised are at little variance with those of Cockayne and some of the species lists are quoted directly, for example, that of the scrub level. Schweinfurth's main contribution was twofold : firstly his observations regarding the physiognomy of the canopy species, and secondly comments regarding Egmont's vegetational relationships with the South-West Pacific. Supporting the discussion with height/diameter measures he described the ways in which _W. racemosa_ and _L. bidwillii_ in particular are affected by exposure to wind. Tree species tend to become more huddled with a denser canopy - locking together which "seen from a greater height... appears as a dense continuous "defensive front"... when a tree stands in isolation of the edge of the forest it develops a typical calotte-shaped crown." (Schweinfurth, 1962, 7-8.) Schweinfurth pointed to the need to consider the patterns exemplified on Egmont in light of the major patterns of variation latitudinally and with regard to the range and number of species present on Egmont. As noted Mt Egmont is the last location of sufficient altitude before the tropics which enables contrasts or comparisons to be drawn. Both floristically and physiognomically Schweinfurth described similarities apparent when comparing the vegetation of Mt Egmont with that of Tasmania and the humid tropics. The approach of defining vegetation groupings associated with particular altitudes is similar to that of the previously mentioned authors, however, like Cockayne, indications that the vegetation was not necessarily viewed as discrete zones are apparent: "the eastern slope of Egmont offers ample opportunity of studying the continuously changing transition between mountain forest and shrub belt." (Schweinfurth, 1962, 14.)

Druce (1964) in the Egmont National Park Handbook makes the first attempt to give a quantitative basis to the changes in species distribution with altitude. Following a nomenclature of zones similar to the other authors with major groupings of Lower Forest, Upper Forest, Scrub, Tussock, Mossy Herbfield, and Alpine region Druce drew attention to the fact that species change gradually in representation from one zone to another. Focusing on the Stratford approach route he described this change in species representation giving some quantitative (relative cover) values to illustrate the changes. In summary Druce described a lower forest composed of _Metrosideros robusta_ and _Dacrydium cupressinum_ (no more than one eighth cover) with smaller trees mostly _Weinmannia racemosa_ and _Melicytus ramiflorus_ making up by far the greater part of the cover. With increase in altitude _Metrosideros_ and _Dacrydium_ give way until only the second tier trees (smaller trees above) are left with _W. racemosa_ outnumbering any other. Further increase in altitude sees the appearance of _Podocarpus hallii_ in the canopy 2,750' (837m) and the _Weinmannia_ 66 per cent of the forest at this altitude decreases rapidly. Emergent _P. hallii_ and L. _bidwillii_ were described as making up the upper forest zone with the smaller trees between mainly G. littoralis, F. excorticata, and P. colensoi. "The forest does not suddenly give way to scrub in the next zone; the kaikawaka (L. bidwillii), totara (P. hallii), broadleaf (G. littoralis), and fuchsia (F. excorticata) all decrease gradually. In their place grow koromiko (H. stricta), leatherwood (S. elaeagnifolius), and increased numbers of mountain fivefinger (P. colensoi) which together form a dense cover, six or more feet high and deceptively smooth looking on top." (Druce, 1964, 42-43.)

By 4,000' (1,218m) Senecio elaeagnifolius reaches its maximum (66 per cent) cover decreasing above this altitude with H. stricta, C. pseudocuneata, C. vauvilliersii, and D. filifolium becoming prominent. The shrubs give way in turn to C. rubra and herbs with scattered shrubs of H. odora and C. vauvilliersii remaining.

"The area occupied by herbs increases with altitude till at 5,000' (1,523m) (on a north face) it is much greater than that covered by tussock (C. rubra) and koromiko (H. odora) is the only shrub left. Above this altitude (lower on a south face) there comes the zone of mossy herbfield. The short compact turf is composed for the most part of mountain daisies (Celmisia spp.) forstera (F. bidwillii var. densifolia) anisotome (A. aromatica), creeping coprosma (C. pumila), everlasting daisy (H. bellidiodes), snowberry (G. depressa) and patches of two conspicuous mosses Rhacomitrium spp. Beyond 5,500' (1,6 75m) (much lower in places) there is no longer a continuous cover of plants; from a distance the mountain sides appear practically bare but mosses, lichens and more than thirty different kinds of flowering plants many of them abundant, still grow on the debris slopes, cliffs and steep lava flows." (Druce, 1964, 43-44.)

Druce noted that the number of flowering plants present is halved by 6,500' (1,980m), reduced to ten species by 7,500' (2,285m), and only one species (Colobanthus) remains near the summit. Perhaps the key statement is made in Druce's summing up of the overall vegetation pattern.

"Now that we have completed our general look at the sequence of vegetation up the mountains, it is not difficult to see how each species making up the cover has its greatest expression at a particular altitude, above and below which it fades away, sometimes quickly, sometimes gradually. This gives the vegetation a large measure of continuity without any sudden changes." (Druce, 1964, 44-45.) Along with this emphasis on continuity of change up the mountain Druce also drew attention to the fact that the pattern around the mountain either abrupt or gradual depends mainly on slope, aspect, and exposure of land and on the history of catasrophes including eruptions, deluges, gales, and fire factors.

The effects of volcanic activity on species composition and regeneration are also noted in Druce (1966) and in summary there are two major effects described. Firstly some of the canopy species still present have been structurally affected by past eruptions for example L. bidwillii with short boles and lateral branching. Secondly the species composition in many locations may reflect recent ash and pumice showers for example the replacement of W. racemosa in locations partially destroyed by eruption and with subsequently increased fertility resulting from the "topdressing of ash." Druce described sites near Dawson Falls with Kanuka (Leptospermum ericoides) and Fuschia (F. excorticata) in the canopy as indicating the formation of numerous gaps in the canopy following eruption and the subsequent establishment of these species in the well lit sites. Druce also pointed to the fact that the species regeneration today is not the same as it was,citing the lack of replacements for rimu (*D. cupressinum*) in the last 300 to 400 years. Thus long term changes as well as the more recent ones resulting from the introduction of noxious animals, namely goats and oppossums, are changing the vegetation composition. Goat browsing is described by Druce as depleting the undergrowth causing degradation to lower types such as *Uncinia spp.*, *Microlaena avenacea*, *Coprosma spp.*, *P. colorata*, *M. salicina*, *C. smithii*, and *Histiopteris incisa*. Oppossums on the other hand were reported as causing serious but less extensive damage to species such as *D. spectabile*, *W. racemosa*, *F. excorticata*, *A. serrata*, *Pseudopanax spp.* and *Senecio elaeagnifolius*.

Overall, Druce (1964, 1966) provided a much more detailed look at the factors affecting vegetation on Mt Egmont and in recognising zones or belts of vegetation emphasised continuity and provided some quantitative cover values for the major species in the zones delineated. As well, he raised the notion of regarding Egmont's flora as an island one in that its isolation has resulted in a unique species complement lacking particularly in mountain species and containing a relatively high proportion of endemics.

George (1965), in an article entitled "Egmont - The Vegetation Belts", follows the stated intention of detailing the various vegetation belts from approximately 1,500ft (457m) above sea level to the summit of the mountain. They appear summarised in Fig 2g. Once again the belts identified approximate those already described and there are no additions to the species already listed. In fact, George states that much of his information is based on an address given by Mason and as such has already been described in this review.

Druce (1974) writing in the Auckland Botanical Newsletter expanded his earlier comments regarding Mt Egmont's unique species complement and also indicated the problems apparent in naming some of the species complexes found on Mt Egmont. Druce concluded that although lacking in a number of plants Mt Egmont's total species complement was still underestimated by earlier workers including Buchanan (1869), Thomson (1917), and Cockayne (1928). Comparison of species absences with the total number of species known to occur in the North Island reveals that the absences are not evenly distributed within plant groups for example "two thirds of the lianes, ferns, and rushes are present, but only about one third of the shrubs. For most other groups (trees, orchids, grasses, sedges, dicot herbs) the fraction is about half." (Druce, 1974, 2.) Druce also comments that while five species appear to be endemic it is only a matter of time before some or all of these species are found elsewhere. The tussock and herbfield communities exhibit the most species absences with many of the approximately 300 "missing plants" (defined by Druce as plants found in the central North Island at the same latitude as Mt Egmont) absent from these communities. Reasons cited for the initial underestimate of Mt Egmont's total species complement include the possibility that workers concentrated on the summit cone taking little notice of the forest and the fact that many of the plants are very locally distributed for example Hoheria glabrata, Podocarpus nivalis and Coprosma colensoi. Two species complexes noted by Druce as presenting nomenclature problems are the Carmichaelia arborea group. The problems centre on deciding whether species growing on Mt Egmont are comparable with species found elsewhere, that is, separating habitat variations from species variations. Forstera bidwillii var. densifolia for example is cited by Druce as a species variety which could merely be a habitat form.

# Chapter 3

# DIRECT GRADIENT ANALYSIS

## The Development of Gradient Analysis

The term gradient analysis was originally applied by Whittaker (1951) to the method of vegetation analysis in which "vegetation samples are arranged and studied according to known magnitudes of (or indexes of position along) an environmental gradient which is accepted as a basis of the study". (Whittaker, 1967, 209.) This approach was later termed direct gradient analysis to distinguish it from the complementary approach, indirect gradient analysis, in which "vegetation samples are compared with one another in terms of degrees of difference in species composition and on the basis of these degrees of difference are arranged along axes of variation. The axis may or may not correspond to environmental gradients; but if they do correspond, the approach to environmental gradients is indirect or inferential". (Whittaker, 1967, 209.) The earlier gradient analyses of Whittaker (1948, 1956), Curtis and McIntosh (1951), Curtis (1955), Curtis (1959), Brown and Curtis (1952), and Bray and Curtis (1957), fall into both categories of direct and indirect gradient analysis. Whittaker's work was primarily direct gradient analysis while that of Curtis and his associates (the School of Wisconsin) was indirect gradient analysis. Both these approaches developed during the same time period as did work by Ellenberg in Germany (1948, 1950, 1952) and gave convergent results, namely the emphasis on vegetation continiuity, binominal or Gaussian distributions of species populations, and individualistic species distributions. It is important to remember that these results had been embodied much earlier in Gleason's 1926 paper "The individualistic concept of plant association" particularly the two central ideas restated by Whittaker (1967) as:

"1. The principle of species individuality - each species is distributed in relation to the total range of environmental factors (including effects of other species) it encounters according to its own genetic structure, physiological characteristics and population dynamics. No two species are alike in these characteristics, consequently with few exceptions, no two species have the same distributions.

2. The principle of community continuity - communities which occur along continuous environmental gradients usually integrate continuously, with gradual changes in population levels of species along the gradient." (Whittaker, 1967, 209.)

As well Gleason's ideas had been paralleled by Lenoble (1926, 1928) in France and Ramensky (1924) had outlined similar ideas in Russia. Ramensky (1930) took these ideas much further with extensive research on species distribution and community relationships and thus Whittaker (1967) clearly states that "it is Ramensky, rather than Gleason, Lenoble, Ellenberg or the recent Americans, who should be recognised as the originator of gradient analysis". (Whittaker, 1967, 210.) Despite this genealogy it has been Whittaker's contributions to gradient analysis that have popularised this concept, and Whittaker has most clearly stated the techniques, results, and conclusions most relevant to the present study. A comprehensive review of the many other gradient analyses both direct and indirect is also provided by Whittaker (1967, 1973a). Whittaker's original direct gradient analysis, a Ph.D. Thesis (1948) entitled "A Vegetation analysis of the Great Smoky Mountains", and the resulting paper (1956), was designed to test the community-unit theory and individualistic hypothesis. Two sampling designs were employed in this study : "field transects" and "site transects". Field transects involved a layout of plots along predetermined intervals of a gradient (either a predetermined horizontal distance or a predetermined elevational interval). Since the predetermined sample location did not always satisfy the "uniform site" criterion Whittaker relaxed his more objective "field transect" sampling into the "site sample" layout. This involved sampling areas along mountain trails that satisfied the site-uniformity criterion to accomplish a "random" coverage of the vegetation. Random not in the statistical sense since sampling was limited by access but random in the sense that Whittaker tried to achieve a geographically representative sampling across the elevation belt. Sample size at each site varied with the number of trees thought necessary to indicate stand composition and ranged from 50 to 300 trees. Two gradients were used in the study : elevation, and a topographic moisture gradient. Elevation ranged from 1,500ft (460m) to 6,600ft (2,010m). The topographic moisture gradient depending on the site moisture range within an altitudinal belt was divided into six to ten steps, and each step was sampled with up to five vegetation samples (replicates). Each step was defined by a topographic position-type, for example North facing slope, lower slope, ravine bottom etc. and these were arranged into a step-wise series of topographic positions or site types judged by experience to vary from moist to dry within the defined altitudinal belt. Whittaker relied mainly on the 300 site samples collected, a total of 25,000 stems, to describe and analyse the vegetation patterns through the two gradients defined.

"The site samples were finally arranged in composite transects in terms of elevation, or topographic site, or of moisture conditions as indicated by the vegetation itself. For the elevation transects some means of comparing stands of equivalent moisture conditions was needed. The site samples were consequently classified into four groups, according to which moisture class of trees was predominant in a given sample. Within each of the four classes of stands of the site samples were grouped by 200ft and 300ft intervals. Four composite transects were thus arranged to cover the whole of the vegetation pattern, showing changes in the levels of plant populations from low elevations to high in each of the four classes of stands and sites recognised." (Whittaker, 1956, 6.)

For both gradients Whittaker presented ordinations of the species distributions using as the abscissa the environmental gradient (i.e. the topographic moisture gradient or the elevation gradient) and on the ordinate the quantitative value obtained for the species in the stand at the sampling position along the gradient. It is important to remember that the quantitative species value is in fact an average obtained from usually five composite samples and further it is a relative rather than an absolute measure. Tree and tall-shrub species were expressed as relative densities (percent of stand) and for herbs and shrubs as relative cover (coverage). All of the species ordinations produced in this way showed series of bell shaped (Gaussian) species curves each with an individual position with regard to curve peak (mode) and range. Little or no association of species in terms of mode or range was apparent so that each species progressively reached a maximum representation, declined, and was replaced along the gradient by other species. Vegetation types were with some exceptions considered fully continuous with one another. The distribution of undergrowth species did not correspond with those of dominant species, and change in floristic composition of communities was continuous through vegetation types defined by dominant species. As well Whittaker produced mosaic charts (nomograms) in which the two major gradients were used as axes with elevation from 1,500ft to 6,600ft (460-2,010m) on the ordinate and moisture-balance as indicated by site on the abscissa. Thus when 300 site-samples were plotted by elevation and topographic position using the 15 forest types already classified and important species isorithms a generalised pattern of the vegetation was obtained. Whittaker also plotted individually the relative density (stand percentage) of 44 major tree species on the two gradients forming nomograms of the tree population levels in relation to the gradients. These population figures could be visualised in three dimensions as hills with their summits representing environmental optima for species and with slopes of decreasing population density with increasing departure from the optima. The species nomograms showed little evidence of association between species with each species optimum being located separately in two dimensional space. Details of the vegetation patterns noted by Whittaker included general decrease of tree stature and coverage along the moisture gradient (mesic to xeric) but with a greater number of stems in mesic sites; maximal species diversity in low elevation stands, transitional diversity between cove forests and oak forests, and decreasing diversity from these stands towards more mesic or more xeric conditions and towards higher elevations, dominance at low elevations of deciduous trees other than oaks in mesic sites, oaks in intermediate sites, and pines in xeric sites; self-maintenance of forests in undisturbed sites; general increase in coverage of the shrub stratum along the moisture gradient towards xeric sites; dominance of deciduous non-ericaceous shrubs in mesic site, evergreen ericaceous shrubs in intermediate sites, and deciduous ericads in xeric sites; an inverse relationship between shrub and herb coverage; dominance of ferns and delicate umbrella shaped herbs in mesic sites decreasing along the moisture gradient with increasing dominance of rosette plants, grasses, and ground heather; dominance of *Picea rubens* in lower subalpine forests and *Abies* fraseri in upper subalpine forests; little difference in subalpine canopy composition along the moisture gradient but striking differences in undergrowths; occurence in valleys of the same herbs and shrubs present in mesic deciduous forests; a complex undergrowth of five strata occurring on north and east slopes and decreasing in coverage around to west and south slopes; and a dense *Rhododendron* heath occurring in spruce-fir stands on ridges. The major observations made by this study were clearly those concerning the nature of species population distributions and they lead Whittaker to reject the assumption that species are organised into associations (the association unit theory) in favour of the individualistic hypothesis of Ramensky and Gleason. Whittaker thus interpreted the vegetation as a complex and largely continuous population pattern. As to the reasons for this type of vegetation pattern Whittaker considered the factors outlined in Gleason's principle of species individuality to be all important (genetic structure, physiological characteristics, and population dynamics). Thus species distributed individually according to their own physiology and genetic pattern; for example Whittaker noted the possible effects of genetic patterns of the species found in the Great Smoky Mountains These included the presence of two or more ecotypes of some major species, and the occurence of clines of introgressive hybridization, polyploidy and apomixis. Competition was also considered to affect the distributional patterns in many ways:

1. formation of plateau distributions with competition occurring within species
2. depression of population levels through competition with other species
3. competitive splitting of a species distribution
4. displacement of the environmental mode from the physiological optimum.

In spite of Whittakers emphasis on the continuity of vegetation he recognised that "some vegetation types of more extreme environments are separated from the rest of the vegetation pattern by relative discontinuities". (Whittaker, 1956, 63.) These discontinuous types or zones were characterised flattened or 'plateau' distributions of dominant species or growth forms and zonation could thus be distinguished from gradation as a tendency toward partial segmentation of the vegetation continuum. Ecotones were thus interpreted as communities themselves rather than boundaries (characterised by commodal grouping of smaller woody sp.) between communities. Whittaker also stated that the fifteen climax vegetation types defined for the Great Smoky Mountains were units of recognised subjectivity in terms of physiognomy and dominance in direct contrast to the traditionally accepted practice of classification in which vegetation types were accepted as natural units inherent in the vegetation. Whittaker's approach was thus one of relating gradients of plant populations and community characteristics to gradients of environment - gradient analysis.

## Recent contributions to Direct Gradient Analysis

Recent contributions to direct gradient analysis which add new dimensions and directions to previous direct gradient analyses are those of Beals (1969) and Reeder and Riechert (1975). Both in terms of the interpretation of vegetation pattern and the methods suitable for vegetation analysis they are particularly relevant to present study.

Beals(1969) in a direct gradient analysis conducted in two areas of Ethiopia focused on the question of relative continuity of vegetation. Firstly outlining the two major schools of thought,the continuum school of thought and the discrete community school of thought,Beals expressed the view that vegetation was capable of exhibiting both continuity and discontinuity. This being the case "the question is, What factors determine the relative continuity of the vegetation? Are there factors operating besides the obvious ones, such as predominance of certain combinations of conditions in an area, or inherent environmental discontinuity or random fluctuations". (Beals, 1969, 981.) In order to answer these questions Beals compared the effects of steep and gentle altitudinal gradients on vegetational change. The steep gradient ( a vertical change of 1,250 metres in 20 kilometres horizontal distance) was located on the Rift escarpment between the village of Bati and the town of Combolchia Ethiopia and the gentle gradient ( a vertical change of 900 metres in 300 kilometres horizontal distance) was located in the Rift Valley between Awash and Shashamanne Ethiopia. The vegetation was sampled at approximately 10 metre altitudinal intervals in both areas with a sample consisting of ten plots each 20 x 10 metres giving a total area sampled of 0.2 hectares at each location. For analysis these samples were further aggregated into segments of five combined samples each representing 50 metres of elevation. Calculation of Sorenson's coefficient of similarity ($S = 2W/(a+b)$ where $W$ = number of species common to two samples, $a$ = total number of species in sample a, and $b$ = total number of species in sample b) revealed a marked difference in the distribution of coefficients between the two areas. The gentle Awash gradient coefficient distribution was symmetrical and apparently normal while for the steep Bati gradient the distribution was highly skewed. Application of a chi-squared test on the coefficient distributions revealed statistically significant uniformity in the rate of change for the gentle gradient and irregularity for the steep gradient. Graphing of the coefficient of dissimilarity (1 - coefficient of similarity) for adjacent segments also pointed to a more marked vegetation zonation occuring along the steep Bati gradient. Species distributions for example _Acacia senegal, Acacia flaxa, Acacia tortilis, Euphorbia candelabrum, Carissa edulis, Euclea schimperi_ and _Croton dichogamus_ all showed marked differences in the two areas. Beals stated there was a distinct trend toward more sudden appearance and disappearance of species along the steep gradient (Bati) than along the gentle one (Awash). A range of factors was considered in attempting to explain the reasons for the difference in degree of vegetation continuity. These included several facets of species competition including the spatial pattern of distribution of both seeds and plants along steep and gentle gradients, and the enhancement of abrupt distributions by dominance. Environmental factors: climate, rainfall, temperature, and substrate were also considered in that a discontinuity in these variables would be reflected by the vegetation. There was no significant climatic difference detected between the two sites while there were some signficant differences in terms of substrate. Beals concluded however that none of the environmental factors exhibited marked discontinuities. A comparison of sites of adjacent segments of the altitudinal gradient showed that those pairs of segments with dissimilarity indices greater than 0.45 had no greater environmental differences than did pairs with dissimilarity indices less than 0.45.

"Thus no environmental discontinuity was detected along the steep gradient, except for the talus - bedrock transition. None was detected along the gentle gradient, although several factors did show more variability there than on the steep slope." (Beals, 1969, 984.)

In contrast the vegetation of the two slopes exhibited discontinuity on the steep slopes and continuity on the gentle slopes. Beals noted that abrupt distribution of dominant species will in itself cause some discontinuity in the vegetation if the vegetation is analysed quantitatively but there are other species whose change in density is correlated with the dominants, and these reinforce the discontinuity thus in the transition between dominants on the steep gradient many other species also either disappear or appear as the transition is made from one dominant species to another. On the gentle gradient however few simultaneous changes of dominants and sub dominants were detected. Beals thus considered the "correlations of species limits along the steep slope may be brought about by direct biotic interactions - or perhaps chemical interactions - or more commonly by sudden change in the physical environment caused by sudden change in species density". (Beals, 1969, 985.)

Euphorbia candelabrum for example with a different physiognomy to other plants in the area (succulent, leafless, "candelabra" branches) and possible chemical interactions due to its poisonous latex caused the most rapid vegetational change on the steep and gentle gradients. In conclusion Beals (1969) claimed that along the steep gradient the vegetation itself imposed disjunctions on an extrinsically continuous environmental gradient, whereas along the gentle gradient this did not occur. Possible causes for the development of the disjunctions identified were dispersal rates, vegetative reproduction,the competitive - exclusion principle which was probably influential in demarcating plant communities as defined by dominant species along a rapidly changing environmental gradient. Thus as Beals states "the question that should bother ecologists is not really whether vegetation forms a continuum or forms natural and discrete groupings. It is obviously capable of forming both ... The quesion that should be asked is, what methods should be used in the analysis of vegetation - a continuum approach or a classification approach?" (Beals, 1969, 985.) In answer to this question,and contrary to previous opinion,Beals (1969) considered the continuum and classificatory approaches as not necessarily incompatible although he considered the continuum or gradient analysis approach capable of detecting discontinuities whereas the classificatory system could not. Thus for "the purposes of mapping or landscape inventory, classification is necessary and informative; for understanding the sociology of plant communities, some kind of gradient analysis, appears to be more efficient". (Beals, 1969, 985.)

Reeder and Riechert (1975) in a paper entitled "Vegetation change along an Altitudinal gradient, Santa Cruz Island, Galapagos", described the results of a direct gradient analysis along a limited altitudinal gradient (183 metres rise in 12,900 metres traverse).

Sampling occurred at 10 metre altitudinal intervals with five linearly arranged contiguous 10 x 10 metre quadrats located along the contour. The data from the five quadrats was combined so that the total area sampled at each site was 500 sq.metres. Calculation of the dissimilarity index (1 - similarity index) between adjacent samples in the same way as Beals (1969) revealed breaks in the continuity of vegetation change at several points along the gradient. The breaks in the continuity of the vegetation enable the recognition of several vegetation zones: a Mangrove - coastal zone, a Cryptocarpus zone, an Arid zone, and a Protean zone. Canonical analysis was also carried out on the samples and results coincided closely with those obtained using the dissimilarity index. Examination of climatic data (moisture gradients and substrate) revealed no specific breaks in environmental continuity which might explain the discontinuities in the vegetation. The second canonical variate extracted suggested the cause of the observed discontinuities in that it separated out all the samples at which the greatest discontinuity occurred and all except one exhibited "a 10m rise in altitude over a relatively short distance when compared with altitudinal samples along the remainder of the transect". (Reeder and Riechert, 1975, 168.) Thus they concluded that the discontinuities in the vegetation represented slope effects and two major possibilities for slope effects were proposed:

1. the physical environment and differences in terms of water runoff and soil deposition
2. the plant species themselves imposing disjunctions on a steep slope - increased competition might occur where little marginal habitat is offered by mutual invasion by similar species.

Differences in the physical environment resulting in structural stand differences were thought to be more important with a much higher representation of small height class individuals on steep slopes than on other parts of the gradient. Structural features rather than species representation contributed much to the variability exhibited in the vegetation with zonation being related to tree-species equitability and richness (zone separation in the form of a greater number of equally dominant plant species). Discontinuities identified in the vegetation by Reeder and Riechert (1975) were more in terms of total stand character than in sudden changes in species composition. The discontinuities were characterised "by unusually large numbers of young trees on steep slopes... in what otherwise might have been considered continuous vegetation change with altitude". (Reeder and Riechert, 1975, 174.)

## New Zealand Altitudinal Gradient Analyses

A number of New Zealand researchers have followed the original work of Whittaker (1948, 1956) and Curtis and McIntosh (1951) and performed direct gradient analyses on the vegetation in New Zealand using altitude as the principal gradient. They include: Mark and Sanderson (1962) in the Hollyford Valley Fiordland, Mark (1963) at Secretary Island Fiordland, Wells and Mark (1966) on Mt Anglem Stewart Island, Mark and Burrell (1966) on the Humboldt Mountains Fiordland, Daly (1967) in Central Otago, Gibbs (1966) in Tongariro National Park, Ogden (1971) on Mt Colenso in the Ruahine Ranges and Clarkson (1974) in the Tongariro National Park.

Mark and Sanderson (1962) analysed the forest on the eastern side of the Hollyford Valley in the vicinity of Deadman's Hut - Harris Saddle Track (See Figure 3) "to describe the changes in composition, structure and regeneration of the forest associated

Figure 3

LOCATION OF NEW-ZEALAND GRADIENT ANALYSES

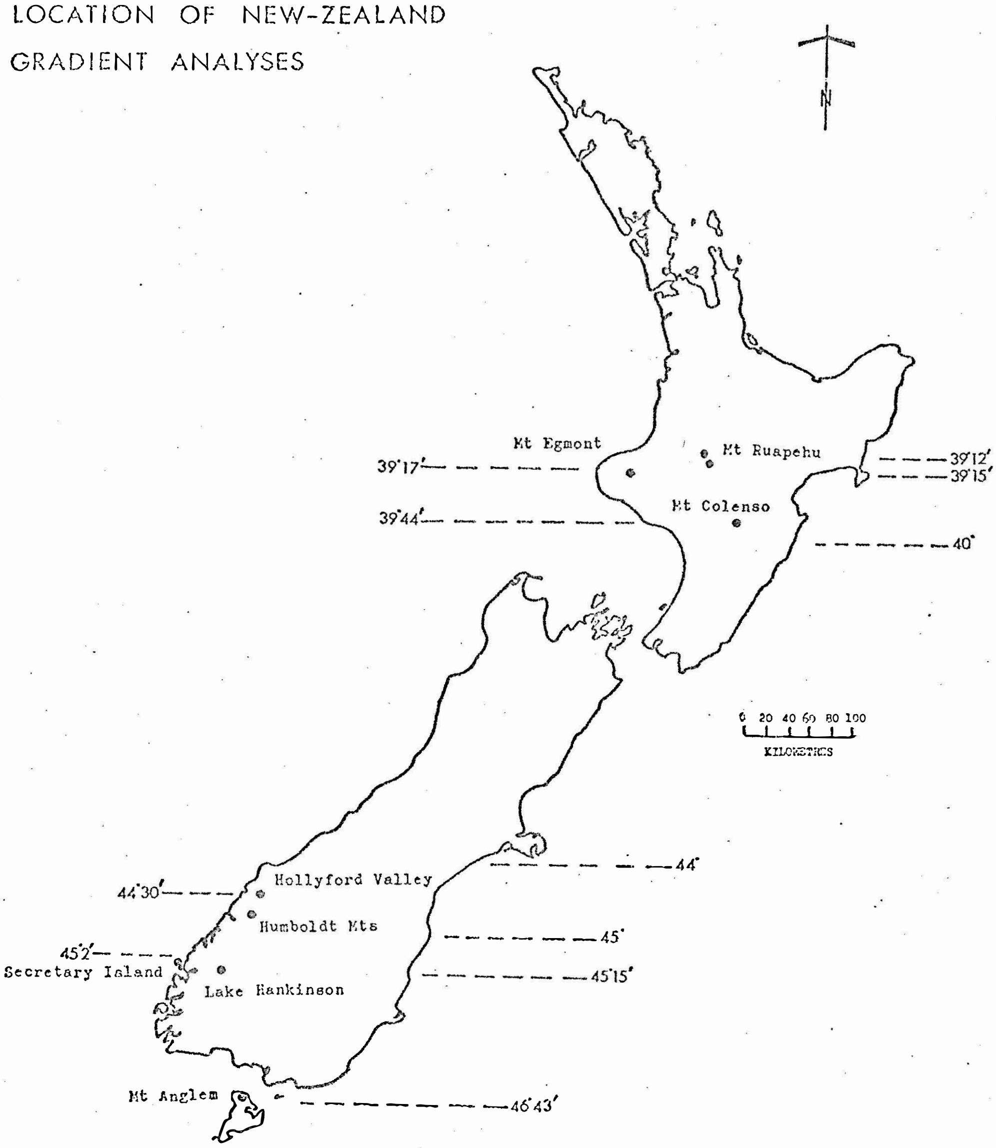


Table 3. Comparison of New Zealand Direct Gradient Analyses:

| Author | No. of samples | Sample size |
|---|---|---|
| Mark and Sanderson (1962) | 6 sites<br>X 10 sections | 835sq m Trees<br>417sq m Shrubs etc |
| Mark (1963) | 14 | first 200 trees |
| | 7 | 835sq m Trees<br>417sq m Shrubs etc |
| Scott et.al. (1964) | 6 sites | 835sq m Trees<br>417sq m Shrubs etc |
| Wells and Mark (1966) | 8 sites x 25<br>points - 4<br>trees each point | Plotless |
| | 15m x 10<br>point intercept<br>every 30 cm | 500 pts x 10 |
| Mark and Burrell (1966) | 6 sites | 15 x 10m<br>transects<br>point intercept<br>every 30 cm |
| Gibbs (1966) | 18 sites<br>(270 quadrats) | multiples of<br>2sq m Max.<br>pooled data<br>38 x 2sq m |
| Daly (1967) | 10 sites<br>(99 stands) | line transects<br>30 x 30cm<br>-1.21m point intercept<br>20 x 30m<br>60 cm point intercept |
| Ogden (1971) | 4 sites | 1 hectare |
| Clarkson (1974) | 73 transects | line transects<br>5 m |

| Sampling procedure | | |
|---|---|---|
| Maximum altitudinal interval | Average altitudinal interval | Altitudinal |
| 182m | 149m | 91.40 - 990.16m<br>(898m) |
| 76m<br>73m | 76m<br>144m | 0 - 898.76m<br>(898m) |
| 182m | 137m | 213.26 - 914.00m<br>(700m) |
| 170m | 132m | 0 - 976.[illegible]0m<br>(976m) |
| 210m | 140m | 1080.00 - 1640.00m<br>(560m) |
| 60m | 28m | 1218.66 - 1706.13m<br>(487m) |
| 243m | 104m | 91.40 - 1645.20m<br>(1553m) |
| 198m | 157m | 639.80 - 990.16m<br>(350m) |
| 3.0m | 2.7m | 1172.96 - 1371m<br>(198m) |

with change in altitude from the valley floor at 300ft a.s.l. (91.40m) to the tree line of 3,240ft (990.16m)". (Mark and Sanderson, 1962, 17.) Rectangular plots 500ft (152.33m) in length were used to sample vegetation at six sites approximately 500ft (152.33m)apart on the altitudinal gradient. The data collected was used to calculate Importance Values as in Curtis and McIntosh (1951). Results showed changes in both composition and structure through altitude and a general lack of ecological interdependence between species, the individual range of each species being determined by its individual environmental tolerance limits. Mark and Sanderson (1962) stated however that rather abrupt changes both in vegetation composition and structure apparent at 1,500ft (457m) made it possible to define a lowland mixed beech - podocarp - kamahi forest and an upland pure silver beech forest. Of the sixty-seven species recognised, two groups: those not venturing above 1,500ft (457m) (twenty-two species), and those occurring only above that level (twenty species) were apparent,so that "although the composition of the forest varies continuously with altitude, it is also possible to recognise two distinct forest types; beech - podocarp - kamahi forest below, and silver beech forest above". (Mark and Sanderson, 1962, 25.)

Mark (1963) analysed the forest along a spur running north westward from the shoreline at Blanket Bay Secretary Island to the treeline at 2950ft (898.76m) (See Figure 3) "to describe variations in composition, density, and dominance of the forest strata (except ground cover, epiphytes, and lianes) along this altitudinal gradient". (Mark, 1963, 108.) Data collected on two separate occasions was combined and Importance Values calculated as in the study by Mark and Sanderson (1962). The sampling interval ranged from 250ft (76.16m) for plots in which trees only were recorded up to 550ft (167.56m) in plots where shrubs and ground cover were recorded as well. Maximum plot sizes were 1,000sq yds (835sq m) for mature and developing trees and 500sq yds (417sq m) for shrubs, herbs, and small tree seedlings. Plots were selected to avoid steep bluffs and other anomalous sites and those examined ranged between 7-35$^{o}$ slope angles with aspects between east and south. Results showed a rather abrupt change in composition and structure of the tree, small tree, and shrub strata near the 1,500ft (457m) contour. This forest was regarded as "transitional between a lowland mixed forest, dominated chiefly by kamahi (W. racemosa), rata (Metrosideros umbellata) and the podocarps with a moderate beech component, chiefly mountain beech (N. solandri var. cliffortioides); and an upland beech forest, dominated by silver beech (N. menziesii) with mountain beech co-dominant or dominant on relatively dry, exposed sites". (Mark, 1963,192.) In terms of altitudinal distribution species could be divided into five broad groups: those confined to the shoreline, lowland species occurring generally below 1,500ft (457m), continuous or near continuous species, high altitude species, and species with discontinuous distributions. Rata (M. umbellata) was considered to exhibit a unique distribution (sealevel to about 2,350ft (715.96m)). Overall in fact the sixty-nine species listed in the four strata showed little or no interdependence in their distributions. In concluding Mark (1963) cited his objectives as being twofold: firstly to discover the results of an altitudinal gradient analysis in unmodified New Zealand forest and secondly to provide data of use in assessing damage by exotic animals in other parts of Fiordland. With regard to the first objective the extensive overlap of species ranges was interpreted as supporting the proposition that species respond individually to the environmental gradient associated with increasing altitude as a result of their individual tolerance and competitive ability. With regard to the second objective the usefulness of the data in providing a basis of comparison for animal damage within Fiordland was considered limited because of the complexity of Fiordland forest vegetation.

Scott et. al. (1964) investigated the changes in forest composition and structure associated with increasing altitude upon a spur on the north side of the valley between Lakes Thomson and Hankinson, north-west from the Hankison Hut in Fiordland. (See Figure 3) Sampling was carried out at six sites between the valley floor 700ft (213.26m) and the tree-line at 3,000ft (914.00m), the altitudinal interval averaging 137m. The quadrat sizes were the same as those of Mark and Sanderson (1962) as was the sampling procedure and the data collected was used to calculate the relative density and basal area of species recorded. The forest was "dominated throughout by N. menziesii (silver beech) constantly accompanied by the understory species: Neopanax simplex, Coprosma foetidissima, Myrsine divaricata, Blechnum minus, and Astelia nervosa" (Scott. et.al., 1964, 311.) with all other species exhibiting some restriction in their altitudinal range. Scott et. al. (1964) considered the canopy and subcanopy species showed a gradual and continuous change in composition making it impracticable to subdivide the forest into discrete communities although two different facies were apparent: upland and lowland. The greatest discontinuities noted occurred just below the tree line where many subalpine grassland species penetrated into the forest and near the 2,000ft (609.33m) mark the upper limit of the important lowland species: *P. hallii, P. colorata, M. umbellata, G. littoralis,* and W. racemosa.

Wells and Mark (1966) described quantitatively the altitudinal gradient in vegetation on the north-eastern slope of Stewart Island's highest peak Mt Anglem. (See Figure 3.) Eight sites between sea level and the summit 976m were sampled using the Point centre quarter method of plotless sampling of Cottam and Curtis (1956). Twenty-five points at each site were sampled giving 100 determinations for Trees, Small trees, Shrubs and Herbs (as defined by Wells and Mark 1967, 269). Data obtained was used to calulate total and relative density and basal area although in the alpine herb moor of the summit the point-intercept method was used to give measures of dominance and cover. The average altitudinal interval between sites was 132m. The quantitative results of the sampling enabled Wells and Mark to recognise four major plant communities separated by discontinuities both in physiognomy and floristic composition. The four groupings identified supported the qualitative descriptions given previously by Cockayne (1909). The four community types: Lowland Podocarp - Broadleaf Forest, Montane Leptospermum - Dacrydium Tall Shrubland, Sub-alpine Scrub, and Alpine Herb Moor are best described in terms of the altitudinal distribution of their dominants. The Lowland Podocarp - Broadleaf forest was described as occupying the area up to 300m being dominated by *Dacrydium cupressinum, Podocarpus ferrugineus,* and *Weinmannia racemosa* all of which reached their maximum densities and basal areas below this altitude. Montane *Leptospermum* - *Dacrydium* Tall shrubland occupies a zone between 320m and 410m and is separated by a narrow belt of transitional vegetation. *Leptospermum coparium* and *Dacrydium biforme* reach their maximum densities at those altitudes and are important in the shrub layers only past 410m. The subalpine scrub between 410 - 650m is dominated by *Olearia colensoi* the transition between it and the tall shrubland being characterised by the increasing dominance of *O. colensoi* and the decreasing importance of *L. scoparium* and *D. biforme.* The Alpine Herb Moor, essentially continuous above 850m, is characterised by greater floristic richness than the other three communities and the dominance of *Dracophyllum politum, Chionochloa pungens* and *Raoulia goyenii.* In contrast to the previously described work then Wells and Mark (1966) interpreted the altitudinal sequence of vegetation in terms of four major community types defined by discontinuities both in floristics and physiognomy.

Mark and Burrell (1966) quantitatively analysed a series of sample plots at six sites between 1080m and 1640m on the Humboldt Mountains overlooking the Hollyford Valley in Northern Fiordland. (See Figure 3) "Since the transect began within 3km of the Deadman's Harris Saddle Track, it could be considered as an upward extension of the altitudinal gradient already described for the forest (Mark and Sanderson 1962". (Mark and Burrell, 1966, 12.) The purpose of the study stated was to determine whether or not changes in the composition and cover of the grassland vegetation between the silver beech (*N. menziesii*) timber line and the upper limits of closed vegetation at about 1,640m conformed to a gradient or whether discrete communities could be recognised. The maximum altitudinal interval between sites was 210m while the average interval was 140m. Sampling at all of the six sites took the form of 10 X 15m transects using the point intercept method, the point interval for the top stratum being 30cm. On the basis of physiognomy three communities were obvious: the first a mixed snow tussock scrub dominated by

*Chionochloa flavescens* at about 1,000m; the second a tussock grassland dominated by *C. flavescens* and *C. crassiucula* above 1,100m; and the third dominated by the dwarf tussocks *C. oreophila, Poa colensoi* and the mountain daisy *Celmisia hectori* above 1,500m. Calculation of similarity indices to compare the sites both floristically (presence and absence of species) and vegetatively (species cover values) indicated the presence of an altitudinal gradient in that the flora from adjacent sites tended to be more closely related than distant sites. Further to this, lack of ecological interdependence between species was obvious with the exception of the ecotone between forest and grassland. Mark and Burrell concluded however that despite the gradient in composition,the abrupt changes in structure and composition of dominant and subordinate species (1,100m and 1,500m) enabled the recognition of separate communities; the low alpine snow tussock - scrub, low alpine snow tussock grassland, and high alpine dwarf tussock grassland.

Daly (1967) attempted to relate variation in the grassland continuum in Central Otago to the principal environmental gradients altitude and moisture status,however the results of only the altitudinal gradient analysis will be reviewed. Ninety-nine stands were "sampled to represent the wide range of variation exhibited by the grassland and related vegetation" (Daly, 1967, 63) and the altitudinal range was between 300ft (91.4m) and 5,400ft (1,645.2m). The maximum altitudinal interval was 243m while the average interval was 104m. Sampling in each of these stands took the form of line transects; for example, for the grassland and shrubland 30 x 100ft (30.46m) lines with point intercepts recorded at 4ft (1.22m) intervals. The results were analysed according to the Bray-Curtis (1957) method of ordination and graphing of relative cover values for species in a linear arrangement of communities. Results showed each species reaching a peak contribution in terms of relative cover at different altitudes and exhibiting an individual range of tolerance to different altitudes. Daly thus concluded that these overlapping distributions indicated a continuum of vegetation along a gradient of increasing altitude and changing moisture status.

Gibbs (1966) sampled 18 sites in an area above the Timberline on the North West slopes adjoining Bruce Road Mt Ruapehu between 4,000ft (1,218.66m) and 5,500ft (1,706.13m). (See Figure 3.) Multiple sampling using 2sq m quadrats took place at each site with a maximum of 38 quadrats and a minimum of two quadrats at any one site. The altitudinal interval maximum was 220ft (67m) and the average interval approximately 92ft (28m). Species were rated on a 1 - 5 scale for sociability and dominance within each quadrat and frequency determined as the percentage occurrence in the total quadrats collected at each site. Importance Value Indices the same as Curtis and McIntosh (1951) were calculated for all species and used to assess their distribution. Different species exhibited different altitudinal limits of growth: twelve species at 4,500ft (1,371m), six species at 5,000ft (1,523.3m), while seven species were recorded throughout the altitudinal range from 4,000ft (121.86m) to 5,600ft (1,706.13m). The remainder of the total of seventy-four species exhibited varying individual altitudinal limits. Comparison of the species distributions pointed to floristic changes in sample composition around 4,500ft - 4,600ft (1,371m - 1,401.46m) and 4,900 - 5,000ft (1,492.86m - 1,523.33m) although physiognomically the vegetation appeared to belong to one plant association in which Dracophyllum recurvum, Rhacomitrium lanuginosum, Celmisia spectabilis, Senecio bidwillii, Anisotome aromatica and Gaultheria colensoi were the important species. On the basis of these floristic discontinuities Gibbs suggested the division into three plant communities: a Gleichenia - *Chionochloa* - *Dacrydium laxifolium* community between 4,000ft and 4,600ft (1,218.66m - 1,401.46m), a *Dracophyllum* recurvum - Rhacomitrium - *Celmisia spectabilis* community between 4,500 and 5,100ft (1,371m - 1,553.8m), and a *Rhacomitrium* - Dracophyllum recurvum - *Gaultheria colensoi* community above 5,100ft (1,553.8m)

Ogden (1971) quantitatively described the altitudinal distribution of the species on Mount Colenso in the Ruahine Range. (See Figure 3). The point centred quarter method of Cottam and Curtis (1956) was used to sample four stands of approximately 1 hectare in area. Stands ranged from 2,100ft (639.8m) to 3,250ft a.s.l. (990.16m) with an average altitudinal interval of 576.66ft (137.41m). Graphing of the distributions of the main species showed overlapping altitudinal ranges "so that no clear cut altitudinal 'zones' or 'belts' can be distinguished even if canopy species only are considered". (Ogden, 1971, 59.) Ogden thus considered the forests on the Kauwhatau spur of Mt Colenso to form a continuum of overlapping species distributions ranging from mixed beech-podocarp forest on the terraces, through red beech (N. fusca) dominated forest at intermediate heights, *Libocedrus bidwillii* - *Dacrydium biforme* forest near the tree line, merging gradually with Olearia - Hebe - *Cassinia* scrub and finally into tussock grasses and herbs. The altitudinal distribution of ground cover herbs and ferns was also interpreted as a continuum of species similar to that seen in the canopy trees and shrubs. In conclusion Ogden repeated Elder's (1965) statement "in averaging out (the altitudinal range of different species) it became clear that the representative species are not grouped in altitudinal zones, but appear in an overlapping gradation". (Ogden, 1971, 65.) He also made the point that if an empirical classification of this vegetation continuum had to be devised it would be best to recognise a few main communities with broad ecotones between them.

Clarkson (1974), in an unpublished field report, described a direct gradient analysis carried out in the Taranaki Falls area of Mt Ruapehu between 3,850ft and 4,500ft (1,172.96m - 1,371m). Seventy-three 5m line transects at an average altitudinal interval of 2.70m were used to record the presence of all species throughout the altitudinal range. Similarity indices were calculated to compare the transects on a floristic (presence and absence of species) basis. On the basis of these similarity indices and the species distributions four separate sub-associations were recognised: a Dracophyllum recurvum - Dacrydium laxifolium - Gaultheria colensoi sub-association between 4,100 and 4,500ft (1,249.13m - 1,371m), a Coprosma cheesemanii - Dracophyllum recurvum - Cyathodes sp. sub-association between 4,000 and 4,100ft (1,218.66m - 1,249.13m), a Dracophyllum recurvum - Celmisia spectabilis - Coprosma cheesemanii sub-association between 3,900ft and 4,000ft (1,182.20m - 1,218.66m), and a Celmisia spectabilis - Dracophyllum recurvum - Gleichenia circinata sub-association between 3,850ft and 3,900ft (1,172.96m - 1,188.20m). Apart from the principal changes in composition along the altitudinal gradient, factors including slope, aspect, and lithology were recognised as important in determining the distribution of the sub-associations identified. Overall high similarity indices between transects and the vegetation physiognomy pointed to the fact that all the sub associations identified were part of one plant association dominated by species found throughout the altitudinal range including D. recurvum and C. spectabilis.

# Chapter 4

# METHODS

## Data Collection

Data from forty-eight quadrats was collected on four major ridges of Mt Egmont: York Road Track Ridge, North Egmont (Blundell's Track and Razorback), Dawson Falls (Summit Track), and Lake Dive Track Ridge. (See Figure 1) Of these quadrats twenty-three were collected to describe the vegetational change through the altitudinal gradient along the York Road Track Ridge, while the twenty-five collected at the North Egmont, Lake Dive, and Dawson Falls locations provide further comparisons of the tree-shrub and shrub-tussock interface. Twelve samples collected on the Stratford side in 1972 with the assistance of the Massey University Extension Course have been included as well bringing the total to sixty quadrats. All sampling except for the twelve quadrats from the Stratford side was conducted between 28/8/75 and 13/6/76 and employed a predetermined sampling procedure as outlined below.

## Sampling procedure: an outline

1. Quadrats to be located altitudinally at thirty metre intervals between 853m (2,800ft) and 1,858m (6,100ft).
2. No sampling within two metres of tracks or ridge sides.
3. Quadrat size to vary according to minimal area checks and accepted quadrat sizes as described by Mueller-Dombois and Ellenberg (1974) p. 67-80.
4. Sample on North facing slopes only.

5. Always sample in medium drainage conditions - avoid extremes of free-draining or poorly drained.
6. No sampling on sites where the slope angles exceeds $50^0$ (cliffs, banks, etc.).
7. Avoid marked changes in substrate, in particular exposed rock faces.

The sampling procedure was designed specifically to hold as many environmental parameters constant as possible so that the altitudinal gradient would be the prime one reflected by the vegetation.

Sample size: a justification

The final quadrat size was determined after reconnaisance of the entire ridge, the most important restriction in many places being ridge width. At locations where ridge width was the major criterior for quadrat size the practice was to sample as large an area as possible. As well quadrat size was also determined by attention to two critical factors. The first was the need to retain sufficient internal sample homogeneity, a characteristic noted by Mueller-Dombois and Ellenberg (1974) as particularly important in mountainous terrain, and the second was the need to achieve a minimal quadrat size for obtaining a representative combination of species. Three examples of minimal area checks have been included to show the minimal area required in shrub-tussock communities, lower altitude forest, and the herbfield (See Figures 4, 5, and 6 and Table 4). The point at which species representation levels off to within five or ten percent of the value recorded in the preceding sample area is generally accepted as the minimal area to be sampled if a representative combination of species is to be achieved. For the shrub-tussock samples it is obvious that if line transects are to be employed at least three ten metre lines

Table 4. Minimal Area Checks: Relative Density of given species as a function of quadrat size or line transect length.

A. Shrub-Tussock 1,325m (4,350ft) York Road Track Ridge

| | | | | | |
|---|---|---|---|---|---|
| Senecio elaeagnifolius | 12.50 | 7.14 | 8.06 | 6.59 | 6.54 |
| Chionochloa rubra | 3.12 | 28.57 | 17.74 | 17.58 | 14.95 |
| Hebe odora | 6.25 | 17.85 | 25.80 | 19.78 | 19.62 |
| | 0-5m | 0-10m | 0-20m | 0-30m | 0-40m |

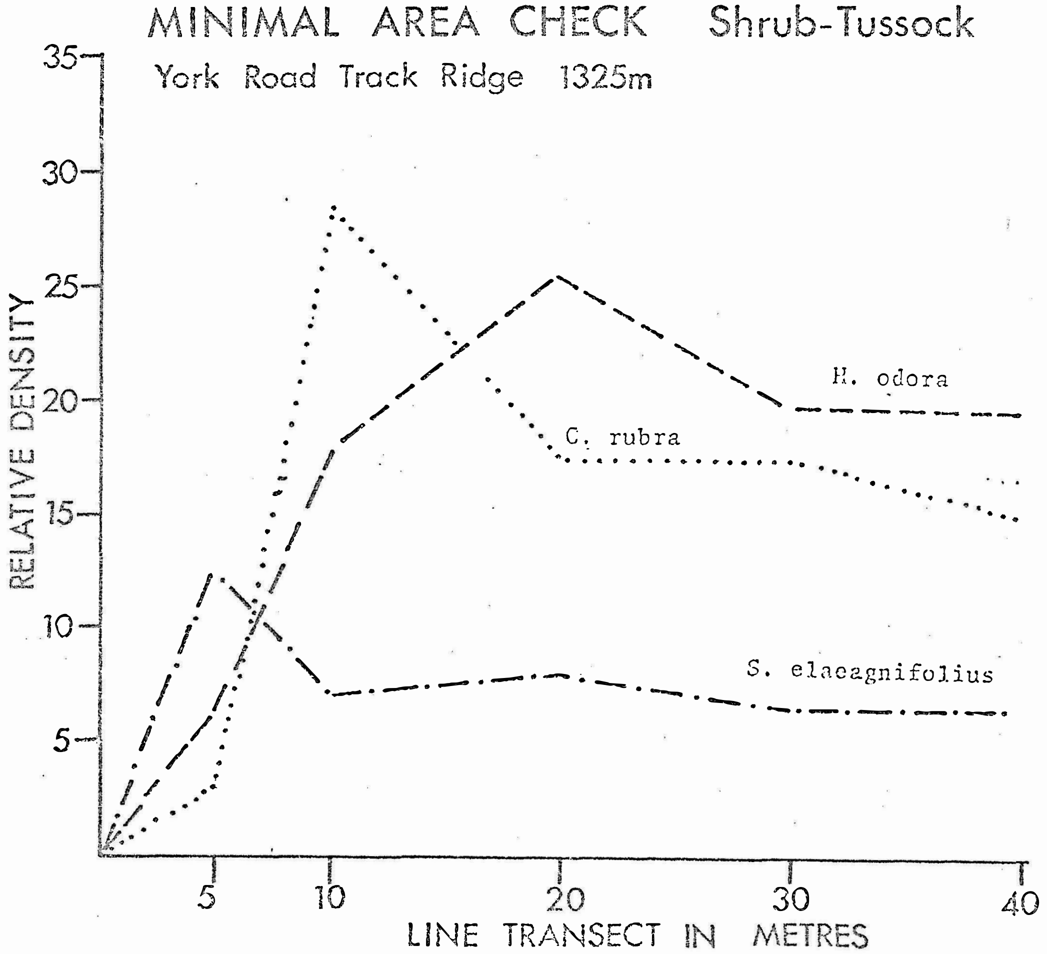
B. Forest 935m (3,070ft) Dawson Falls

| | | | | | |
|---|---|---|---|---|---|
| Podocarpus hallii | 100.00 | 40.00 | 21.40 | 14.70 | 17.07 |
| Griselinia littoralis | 0 | 20.00 | 7.14 | 11.76 | 12.19 |
| Weinmannia racemosa | 0 | 40.00 | 71.40 | 73.52 | 70.73 |
| | 5x5m | 7x7m | 10x10m | 10x20m | 10x30m |

C. Herbfield 2,096m (5,570ft) York Road Track Ridge

| | | | | | |
|---|---|---|---|---|---|
| Poa colensoi | 38.09 | 42.85 | 34.48 | 31.57 | 29.75 |
| Gaultheria sp. | 9.52 | 7.14 | 9.19 | 8.77 | 9.09 |
| Montia sp. | 0 | 0 | 0 | 0 | 1.65 |
| | 0-5m | 0-10m | 0-15m | 0-20m | 0-25m |

Figure 4



MINIMAL AREA CHECK Shrub-Tussock

York Road Track Ridge 1325m

Figure 5

MINIMAL AREA CHECK Forest

Dawson Falls 935m

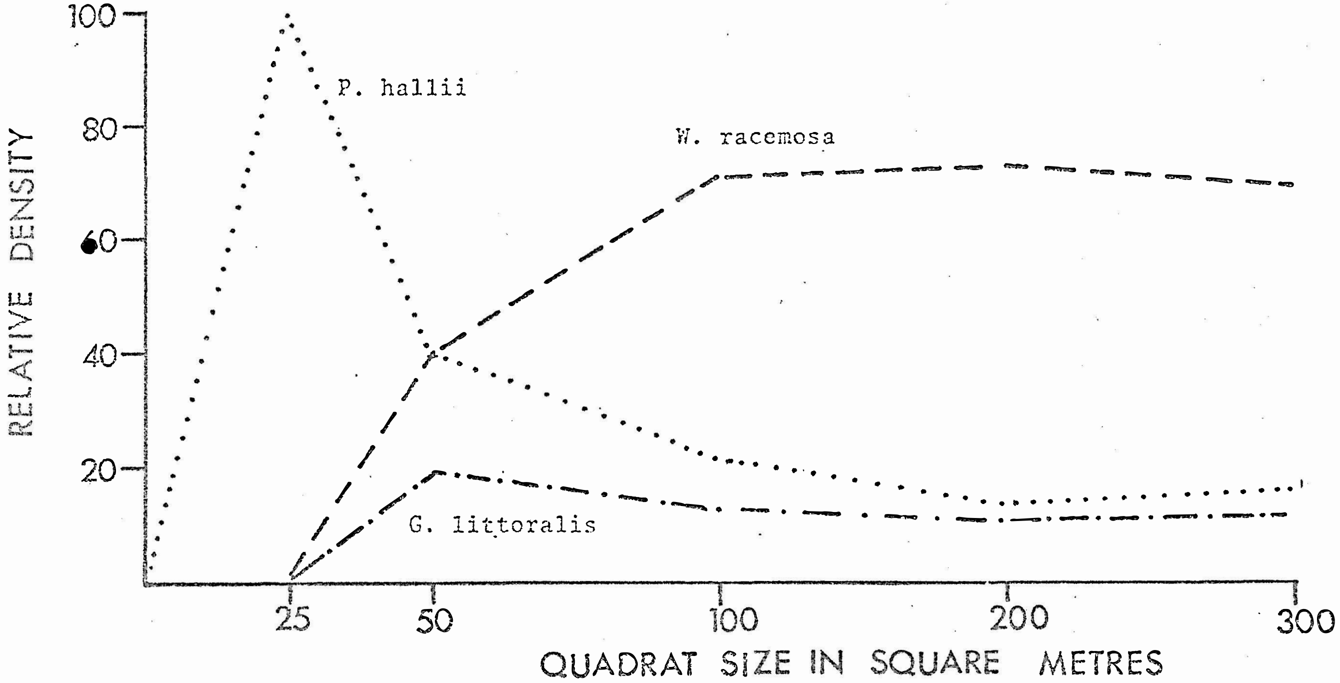
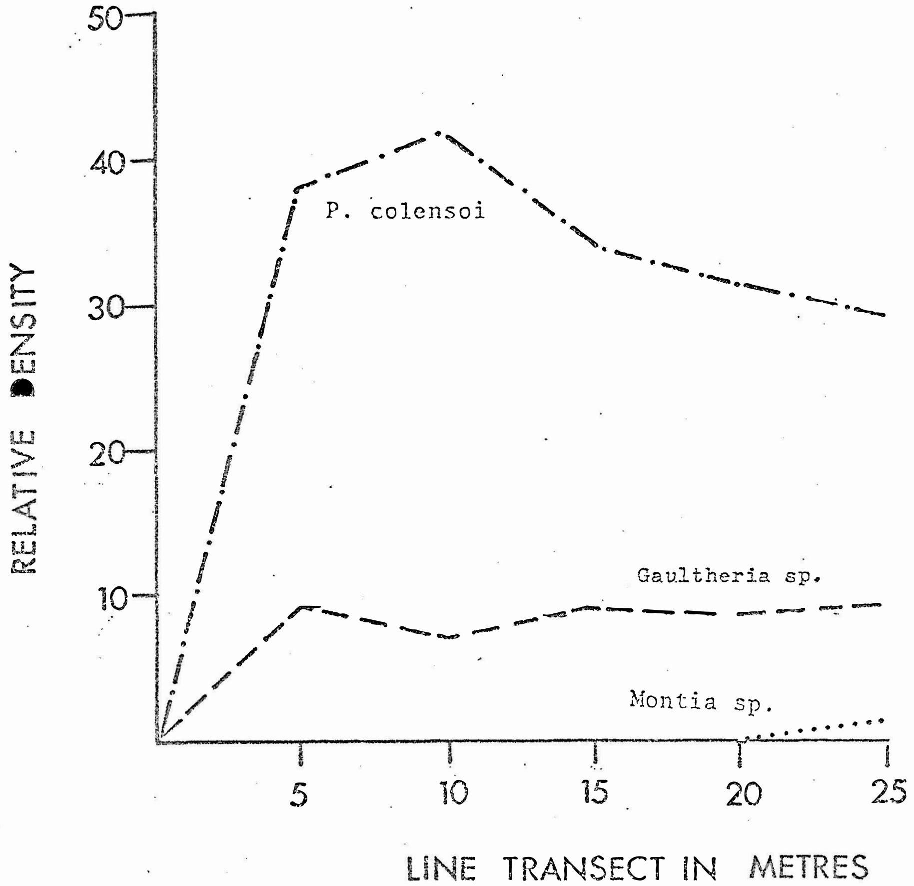


Figure 6

## MINIMAL AREA CHECK Herbfield

York Road Track Ridge 2096m



are required to achieve a representative combination of species. In contrast the minimal area required in the lower altitude forest is closer to 200sq m. Five 5m line transects at least are required for the herbfield and in fact this may be insufficient although the requirement of substrate homogeneity becomes almost impossible to meet if the sample exceeds 5sq. m. Further justification for the quadrat sizes finally used includes the data of Westhoff and Van der Maarel, who list minimal areas for various communities in Whittaker (1973), and Mueller-Dombois and Ellenberg (1974) who list minimal areas for temperate-zone vegetations. The final quadrat sizes thus determined were: Forest 20 x 20m, Scrub-Forest 15 x 15m, Scrub 10 x 10m, Tussock grassland and herbfield 5 x 5m (or in the case of the latter two, modified to line transects at least 3 x 10m lengths). The fact that quadrat size would have to be increased to 50 x 50m or even greater in the forest below 853m (2,500ft) was the major reason for dealing with the vegetational change along the altitudinal gradient between 853m and 1,858m.

Vegetation was recorded in the categories listed below:

1. Canopy - trees with more than fifty percent of their crowns in full sunlight.
2. Sub canopy - trees not reaching full sunlight - shaded by the canopy.
3. Shrubs - less than 2m.
4. Ground cover - the herbaceous layer of grasses, ferns, seedlings etc.
5. Epiphytes - perching plants including seedlings of tree species.
6. Lianes - climbing plants, creepers, vines.

Species nomenclature throughout follows that of Druce's Unpublished "Checklist of the Higher Plants of Mount Egmont including Pouakai and Kaitake Ranges", Third Approximation November 1973 and including Corrections: August 1974, October 1974, July 1975 and April 1976.

Diameter at breast height (d.b.h. at 1.50m) was recorded for canopy and subcanopy species. Density was recorded for canopy, subcanopy and shrubs. Cover was recorded employing the line-inter intercept method (described by Mueller-Dombois and Ellenberg, 1974, 90) and line transects (continuous cover) in shrub quadrats. Ground cover was recorded along a line stretched across the quadrat 1 metre from the most northerly side. As well as this quantitative measure of ground cover all ground cover species present in the quadrat marked out were noted. Therefore in all the forest quadrats ground cover species present was recorded in an area 20 x 20m. Special attention was paid to the presence or absence of seedlings of the canopy species and estimates of seedling numbers for the major canopy species were made in the whole quadrat. The presence of epiphytic and liane species was also noted. Table 5 summarises the data recorded for each stratum of the vegetation at each site.

Table 5. Summary of Vegetation Data recorded at each site.

| | Presence | Relative cover | Relative density | Relative Basal Area |
|---|---|---|---|---|
| Canopy | X | X | X | X |
| Subcanopy | X | | X | |
| Shrubs | X | | X | |
| Ground cover | X | X | | |
| Epiphytes | X | | | |
| Lianes | X | | | |
| Seedlings | X | | | |

Canopy height was measured in the majority of quadrats and estimated where measurement proved difficult, for example in the lowland forest. Slope and aspect were recorded for all quadrats although ridge alignment in each of the sampling areas summarises the aspect of all the quadrats. The altitude for each quadrat was determined using an altimeter (13-2000-IN Aircraft Inst. Develop. Inc. Wichita, Kansas) and known spot heights on the ridges examined particularly those of Huts, Trig stations, Track junctions, and National Park markers. The altimeter proved to be accurate to within ± 10ft (9.14m) on days in which the weather was stable, however, because of Mt Egmonts unstable climate, altitudes required checking up to four times on some sites. General notes were also recorded for each quadrat including descriptions of substrate, drainage, vegetation physiognomy and structure, and regeneration performance of the major canopy species.

## The use of the Importance Value (I.V.)

The Importance Value (I.V.) was first used in vegetation studies by Curtis & McIntosh (1951) and was defined as the sum of Relative Density, Relative Frequency, and Relative Dominance values for a given species in a given stand of vegetation:

$$\text{Relative Density} = \frac{\text{Number of individuals of a species}}{\text{Total number of individuals of all species}} \times 100$$

$$\text{Relative Frequency} = \frac{\text{Frequency of Species A}}{\text{Sum of frequency values of all species}} \times 100$$

$$\text{Relative Dominance} = \frac{\text{Basal Area (or Cover) of Species A}}{\text{Total Basal Area (or Cover) of all species}} \times 100$$

So defined, the Importance Value ranges from 0 (where a species is unrepresented) 300 (where a species forms a monodominant stand). Mueller-Dombois and Ellenberg (1974) make the point that any one of the three parameters may be interpreted as an importance value depending on which of the values the investigator considers most important for a particular species, group of species or community. Several workers including Fosberg (1961), Rice (1967), and Daubenmire (1968) have criticised the use of relative rather than actual parameters because densely vegetated and sparsely vegetated habitats can record the same relative densities, relative basal areas, and relative frequencies giving no indication of species biomass or cover which are considered of greater ecological significance in plant distribution. In the light of these criticisms the importance value used in this study is presented and justified. The Importance Value (I.V.) for Canopy (Top Stratum) Species may be summarised as

$$\text{I. V.} = \text{R. D.} + \frac{(\text{R. C.} + \text{R. B.})}{2}$$

$$\text{Importance Value} = \text{Relative Density} + \frac{(\text{Relative Cover} + \text{Relative Basal Area})}{2}$$

Three aspects require justification in the use of this proposed importance value in this study. The first is the ommission of the Relative Frequency value, the second the combination or averaging of Relative Cover and Relative Basal Area, and the third the use of relative rather than absolute values. The Relative Frequency value could not be computed because only one quadrat was measured at each specified altitude because of site restrictions that is the limitation imposed by ridge width at many locations along the York Road Track Ridge. Relative Cover and Relative Basal Area were averaged on the grounds that "instead of crown area, cover may also imply the projection of the basal area to the ground surface". (Mueller-Dombois and Ellenberg, 1974, 118.) and therefore, the cover of the crown of a canopy species or the diameter breast height (d.b.h.) are essentially measures of the same parameter that is, the area taken up by a species within a reference area and relative to the area taken up by other species. A comparison of the data obtained in sampling for both Relative cover and Relative Basal Area shows a variable relationship between the two measures for example in Table 6.

Table 6. Relative Cover and Relative Basal Area for *Podocarpus halli* and *Griselinia littoralis* on the York Road Track Ridge

| Altitude in metres | *P. hallii* | | *G. littoralis* | |
|---|---|---|---|---|
| 897 | 26.08 | 32.13 | 36.95 | 16.93 |
| 959 Regeneration quadrat | 82.60 | 79.65 | — | — |
| 959 | 37.83 | 36.04 | 32.43 | 41.04 |
| 999 | 38.19 | 37.19 | 50.31 | 49.84 |
| | R.C. | R.B. | R.C. | R.B. |

Table 6. shows that in some instances the values for Relative Cover and Relative Basa Area are within 1 percent of each other while in one case (*G. littoralis* at 897m) a variation of up to 20 percent is apparent. This is also an indication of the problem of measuring a species exhibiting a multistemmed spreading growth habit.

On the basis that both cover and basal area are an attempt to quantify dominance, where available, the two values have been averaged to give a more accurate indication of this parameter for this study. Relative values for density and dominance have been used to focus on the relative species composition at each altitude.

This gives a false impression when comparing say a high altitude sample (No 1 at 1,855m) with a total cover value of only 13 percent with a low altitude sample (No 21 at 897m) with a total cover of 92 percent in the canopy alone but this is compensated by presenting the data for absolute (total) cover separately. In this way the change in species composition through the major altitudinal gradient (York Road Track Ridge) is examined on the same Importance Value range 0 - 200 throughout.

## Altitude as an indicator of the environmental gradient

Altitude,that is height above sea level in metres,is the measure used to order the vegetation data,and thus relate changes in composition, physiognomy, and structure directly to environmental factors. It is recognised that as stated by Whittaker (1973b) altitude itself has no bearing on plant physiology and thus upon species distributions. Rather altitude has been employed as an index of sample position along a complex environmental gradient. This complex environmental gradient includes changes in many environmental factors including temperature, wind velocity, precipitation, insolation (aspect), slope, and substrate characteristics. The attempt to hold constant drainage,substrate conditions, slope and aspect has already been described in the sampling procedure. Consequently for this study it is assumed that the major environmental changes reflected by the vegetation are those of temperature, wind velocity, precipitation, and humidity. Whitmore (1975) summarises the changes through elevation for these factors in tropical montane climates and along with the description by Coulter (1976) of "Weather in Egmont National Park" the assumed changes in these factors through altitude can be postulated.

Temperature decreases with increasing altitude and Coulter (1976) claims that "air temperatures near the ground decrease on average by approximately six degrees C. per 1,000m" (Coulter, 1976, 52) with variation from place to place and time to time according to the general weather prevailing and on account of local topographic influences on climate. Druce (1976) also states, "the usually accepted three degrees F. per 1,000ft (one degree C. per 200m) decrease in mean temperature should apply fairly well to Egmont, at least up to 1,200m". (Druce, 1976, 44.) Using these values as the standard this would mean a difference of nearly six degrees C. mean temperature between the lowest altitude quadrat sampled (897m) and the highest altitude quadrat (1,855m). Freezing level is described by Coulter (1976) as occurring "at approximately 3,500m an average (it lies between 2,800m and 4,200m for about two-thirds of the time) in mid summer while in mid winter the corresponding levels are 1,750m (1,150m, 2,350m)". (Coulter, 1976, 52.)

Precipitation is related to temperature in that "the degree of saturation of a given air body increases as its temperature falls and with increasing elevation the dewpoint (that is the temperature at which condensation occurs and cloud forms) depends on the temperature lapse rate and the initial moisture content". (Whitmore, 1975, 209.) Thus it is generally accepted that precipitation increases with increasing altitude although the relationship is not simple with much local variation due to local topography and conditions. Coulter (1976) notes that the mean annual rainfall for Taranaki" amounts to about 1,500mm near the North Taranaki coast, around 1,100 to 1,300mm near the South Taranaki coast, and increases more or less parallel with the contours of land to about 6,500mm at the 1,000m level and probably to about 8,000mm near the 2,000m line, but with somewhat more rain on the northern and western slopes than elsewhere". (Coulter, 1976, 52.) This would mean a difference of approximately 3,500mm between the lowest and the highest quadrat sampled on the York Road Track.

Wind velocity or rather exposure to wind also increases with increasing altitude. Coulter (1976) gives estimates of average wind speed for Stratford 300m a.s.l. of 11km per hour and for the summit of Mt Egmont 2,518m a.s.l. of about 40km per hour. These estimates indicate that the differences between the lower altitude and upper altitude quadrats in terms of wind exposure would be marked.

Overall a great range of environmental factors change along the altitudinal gradient only some of which (for example temperature, wind velocity and precipitation) have been estimated at various locations on Mt Egmont. No reliable climatological data is available at all for the majority of sites sampled although slope, aspect, and substrate conditions were recorded. It is also recognised that the volcanic history of Mt Egmont and in particular the recent ash and lapilli showers (Burrell Formation dated 1655 A.D. according to Neall (1976)) have affected vegetation composition at some of the locations sampled. These effects have already been noted in Chapter 2 (See Druce, 1964, 1966) and add further complexity to the environmental gradient described.

The approach of this study then is one of direct gradient analysis using altitude (height above sea level in metres) merely as an index of sample position along a complex environmental gradient in which temperature decrease, precipitation increase, and wind velocity increase are assumed to be the major factors underlying a general environmental deterioration.

# Chapter 5

## SITE DESCRIPTION OF THE YORK ROAD TRACK RIDGE

The York Road Track Ridge was selected as suitable for sampling for a number of reasons,the prime one being that between 1,087m a.s.l. and 1,489m a.s.l. at least,it displayed a relatively regular increase in elevation. Coupled with this it seemed possible to hold other factors such as aspect, drainage conditions, substrate, and degree of exposure to wind relatively constant throughout the length of the ridge. Other factors influencing the selection of this ridge for sampling included access and the proximity of hut accomodation at each end of the ridge. The York Road Track Ridge is located in the eastern sector of Egmont National Park between G.R. 647750 and G.R. 632669 (N.Z.M.S. I Stratford Sheet N 119) (See Figures 1 and 7). For the purposes of this study sampling was continued past the end of the York Track but following the same and adjacent ridge to G.R. 632654. Sampling took place between an altitude of 897m and 1,855m,an increase of 958m in a 2,700m traverse. The details of these samples and their locations are summarised in Table 7 and Figure 1.

The section of the York Road Track Ridge beginning at 875m rises gradually at first (1:7) to the York Road Hut (Waipuku) and Maketawa Track Junction. There is a more sudden increase in elevation (1:2) in the area known as Quarry Bluff where a large section of exposed rock and gravel detracts from the general vegetation pattern and subsequently has not been sampled. Past history of human activity at the nearby quarry site abandoned

Table 7. Location and Description of York Road Track Ridge Samples

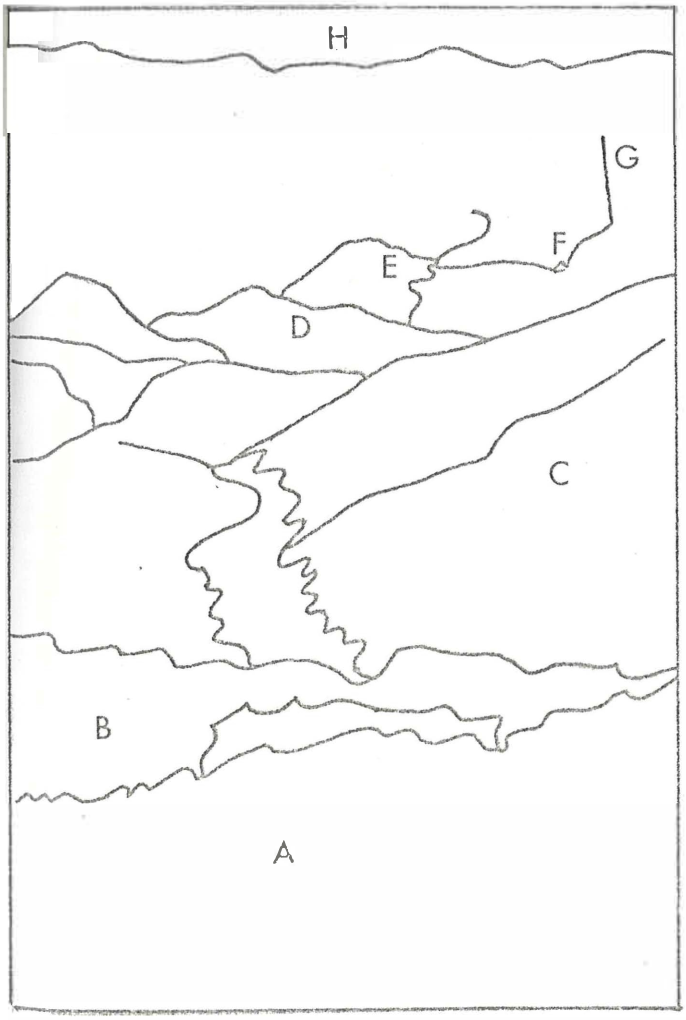
| No. | Altitude in metres | Difference in metres | Altitude in feet | Area / Aspect Length | Mean Slope Angle | Location Notes |
|---|---|---|---|---|---|---|
| 1 | 1855 | | 6090 | 5sq m N.N.E. | 25° | |
| 2 | 1797 | 58 | 5900 | 5sq m N.E. | 33° | |
| 3 | 1751 | 46 | 5750 | 5sq m N.E. | 15° | |
| 4 | 1706 | 45 | 5600 | 5sq m N.E. | 15° | Adjacent to Lion Rock |
| 5 | 1584 | 122 | 5200 | 5sq m N.E. | 30° | |
| 6 | 1547 | 37 | 5080 | 5sq m N.N.E. | 270° | Adjacent to Warwick Castle |
| 7 | 1489 | 58 | 4890 | 5sq m E.N.E. | 20° | |
| 8 | 1416 | 73 | 4650 | 50m N.E. | 20° | 20m above Round-the-Mountain Track Junction |
| 9 | 1355 | 61 | 4450 | 40m N.E. | 10° | 40m below Round-the-Mountain Track Junction |
| 10 | 1325 | 30 | 4350 | 40m N.E. | 7° | |
| 11 | 1294 | 31 | 4250 | 40m N.E. | 7° | |
| 12 | 1261 | 33 | 4140 | 10sq m N.E. | 15° | Manganui Ski Lodge siting |
| 13 | 1218 | 43 | 4000 | 10sq m E. | 7° | |
| 14 | 1176 | 42 | 3860 | 10sq m E | 18° | |
| 15 | 1145 | 31 | 3760 | 10sq m E. | 4° | |
| 16 | 1087 | 58 | 3570 | 10sq m N.E. | 30° | Top of Quarry Bluff |
| 17 | 999 | 88 | 3280 | 15sq m E.N.E. | 30° | |
| 18 | 959 | 40 | 3150 | 20sq m N.E. | 2° | Near Maketawa Track Junction |
| 19 | 897 | 62 | 2945 | 20sq m E. | 20° | 400m below York Road (Waipuku) Hut |
| 20 | 959*R | | 3150 | 10sq m E.S.E. | 5° | Dray Track Entrance-Regeneration sample |
| | In addition Ground Cover only | | | | | |
| 21 | 1337 | | 4390 | 5sq m E.N.E. | 22° | |
| 22 | 1349 | | 4430 | 5sq m E. | 4° | |
| 23 | 1386 | | 4550 | 5sq m E. | 5° | |

since 1923 and previously much higher goat populations may have contributed to these differences. From the top of Quarry Bluff the vegetation cover resumes and the ridge becomes narrower, steep-sided, and more clearly defined. Increase in elevation is once again steady although the gradient is greater than near the York Road Hut (1:5.5) and continues almost unbroken to the Round-the-Mountain Track. Exceptions are sections of the ridge above Quarry Bluff which undulate gently to form several hollows which are more sheltered than the rest of the ridge at this altitude. Care was taken to avoid these sites. After a slightly steeper climb (1:4.5) 500m before reaching the Round-the-Mountain Track the increase in altitude is particularly even on the section of ridge up to the Round-the-Mountain Track in which the shrub species gradually give way to *Chionochloa rubra* and herb species. Above the Round-the-Mountain Track the gradient becomes steeper (up to 1:4) and it becomes increasingly difficult to hold degree of exposure, drainage and substrate factors constant. As a result the ridge which is in fact the continuation fo the York Track Ridge was eventually abandoned at 1,547m and sampling continued on the adjacent ridge 600m north up to an alitude of 1,855m. The substrate factor in particular became impossible to hold constant so that the elevation interval between samples 4 and 5 reaches 122m in order to avoid a steep region (1:2 in places) of solid rock outcrop and its associated change in drainage conditions. Even with the ommission of such sites from 1,489m onwards it became increasingly difficult to maintain defined sampling procedures, and this will be brought out fully in examining the results of these higher altitude samples. Therefore in terms of the established sampling procedure samples 5 to 20 can be considered

Figure 7

YORK ROAD TRACK RIDGE

Aspect East
Altitude 1,550m



| | |
|---|---|
| A | Moss-Herbfield major species:<br>*C.gracilenta var.*,<br>*R.lanuginosum var.pruniosum*,<br>*F.bidwillii var.densifolia*. |
| B | *C.rubra* upper altitudinal limit. |
| C | Slopes below Warwick Castle. |
| D | Shrub-Tussock Interface. |
| E | Tree-Shrub Interface. |
| F | York Road(Waipuku)Hut. |
| G | York Track. |
| H | Boundary of Egmont National Park. |

as satisfying all criteria and overall the York Road Track Ridge can be viewed in terms of three major sections: the lower section including samples 19 and 20 with the most gradual increase in elevation; a middle section above Quarry Bluff and below the Round-the-Mountain Track including samples 9 to 17 exhibiting a more rapid but even increase in elevation with exception of several hollows near the top of Quarry Bluff; and an upper section including samples 1 to 8 with an even greater gradient in which the problems associated with substrate, degree of exposure, and drainage conditions eventually became impossible to hold constant.

# Chapter 6

# RESULTS AND ANALYSIS

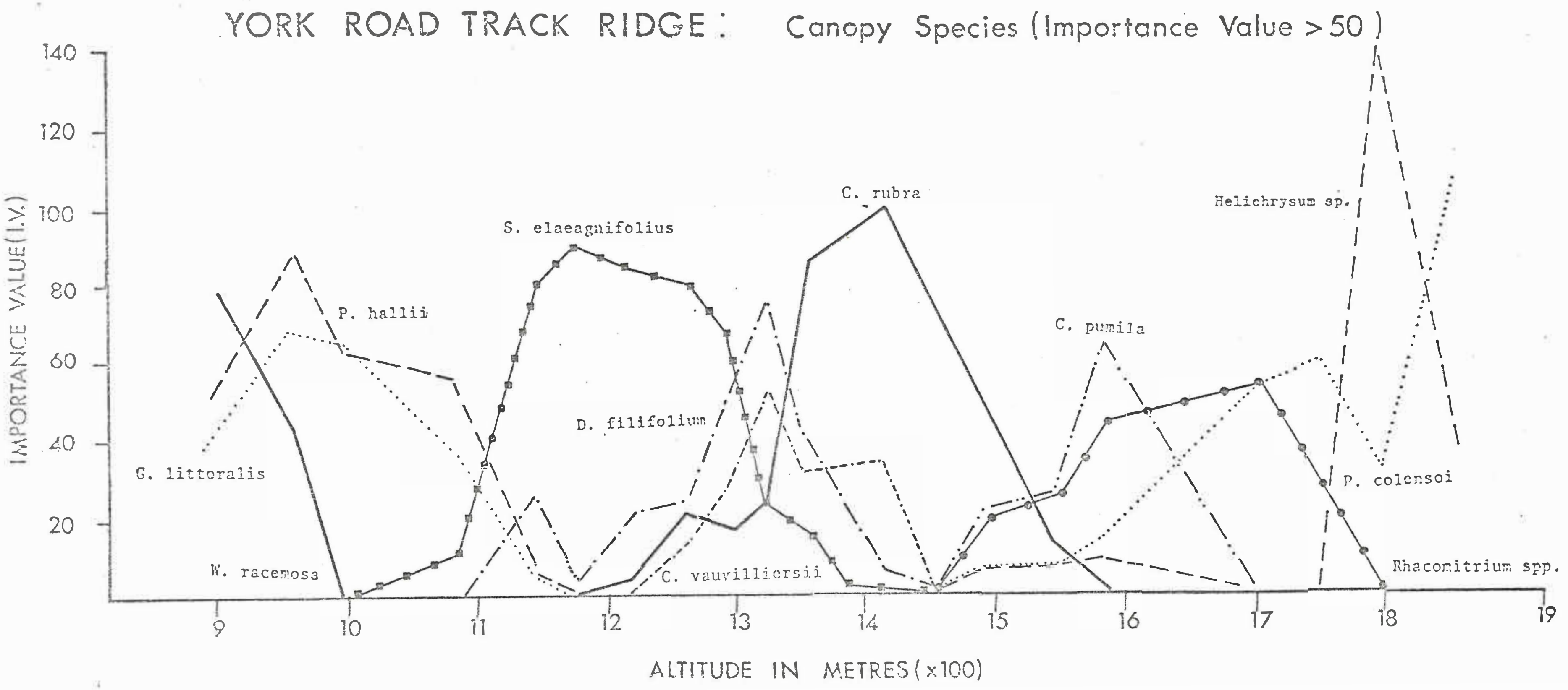
## York Road Track Ridge Species Distributions

### Canopy Species > 50 Importance Value

The distributions of canopy species with > 50 importance values between 897m and 1,855m on the York Road Track Ridge are summarised on Figure 8. There is a clear progression of species dominance with increasing altitude and a varying degree of association between species. The altitudinal range of *W. racemosa* is shown in part only but it is clearly the most important species in the 897-920m altitudes with a maximum importance value of 80. *P. hallii* and *G. littoralis* show a high degree of association ($r = + 0.984$ $p = 0.001$) with the species reaching peak importance values of 89 and 68 respectively at 959m. *Griselinia* overshadows *Podocarpus* in importance only once at 1,087m and by only one importance value unit. The reason for the species association is obvious for in almost every quadrat where the two species appear there is evidence that *Griselinia* began as an epiphyte on *Podocarpus* eventually overtopping *Podocarpus* to reach the canopy. Whether this is a logical progression ending when *Podocarpus* becomes senescent, or whether the death of *Podocarpus* results from the overtopping by *Griselinia* requires further examination. With increase in altitude *S. elaeagnifolius* takes over from

*P. hallii* reaching a maximum importance value of 90 at 1,176m and giving way in turn to *D filifolium* and *C. vauvilliersii* both reaching maximum importance values of 75 and 52 respectively at 1,325m. *C. rubra* first recorded at 1,218m amongst the smaller shrubs gradually becomes dominant reaching its maximum importance value of 100 at 1,410m. A further 42 metres of elevation sees the last of the shrub species and the beginnings of the decline of *Chionochloa* dominance. By 1,547m *C. pumila* has reached its maximum importance value 68 and *Chionochloa* is no longer represented. At this point *P. colensoi* and *Rhacomitrium spp.* are becoming important components of the top stratum, *Rhacomitrium spp.* reaching their maximum importance value of 63 at 1,751m and *P. colensoi* peaking with an importance value of 109 at 1,855m. *Helichrysum sp.* (unnamed) exhibits a fluctuating distribution with a maximum importance value of 147 at 1,797m and this is probably due to its sensitivity to changes in substrate and drainage conditions at these higher altitudes. As well as the obvious association of *Podocarpus* and *Griselinia* the distributions of *Dracophyllum* and *Cassinia* are significantly correlated ($r = + 0.820 \quad p = 0.001$). The strength of the association is not as great as that of *Podocarpus* and *Griselinia* however with the *Dracophyllum* more important at lower altitudes and the *Cassinia's* upper altitudinal limit extending above that of *Dracophyllum.* Both species reach prominence in quadrats near the upper limit of *S.elaeagnifolius* and the lower limit of *C. rubra* possibly as the result of competitive release as *Senecio* reaches the margins of its tolerance and *Chionochloa* is still unable to compete successfully with the shrub species until the advantages of its greater tolerance to altitude (temperature, etc.) becomes apparent at higher elevations.

Figure 8


YORK ROAD TRACK RIDGE : Canopy Species (Importance Value > 50 )
IMPORTANCE VALUE (I.V.)
140
120
100
80
60
40
20
ALTITUDE IN METRES (x100)
9
10
11
12
13
14
15
16
17
18
19
P. hallii
G. littoralis
W. racemosa
S. elaeagnifolius
D. filifolium
C. vauvilliersii
C. rubra
C. pumila
Helichrysum sp.
P. colensoi
Rhacomitrium spp.

The shape of the distribution of Dracophyllum and Cassinia wedged between Senecio and Chionochloa appears to point to the fact that the altitudinal space available between the optimum locations for Senecio and Chionochloa is very limited. The difficulty of holding environmental parameters constant at higher altitudes are well illustrated by the distributions of Coprosma pumila, Rhacomitrium spp., Helichrysum sp. (unnamed), and P. colensoi particularly in the top three quadrat samples (1-3) where degree of exposure, slope angle, and drainage conditions appear responsible for the greater degree of fluctuation of importance value apparent at these elevations. In summary the major features of these species distributions are: the gradual progression as one canopy (top stratum) species takes over from another reaching its maximum importance value and giving way until it is no longer represented in the top stratum; the generally unimodal Gaussian type species distributions; and the lack of species association with the exception of Podocarpus and Griselinia and Dracophyllum and Cassinia.

## Canopy Species <50 >20 Importance Value

Distributions of species with Importance less than 50 but greater than 20 are summarised on Fig. 9. Like the species with Importance Values >50 there is a clear progression of species dominance with increasing altitude. The altitudinal range of C. serratus is shown in part only with its upper limit occurring at 959m. P. colorata is first recorded at 999m, where it reaches its maximum importance value 44, and declines in importance until at 1,145m it is no longer represented in the canopy. P. simplex var. sinclairii is also recorded first at 999m but its distribution extends much higher finishing at 1,294m and with its

Figure 9
YORK ROAD TRACK RIDGE Canopy Species (Importance Value >20 <50)

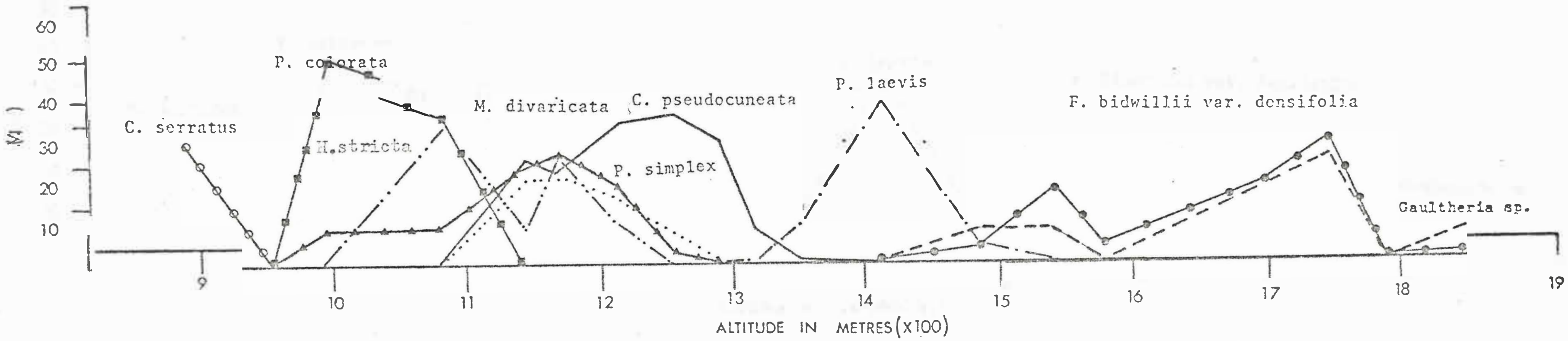
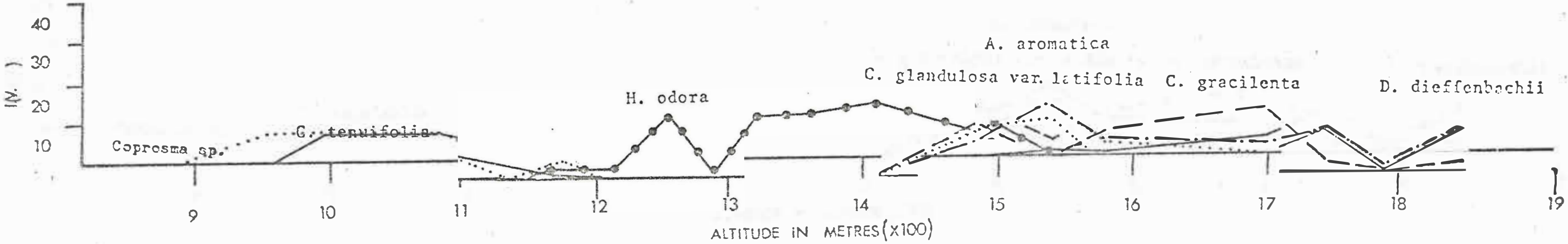


Figure 10
YORK ROAD TRACK RIDGE Canopy Species (Importance Value <20)



maximum importance value 26 occurring at 1,176m. *H. stricta* is first recorded at 1,087m where it reaches its maximum importance value of 34. Its distribution is bimodal with a second peak importance value 25 occurring at 1,176m. Its last occurrence in the canopy is at 1,218m. *M. divaricata* and *C. pseudocuneata* are both recorded first in the canopy at 1,118m however *Myrsine* cuts out at 1,294m while *Coprosma* is last recorded at 1,416m. *Myrsine* reaches its maximum importance value 21 at 1,176m and *Coprosma* importance value 36 at 1,261m. *P. laevis* is first recorded at 1,294m and increases in representation until 1,416m where it achieves its maximum importance value 39. It then declines in importance being last recorded in the top stratum at 1,481m. The last species distribution depicted on Fig. 9 is that of *F. bidwillii var. densifolia*. Its distribution is bimodal and skewed probably the result of the inability to hold constant substrate factors in sampling the upper quadrats. *Forstera* is first recorded at 1,489m, reaches its maxiumum importance value 30 at 1,751m and is still represented in the upper quadrat at 1,855m.

## Canopy Species <20 Importance Value

Distributions of species with importance values <20 are depicted on Fig. 10. *C. tenuifolia* is first recorded at 999m, achieves an importance value of 7 at 1,087m and 1,118m and is last represented at 1,145m. *Coprosma sp.* (unnamed) achieves similar importance values but its distribution is much wider extending from 959m up to 1,176m. *H. odora* is represented in the canopy between 1,176m and 1,547m but its distribution is uneven reaching an importance value of 16 at 1,261m declining to present only at 1,294m and then increasing again to its maximum representation importance value 18 at 1,416m. The last representation of H. odora in the canopy at 1,547m is significant in that it is the upper altitudinal limit for shrub species although the majority of the other shrub species rarely extend past 1,355m. The uneven distribution of H. odora could be in part caused by the fact that it extends into the tussock dominated quadrats thus increasing in representation again as it competes with Chionochloa but eventually reaching its upper tolerance limit in terms of altitude (temperature etc.). A. aromatica,C. gracilenta var., C. glandulosa var. latifolia, and D. dieffenbachii are all recorded in the top stratum first at 1,489m although this degree of distributional coincidence is in part enhanced by the large altitudinal interval between quadrats 7 and 8 and the fact that the canopy (top stratum) category is no longer separable from the ground cover stratum. The distributions of A. aromatica, C. gracilenta var., and D. dieffenbachii extend to the uppermost sample while C. glandulosa var. latifolia both achieve maximum importance values of 18 and 15 respectively at 1,547m while C. gracilenta var. reaches its importance value 17 at 1,706m and D. dieffenbachii 12 at 1,797m.

Species with limited distributions

A number of species distributions are not depicted on Figs. 8, 9, and 10 either because they have a very limited distribution or because they do not achieve importance values above 5. These include Luzula sp., Colobanthus sp., Epilobium spp., Pentachondra pumila, Lycopododium fastigatum, Geranium microphyllum, Aporostylis bifolia Festuca rubra subsp. commutata, Coriaria pteridoides, Ranunculus nivicola, Oreobolus pectinatus, Euphrasia cuneata, Gunnera monoica var. monoica, Astelia sp. (unnamed), Gahnia procera, and Ourisia macrophylla. The occurrence of these species is summarised on Table 8 which includes the altitude where their maximum importance value was recorded. (See Appendix 2 for complete Canopy Species List)

Table 8. Species < 5 Importance Value or single occurence (Canopy Top Stratum)

| | Importance Value | Altitude in Metres |
|---|---|---|
| Luzula sp. | 2 | 1,584 |
| Colobanthus sp. | 4 | 1,751 |
| Epilobium sp. | 19 | 1,797 single occurrence |
| Pentachondra pumila | 17 | 1,547 |
| Lycopodium fastigiatum | + | 1,584 |
| Geranium microphyllum | + | 1,489 |
| Aporostylis bifolia | + | 1,489 |
| Festuca rubra | + | 1,489 |
| Coriaria pteridoides | + | 1,325 |
| Ranunculus nivicola | 1 | 1,489 |
| Oreobolus pectinatus | 24 | 1,547 single occurrence |
| Euphrasia cuneata | + | 1,584 |
| Gunnera monoica | 8 | 1,584 |
| Astelia sp. (unnamed) | 2 | 1,294 |
| Gahnia procera | 1 | 1,145 |
| Ourisia macrophylla | 2 | 1,547 |

The distribution of species with importance values less than 20 highlights the fact that in the upper altitude quadrats a greater number of species are represented in the category canopy (top stratum). The categories adopted affect this apparent pattern in that the top stratum and the ground stratum are one and the same at higher altitudes and the comparison of number of species represented at upper altitudes as compared to lower altitudes is not a valid one in that the categorisation for the major part determines the result. When the lower altitude ground stratum species diversity is compared with the upper altitude ground (top stratum) diversity in fact the trend is the reverse with greater numbers of species represented in the lower altitudes.

Subcanopy and Shrubs >25 percent Relative Density

Few subcanopy and shrub species achieve representation to the extent of 25 percent relative density. The subcanopy and shrub strata are rather characterised by the dominance of P. colorata. P. colorata consistently exceeds 50 percent relative density up to 1,087m in subcanopy and 999m in the shrub strata. P. hallii is important as a subcanopy species at 999m and 1,087m reaching its maximum density 100 percent in the latter site. This is the last site at which canopy and subcanopy were structurally distinguishable and the fact that only two individuals make up this relative density value must be taken into account. The paucity of species notably the more palatable ones characteristic of other sites at similar altitudes (Coprosma spp. Alseuosmia macrophylla etc.) and the dominance of P. colorata in these strata appears to reflect previously much higher goat populations known to have been centred near Quarry Bluff. Shrub and subcanopy strata were no longer recognised after passing an elevation of 1,087m and from this point only the canopy (top stratum) and ground cover are depicted on Figs. 8 and 12.

Species of comparatively minor importance in the subcanopy and shrub strata include M. divaricata, P. simplex var. sinclairii,

Figure 11a

## YORK ROAD TRACK RIDGE Subcanopy

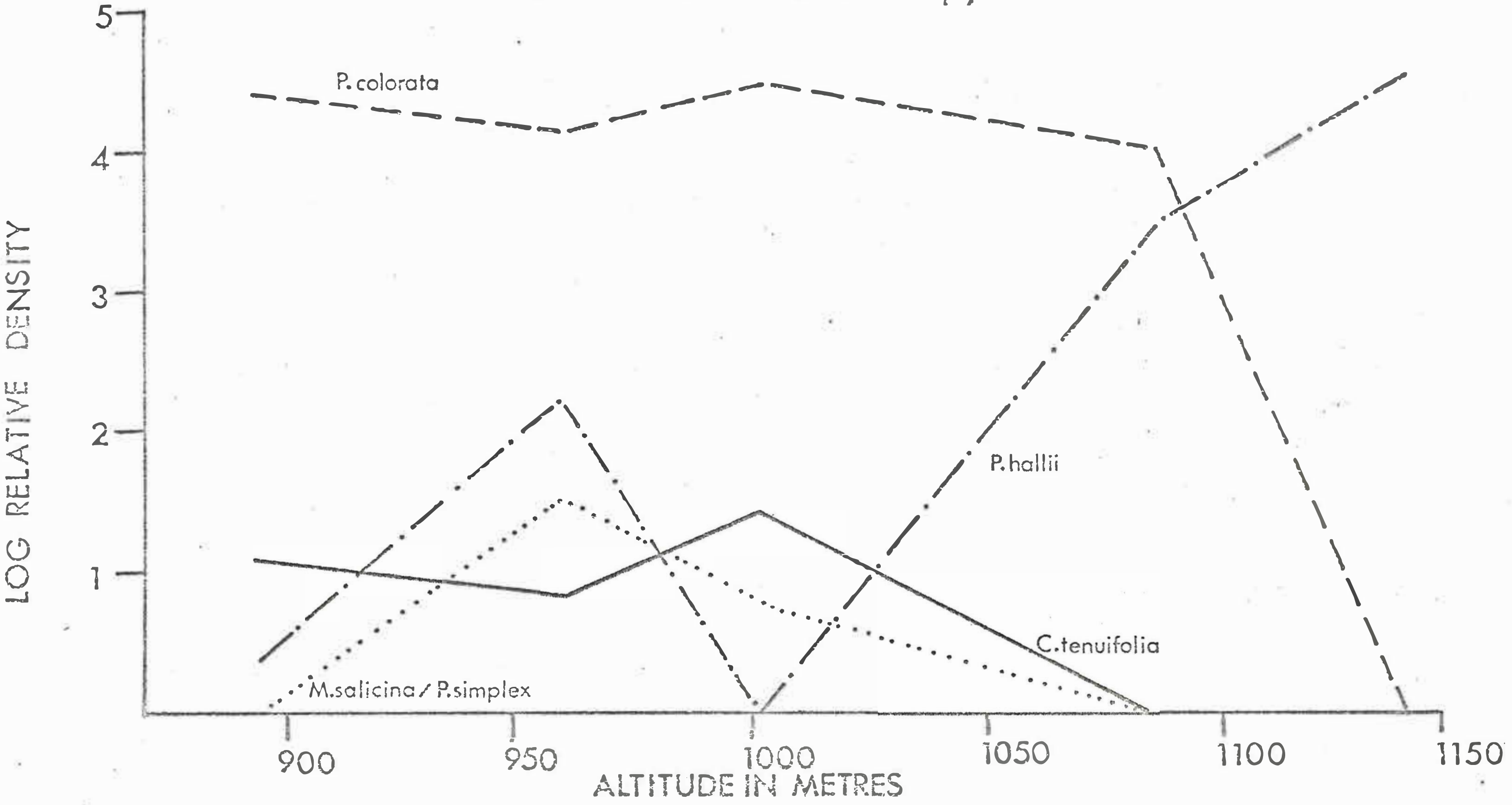
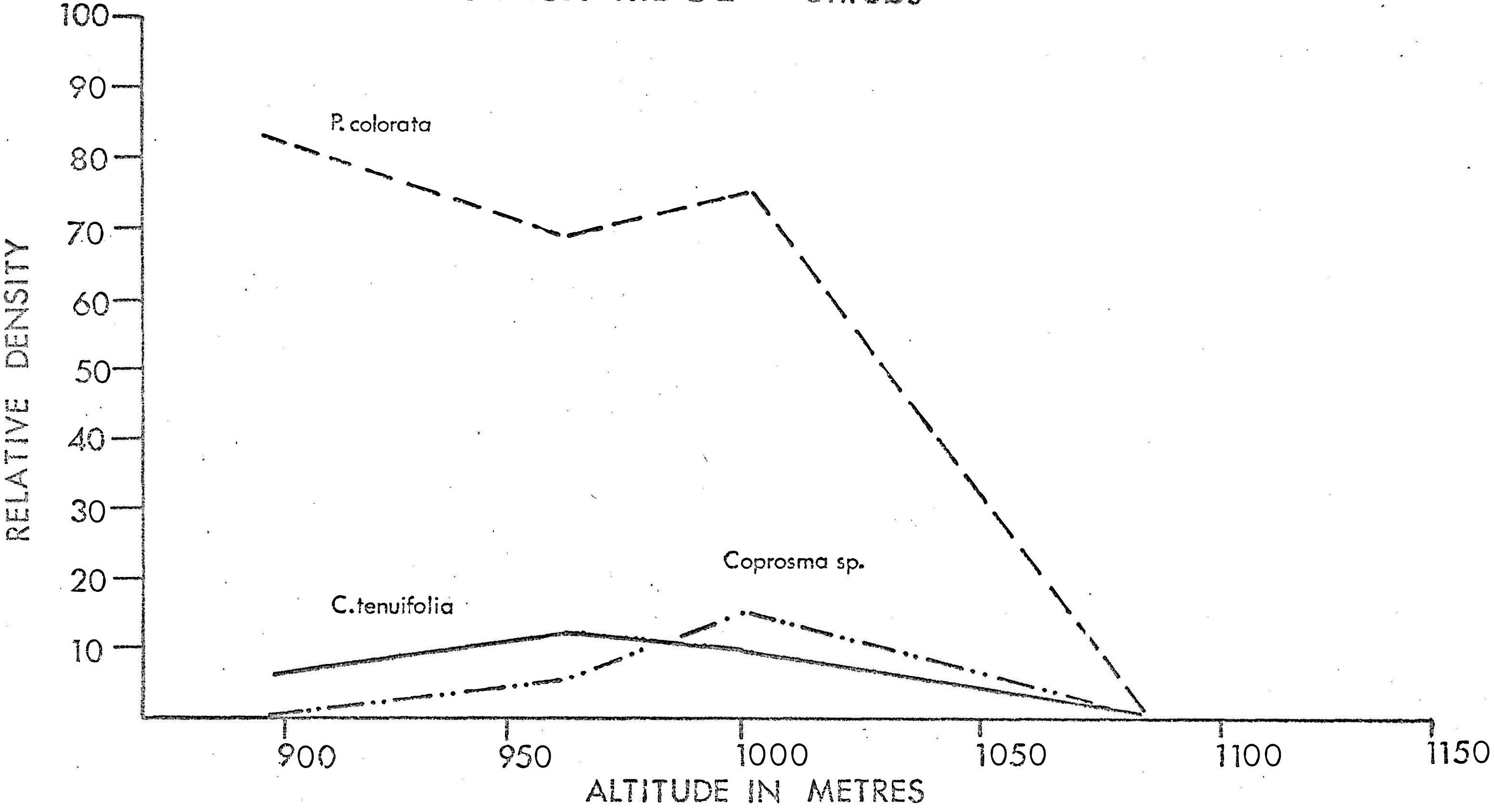


Figure 11b

YORK ROAD TRACK RIDGE Shrubs



C. tenuifolia, and Coprosma sp. (unnamed). Graphing log relative density on the abscissa of Fig. 11a the distributions of these species is made easier to compare with the distributions of the major subcanopy and shrub species. C. tenuifolia is essentially a lower altitude component of these strata being represented in quadrats 17, 18, and 19 between 897m and 999m and never exceeding a relative density of 4 percent. M. divaricata and Pseudopanax simplex var. sinclairii share a similar distribution pattern both reaching their maximum relative density of 4 percent in quadrat 18 959m a.s.l. Coprosma sp. (unnamed) reaches its maximum relative density 15 percent in the shrub layer at 999m.

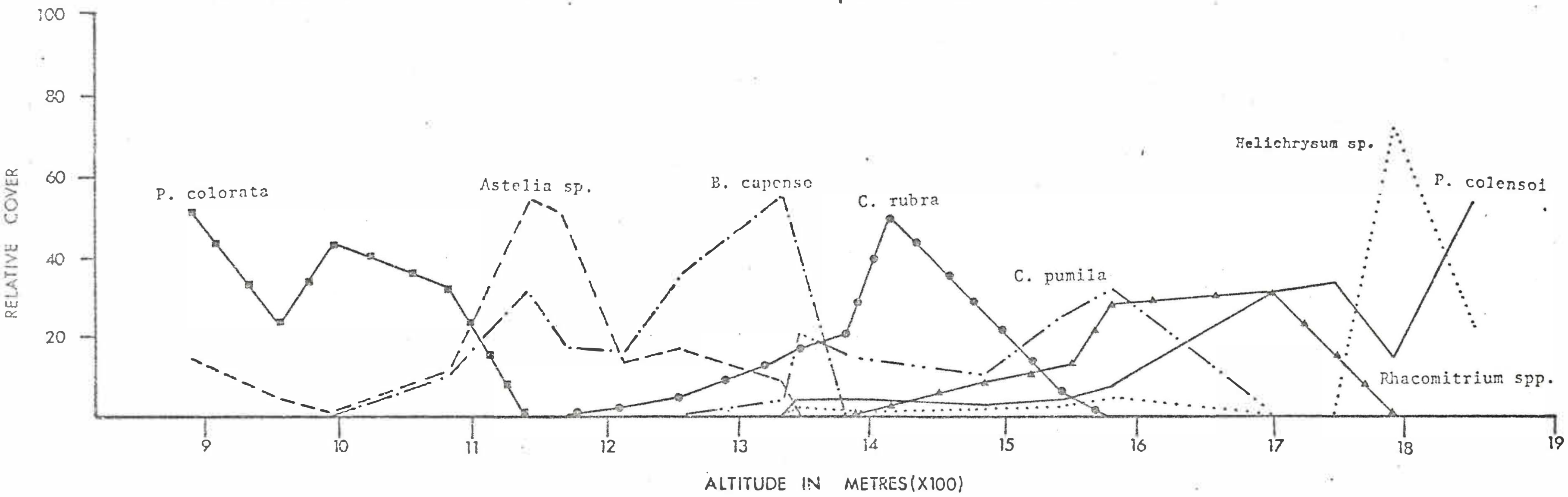
Perhaps the most important feature of all these distributions is the fact that in most cases they represent the lower altitudinal range of the species concerned in that many become components of varying importance in the canopy or top stratum from 1,087m onwards. Thus for example P. simplex var sinclairii while only represented at a maximum of 4.87 relative density at 959m reaches importance values of up to 26.68 at 1,145m. Shrub and subcanopy species unable to reach the top stratum (canopy) in the lower altitude samples because of competition from the larger tree species P. hallii, W. racemosa, and G. littoralis eventually become part of the canopy in higher altitude quadrats.

## Ground Cover >25 percent Relative Cover

The distribution of ground cover species exceeding 25 percent relative cover is summarised on Fig. 12. Again there is a clear progression of species dominance moving from 897m to 1,855m a.s.l. P. colorata has its maximum relative cover 52 percent of 897m and from there, declines in importance until it is no longer recorded at 1,118m. Astelia sp. (unnamed) a species which has a particularly

Figure 12

YORK ROAD TRACK RIDGE Ground Cover Species > 25% Relative Cover



wide distribution from 897m to 1,337m then becomes dominant reaching a maximum relative cover of 54 percent at 1,118m. In turn it gradually gives way to B. capense which peaks at 1,337m with a relative cover of 55 percent. From this altitude the ground cover species are the canopy or top stratum species and their distributions have already been described. However an important feature of the distributions of these species is that their distribution in the category ground cover is wider than in the canopy (top stratum) category. C. pumila, Helichrysum sp. (unnamed), and Rhacomitrium sp. all form a substantial part of the ground cover category at 1,337m, at which altitude C. rubra dominates the top stratum. The species distributions in the ground cover category thus parallel the pattern observed in the canopy with a progression of unimodal 'curves' as one species takes over from another with increasing altitude.

## York Road Track Ridge Canopy Species Correlation

### The use of the Linear Regression Model for testing Species Association

There are several assumptions implicit in the use of the linear regression model (and in particular Pearson's Product Moment Correlation Coefficient) and these are summarised by Poole and O'Farrell (1970). Two of these assumptions are particularly relevant to vegetation data analysis in the sense that they may be difficult to meet.

They are: 1. that the distribution of the variables to be correlated have a joint normal distribution and that the conditional variance of one variable given the other is the same, and 2. that the relationship between the two variables is linear.

Few of the species correlations performed in the literature on vegetation analysis seem to take full account of the assumptions to be met before employing the linear regression model and consequently the conclusions obtained regarding species correlation may be innacurate. With regard to the first assumption listed Goodall (1973) notes that "ecological data is often very far from being normally distributed - in fact, a distribution curve with a mode substantially below the mean is usual - and in this case, though the correlation coefficient may provide acceptable measure of association, its distribution is unknown, and to rely on published tables may lead one far astray". (Goodall, 1973, 119.) With regard to the second assumption listed Goodall (1973), notes that non-linear relations between species are not uncommon and "that where observations cover a fairly wide range of ecological conditions, different species may occur in maximum quantity at different environmental values, and decrease both above and below this optimum. Where the modes of the two species do not coincide, this means that a linear model may fail to reveal the relationship between them". (Goodall, 1973, 126.)

It is possible to correct for situations in which data does not fulfil the assumptions of the linear regression model in some instances. Possible compensations for 1) include normalising the data by transformation or the use of a non-parametric statistic for example Spearman's Rank Correlation Coefficient which makes no assumption regarding the nature of the variable distributions. Possible compensations for 2) include linearisation of the data using a logarithmic or polynomial (quadratic) function or the use of non-linear statistics. An examination of the data matrix and graphs of species distributions for the 30 major canopy species on the York Road Track Ridge revealed problems as far as meeting these two assumptions of the linear regression model was concerned. The calculation of the species correlations was thus carried out with the assumptions in mind and where possible data transformation was attempted. The possibilities for transformation have not been exhausted however as many of the alternatives, in particular the use of non-linear statistics and higher order polynomial transformations, are beyond the scope of this study. Keeping this in mind species correlation coefficients were calculated first using the unmodified quantitative data (Pearsons Product Moment Correlation Coefficient), second after natural logarithmic transformation (Pearsons Product Moment Correlation Coefficient) and finally using ranked data (Spearmans Rank Correlation Coefficient). Results were then compared to determine whether or not the different methods detected different patterns of statistically significant species correlation. The patterns proved to be similar with the most noticeable difference an increase in the number of statistically significant correlations between species where the natural logarithmic transformation and Spearman Rank Correlation Coefficient were concerned. The number of statistically significant correlations $p = \leqslant 0.005$ increased from (30) in the unmodified data to (56) and (64) for the natural logarithmic transformation and Spearmans Rank Correlation respectively. The trend is an important one in that it suggests that the logarithmic transformation in particular has in part corrected the tendency to non-linearity in the data subsequently increasing the number of statistically significant species intercorrelations (increasing the cohesiveness of the clusters identified) in the species clusters identified. In the use of Spearmans Rank Correlation the increase in statistically significant species correlations are more the result of the conversion of quantitative data to rankings and the subsequent loss of detail. To offset this however the use of this non-parametric statistic requires no assumptions be met regarding the nature of the variable distributions.

The species groupings or clusters identified are presented with the caution that the assumptions of the linear regression model are not met totally in each of the three cases. However the overall degree of similarity in the pattern of species correlation detected supports the suggestion that the groupings identified are natural ones based on similar altitudinal distributions of the species involved.

## Canopy Species Correlation Pearsons Product Moment Correlation Coefficient (unmodified data)

Calculation of the Pearsons Product Moment Correlation Coefficient to test the statistical significance of association amongst the 30 major canopy species (determined by importance values $>5$ or with $\geqslant 2$ occurrences in the canopy) reveals some statistically significant species association. Species correlations achieving the normally accepted significance level $p = \leqslant 0.005$ are depicted on a linkage analysis Fig. 13 employing the method of McQuitty (1957). Five species clusters are formed at this level of significance and they are ecologically meaningful in that the species clusters obtained are of species with similar altitudinal distributions. Cluster 1 consists of *W. racemosa* and *C. serratus*. Cluster 2 includes a range of middle altitude tree and shrub species Cluster 3 includes three shrub species which tend towards the upper altitudinal limit for shrub species (*C. vauvilliersii*,

## Key to Species in Figures 13and14

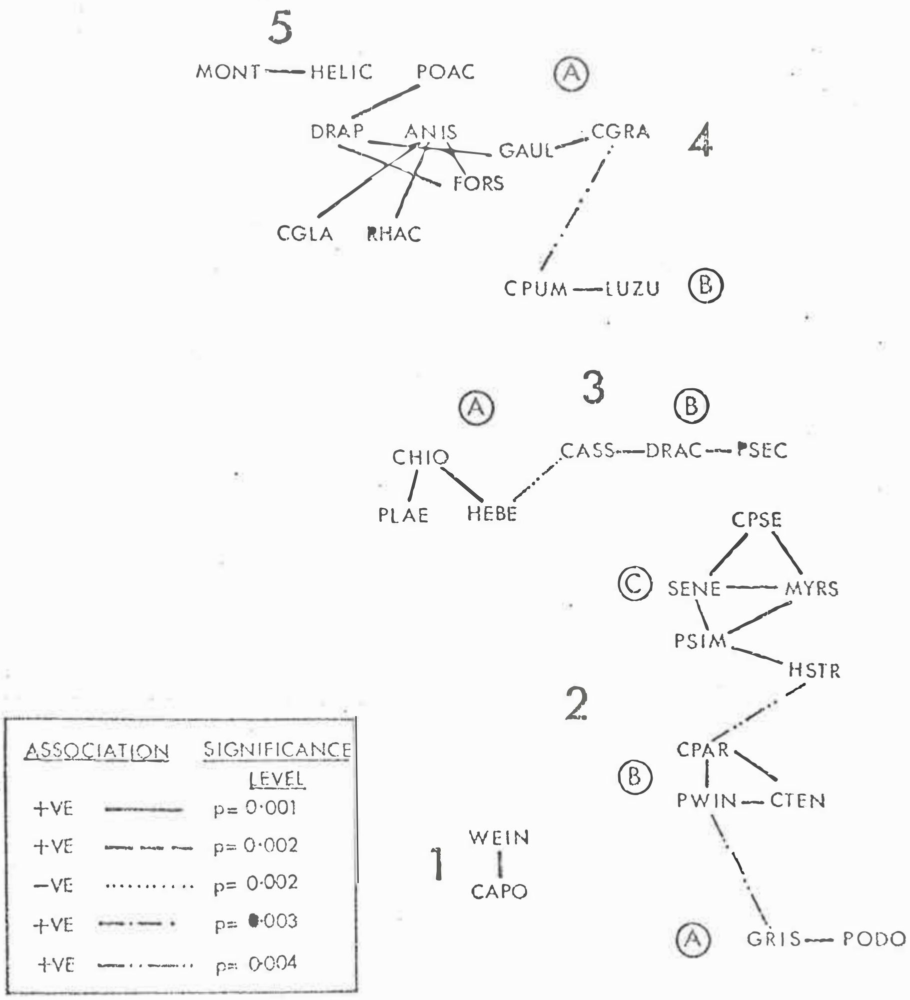
| | |
|---|---|
| GAUL | *Gaultheria sp.(unnamed)* |
| MONT | *Montia sp.* |
| HELIC | *Helichrysum sp.(unnamed)* |
| POAC | *Poa colensoi* |
| FORS | *Forstera bidwillii var.densifolia* |
| DRAP | *Drapetes dieffenbachii* |
| ANIS | *Anisotome aromatica* |
| CGRA | *Celmisia gracilenta var.* |
| CGLA | *Celmisia glandulosa var.latifolia* |
| RHAC | *Rhacomitrium spp.* |
| CPUM | *Coprosma pumila* |
| LUZU | *Luzula sp.* |
| CHIO | *Chionochloa rubra* |
| CASS | *Cassinia vauvilliersii* |
| PLAE | *Poa laevis* |
| HEBE | *Hebe odora* |
| DRAC | *Dracophyllum filifolium* |
| SENE | *Senecio elaeagnifolius* |
| CPSE | *Coprosma pseudocuneata* |
| MYRS | *Myrsine divaricata* |
| PSEC | *Pseudopanax colensoi* |
| PSIM | *Pseudopanax simplex var.sinclairii* |
| HSTR | *Hebe stricta* |
| CPAR | *Coprosma sp.(unnamed)* |
| PWIN | *Pseudowintera colorata* |
| CTEN | *Coprosma tenuifolia* |
| WEIN | *Weinmannia racemosa* |
| CAPO | *Carpodetus serratus* |
| GRIS | *Griselinia littoralis* |
| PODO | *Podocarpus hallii* |

Figure 13

## YORK ROAD TRACK RIDGE

Canopy Species Correlation

(Pearsons Product Moment Correlation Coefficient)



*D. filifolium*, and *P. colensoi*) and the major species from the tussock dominated quadrats. Cluster 4 is comprised of upper altitude herbfield species and is a more cohesive group in that there are many interconnections (significant positive correlations) between the group members. The final cluster, Cluster 5 is comprised of two species only (*Helichrysum sp.* (unnamed) and *Montia sp.*) both represented in the extreme upper altitudinal quadrats. In total there are 30 statistically significant species correlations $(p = \leqslant 0.005)$ out of a possible of 435 and further to this a total of 7 of the 30 canopy are signficantly associated with only one other species. (See Appendix 2.) The *W. racemosa* - *C. serratus* positive association results from the almost identical altitudinal distribution of the species throughout the lower altitude quadrats although it must be noted that the complete distribution for these species has not been sampled. Therefore thesignificant correlation may simply result from this fact although field observations in sites lower than those formally sampled supports the correlation obtained. The species correlations in Cluster 2 as a whole are ecologically meaningful in that there is a logical grouping together of *Griselinia* and *Podocarpus* from the upper forest which is connected via the *Griselinia* - *Pseudowintera* correlation to the lower altitude scrub species and then via the *Hebe stricta* - *Coprosma sp.* (unnamed) correlation to the upper altitude scrub species. When only correlations of $\leqslant p = 0.001$ are considered cluster 2 divides logically into these three sub groups. Likewise the species correlations in cluster 3 are ecologically meaningful. The shrub species found at the upper altitudinal limit of shrubs are connected via the *Cassinia* - *H. odora* correlation to the tussock species. When only the correlations significant at $p = 0.001$ are considered cluster 3 divides logically into two subgroups the upper altitude shrub species and the tussock species along with *Hebe odora.* The species intercorrelations in the herbfield cluster 4 are more complex and appear to be related not only to altitudinal limits but also to substrate conditions although this is difficult to prove without further investigation. The correlation of *Anisotome* , *C. glandulosa var. latifolia*, *Rhacomitrium spp.* appears to be moisture based in that these three species tended to occur together in poorer drained sites in upper altitude quadrats. It is also possible that the intercorrelations between *Gaultheria*, *C. gracilenta var.*, *Drapetes*, and *Forstera* represent drier substrate conditions. However the pattern is not straight forward and the pattern of intercorrelation could also be partly explained purely in terms of altitude with *C. var. latifolia* for example distributed at lower altitudes to *C. gracilenta var.* When only correlations significant at $p = 0.001$ are considered *Luzula sp.* and *C. pumila* form a subgroup apart from the rest of the herbfield species. A possible explanation is their occurrence on sites exhibiting ridge - hollow terracing. Overall the species correlations in this herbfield cluster 4 are complex and any explanation in terms of altitudinal limits alone is difficult because of the influence of other factors such as substrate conditions. The correlation of *Helichrysum* and *Montia* appears to result from their similar distribution centred on the upper most quadrats and in the unstable substrate conditions on scree slopes.

## Canopy Species Correlation Pearsons Product Moment Correlation (natural logarithmic transformation)

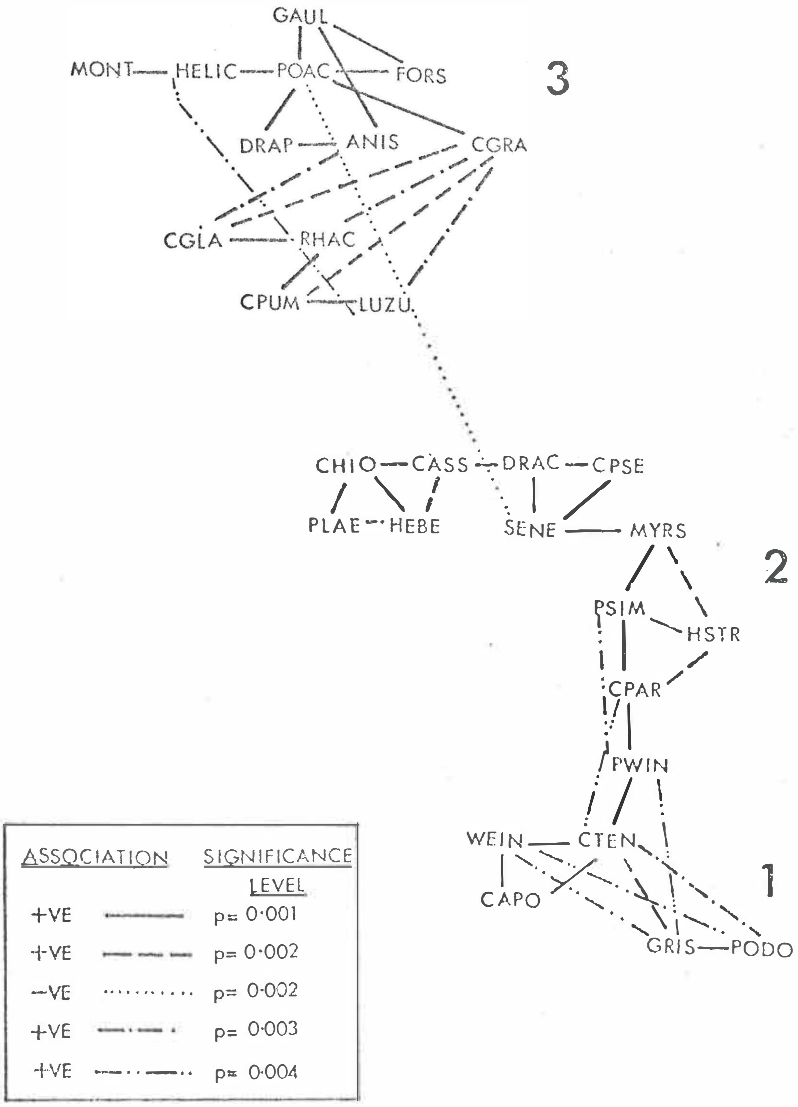
The data was transformed to natural logarithms and again Pearsons Correlation Coefficient was used to determine the number of statistically significant species associations. (See Appendix 3.) The correlations which achieve the generally accepted significance level $p = \leqslant 0.005$ are depicted on a linkage analysis in the same way as the unmodified data (See Fig. 14). At this level of significance only two species clusters are defined the first a cluster comprised of intercorrelated herbfield species and the second a cluster comprised of intercorrelated shrub, tussock, and forest species. The natural logarithmic transformation thus has the effect of increasing the number of statistically significant correlations (from 30 to 56) and consequently causing 'chaining' of the clusters previously delineated in the unmodified data. The same overall pattern of species association is thus apparent, for example the highest correlation coefficients (those approaching closest to 1.00) are exhibited by the same species pairs as in the unmodified data. As well subgroups or noda where a higher degree of intercorrelation occurs within each of the clusters identified correspond with the clusters delineated in the unmodified data. When positive correlations significant at $p = \leqslant 0.001$ only are considered three species clusters are apparent the first composed of two forest species <u>G. littoralis</u> and <u>P. hallii</u>, the second all the remaining forest and shrub species, and the third the herbfield species. Again the pattern of species intercorrelation appears to be ecologically meaningful in that species with similar altitudinal distributions are grouped together and 'chaining' within clusters occurs in a logical progression from

Figure 14

YORK ROAD TRACK RIDGE

Canopy Species Correlation

(Pearsons Product Moment Correlation Coefficient
Logarithmic Transformation)



lower altitude species through to higher altitude species. The pattern of intercorrelation in the herbfield cluster is more complex because of the often mentioned difficulty in holding constant other factors including substrate conditions. The same patterns described for the unmodified data appear applicable in that particularly when correlations significant at $p = \leqslant 0.001$ only are considered similar noda of species intercorrelation are apparent.

### Canopy Species Correlation Spearmans Rank Correlation Coefficient

Finally Spearmans Rank Correlation Coefficient was calculated for each of the 435 possible species combinations and the statistically significant $p = \leqslant 0.005$ species associations are listed in Appendix 4. Spearmans Rank Correlation Coefficient uses ranked data and thus the quantitative species data collected was reduced to species rankings consequently suffering a loss of information and simplifying relationships. The advantages of this approach have already been described. At the $p = \leqslant 0.005$ significance level two species clusters only are delineated both identical to the logarithmic transformation result with regard to cluster membership and very similar with regard to the pattern of intercorrelation. Again the overall pattern of species association is the same as that of the unmodified data with the highest correlations exhibited by the same species and subgroups or noda where a high degree of intercorrelation occurs corresponding to the clusters indentified in the unmodified data. The conversion of the data to ranking doubled the number of statistically significant species correlations causing an even greater degree of 'chaining' of the clusters delineated in the unmodified data. Two clusters are apparent until the $p = 0.004$ significance level at which point W. racemosa and C. serratus separate to form a distinct cluster.

No further clusters separate by continuing to increase the significance level accepted for cluster definition but the number of interconnections or degree of cohesiveness decreases as more rigorous levels of significance are set.

Each of the linkage analyses described has the same basic pattern in which clusters of species with similar altitudinal distributions can be identified. The species associations are of two main types first where one species distribution tends to parallel that of a dominant species (dominant - subdominant) and second where two species share similar altitudinal distributions and are codominants for example W. racemosa - C. serratus in the first instance and G. littoralis - P. hallii in the second instance. The total number of statistically significant species associations appears to be much higher than that generally reported in direct gradient analyses. This appears in part at least to be a function of the gradient range and of the altitudinal interval employed, possibilities discussed in Chapter 7. Further to this the relatively high degree of species association also points to the fact that a classificatory strategy in which clusters or groups of species which associate (associations, communities) together are identified is the most useful approach for this data. Finally the clusters or groups identified appear to be 'natural groups' rather than artifacts of the data and thus support in part the discrete community type hypothesis.

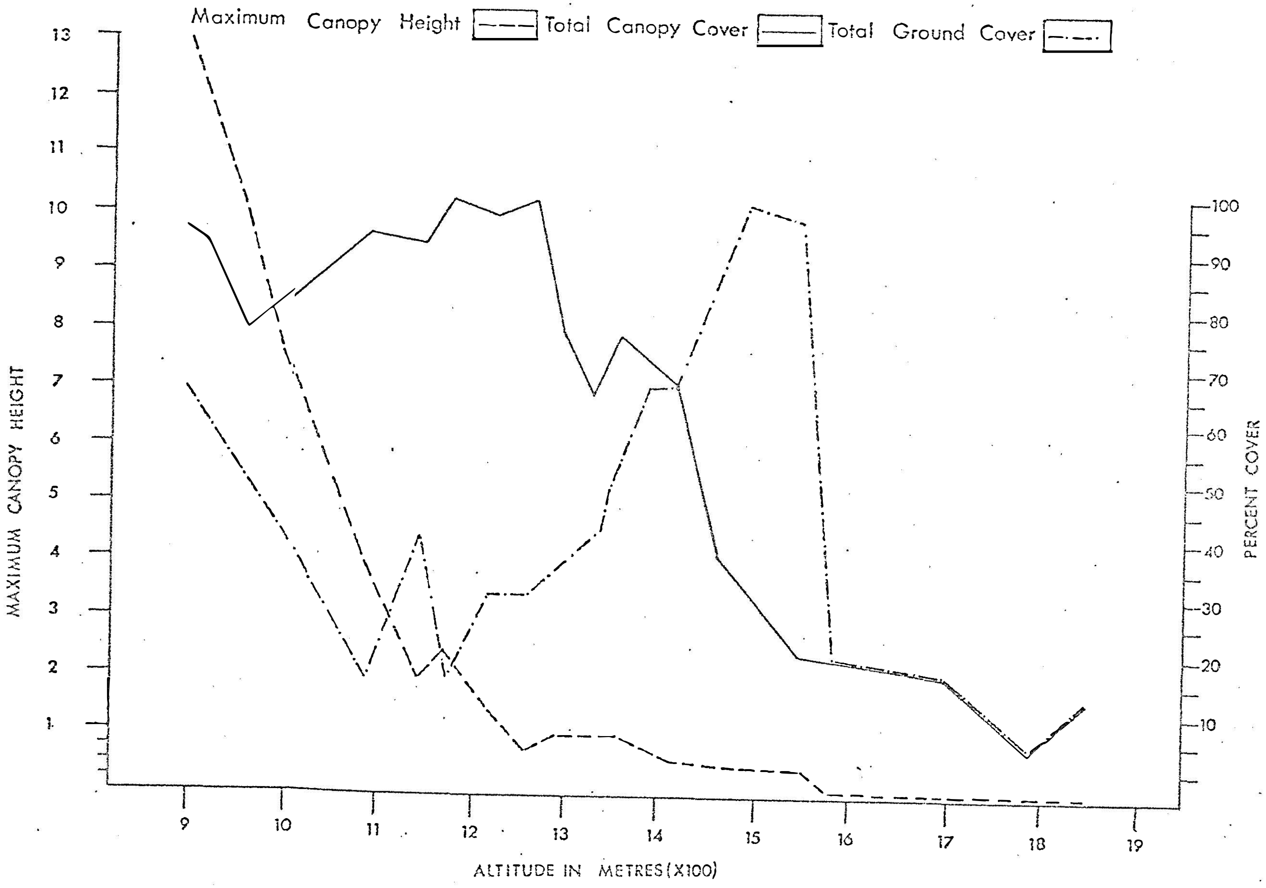
## York Road Track Ridge Species Physiognomy

### Total Canopy Cover and Maximum Canopy Height

Both Total Canopy Cover and Maximum Canopy Height are quantitative expressions of a whole range of physiognomic and structural changes which take place along the altitudinal gradient. (See Fig. 15.) Maximum canopy height decreases with increasing altitude from the highest maximum canopy height of 13m recorded in the W. racemosa dominated quadrat at 897m through to 5cms max. canopy height recorded in the Helichrysum sp. dominated quadrat at 1,797m. Maximum canopy height was selected to represent the differences in canopy height through altitude because it could be determined rapidly whereas mean canopy height or range of canopy height would have involved multiple estimations of canopy height. In most cases maximum canopy height is a reflection of one or two dominant species which achieve the greatest stature at any given quadrat. Thus in the lower forest quadrats the maximum canopy height is usually exhibited by Weinmannia or emergent Podocarpus while in the shrub dominated quadrats the maximum canopy height is exhibited by S. elaeagnifolius. The maximum canopy height may in fact be an extreme value in that it may only be exhibited by a minority of the canopy species in terms of relative cover or relative density. For this reason major changes of slope on the line representing maximum canopy height are clear cut. From 897m through to 1,118m the major canopy species recorded for maximum canopy height was P. hallii and it declines steadily from 13m to 2m. From 1,118m to 1,218m P. hallii is no longer emergent above the rest of the canopy and in fact is more part of a closed canopy in which S. elaeagnifolius is beginning to dominate. By 1,218m S. elaeagnifolius

## Figure 15

YORK ROAD TRACK RIDGE



clearly dominates and thus the maximum canopy height recorded again shows a steady decline until 1,547m. At this point C. rubra, which shared the maximum canopy height with Senecio in the upper shrub quadrats and then replaced it in the tussock dominated quadrats, reaches its upper altitudinal limit. From 1,547m onwards the maximum canopy height is that of the ground cover stratum including Poa colensoi and Helichrysum sp. Key points along the line representing maximum canopy height are therefore where Senecio replaces Podocarpus, where Chionochloa finally dominates Senecio in terms of maximum canopy height, and where Chionochloa reaches its upper limit and is replaced by the much smaller herbfield species.

Total Canopy Cover like Maximum Canopy Height reflects the changes in species composition and their subsequent effects on physiognomy and structure of the vegetation. (See Fig. 15.) In the lower altitude forest where Weinmannia and Podocarpus dominate there is a deal of fluctuation in the total canopy cover which appears in part to reflect the growth habits of these two species (the tendency for Weinmannia to form a more closed canopy as compared to the emergent Podocarpus). Thus the relative composition of these major species appears to be reflected in total canopy cover with the highest value in the lower altitude forest; 96 percent occurring where Weinmannia is clearly dominant. Total Canopy cover thus decreases as Podocarpus become dominant between 959m and 1,087m. Then as Podocarpus decreases in dominance and more and more shrub species are represented in the canopy (top stratum) there is a tendency for much higher total cover values. Thus from 1,087m onwards as Senecio joins the canopy, Podocarpus is no longer emergent, and Griselinia is more of a low growing spreading shrub, total canopy cover values consistently reach above 90 percent. From 1,261m onwards the shrub species begin to reach their upper limit and as the relative proportion of tussocks increases total cover values for the top stratum decrease to 70-80 percent. From this point the definition of the top stratum becomes critical for the tussocks decrease in stature until they begin to merge with smaller herbfield species such as *Celmisia sp.* and *Helichr sum sp.*, in other words the ground stratum. Thus if the category top stratum is retained strictly until this change over is complete and the ground stratum is in fact the top stratum total cover steadily declines through altitude until by 1,797m a total cover of only 3 percent is recorded. This however conceals on important change in vegetation pattern in that much of the decrease in total cover at high altitudes is the result of the harsher environmental conditions, the inability of species to colonise and survive, and the increasing area of "uncolonisable" rock. At the point where the tussocks of the top stratum and the ground cover species become difficult to separate the total ground cover reaches above 90 percent and includes many of the same herbfield species which only achieve total cover of 20 percent or less above 1,547m. This pattern is however outlined in detail in the discussion relating to Total Ground Cover.

To summarise then the major changes in total canopy (top stratum) cover through altitude relate to the species composition at any given altitude. There is a tendency for much higher canopy cover to occur in the shrub dominated quadrats. Total cover declines as the shrub species upper limit is reached and the tussocks become dominant. Finally the herbfield species reach maximum cover between 1,489m and 1,547m and progressively decline as conditions become more extreme towards 1,855m The lowest total cover of 3 percent is recorded near a recent scree slide at 1,797m. Changes in physiognomy and structure are also described in more detail in the Sections on the Tree-Shrub and Shrub-Tussock interfaces.

In conclusion it must be noted that maximum canopy height and total canopy are absolute values and therefore give an indication of total species biomass at each of the sites recorded. As noted in Chapter 4 absolute measures have a greater ecological significance than relative measures of species density or cover in that they enable comparison of actual species biomass at each site rather than just the relative species composition. The importance of this data is obvious then for whereas the values for relative density and cover (importance values) result in all quadrats appearing to contain equal total quantitative values of species composition presentation of the maximum canopy height and total cover data demonstrate the marked differences in biomass between the quadrats. The difference between lower altitude forests and upper altitude herbfields in terms of biomass are extreme. The <u>Weinmannia</u> dominated quadrat at 897m thus may be considered as a four tiered structure - canopy, subcanopy, shrubs and ground cover reaching up to 13 metres in height with a total canopy cover of 96 percent and a total ground cover of 65 percent. The highest altitude quadrat dominated by <u>P. colensoi</u> in comparison has only a single stratum of vegetation reaching up to 5cms in height and a total cover of 13 percent. A very approximate quantitative difference between these quadrats in terms of plant biomass can be obtained by multiplying the unit area occupied by vegetation by the maximum canopy height. At 897m and including the canopy only this is 598 cu metres / 25 sq m as compared with 1.625 25 sq metres in the quadrat at 1,855m. Total plant biomass thus decreases dramatically with increasing altitude and although more floristic data than physiognomic structural data has been collected in this study the significance of the latter is fully recognised.

## Total Ground Cover

Total ground cover for the York Road Track Ridge is also depicted on Fig. 15. At the lowest altitude quadrat (897m) total ground cover is 65 percent but it declines steadily as the shrub species begin to dominate from 999m onwards. Values as low as 15 percent are recorded in quadrats dominated by P. colorata and S. elaeagnifolius. Total ground cover remains low until the upper altitudinal limit of the shrub species is approached (1,337m) where it increases rapidly reaching a maximum value of 98 percent at 1,489m. From this point onwards total ground cover declines again rapidly to 18 percent at 1,584m and reaches its minimum at 1,797m with only 3 percent total ground cover. Attention has already been drawn to the fact that the definition of canopy (top stratum) and ground cover (ground stratum) is critical at the point where the tussocks merge with the smaller herbfield species. The two maximum total ground cover values are recorded in the quadrats where this occurs and the rapid decline from this point onwards appears to result more from the unfavourable environmental conditions of higher altitudes and the consequent inability of species to invade and colonise the higher altitude slopes. In the quadrats where the separation of the canopy and ground stratum is clear cut there is an inverse relationship between total canopy cover and total ground cover. Three factors appear to contribute to this relationship. The first is the obvious limiting of total ground cover caused by a close-knit canopy reducing the amount of light reaching the ground. The second is the different growth habits of the lower altitude ground cover species for example *Astelia nervosa* and *Blechnum discolor* with their more robust growth forms would be expected to achieve much greater coverage than the much smaller species *A. aromatica, O. macrophylla, R. nivicola,* and *Celmisia spp.* growing at higher altitudes. The third possible factor is the shrub canopy floristic composition. *D. filifolium* for example produces a litter of dead 'needles' which appear to inhibit the ground cover growth. The fact that *D. filifolium* forms such a close knit canopy may be an inhibiting factor as well however the effect of the needle litter deserves more detailed investigation. To summarise the overall ground cover pattern is one of increasing total ground cover with decreasing total canopy cover. Beyond 1,584m however the more unfavourable environmental conditions begin to show their full effect and total ground cover decreases markedly with increasing altitude. The minimum total ground cover recorded 3 percent at 1,797m occurs where recent scree movement has obviously affected the degree of coverage achieved by the vegetation.

## Tree-Shrub Interface

In order to examine more closely the discontinuites in canopy species composition, physiognomy, and structure apparent at the tree-shrub interface data from four locations, Lake Dive, North Egmont, Dawson Falls, and York Road is presented on Figures 16, 17, 18, 19, 20, 21 and 23. This includes Canopy Relative Density, Canopy Maximum Height, Number of stems per 100 sq m, and Vegetation Stratification. Quadrat data for slope angle, gradient, aspect, and altitudinal range is summarised on Table 9 and the altitude for each quadrat is listed in Table 10.

Figure 16
NORTH EGMONT Tree-Shrub Interface

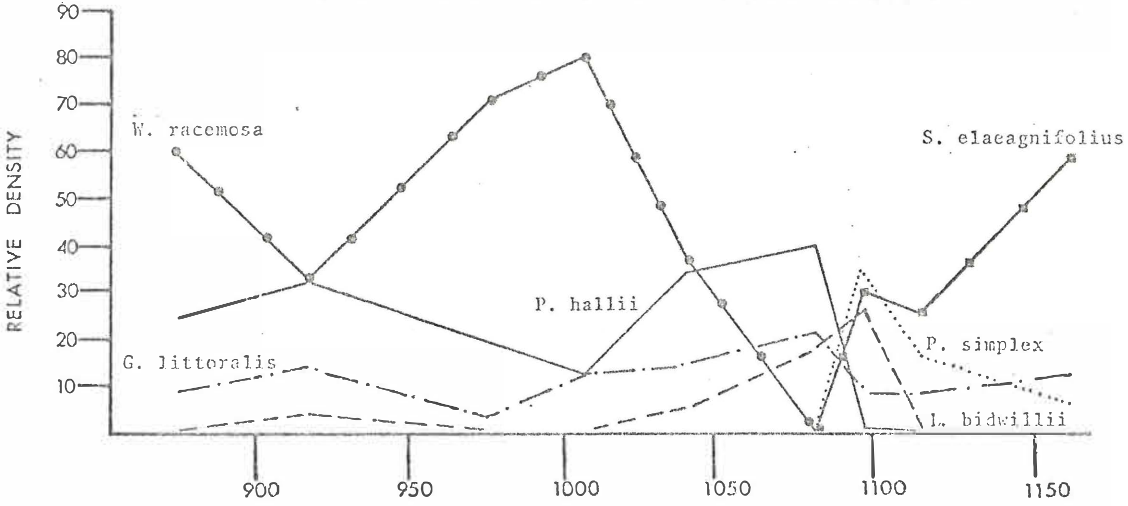


Figure 17
YORK ROAD Tree-Shrub Interface

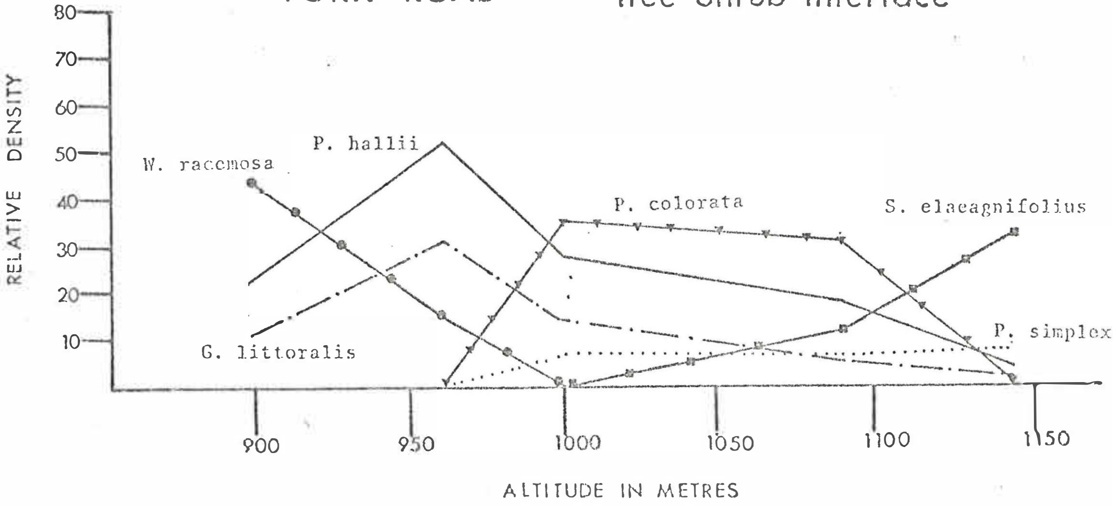


Figure 18
DAWSON FALLS Tree-Shrub Interface

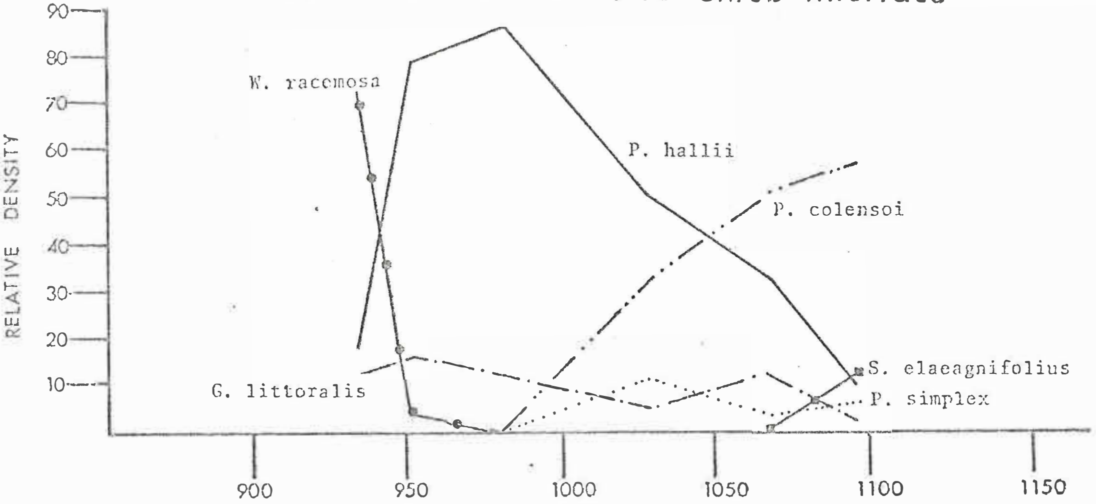


Figure 19
LAKE DIVE Tree-Shrub Interface

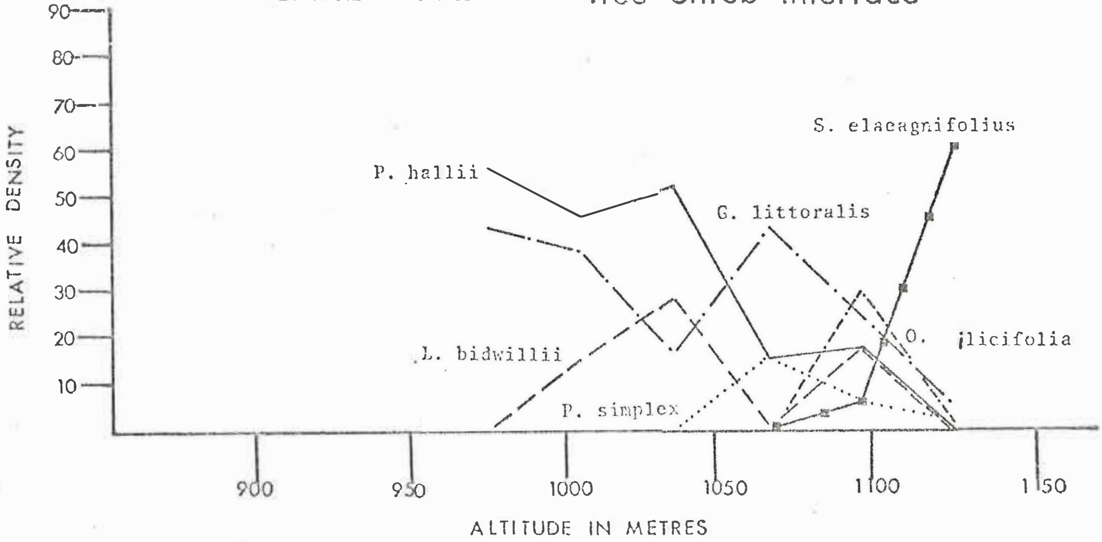


Table 9. Tree-Shrub Interface Quadrat Environmental Data

| | Quadrat Slope Angle | Aspect (Ridge alignment) | Gradient | Altitudinal Range |
|---|---|---|---|---|
| North Egmont (Figure 16) | 40.22° | N.E. | 1:5.63 | 292m |
| York Road (Figure 17) | 17.00° | E. | 1:6.47 | 198m |
| Dawson Falls (Figure 18) | 8.50° | S.E. | 1:4.93 | 163m |
| Lake Dive (Figure 19) | 13.80° | S | 1:2.64 | 152m |

Comparison of Canopy species reveals major differences in species complement, rate of change in dominance from tree species to shrub species with increase in altitude, the relative density of species at comparable altitudes, and the overall altitudinal range of species at the four locations.

## Lake Dive Track Ridge

The major canopy species represented at the Lake Dive location are *P. hallii*, *L. bidwilli*, *G. littoralis*, *P. simplex var. sinclairii*, *O. ilicifolia*, and *S.elaeagnifolius*. (See Fig. 19.) At the lower altitudes 974m - 1,035m *P. hallii* dominates with a maximum relative density of 56percent at 974m. *G. littoralis* which parallels the *Podocarpus* distribution but is subordinate to it up to 1,035m becomes dominant at 1,066m reaching its maximum relative density of 42 percent. *Griselinia* is replaced in turn by *Olearia ilicifolia* at 1,096m with a relative density of 29 percent and *S.elaeagnifolius* dominates at 1,127m with a relative density of 60 percent. Thus the progession of dominance by one canopy species and its replacement by another results in a change from *Podocarpus* - *Griselinia* - *Libocedrus* forest to *Senecio* dominated scrub. This

Table 10. Tree-Shrub Interface Quadrat Altitude

| | Altitude | |
|---|---|---|
| | Feet | Metres |
| | York Road | |
| 1 | 2,945 | 897.24 |
| 2 | 3,150 | 959.70 |
| 3 | 3,280 | 999.30 |
| 4 | 3,570 | 1,087.66 |
| 5 | 3,760 | 1,145.55 |
| | Dawson Falls | |
| 6 | 3,600 | 1,096.80 |
| 7 | 3,500 | 1,066.33 |
| 8 | 3,380 | 1,029.77 |
| 9 | 3,270 | 996.26 |
| 10 | 3,170 | 965.79 |
| 11 | 3,065 | 933.8[illegible] |
| | North Egmont | |
| 12 | 2,865 | 827.87 |
| 13 | 3,005 | 915.52 |
| 14 | 3,200 | 974.93 |
| 15 | 3,305 | 1,006.92 |
| 16 | 3,410 | 1,038.91 |
| 17 | 3,550 | 1,081.56 |
| 18 | 3,600 | 1,096.80 |
| 19 | 3,660 | 1,115.08 |
| 20 | 3,825 | 1,165.35 |
| | Lake Dive | |
| 21 | 3,200 | 974.93 |
| 22 | 3,300 | 1,005.40 |
| 23 | 3,400 | 1,035.86 |
| 24 | 3,500 | 1,066.33 |
| 25 | 3,600 | 1,096.80 |
| 26 | 3,700 | 1,127.26 |

change is complete by 1,127m, however the actual tree line defined in terms of a change in growth habit or physiognomy occurs at approximately 1,081m. One species distribution, that of G. littoralis, detracts from the floristic discontinuity in that it extends into the Senecio dominated scrub. However physiognomically it adopts the shrub growth form. Libocedrus bidwilli is represented in the canopy between 1,005m and 1,096m reaching its maximum relative density of 28 percent at 1,025m. Its distribution is particularly clumped or discrete and in fact it dominates to the extent of 90 percent relative density at several locations between the quadrat sites.

The Lake Dive location (See Fig. 19) exhibits a particularly rapid rate of change from dominance by tree species to dominance by shrub species. For example the rate of increase in relative density for S.elaeagnifolius from the quadrat immediately before its appearance in the canopy to its maximum representation of 60 percent at 1,127m is 27 percent per 30 metres. This rate of increase should be compared with those of the locations following to give an indication of the abruptness of change or degree of discontinuity in canopy composition. The rate of change exhibited by the Lake Dive location in particular with reference to S.elaeagnifolius is the most rapid of the four and this can probably be attributed in part to two of the environmental factors recorded in Table 9. Firstly the elevation gradient is very steep (1:2.64) indicating a 1 metre rise in elevation for every 2.64 metres horizontal distance. Beals (1969) noted that disjunctions along an altitudinal gradient in Ethiopia were caused by competitive exclusion occurring in the limited horizontal distance afforded by steep slopes and this explanation will be considered later when the data of all four locations is compared. Secondly the southerly (S. - S.S.W.) aspect of the ridge may also contribute to the rapidity of change in species composition. Although only very limited climatic data is available for Egmont National Park the southern side of Mt Egmont is generally considered to be less favourable than the northerly and easterly aspects because of the longer winter snow-lie, lower insolation in late afternoon, and exposure to salt-laden sea winds.

### York Road Track Ridge

In marked contrast to the Lake Dive location is the York Road Track Ridge (See Fig. 17). The major canopy species represented are *W. racemosa, P. hallii, G. littoralis, P. colorata, P. simplex var. sinclairii*, and *S.elaeagnifolius.* At 897m *W. racemosa* dominates with a relative density of 44 percent. *Weinmannia* gives way to *P. hallii* at 959m (relative density 52 percent) which continues to dominate until 1,087m. The distribution of *G. littoralis* parallels that of *P. hallii* throughout its altitudinal range and its maximum relative density of 31 percent occurs at 959m. *P. colorata* becomes the major canopy component at 999m with a relative density of 35 percent and it retains dominance until 1,087m. *Senecio* first recorded in the canopy at 1,087m reaches a relative density of 33 percent by 1,145m. The change from *Podocarpus - Griselinia* forest through to *Senecio* dominated scrub is thus complete by 1,145m and the tree-line defined in terms of a change in species growth habit occurs at approximately 1,100m. *L. bidwillii* is absent from the canopy on the York Road Ridge.

The rate of change from tree species to shrub species is much slower on the York Road Track Ridge than on the Lake Dive Ridge. The rate of increase for *S. elaeagnifolius* from the quadrat immediately before its appearance in the canopy to its maximum representation is

4 percent per 30 metres. This much slower rate of change appears to result for the most part from the gradual gradient 1:6.47 of this section of the York Road Track. The easterly aspect of the York Road Ridge would also provide more favourable climatic conditions than those of the Lake Dive Ridge.

## Dawson Falls

The major canopy species represented at the Dawson Falls location include P. hallii, W. racemosa, G. littoralis, P. colensoi, S. elaeagnifolius, and P. simplex var. sinclairii. (See Fig. 18.) W. racemosa is dominant at 933m with a relative density of 79 percent but is quickly replaced by P. hallii at 965m. P. hallii continues to increase in dominance up to 996m where its maximum relative density 86 percent is recorded. P. colensoi, first recorded in the canopy at 1,029m, progressively increases in representation until at 1,096m a relative density of 57 percent is recorded. G. littoralis is recorded in all quadrats and is always one of the subordinate species. S. elaeagnifolius is first represented at 1,096m with a relative density of 12 percent. This is only the beginning of its representation in the canopy and although no formal data was collected above 1,096m its estimated relative density at 1,127m is 50 percent making it the most highly represented species in the canopy. P. simplex var. sinclairii is first recorded at 999m with a relative density of 11 percent a value it never exceeds in the remainder of its distribution. In terms of species complement Dawson Falls differs from the two locations already described in the importance of P. colensoi as a canopy species. Although physiognomically dissimilar P. colensoi at Dawson Falls and P. colorata at York Road form a definite zone of representation between the P. hallii dominated forest and the Senecio dominated scrub. The data presented does not show the presence of L. bidwillii in the canopy. As a result of the clumping or discrete grouping characteristic of this species it was not recorded in the quadrats although in fact it is present at two sites between 933 and 996m. It does not achieve the dominance characteristic of sites at Lake Dive or North Egmont however.

The rate of change from tree to shrub species at Dawson Falls is similar to that of Lake Dive. For example the rate of increase for P. colensoi is 14 percent relative density per 30m. The comparison is not as valid as that of Lake Dive and York Road however in that classification of P. colensoi as a shrub is arbitrary. P. colensoi in fact may be more properly viewed as a species which dominates a transitional zone between Podocarpus dominated forest and Senecio dominated scrub. The tree-line defined in terms of change in growth habit occurs at approximately 1,200m.

### North Egmont

The major canopy species represented at North Egmont are W. racemosa, P. hallii, G. littoralis, L. bidwillii, P. simplex var. sinclairii and S. elaeagnifolius. (See Fig. 16.) W. racemosa dominates between 872 and 1,006m with a maximum relative density of 75 percent. P. hallii and G. littoralis remain subordinate to W. racemosa until 1,096m when P. hallii assumes dominance with a relative density of 39 percent. G. littoralis is subordinate to P. hallii throughout the lower altitudinal quadrats but its distribution continues into the higher altitude quadrats above 1,081m where P. hallii is no longer represented. P. simplex var. sinclairii becomes dominant at 1,096m with a relative density of 34 percent and gives way in turn to S. elaeagnifolius at 1,115m. Senecio continues to increase in dominance reaching a relative density of 58 percent at 1,165m. *Libocedrus* is distributed between 1,038m and 1,096m forming a minor component of quadrats dominated by *Podocarpus* but also extending into the shrub dominated quadrats. In the latter it tends to be emergent above the more closed canopy of *Pseudopanax* and *Senecio*. *Libocedrus* is found in discrete groups similar to the distribution pattern already described for Lake Dive although it is particularly well represented at North Egmont. Many sites not formally sampled exhibit relative densities of 80 percent or more and the ridge sides and valleys between 974m and 1,096m support dense stands of *Libocedrus*. The change from a *Weinmannia* *Podocarpus* - *Griselinia* forest to *Senecio* - *Pseudopanax* scrub is complete at 1,115m although *Griselinia* remains a minor component of the scrub canopy. Tree-line defined in terms of a change of growth habit is at approximately 1,100m. In contrast to the three locations already described the upper altitudinal limit of *Weinmannia* is 1.006m approximately 50m higher than the upper limit at Dawson Falls. This is a possible indication of more favourable climatic conditions at North Egmont in the lower quadrats at least. Another possible explanation however is that of Druce (1961) who notes "on Mt Egmont areas that have received recent additions of ash are distinguished from those that have not by the absence or lesser abundance of kamahi". (Druce, 1961, 107.)

The rate of increase in representation by *S.elaeagnifolius* is second only to that of Lake Dive at 21 percent relative density per 30 m. This is in direct conflict with the higher altitudinal limit exhibited by *W. racemosa* and may be explained in terms of more rapid environmental deterioration in the upper quadrats. The overall elevation gradient is 1:5.63 which is similar to that of York Road however the gradient of the upper quadrats is closer to

1:3 and could account for the rapid changes in canopy species representation between 1,006m and 1,115m.

In conclusion the four locations described vary with respect to three major considerations:

1. the total species complement
2. the rate of change in representation from tree species to scrub species
3. the altitudinal limits and degree of representation of the major canopy species.

All four locations have most of the major canopy species in common including S. elaeagnifolius, P. hallii, G. littoralis, and P. simplex var. sinclairii. (See Apendix 5.) Major differences occur with the absence of L. bidwillii from York Road and Dawson Falls although in the latter case the absence is from quadrat data only. W. racemosa is represented at all four locations although at Lake Dive collection of data to a lower altitudinal limit of only 974m prevents comparison of its distribution at this location. P. colensoi is notable in forming a distribution transitional between Podocarpus - Griselinia forest and Senecio dominated scrub at Dawson Falls. P. colorata is notable in forming a distribution transitional between Podocarpus-Griselinia forest and Senecio dominated scrub at York Road and in one quadrat only at North Egmont. O. ilicifolia dominates one quadrat between Podocarpus - Griselinia forest and Senecio dominated scrub at Lake Dive only.

The total species complement at each of the locations may also affect the rate of change from forest to scrub species in the sense that some species reach their maximum or at least important representation in quadrats intermediate between forest and scrub. For example the often mentioned O. ilicifolia at Lake Dive,

P. colorata at York Road, and L. bidwillii at North Egmont and Lake Dive. Where a greater range of species is present, particularly in transitional quadrats, the nature of the change becomes more complex for example at North Egmont.

A comparison of the four ridge locations enables the more common species interactions to be characterised. For example P. hallii generally dominates over G. littoralis although G. littoralis has a marginally higher upper altitudinal limit. W. racemosa quickly dominates over P. hallii and G. littoralis in lower altitudes (below 1,000m) but the latter species remain as important components in the canopy. L. bidwillii exhibits particularly clumped or discrete distributions and its presence in the canopy is usually at the expense of representation by P. hallii and G. littoralis particularly as the upper altitudinal limits of the latter are reached. Senecio is usually represented as a minor canopy component with a more tree-like growth habit 30 metres or more below the point at which it assumes dominance in the shrub canopy.

The rate of change in importance from one species to another particularly from tree species to shrub species appears in part related to the elevation gradient and aspect differences of the four locations. The Lake Dive and York Road locations give the best support for the elevation gradient in particular. Comparison of these two ridges supports the contention of Beals (1969) that the limited horizontal distance afforded by steep slopes causes competitive exclusion of species and thus disjunctions or discontinuities in species representation along the altitudinal gradient. Less favourable climatic conditions related to aspect already described for Lake Dive could accentuate this discontinuity. Other factors affecting this could be the number of species involved in the interaction and unrecorded climatic variables. The latter in particular could provide the strongest effect on this rapidity of change or discontinuity because the decrease of say temperature with increasing altitude may also be discontinuous. Rather sudden changes could occur for example as the ridges described become more exposed upon rising above the altitude of protective flanking ridges.

The altitudinal limits and the degree of representation of the major species varies at all four locations. Relative density of these species at any given altitude would be affected in two major ways: firstly by the number of species competing at that altitude, and secondly by the relative climatic limitations imposed at that altitude for each of the ridges. Thus at 965m at Dawson Falls P. hallii reaches a relative density of 79 percent the only other canopy species being G. littoralis and W. racemosa. Further to this W. racemosa is near its upper limit and is presumably less competitive. In contrast on the North Egmont ridge at 1,081m P. hallii has a relative density of 39 percent with L. bidwillii, P. colorata, P. tenuifolium and G. littoralis making up the remainder of the canopy. The indirect evidence of species distributions on the four ridges points to the least favourable conditions being those of the Lake Dive location. York Road and Dawson Falls appear to be similar on the basis of the upper limit of W. racemosa while North Egmont is anomalous with W. racemosa extending up to 1,038m followed by an extremely rapid change to Senecio dominated scrub. The general climatic descriptions available support the suggestion that the Lake Dive location would have the least favourable climatic conditions but little difference is reported between York Road, North Egmont, and Dawson Falls.

## Physiognomy and Structure

The tree-shrub interface may be examined in terms of the species physiognomy and vegetation structure as well as floristically. The floristic discontinuity described for the four locations examined is further emphasised by the discontinuities of physiognomy and structure. Reference has already been made to the change in growth habit at the tree-line at each of the four locations and this change in growth habit is quantitatively measured as maximum canopy height and number of individuals per 100 sq m. The change in growth habit is essentially one from the tall upright pyramidal or fusiform habit exhibited by P. hallii, L. bidwillii, and W. racemosa to the low growing, spreading, and compact canopy of the Senecio dominated scrub. Accompanying this is the change from a few large individuals per 100 sq m to many smaller individuals per 100 sq m. Figures 20 and 21 depict these changes along the altitudinal gradient for the four locations. York Road and North Egmont provide the best evidence for a physiognomic discontinuity because sufficient quadrats from the shrub dominated areas are included to show the actual change in slope of the lines representing canopy height and number of individuals per 100 sq m. On Fig. 20 the lines representing maximum canopy height for York Road and North Egmont show a change in slope from 1,096m onwards. Fig. 21 supports this observation with the change in slope of the line representing numbers of individuals per 100 sq m occurring between 1,066m and 1,096m. In both cases this points to a discontinuity between the tree dominated and shrub dominated quadrats in terms of physiognomy of the species involved.

In order to clarify interpretation of this data it is presented on Fig. 22 as a scatter diagram of the 26 quadrats measured on the two physicgnomic variables; maximum canopy height and number of

Figure 20

TREE-SHRUB INTERFACE

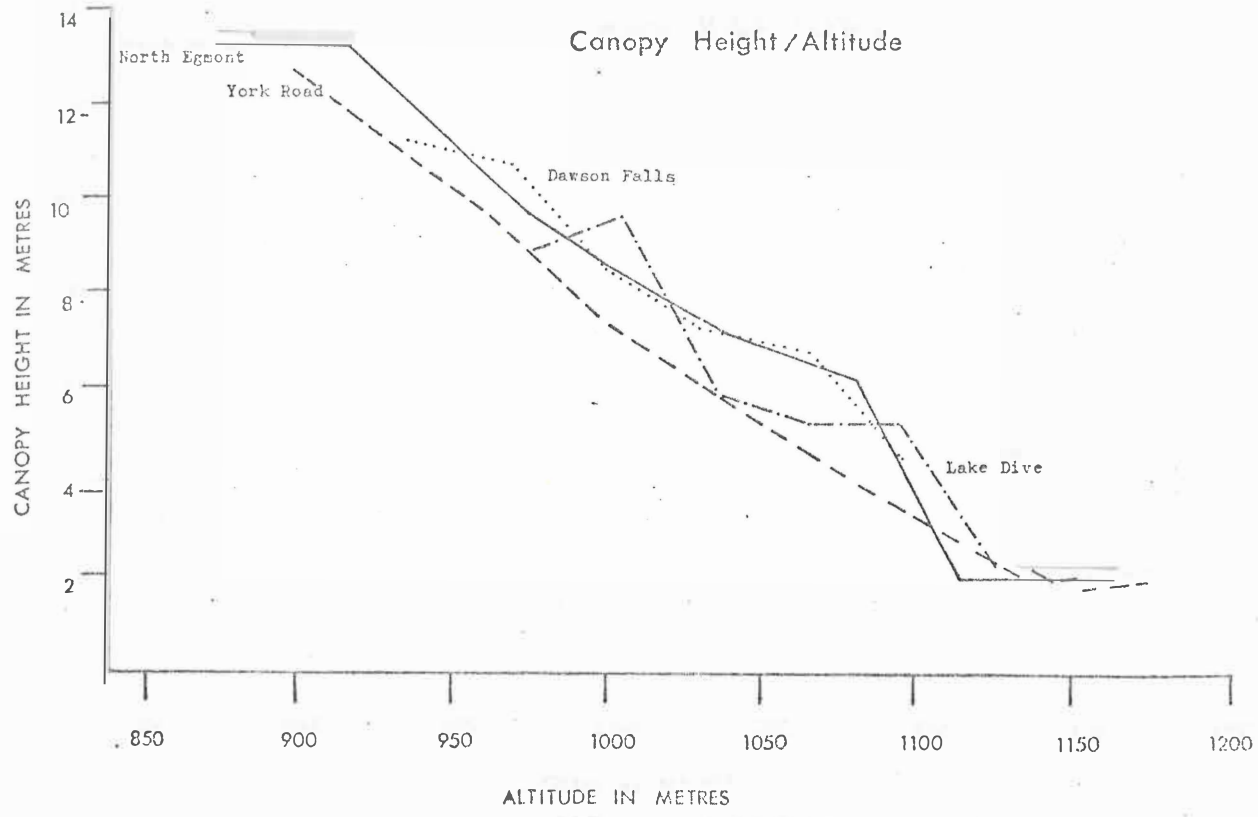
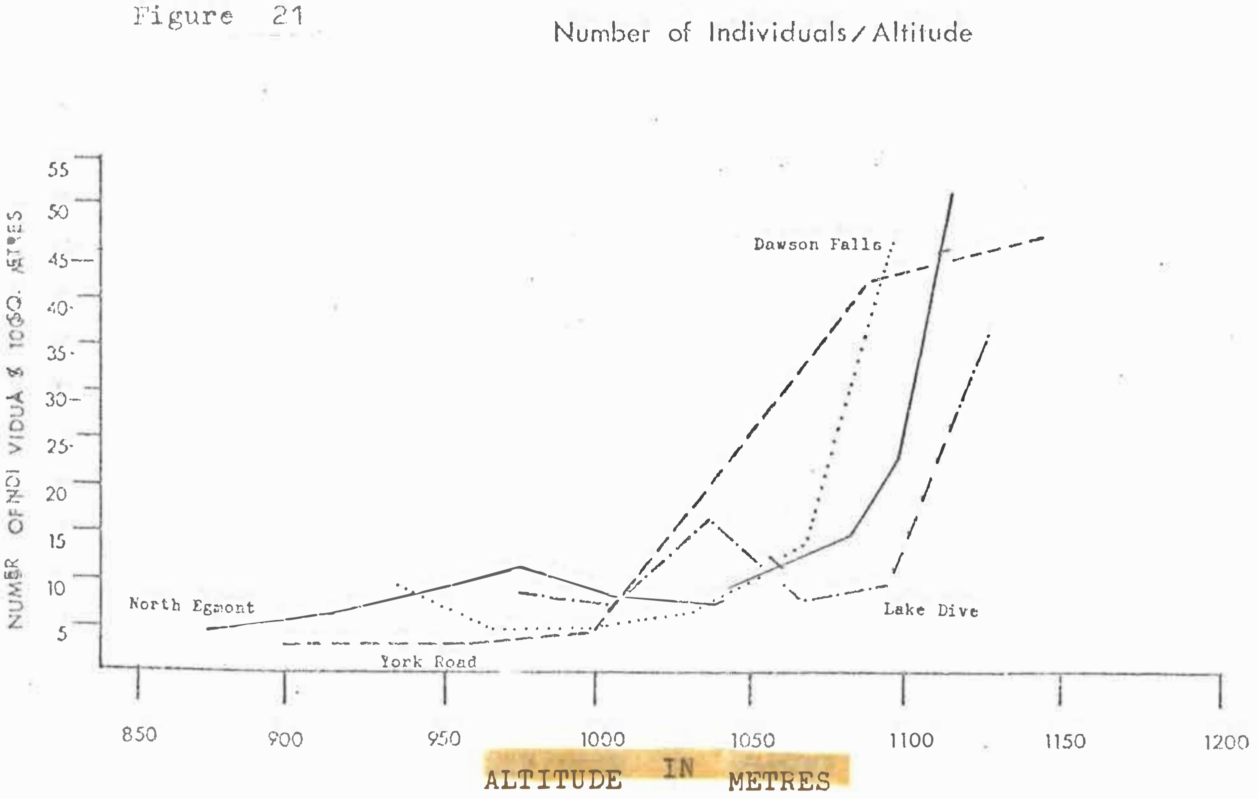


Figure 21



individuals per 100 sq m. The scatter diagram clearly shows the discontinuity between the tree dominated and the shrub dominated quadrats. The cluster labelled A consists in four cases out of the **six** of *Senecio* dominated quadrats (relative cover greater than 40 percent). The cluster labelled B consists in 17 cases out of 20 of quadrats dominated by either *P. hallii*, *G. littoralis*, or *W. racemosa*. The exceptions in both clusters are those quadrats which consist of shrub species capable of approaching tree height, for example *O. ilicifolia*, *P. colorata*, *P. simplex var. sinclairii*, *P. colensoi*, and *S.elaeagnifolius* along with the larger tree species particularly *P. hallii*, *G. littoralis*, and *L. bidwilli.* Quadrats with this type of species composition are the ones which approach closest to the discontinuity, (marked on Fig. 22 as the midpoint between clusters A and B). Cluster B is more properly viewed as a continuous range of quadrats in which one of the major tree species dominates. Canopy height in particular causes the continuous nature of this cluster in that it depends in part on the actual species which dominates how great the value for maximum canopy height will be. Thus for example the canopy height recorded both at lower and middle altitudes could be from the same species, that is emergent *P. hallii.* The discontinuity becomes apparent on the scatter diagram as the much greater difference between the maximum canopy height of the tree species and the shrub species. If the full range of canopy height variation was incorporated into this comparison the discontinuity may not be quite as marked. Inevitably incorporated into this physiognomic discontinuity is a degree of floristic continuity; for example *G. littoralis* and *P. hallii* are represented on both sides of the physiognomic discontinuity. *G. littoralis* in particular adopts a

Figure 22

TREE-SHRUB INTERFACE Physiognomy

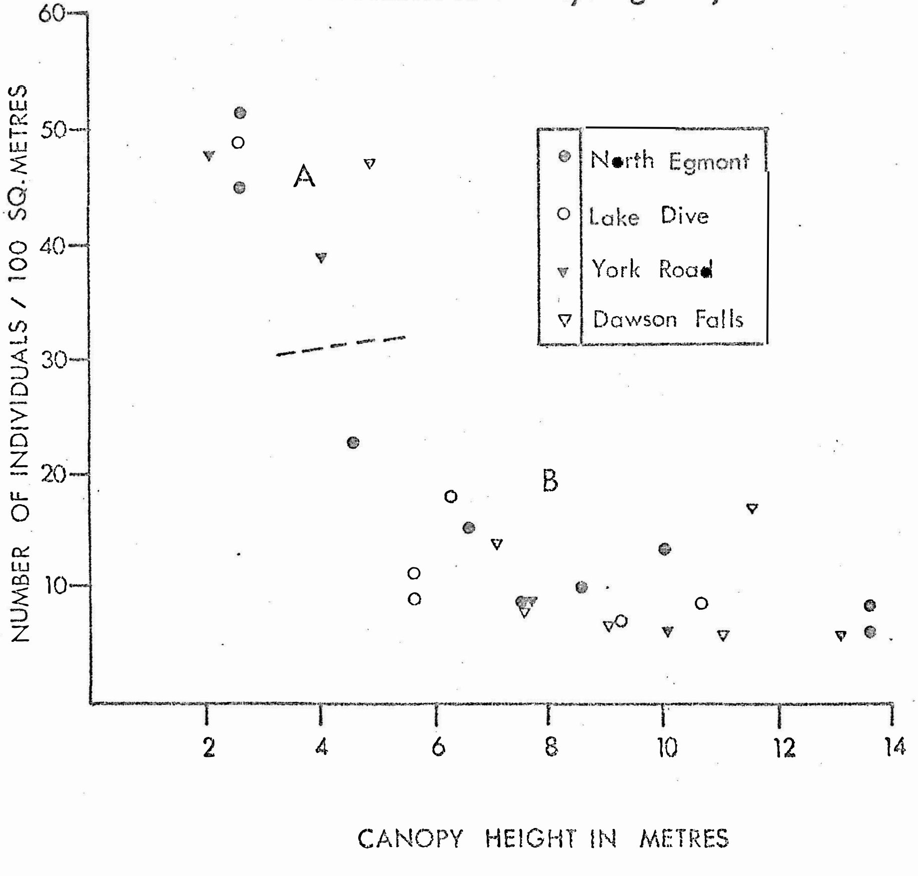
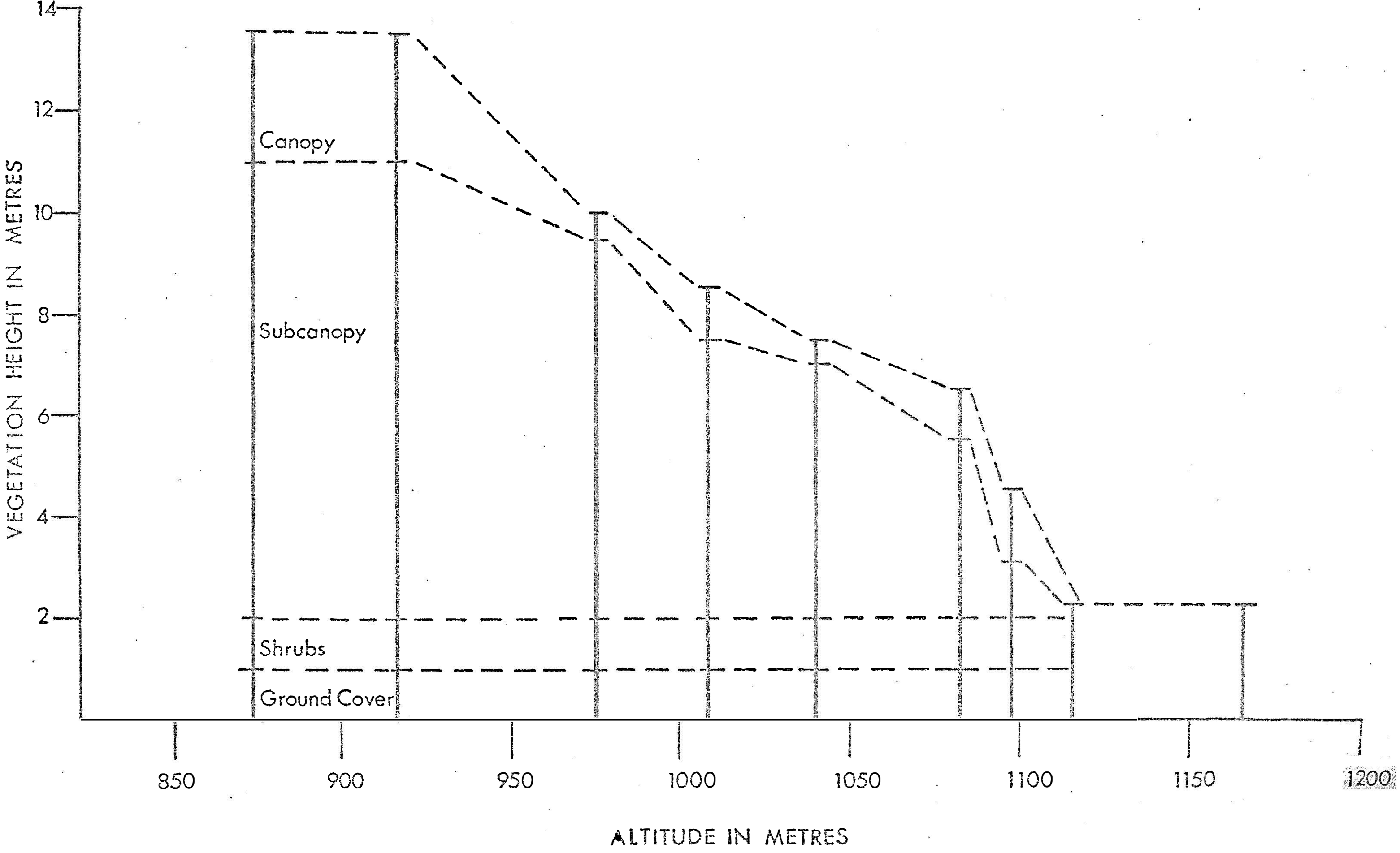


Figure 23

NORTH EGMONT Vegetation Stratification



different growth habit in the upper altitude quadrats making it the physiognomic equivalent of the shrub species. P. hallii on the other hand becomes less and less emergent so that eventually its apical shoots are level with the Senecio dominated shrub canopy.

Vegetation structure, that is the number of strata present in the vegetation, is summarised diagrammatically for the North Egmont location on Fig. 23. The pattern depicted is representative of the pattern at the other three locations with minor exceptions which are noted in the discussion. It must be noted that the categories or strata defined for the vegetation structure are arbitrary, particularly the distinction made between shrubs and subcanopy and between the smaller shrubs and ground cover. Categorisation with height constraints is essential however for accurate recording and comparison of quadrats unless the height of every single individual is recorded. The general pattern of change apparent along the altitudinal gradient is the change from the multilayered forest quadrats through to the shrub quadrats in which the only layers adequately differentiated are the canopy or top stratum and the ground cover stratum. The complexity of the lower forest quadrats is accentuated by the presence of up to 13 epiphytic and two liane species.

The lower altitude quadrats between 872m and 1,038m consist of four major strata along with liane and epiphytic species. The vertical arrangement consists of:

1. the ground cover stratum dominated by B. discolor and A. nervosa (mean height 75cm)
2. the shrub stratum including Coprosma australis, Coprosma lucida C. tenuifolia, Cyathea smithii, P. colorata, Schefflera digitata,

and *Alseuosmia macrophylla* (75cm - 2.00m).

3. The subcanopy including *P. colorata, M. salicinia, P. hallii, C. tenuifolia, P. simplex var. sinclairii, C. serratus,* and *W. racemosa* (2.00m - (7.50 - 11.00m))
4. The canopy including *W. racemosa, P. hallii,* and *G. littoralis* (7.50 - 8.50m / 11.00 - 13.50m)

The maximum canopy height is generally exhibited by emergent *P. hallii* with *W. racemosa* and *G. littoralis* forming a lower more compact canopy surrounding the emergents.

The middle altitude quadrats, 1.038m to 1,096m, consist of four major strata and up to five epiphytic species and two liane species. The vertical arrangement consists of

1. the ground cover stratum dominated by *A. nervosa* and *P. vestitum* (up to 70cm)
2. the shrub stratum which is beginning to become indistinguishable from the subcanopy stratum and is dominated by *P. colorata, C. tenuifolia,* and *C. australis* (70cm - 2.00m)
3. the subcanopy which includes some species which at higher altitudes become part of the *Senecio* dominated scrub (2.00m - (3.00 - 7.00m))

   Dominant species are *P. simplex var. sinclairii, P. colorata, C. australis, C. tenuifolia,* and *S. elaeagnifolius.*
4. The canopy which includes *L. bidwillii, G. littoralis, P. hallii, P. simplex var. sinclairii,* and *P. colorata* (3.00 - 4.50m ( 7.00 - 7.50m))

The maximum canopy height is generally exhibited by emergent *P. hallii* and *L. bidwillii* with a lower canopy limit consisting of *P. simplex var. sinclairii, P. colorata,* and *G. littoralis.*

The upper altitude quadrats, 1,115m to 1,165m, consist of two major strata and a limited representation of epiphytes. The vertical arrangement consist of :

1. the ground cover stratum dominated by *B. capense* and *A. nervosa* (up to 55cm)
2. the canopy or top stratum dominated by *S.elaeagnifolius*, *P. colensoi*, *P. simplex var. sinclairii*, and *C. pseudocuneata* (55cm - 2.25m)

Distinction between canopy or subcanopy strata is impracticable in that most of the top stratum in fact occupies the 1.50 - 2.25m height class and is densely interwoven and compact.

Exceptions to the general pattern described for North Egmont are found at York Road between 1,087m and 1,145m, Lake Dive at 1,086m and Dawson Falls at 1,096m. These exceptions do not detract from the overall pattern, rather they are the result of either disturbance of some form or the differences resulting from the species complement present at that location. At York Road the shrub layer is poorly differentiated from the canopy/subcanopy strata and is dominated by *P. colorata.* This probably results from previously much higher goat populations centred on Quarry Bluff and the dominance of *P. colorata* is usually considered as an indicator of such a disturbance. At the Lake Dive quadrat (1,066m) differentiation between the canopy and subcanopy was difficult. The main canopy species included *Coprosma sp.* (unnamed), *P. hallii*, *P. simplex var. sinclairii* and *H. stricta* with *G. littoralis* dominating. *G. littoralis* is emergent at 5.5m but with a spreading canopy resulting from up to four major leaders per individual. Below this at a maximum of 5m is a complex mix of the species already noted which form a broken and uneven canopy. As well the shrub and subcanopy strata are poorly differentiated because of the relatively large number of *P. hallii* poles and saplings and the presence of many species which at higher altitudes become part of the *Senecio* dominated scrub. These include *H. stricta* and *P. simplex var. sinclairii.* The site is very exposed with some evidence of windfallen canopy trees and this probably accounts for the pattern of stratification exhibited. The canopy at Dawson Falls (1,096m) is composed of *P. colensoi* and *P. hallii* in the main with *P. colensoi* forming a particularly even and compact canopy and *P. hallii* emergent up to 4·80m. The subcanopy is poorly differentiated and resembles more a shrub stratum in that few individuals greater than 2m in height exceed 3m. Goat browsing is in evidence particularly on the *G. littoralis* and *C. australis* individuals in the shrub layer and this along with the compact canopy of *P. colensoi* may account for the poorly developed subcanopy stratum.

### Tree-Shrub Interface: Grouped Data

In order to provide a generalised description of species distributions between 870m and 1,170m and in particular the tree-shrub interface the data collected at all four ridge locations was grouped into 30m segments and averaged. Thus the single ridge quadrats become a composite of quadrats encompassing the vegetation data from twenty six quadrats. This method is comparable to the method of data analysis employed by Whittaker (1956) and described by Whittaker (1973) as a composite transect. "Samples may be grouped by sets of five, say, for thirty metre elevation intervals, or for positions along a topographic moisture gradient. Such grouping tends to average out the irregularities affecting individual samples, and to produce a clear, more easily interpreted picture of species distributions and community change along a gradient." (Whittaker, 1973, 14.)

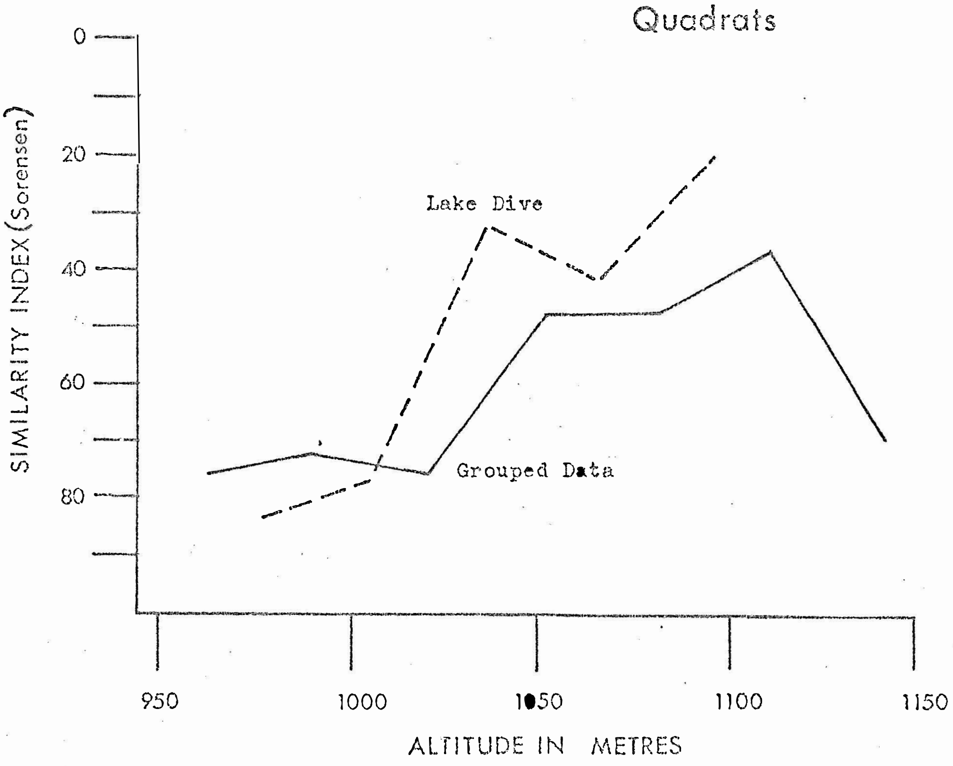
The amalgamation of data has some interesting consequences with regard to the interpretation of species distributions and the conclusions reached in Whittaker"s (1956) study. The species distributions are smoothed by this averaging procedure and further the overlap between the 'tails' of species distributions is increased. Thus where in a single transect presentation, for example Lake Dive, discontinuity between the tree and shrub quadrats is marked the abruptness of change is reduced and continuity between adjacent quadrats is increased by composite transect presentation.

There appears to be reason for critically examining the justification for this averaging procedure employed by Whittaker (1956) if it detracts from discontinuities which are real in vegetation data. Table 11 and Fig. 24 show the discontinuity apparent at Lake Dive compared with the equivalent grouped data. At the quadrats located on the tree-shrub interface the similarity index calculated for Lake Dive is 0.114 while for the grouped data it is 0.371 a clear reduction in the degree of discontinuity apparent at the tree-shrub interface. The major reason for this reduction in data discontinuity is probably the fact that the same altitudes at different ridge locations are not comparable. As altitude is a complex variable including temperature, wind exposue, relative light intensity, relative humidity etc. locations recording the same altitude do not necessary exhibit the same environmental conditions. Thus the averaging of data particularly into 30m segments is in fact measuring and averaging a range of species performances over a range of environmental conditions. This must surely increase the degree of continuity in vegetation data when in fact the discontinuities may be marked on the ground. Kellman (1975) has

Table 11. Similarity Indices between adjacent quadrats

| | Altitude in Metres | Similarity Index for Adjacent Quadrats | |
|---|---|---|---|
| Lake Dive | 1,127.26 | | |
| | 1,096.80 | (0.114) | ( ) Similarity Index |
| | 1,066.33 | 0.436 | at Tree-Shrub |
| | 1,035.86 | 0.342 | Interface |
| | 1,005.40 | 0.775 | (Discontinuity) |
| | 974.93 | 0.846 | |
| Grouped Data | 1,169.76 | | |
| | 1,139.60 | 0.706 | |
| | 1,109.44 | (0.371) | |
| | 1,079.27 | 0.485 | |
| | 1,049.11 | 0.480 | |
| | 1,018.95 | 0.775 | |
| | 988.78 | 0.725 | |
| | 958.63 | 0.762 | |

Figure 24
TREE-SHRUB INTERFACE
Similarity Indices between Adjacent Quadrats



summarised this argument stating "the continuous changes in species populations shown in the displays provided by these techniques were taken by their authors to illustrate the continuous nature of vegetation change in space and the absence of discrete associations. However, some confusion has arisen around this interpretation through a failure to distinguish between continuity in composition, which was demonstrated, and continuity on the ground. The latter was not demonstratable from the data which were derived from spatially separated sites". (Kellman, 1975, 68-69.)

Keeping in mind that this type of data analysis increases the degree of continuity between quadrats, Figs. 25 and 26, still provide a generalisation or summary statement of the canopy species distributions on ridge locations for a large sector of Egmont National Park. Species represented at four or more data groups are depicted on Fig. 25. These species distributions show a gradual progression of dominance from W. racemosa (maximum relative density 60 percent at 868m) at lower altitudes to Podocarpus hallii (maximum relative density 65 percent at 1,168m) at higher altitudes and finally S. elaeagnifolius (58 percent at 1,169m) at higher altitudes. G. littoralis parallels the distribution of P. hallii subordinate for the most part of its range but dominant over P. hallii from 1,109m onwards - P. simplex var. sinclairii forms a minor component of the canopy from 985m to 1.079m but becomes a more important component of the Senecio dominated quadrats at 1,109m with a relative density of 15 percent. L. bidwillii achieves its maximum representation 16 percent relative density at 1,049m but it is only the third most important canopy species at this altitude.

Figure 25

## TREE-SHRUB INTERFACE    Grouped Data

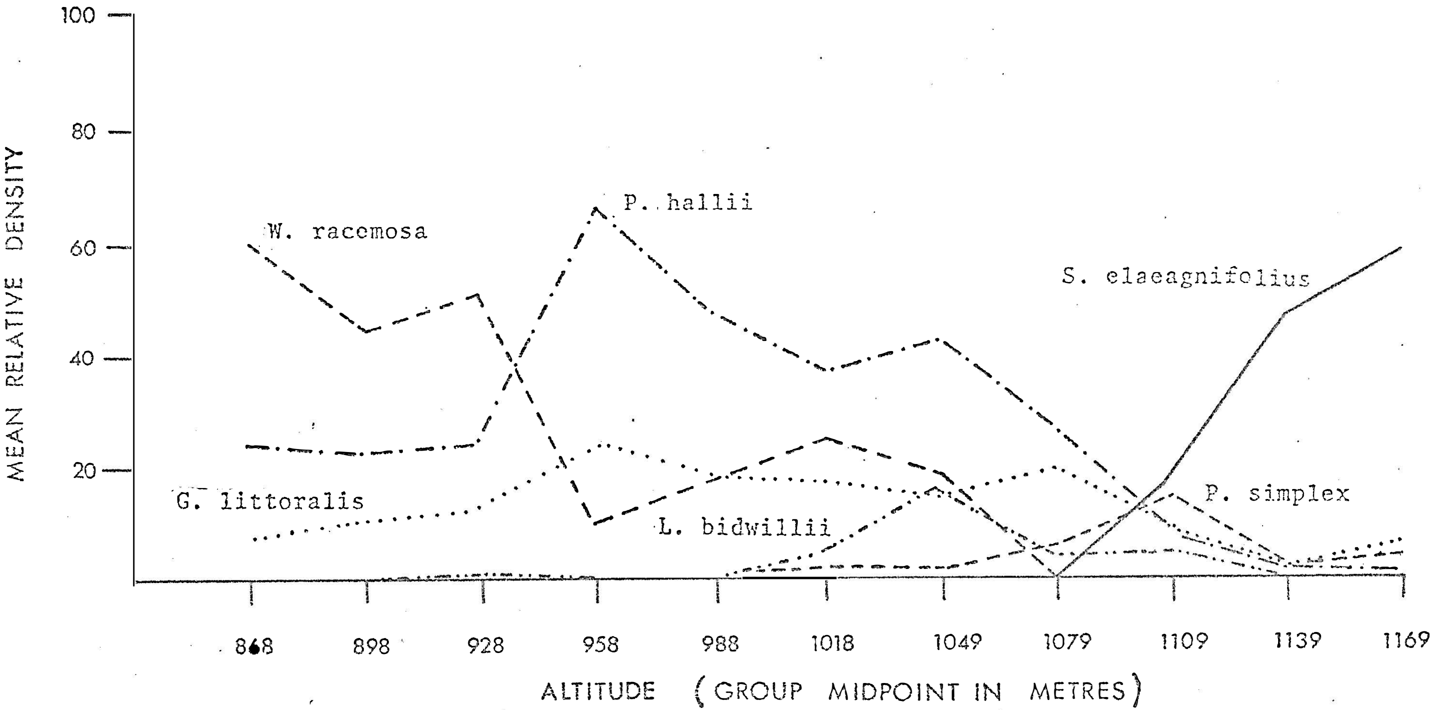
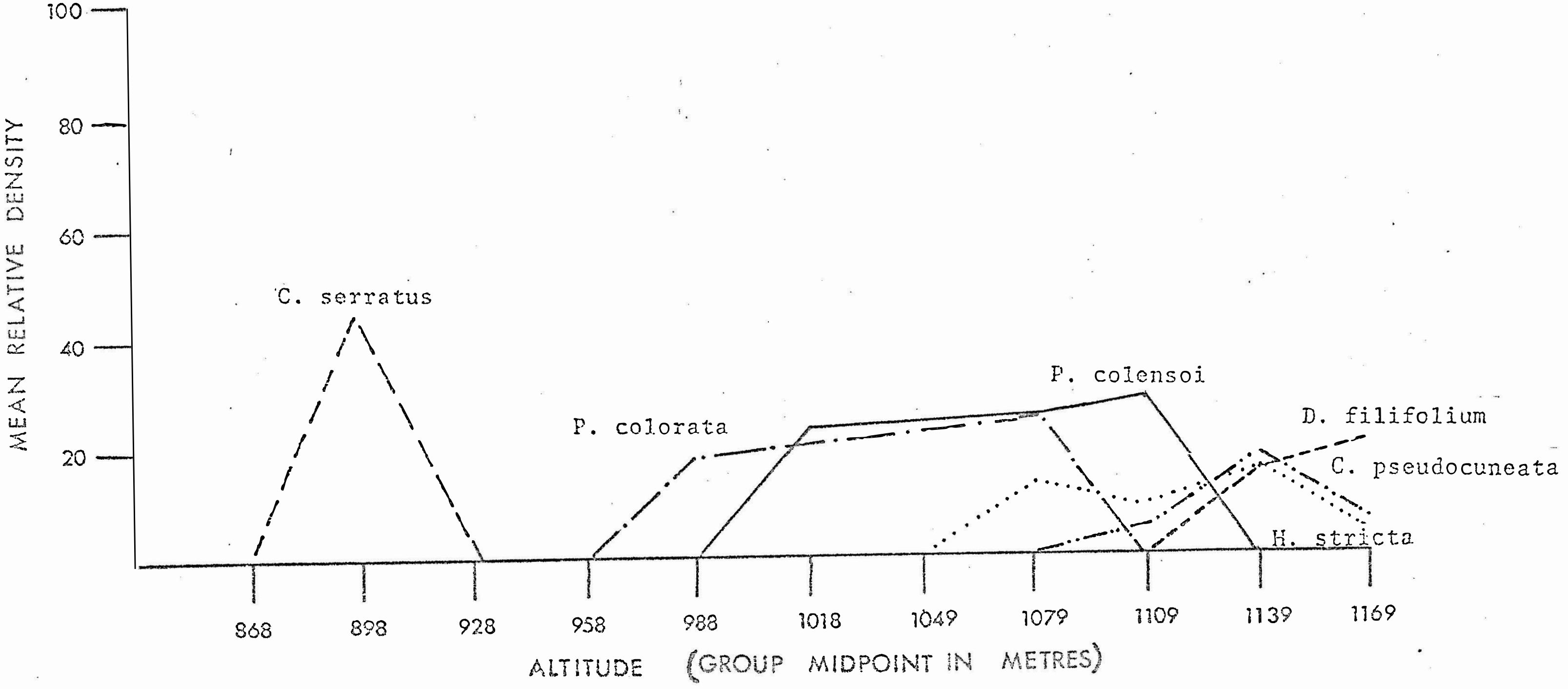


Figure 26

# TREE-SHRUB INTERFACE Grouped Data



Species represented in four or less of the data segments are shown on Fig. 26. C. serratus is an important component (22 percent relative density) of the canopy at 898m but rapidly decreases its representation to 1 percent by 928m. P. colorata and P. colensoi both form minor components of the canopy in the middle altitude further exceeding 15 percent relative density. D. filifolium, Coprosma sp. (unnamed), H. stricta, and C. pseudocuneata all form minor components of the canopy in upper altitudes where Senecio dominates. The distribution of C. pseudocuneata and D. filifolium in the canopy is exclusively in the Senecio dominated sites while H. stricta, and Coprosma sp. (unnamed) provide a degree of continuity to the tree-shrub interface extending down into the forest quadrats at 1,079m.

## Stratford Canopy Species distributions

A further comparison of the Tree-Shrub interface data is provided by data collected alongside the Stratford Plateau Road in 1972 (See Fig. 27) by the Massey University Extension Course in which the author took part. Data was collected using a point-cover sampling technique. The twelve sample locations ranged between 565m and 1,431m a.s.l. with an average altitudinal interval of 78m and a maximum interval of 152m. Two samples of fifty points each about twenty-five paces apart and located on a grid system following the cardinal compass points were collected at each altitude listed (See Table 12). The canopy species at each point was noted and the data thus recorded was converted to percentage point cover for each species encountered. The data provides an interesting comparison to that already described not only in terms of the species distributions described but also with regard to the sample size employed, the altitudinal interval

Table 12. Location and description of Stratford quadrat data.

| Altitude in Metres | Group Number Day 1 | Day 2 | | Study Location (="station") |
|---|---|---|---|---|
| 565.16 | 1 | 12 | 1. | 1,855ft on road. Work both sides of road. |
| 598.67 | 2 | 11 | 2. | 1,965ft on road (both sides). |
| 640.10 | 3 | 10 | 3. | 2,101ft on road (both sides). |
| 679.41 | 4 | 9 | 4. | 2,230ft on road (Cross Tepopo Stream on North side of road, track to swamp on South side. |
| 740.04 | 5 | 8 | 5. | 2,429ft both sides of road. |
| 802.80 | 6 | 7 | 6. | 2,635ft (road) to 2,775ft (Mountain House) Sampling area between road & Patea River below. Enchanted walk track. |
| 860.99 | 7 | 6 | 7. | 2,826ft Track from road to Patea River Cross second stream before starting sampling. |
| 931.37 | 8 | 5 | 8. | 3,057ft Between road and Moss's walk. |
| 1067.86 | 9 | 4 | 9. | 3,505ft Sample on South side of road. |
| 1139.15 | 10 | 3 | 10. | 3,739ft Plateau. Sample on track to Dawson Falls. |
| 1279.60 | 11 | 2 | 11. | Curtis ridge track. Near upper limit of sub-alpine scrub. |
| 1431.93 | 12 | 1 | 12. | Curtis ridge track - tussock grassland. |
| 990.17 | 13 | | | 3,250ft Near V.H.F. Station Tree-Shrub Interface |

1 - 12 Average Altitudinal Interval 78.79m

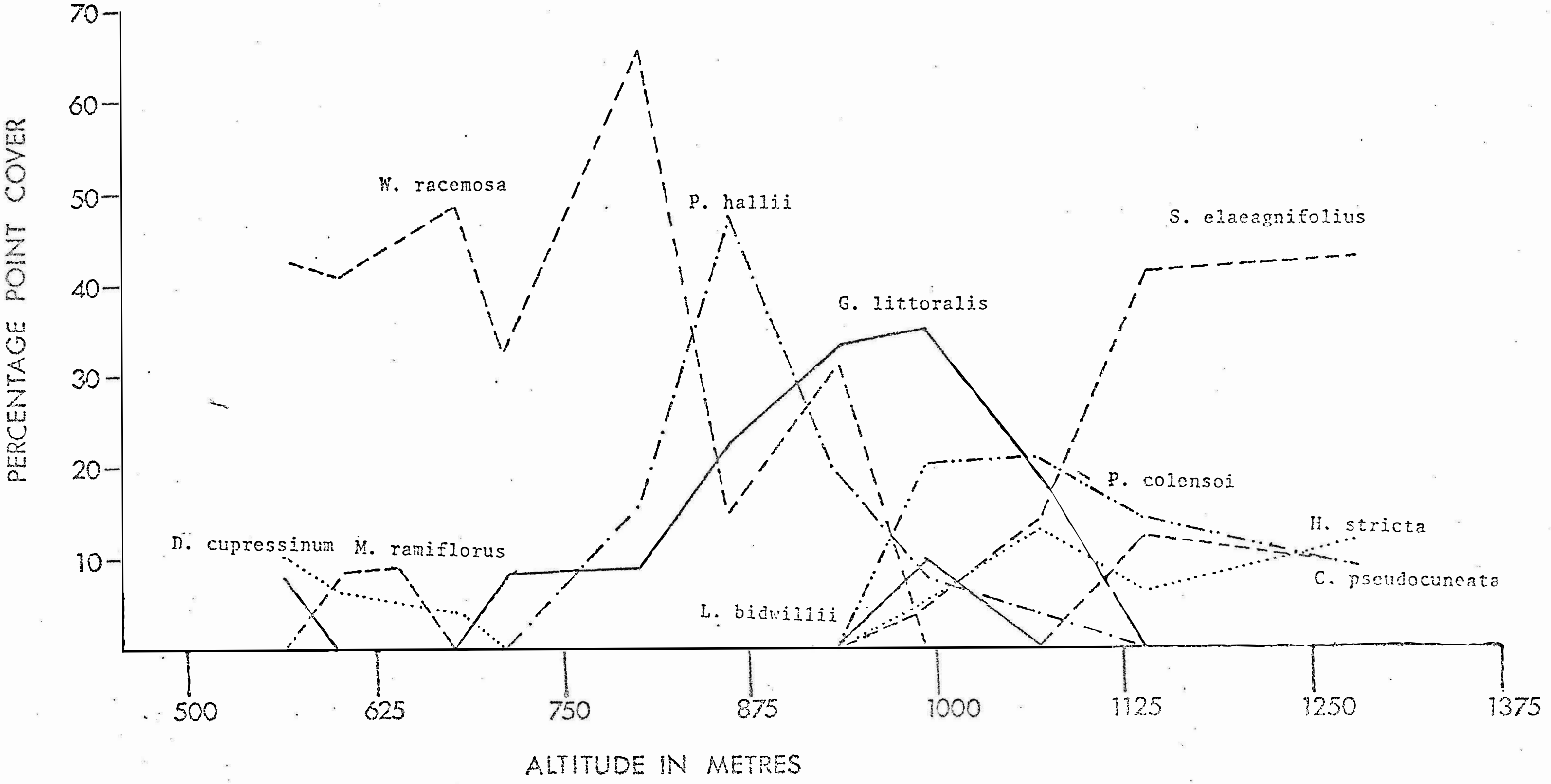
Maximum " " 152.33m

Detete 12 Include 13 : 64.95m

140.45m

Figure 27

STRATFORD Canopy Percentage Point Cover



employed, and their possible effects on data interpretation. The altitudinal interval employed proved inadequate in two locations: the first in the critical area of the tree-shrub interface at approximately 990m (3,250ft) where the major species distributions particularly P. hallii, G. littoralis, S. elaeagnifolius, and P. colensoi were unclear, and the second between 1,279m (4,200ft) and 1,431m (4,700ft) where the maximum altitudinal interval caused inadequate description of the species distributions at these altitudes. As a result of these inadequacies it was decided to omit the 1,431m (4,700ft) altitude sample and provide an additional sample in the critical area of the tree shrub interface at 990m (3,250ft). This data was collected on August 17th 1976 using the same sampling techniques as that employed in the 1972 data collection.

These changes reduced the average altitudinal interval between samples to 64m and the maximum altitudinal interval to 140m. The species distributions at the tree-shrub interface were clarified greatly and a further important canopy species recognised namely L. bidwillii which had previously been missed because of the wide altitudinal interval between samples. Overall, the larger sample area, greater sample heterogeneity, and the much wider spaced altitudinal interval resulted in a smoothing of the major species distributions. Species less common on the other hand tend to have tails or limits of their distributions missed by the much wider altitudinal interval. In spite of these overall differences in sampling method the species distributions depicted on Fig. 27 coincide well with those of the tree shrub interface data from the other ridges and also serve to illustrate the distribution of the major species below 760m which is not included in the other examples because of the minimal sample area constraint already described in Chapter 4.

Beginning at 565m *W. racemosa* is the clear dominant making up 42 percent point cover. *D. cupressinum* attains its maximum percentage point cover 10 at this altitude and declines in representation thereafter. *W. racemosa* continues to dominate up to 802m with its maximum representation 66 percent point cover occurring at this altitude. *M. ramiflorus* forms a minor component in the canopy at 598m and 640m with percentage point covers of 8 and 9 respectively. *P. hallii* first represented at 802m reaches its maximum representation of 47 percent point cover at 860m and then declines being recorded last in the canopy at 1,067m. *G. littoralis* first represented at 565m remains subordinate to W. *racemosa* and *P. hallii* until 931m where it becomes dominant. Its representation continues to increase to a maximum percentage point cover of 35 at 990m and then declines being recorded last in the canopy at 1,067m. *P. colensoi* and *L. bidwillii* form minor components of the canopy at 990m with percentage point covers of 20 and 10 respectively. *P. colensoi* reaches its maximum representation of 21 percent point cover at 1,067m where it is dominant. *G. littoralis* has declined to 18 percent point cover while *S. elaeagnifolius* continues to increase in importance at 14 percent point cover. By 1,139m *S. elaeagnifolius* is clearly dominant with a percentage point cover of 41. Its representation increases a little to 43 percent point cover at the final sample location included 1,431m. The distribution of *H. stricta* a relatively minor canopy component parallels that of *S. elaeagnifolius* being first recorded at 931m and reaching its maximum representation of 13 percent point cover at 1,297m. *C. pseudocuneata* is only represented in the two upper altitude samples with percentage point covers of 12 and 9 respectively.

The species distributions outlined for Stratford are similar in many respects to those described for the tree shrub interface at the four other locations. The distribution pattern of P. hallii in relation to that of G. littoralis resembles closely that of the Lake Dive Ridge Track with G. littoralis becoming dominant to P. hallii near the actual tree shrub interface and providing a degree of floristic continuity into the shrub dominated upper altitudinal samples. The distribution of P. colensoi is similar to that at both York Road and Dawson Falls in that it achieves maximum representation between the samples dominated by P. hallii at lower altitudes and S.elaeagnifolius at upper altitudes. Field observations point to the fact that the distribution pattern of L. bidwillii is not adequately described because of the discrete nature of its distribution pattern and the wide altitudinal interval employed in sampling. However, like both the Lake Dive and North Egmont locations L. bidwillii forms a minor component in the middle altitudes between the tree and shrub dominated samples. The distribution pattern for W. racemosa in particular its interaction with P. hallii and G. littoralis is complex in the 860m and 931m samples. A closer altitudinal sampling interval would probably clarify the fluctuations apparent in representation at these altitudes. The distribution depicted is probably the most similar to that of North Egmont where W. racemosa remains as an important component up to 1,038m as compared with 931m at the Stratford location.

Floristic discontinuity is apparent in that the major shrub species are all recorded first at the same sample and with approximately 200m the change to shrub species is complete. The wide altitudinal interval employed probably exaggerates this coincidence of species. A degree of floristic continuity is provided by the presence of P. hallii and G. littoralis in the shrub dominated samples and conversely by the beginnings of the shrub distributions in the G. littoralis dominated sample. Like all the other locations physiognomic discontinuity is apparent (although not formally recorded) particularly with regard to the change in growth form exhibited by G. littoralis already described for the four other locations.

The data recorded for the lower altitudes (565m -679m) clearly illustrates the relative importance of W. racemosa when compared to D. cupressinum on a cover basis. D. cupressinum is physiognomically dominant at these altitudes towering above the other trees at heights of up to 30m. A measure such as basal area or volume would probably show D. cupressinum as being more important than the maximum percent point cover of 10 apparent at 565m however in terms of percentage point cover this value is in close agreement with Druce's (1964) value for D. cupressinum of one eighth of the cover in altitudes between 550m - 750m on the Stratford side of Mt Egmont.

## Shrub-Tussock Interface

The shrub-tussock interface is another example of the presence of a discontinuity in canopy (top stratum) species composition, physiognomy, and structure. Data from two locations, the Razorback (North Egmont), and York Road Track Ridge is presented in Figs. 28 and 29. Quadrat data for slope angle, gradient, aspect, and altitudinal range is summarized on Table 13. Comparison of canopy species distributions in Figs. 28 and 29 reveals differences in species complement, rate of change in dominance from shrub species to tussock species with increase in altitude, the relative cover of species at comparable altitudes, and the interaction between species.

Canopy (top stratum) Species Distribution: Razorback.

The major canopy (top stratum) species represented at the Razorback location are S. elaeagnifolius, C. pseudocuneata, H. odora, D. filifolium, H. stricta, and C. vauvilliersii. At the two lower altitude quadrats 1,313m and 1,360m S. elaeagnifolius dominates with relative cover values of 66 and 55 percent respectively. By 1,390m Senecio is recorded as present only in the canopy that is less than 1 percent relative cover. The distribution of S. elaeagnifolius is paralleled by that of C. pseudocuneata and H. stricta both of which decline in importance from 1,313m to 1,340m. Field observations points to the fact that although last recorded at the 1,390m quadrat the actual upper altitudinal limit of C. pseudocuneata is some 20 metres above this between the upper quadrats. D. filifolium is distributed throughout the quadrats reaching its maximum representation 40 percent relative cover at 1,421m amongst the tussock. C. vauvilliersii is also distributed throughout the quadrats first as a minor component of the shrub canopy but reaching its peak representation of 29 percent relative cover at 1,390m and then declining rapidly. C. rubra is first recorded at 1,360m, becomes dominant by 1,390m, and achieves its maximum representation with a relative cover value of 45 percent at

Figure 28

SHRUB-TUSSOCK INTERFACE

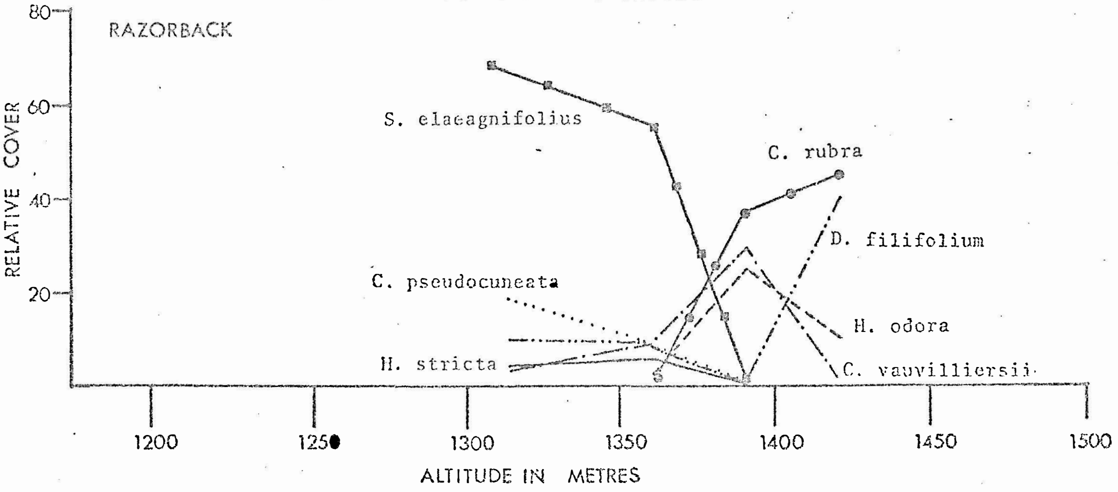
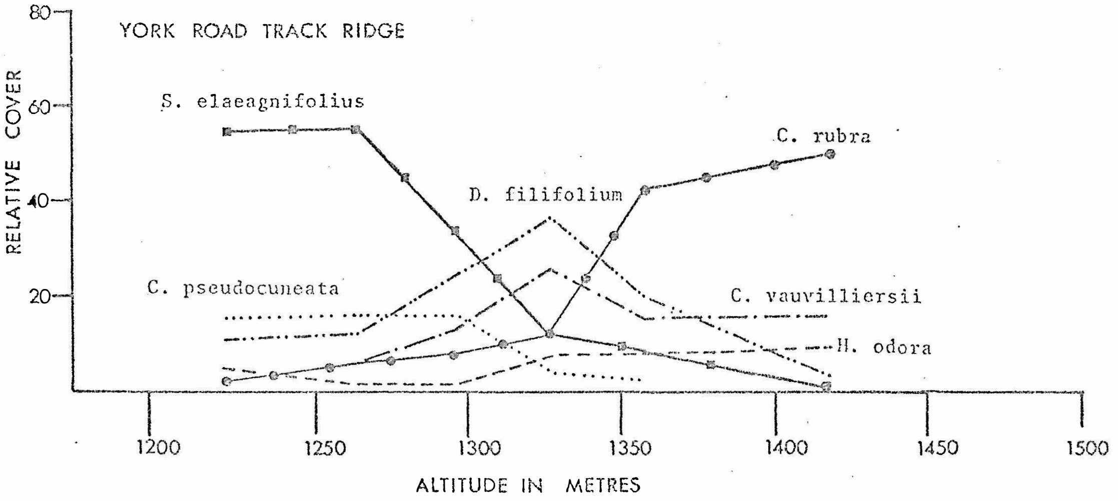


Figure 29



1,421m. H. odora parallels the Chionochloa distribution at first but reaches its maximum relative cover 25m lower at 1,390m and then declines in importance.

Canopy (top stratum) Species Distribution: York Road Track Ridge.

The major canopy species recorded at the York Road location were S. elaeagnifolius, C. pseudocuneata, C. vauvilliersii, H.odora, C. rubra, and P. laevis (see Fig. 29). S. elaeagnifolius dominates in the lower altitude quadrats with a maximum relative cover of 55 percent at 1,261m. From this altitude it declines in representation sharply at first but continues as a very minor component up to 1,416m. The distribution of C. pseudocuneata parallels that of S. elaeagnifolius however its maximum representation occurs higher at 1,294m and field observation showed the upper altitudinal limit to be some 20 metres above the last quadrat in which it was recorded. D. filifolium and C. vauvilliersii have similar distributions in that they both achieve maximum representation at 1,305m of 37 and 26 percent relative cover respectively. However, Cassinia is not recorded in the lowest altitude quadrat and is still an important canopy component (16 percent relative cover) in the upper altitude quadrat whereas Dracophyllum declines to only 3 percent relative cover. C. rubra represented throughout the quadrats rapidly increases in representation from 1,325m onwards and reaches its maximum relative cover of 50 percent at 1,416m. P. laevis is first represented at 1,294m achieving its maximum representation of 19 percent at 1,416m. H. odora is represented throughout the quadrats but achieves its highest relative cover values 7 and 9 percent in the tussock dominates quadrats at 1,355 and 1,416m.

The rate of change in dominance from shrub species to tussock can be measured as the rate of decrease of Senecio in relative cover per 30 metres altitude and the rate of increase of Chionochloa in relative cover per 30 metres altitude. At the Razorback location

(1,313-1,390m) S. elaeagnifolius declines in representation at the rate of 32 percent relative cover per 30m. Chionochloa increases in representation (1,360-1,421m) at the rate of 22 percent per 30m. In contrast the rate of decline in representation for S. elaeagnifolius (1,218-1,416m) at York Road is only 12 percent per 30m and the rate of increase in representation for C. rubra (1,218-1,416m) is only 11 percent per 30m. The rate of change at the Razorback location is much faster with an abrupt change from shrub dominance to tussock dominance while at the York Road location there is a more gradual replacement of shrub species by tussock.

In the tree-shrub interface comparisons the explanation of Beals (1969) was used in part to explain differences in rate of change or degree of discontinuity between locations. The notion of disjunctions occurring along the limited horizontal distance afforded by steep slopes along altitudinal gradients originally described by Beals (1969) in reference to comparative fieldwork carried out in Ethiopia seems highly applicable in this case as well. A comparison of the gradients and quadrat slope angles for the Razorback and York Road locations (see Table 13) clearly shows the major difference between the two ridges is one of gradient and quadrat slope. In the case of the Razorback location the overall gradient is 1:2.62 and the mean quadrat slope angle 26.66°. The overall gradient for the York Road location is 1:3.81 and the mean quadrat slope angle 12.00°. The difference in gradient is even more marked if only the four upper altitude York Road quadrats are considered because the overall gradient for these quadrats is approximately 1:5.00 and the increase in altitude from one quadrat to the next is almost constant. The tree-shrub interface comparison also pointed to the fact that aspect may influence the abruptness of change or degree of discontinuity at the interface. However, the ridge alignment for the Razorback is North East and that of York Road due East and the difference does not appear to be great enough to have influenced the pattern apparent.

A comparison of species interactions on the two ridges reveals that in many cases they are similar at the two locations. For example: C. pseudocuneata's distribution parallels that of S. elaeagnifolius at both locations and its upper altitudinal limit is higher than that of S. elaeagnifolius; and H. odora reaches its maximum representation amongst the tussock at both locations. There are exceptions however and they appear to relate to the differences in gradient and slope angle apparent between the two locations. At York Road D. filifolium and C. vauvilliersii achieve their peak representations between the Senecio dominated and Chionochloa dominated quadrats while at the Razorback both achieve their peak representation in the tussock dominated quadrats. The limited horizontal distance available on the steeper slopes of the Razorback seems to bring D. filifolium, C. vauvilliersii, and C. rubra into more direct competition.

As well there are differences in species complement between the two locations. Hebe stricta forms a minor component in the three lower Razorback quadrats but is represented only once in the lowest altitude quadrat at York Road. P. laevis is an important component in the tussock quadrats at York Road but was recorded in one of the Razorback quadrats only. In both instances these differences are not major ones as in the case of the tree-shrub interface comparison where some canopy species were entirely absent. These differences appear to relate more to the altitudinal range of the quadrats recorded and the fact that a given altitude at one location is not necessarily the environmental equivalent at another location. Thus probably only the lower limit of the P. laevis distribution at the Razorback was sampled.

The similarity index for adjacent quadrats was calculated according to the method of Beals (1969) and also serves to illustrate the degree of discontinuity apparent at the shrub tussock interface for both locations (see Table 13). The abruptness of change from shrub species dominance to tussock dominance at the Razorback location is emphasised by the low similarity index 0.20 between quadrats 8 and 9 located on the shrub-tussock interface.

Canopy (top stratum) Physiognomy and Structure.

The discontinuity apparent floristically at the shrub-tussock interface is further emphasised by an examination of species physiognomy and vegetation structure. At the Razorback location rapid floristic change from shrub to tussock quadrats is accompanied by a rapid change in maximum canopy height and total cover. The two shrub dominated quadrats exhibit the highest maximum canopy heights and the highest total cover values with values of up to 2.75m and 87 percent. The two tussock dominated quadrats exhibit the lowest maximum canopy heights and the lowest total cover values with values as low as 75cm and 42 percent. The discontinuity is not clear cut in terms of maximum canopy height and total cover in that the values for each quadrat are successively lower and no real clustering of shrub or tussock quadrat values is apparent. Further to this the use of maximum canopy height tends to give similar values for the interface quadrats in that inevitably the maximum canopy height is exhibited by shrub species. When the structure of the vegetation in the quadrats is examined however the discontinuity is marked. In the Razorback quadrats for example those dominated by shrub species tend to be composed of two major strata, the canopy (top stratum) up to 2.75m and the ground cover including seedlings of the canopy species. The canopy in fact occupies much of the 1.50 to 2.75m height class and is densely interwoven and compact. In contrast the quadrats above 1,370m are composed of less distinct strata in the sense that height classes or categorization into strata becomes more

Table 13. Shrub-Tussock Interface Quadrat Data

| | Altitude Feet | Altitude Metres | Slope Angle | (Ridge Alignment) Aspect | Adjacent Quadrat Similarity Index |
|---|---|---|---|---|---|
| | York Road | | | | |
| 1 | 4,000 | 1,218.66 | $7^{0}$ | East | |
| 2 | 4,410 | 1,261.32 | $15^{0}$ | | 1/2 0.88 |
| 3 | 4,250 | 1,294.83 | $7 - 10^{0}$ | | 2/3 0.83 |
| 4 | 4,350 | 1,325.30 | $7 - 10^{0}$ | | 3/4 0.65 |
| 5 | 4,450 | 1,355.76 | $7 - 12^{0}$ | | 4/5 0.66 |
| 6 | 4,650 | 1,416.70 | $10 - 12^{0}$ | | 5/6 0.72 |
| | | | $\bar{X}$ 12.00 | | |
| | Razorback | | | | |
| 7 | 4,310 | 1,313.11 | $25 - 30^{0}$ | North East | |
| 8 | 4,465 | 1,360.33 | $25 - 30^{0}$ | | 7/8 0.80 |
| 9 | 4,565 | 1,390.80 | $25 - 27^{0}$ | | 8/9 0.20 |
| 10 | 4,665 | 1,421.27 | $22 - 27^{0}$ | | 9/10 0.49 |
| | | | $\bar{X}$ $26.66^{0}$ | | |

arbitrary. The canopy stratum is a mix of both tussock and shrub species ranging between 20cm and 1.25m and forming a patchwork over the top of an ever increasing area of ground cover principally composed of herbfield species. The area taken up by ground cover exceeds 50 percent in most locations whereas in the quadrats exhibiting the tightly interwoven shrub canopy it rarely exceeds 25 percent cover.

At the York Road location the change is more gradual just as is the case floristically. Thus the maximum canopy height 1.50m is exhibited by the shrub dominated quadrats but it progressively declines until the lowest value 65cm is exhibited in the upper altitude tussock dominated quadrat. Similarly the total canopy cover declines gradually.

# York Road Track Ridge Quadrat Classification

## Classification versus Ordination.

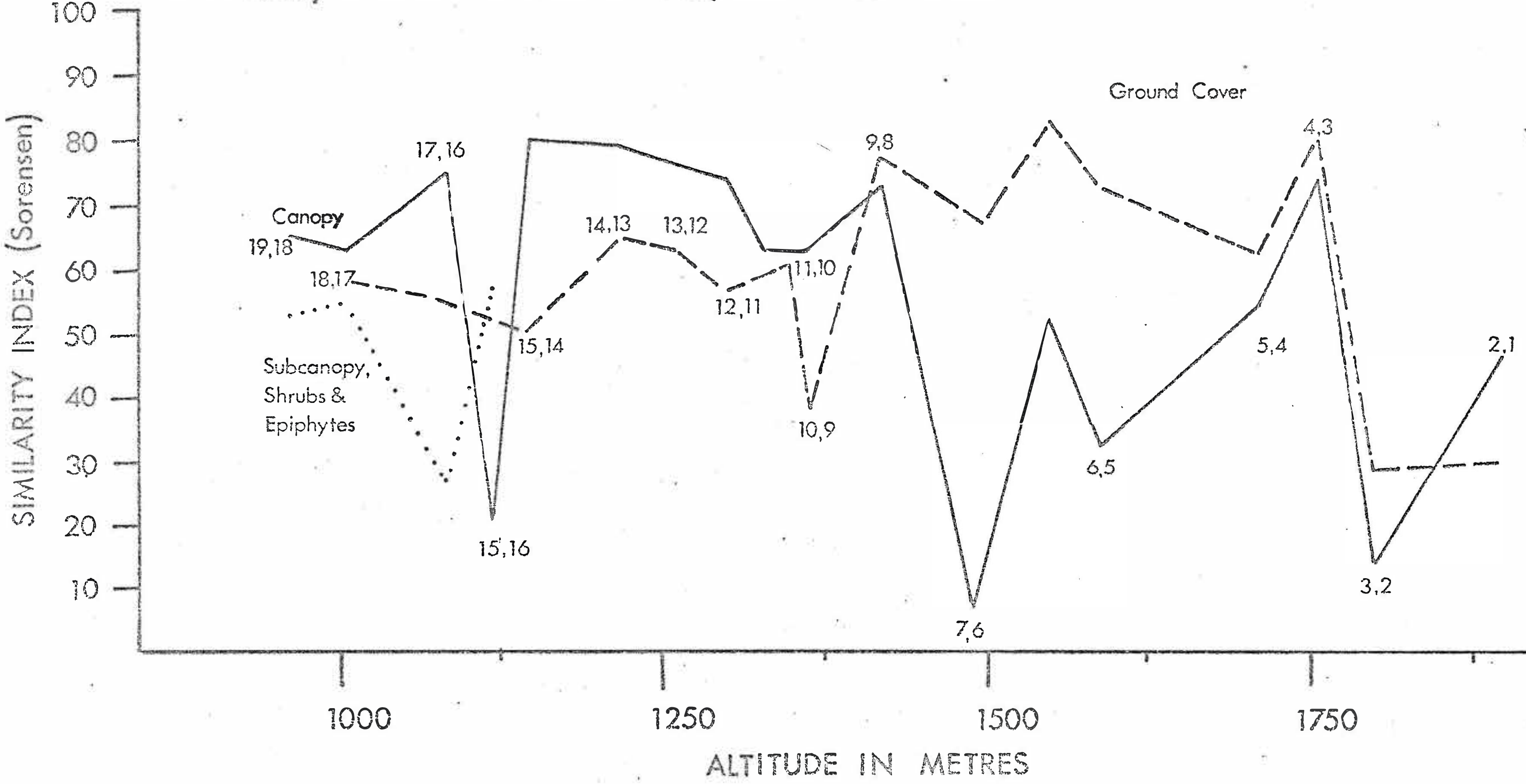
Opinions differ on the use of classification techniques as compared to ordination techniques. The differences relate directly back to the two traditional viewpoints concerning vegetation description and analysis described already in Chapter 2. Advocates of the association unity theory (discrete community types) have traditionally used classificatory techniques to describe and analyse "natural" vegetation groupings while supporters of the continuum concept (individualistic hypothesis) invariably used ordination techniques.Orloci (1975), following Goodall (1963), McIntosh (1967), Beals (1969) and Kellman (1975), has stressed that the strategy adopted in analysing vegetation data should not be a function of rigid assumptions held regarding the characteristics of vegetation distributions. "Ordination of vegetation data has often been mistakenly regarded as the antithesis of its classification. However, if the vegetation data matrix is visualized as an array with each species providing a separate dimension and sites represented by points fused according to these... it can be seen that the two procedures, although differing, are not antithetical. Each seeks orderly tendencies in the data, but of a different sort." Kellman, 1975, 67). On this basis ordination and classification techniques may be considered as different strategies suitable for analysing different kinds of vegetation data. It has been suggested further by Mueller-Dombois and Ellenberg (1974) that "the ordering or ordination of species and stands is a necessary step prior to any good floristic classification" (Mueller-Dombois & Ellenberg, 1974, 212) and by Beals (1963) "that continuum or gradient analysis can detect discontinuities in the vegetation, whereas a classificatory system cannot detect discontinuities". (Beals, 1963, 985). Thus in contradiction to many of the earlier vegetation analyses employing either classificatory or ordination techniques there is a good case for using both these techniques in conjunction with each other, in particular preceding a classification with an ordination to detect the continuous or discontinuous nature of the vegetation data.

The approach of this study is that advocated by Orloci (1975) in that analysis has been approached without a prior commitment to one or another of the broad vegetation hypotheses. Following on from this inspection of the raw data, the similarity matrices (Appendices 5, 6 and 7), and graphing of similarity indices between adjacent quadrats by the method employed by Beals (1963) revealed marked discontinuities or clustering of the quadrat data (see Fig. 30). For the quantitative canopy species data the major discontinuities ( 40 percent similarity index) are evident between quadrats 15 and 16, quadrats 7 and 8, quadrats 5 and 6 and quadrats 2 and 3. These discontinuities have already been described in part in the tree-shrub and shrub-tussock interface results but essentially they coincide with the change from forest to shrub species in the first case, a marked drop in <u>Chionochloa</u> dominance in the second case, a change from moss and herbfield species to <u>Chionochloa</u> and associates in the third case and a substrate effect in the final case. For the qualitative ground cover data the discontinuities are not as marked but are still apparent. The major discontinuities ( 40 percent similarity index) occur between quadrats 9 and 10 and quadrats 2 and 3. In the case of quadrats 9 and 10 there is marked change as the <u>Blechnum-Astelia</u> ground cover gives way to <u>C. rubra</u> and herbfield species, and in the second example, quadrats 2 and 3, the substrate change already noted. The qualitative subcanopy, shrub and epiphyte data shows a marked discontinuity between quadrats 16 and 17 which is related to species diversity and a change from <u>P. hallii</u> to <u>P. colorata</u> in the shrub and subcanopy strata. It must be emphasised that the

Figure 30

## YORK ROAD TRACK RIDGE

Similarity Indices between Adjacent Quadrats



discontinuity exhibited by this graphing of similarity indices does not show the complete extent of discontinuity or clustering of the data. The similarity matrix for quantitative canopy data (Appendix 4) is probably the most extreme example in which clusters of similar quadrats bounded by indices of zero (no species in common) are apparent by simple observation.

## The Choice of a Similarity Index.

The specific similarity indices used in this study are:

1. Sorensen's (1948) similarity index for qualitative comparison (presence of species)

   $IS_s = \frac{2c}{a+b} \times 100$ where c = the number of species common to two quadrats; a = the total number of species in quadrat a, and b = the total number of species in quadrat b.

2. The Bray-Curtis (1957) quantitative modification of Sorensen's (1948) similarity index based on relative values (importance value)

   $IS_{BC} = \frac{\leq MW}{200} \times 100$ where $\leq MW$ is the sum of the smaller quantitative values of species common to both stands.

Mueller-Dombois and Ellenberg (1974) and Whittaker (1973) both discuss the advantages and disadvantages of the various similarity indices. "However, one cannot conclude automatically that one similarity index is superior to another. The value of an index depends on the properties that one intends to emphasise. It is important, however, that one is aware of the diagnostic capacity of a given index." (Mueller-Dombois & Ellenberg, 1974, 222). For the present study it was considered important that the canopy at least should be compared on a quantitative basis to give a more complete description of quadrat similarity, that is not only in terms of species presence but also the amount of each species present. The fact that the data collected for ground cover, subcanopy, shrubs and epiphytes emphasised species presence made the qualitative similarity index more suitable. Ease of calculation and the widespread use of Sorensen's similarity index thus enabling greater comparability of results were considered advantages in favour of this choice of similarity index.

## The Choice of a Classification Technique.

The specific classification technique used in the present study is the average linkage clustering technique of Sokal and Michener (1958) described by both Mueller-Dombois & Ellenberg (1974) and Orloci (1975). It is polythetic (based on the presence of many common characters (species)), agglomerative (groups are formed on the basis of fusions), and hierarchical (small groups are further combined according to their similarities into broader groups). The advantages and disadvantages of the various classification techniques are described by Sokal & Sneath (1963), Everitt (1974), and Orloci (1975). In summary, for the present study it was considered important that the classification was polythetic, that is groupings were distinguished on the basis of as many species as possible (30 in the canopy classification), thus making the classification more sensitive and hierarchical in order to give an indication of overall quadrat similarities at successively lower similarity levels.

Finally it is noted that the choice of either an ordination or a classification technique for analysis necessarily channels the emphasis of the analysis towards either a discrete community interpretation or a continuum interpretation so that the natural discontinuity evident in the data may be further emphasised by the classification strategy adopted.

## Canopy Quantitative Classification.

A classification of the 20 canopy samples for the York Road Track Ridge is summarised on Figure 31 a dendrogram resulting from the average linkage clustering procedure of Sokal and Michener (1958) and described by Mueller-Dombois and Ellenberg (1974) (see Appendix 5). The discontinuities in the data are further emphasised by the resulting classification and at the 50 percent level of similarity

Figure 31

CANOPY QUANTITATIVE CLASSIFICATION

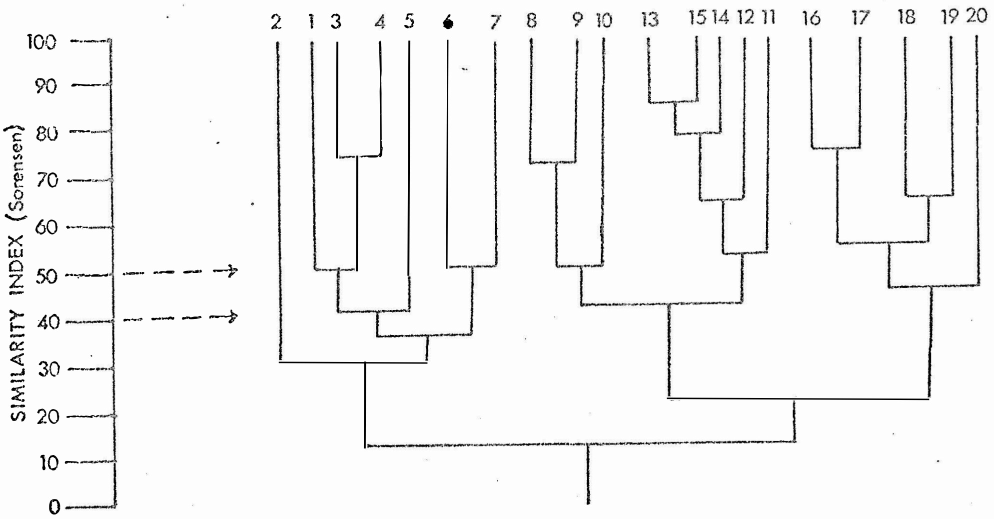


Figure 32 YORK ROAD TRACK RIDGE

G.R.632655 G.R.632711

Canopy Quantitative Similarity Level 50%

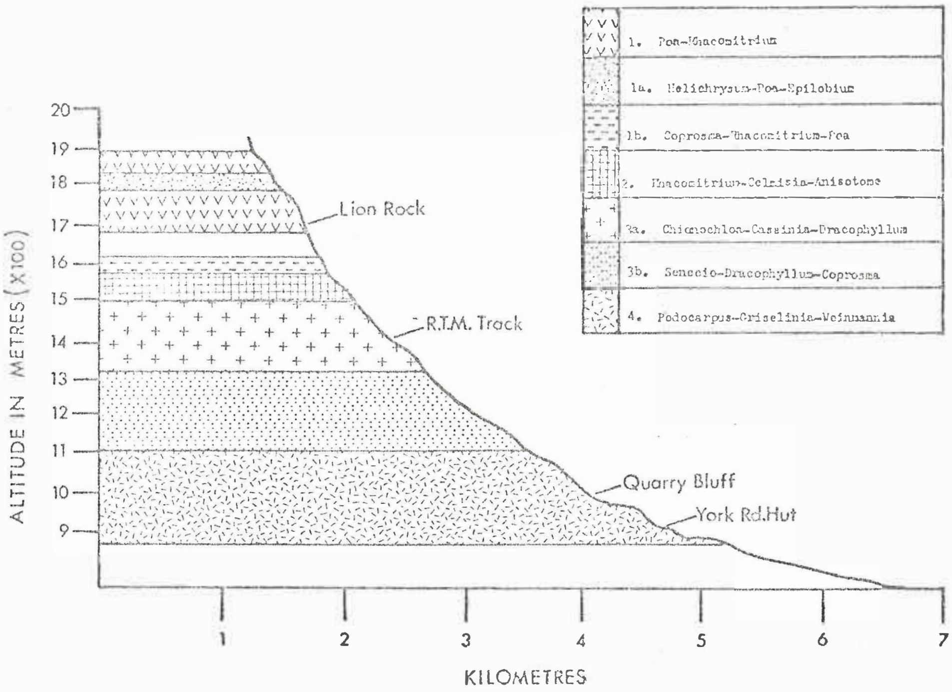


Figure 33 YORK ROAD TRACK RIDGE

G.R.632655 G.R.632711

Canopy Quantitative Similarity Level 40%

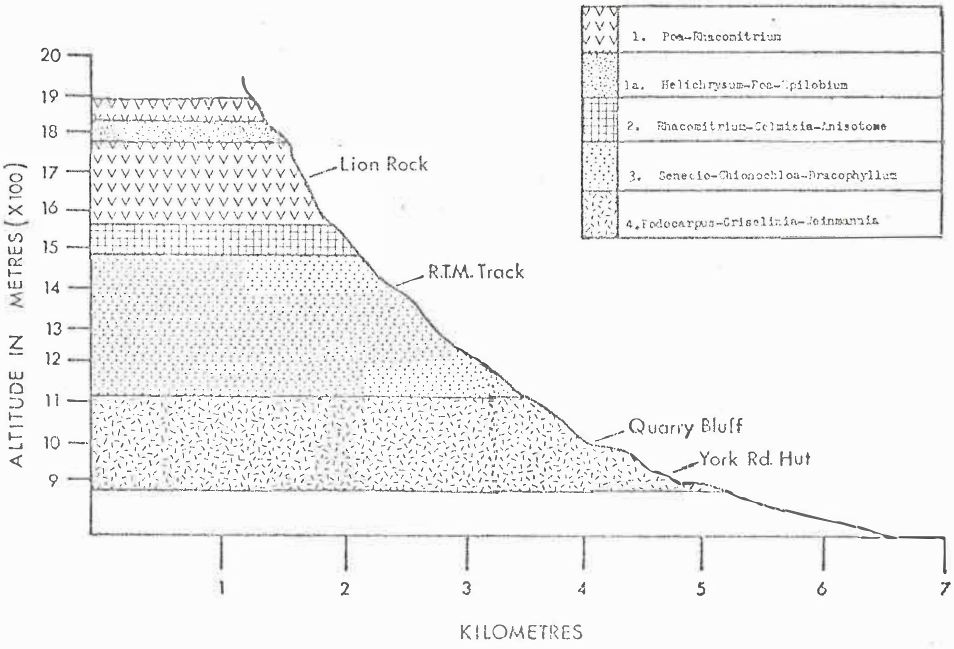


Table 14. York Road Track Ridge Canopy Quantitative Classification
Similarity Level 50 percent

Quadrat Groups, Dominant Species, Mean Importance Value, and Mean Altitude

| | Species | Mean I.V. | Mean Altitude |
|---|---|---|---|
| Group 1<br>Quadrats 1,3,4 | Poa colensoi | 80.78 | 1,770.66m |
| | Rhacomitrium spp. | 29.96 | |
| | Fostera bidwillii var. densifolia | 17.68 | |
| Group 1a<br>Quadrat 2 | Helichrysum sp. | 147.60 | 1,797m |
| | Poa colensoi | 28.56 | |
| | Epilobium sp. | 19.04 | |
| Group 1b<br>Quadrat 5 | Coprosma pumila | 64.48 | 1,584m |
| | Rhacomitrium spp. | 53.68 | |
| | Poa colensoi | 14.34 | |
| Group 2<br>Quadrats 6,7 | Rhacomitrium spp. | 21.35 | 1,518m |
| | Celmisia glandulosa | 13.42 | |
| | Anisotome aromatica | 13.53 | |
| Group 3a<br>Quadrats 8,9,10 | Chionochloa rubra | 70.13 | 1,365.33m |
| | Cassinia vauvilliersii | 38.69 | |
| | Dracophyllum filifolium | 40.76 | |
| Group 3b<br>Quadrats 11,12, 13,14,15 | Senecio elaeagnifolius | 83.04 | 1,207.20m |
| | Dracophyllum filifolium | 24.82 | |
| | Coprosma pseudocuneata | 29.91 | |
| Group 4<br>Quadrats 16,17, 18,19 | Podocarpus hallii | 64.56 | 985.50m |
| | Griselinia littoralis | 51.86 | |
| | Weinmannia racemosa* in 18,19 only! | 30.72 | |
| Group 4a<br>Quadrat 20 | Podocarpus hallii | 114.45 | 959m |
| | P. colorata | 59.95 | |
| | Coprosma sp. (unnamed) | 12.15 | |

Table 15. York Road Track Ridge Canopy Quantitative Classification
Similarity Level 40 percent

Quadrat Groups, Dominant Species, Mean Importance Value, and Mean Altitude

| | Species | Mean I.V. | Mean Altitude |
|---|---|---|---|
| Group 1<br>Quadrats 1,3,4,5 | Poa colensoi<br>Rhacomitrium sp. | 47.56<br>41.82 | 1,677.33 |
| Group 1a<br>Quadrat 2 | SAME AS | LEVEL 50% | |
| Group 2<br>Quadrats 6,7 | SAME AS | LEVEL 50% | |
| Group 3<br>Quadrats 8,9,10,11,<br>12.13.14.15 | Senecio elaeagnifolius<br>Chionochloa rubra<br>D. filifolium | 40.38<br>31.31<br>30.80 | 1,286.26m |
| Group 4<br>Quadrats 16,17,18,<br>19,<br>20 Regeneration Sample | SAME AS | LEVEL 50% | |

indicated on the dendrogram (Figure 31) several major groupings or fusions of the quadrats are apparent. Quadrats 1, 3, and 4 have fused to form a group, while quadrats 2 and 5 remain separate. Quadrats 6 and 7 have fused to form another group and the largest grouping apparent is formed by the fusion of quadrats 11, 12, 13, 14, and 15. Quadrats 16, 17, 18 and 19 fuse to form a single group at 55 percent similarity while quadrat 20 remains separate. Inspection of the dendrogram at 40 percent similarity shows only five remaining groups as opposed to seven at 50 percent similarity. The groups apparent are formed by the fusion of quadrats 1, 3, 4, 5, quadrats 6 and 7, quadrats 8-15, quadrats 16-20, while quadrat 2 remains separate. At 30 percent similarity only three groupings are apparent, quadrats 1-7, quadrats 8-15, and quadrats 16-20. By the 20 percent similarity level only two groups remain, quadrats 1-7 and quadrats 8-20. All the quadrats are fused to form a single group at 13 percent similarity. This classification is ecologically meaningful in the sense that in a theoretical situation where altitude was the prime gradient and discontinuities were apparent in the data it would be expected that quadrats adjacent or near to each other would exhibit greater similarity in their quantitative vegetation composition. As the distance between quadrats increased similarity would decrease. This is certainly the case for the York Road Track Ridge data with only minor exceptions at the 50 percent level of similarity. The classification also provides a more objective basis for recognising community types, zones, or associations than intuitive categorization or observation. Once chosen a similarity level is used systematically to give the groupings recognised titles on the basis of the three quantitatively dominant species. Altitudinal limits and the mean altitude for the groupings recognised at similarity level 50 percent appear on Figure 32 and Table 14. The groupings recognised at similarity level 40 percent appear on Figure 33 and Table 15.

Ground Cover Qualitative Classification.

A classification resulting from a comparison of the ground cover quadrats 1 to 19 on the basis of floristic similarity (see Appendix 6) is summarized on the dendrogram Figure 34 and Figures 35 and 36 which indicate the altitudinal boundaries of the classification. The dendrogram was constructed using the average linkage clustering of Sokal and Michener (1958) and the similarity index used was Sorensen's qualitative similarity index which has already been described.

At the 50 percent level of similarity six groups are apparent: the first consisting of quadrat 2 by itself; the second consisting of quadrats 1, 3 and 4; the third consisting of quadrats 5-9; the fourth of quadrats 10 and 11; the fifth of quadrats 12-14; and the sixth of quadrats 15-19.

The 40 percent level of similarity has only four groupings: quadrat 2 remains separate; quadrats 1 and 3-9 fuse to form the second group; quadrats 10-14 fuse to form the third group; and quadrats 15-19 remain as the fourth group.

The important species in each of the groupings identified at the 50 and 40 percent levels of similarity are summarised in Tables 16 and 17. Important species in this case means species common to all the quadrats fused into a single grouping. As well the dominant species in quantitative terms (relative cover) are listed for further comparison and the mean altitude for the quadrats in the groupings.

Inspection at 20 percent similarity reveals only two groupings, the first formed by the fusing of quadrats 1-9 and the second by the fusing of quadrats 10-19. Finally at 4 percent similarity all the quadrats fuse to form a single group.

Like the classification obtained for the canopy (top stratum) species the prime gradient reflected is that of altitude with quadrats

Figure 34
GROUND COVER QUALITATIVE CLASSIFICATION

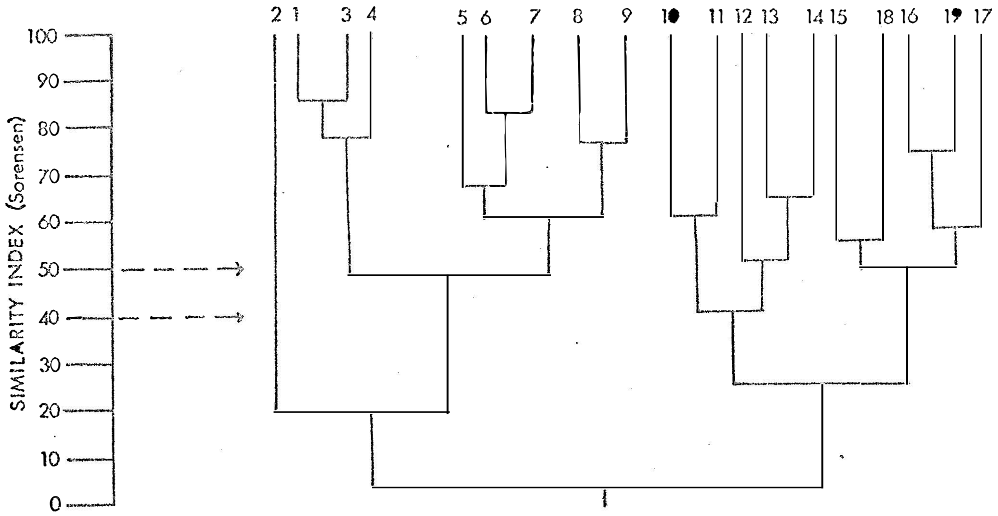


Figure 35 YORK ROAD TRACK RIDGE

G.R.632655 G.R.632711

Ground Cover Qualitative Similarity Level 50%

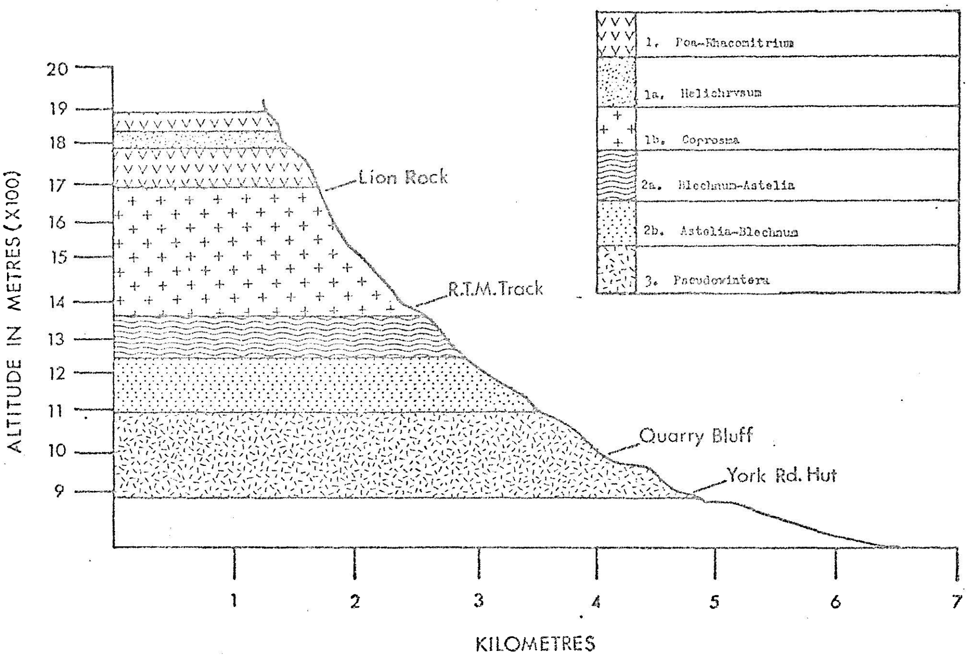
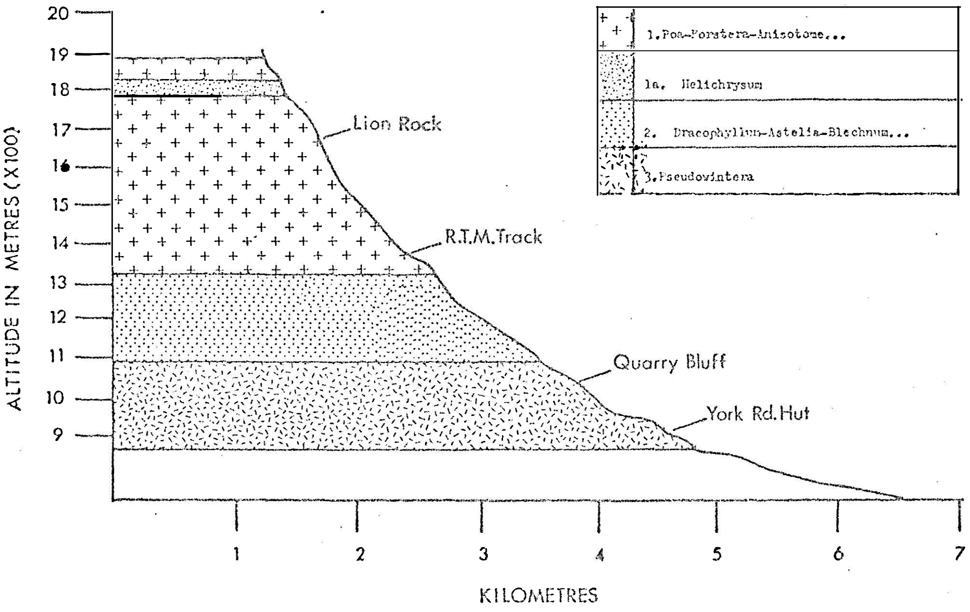


Figure 36 YORK ROAD TRACK RIDGE

G.R.632655 G.R.632711

Ground Cover Qualitative Similarity Level 40%



adjacent or near to each other in terms of elevation grouping together first. Further to this the classification obtained in part parallels that of the canopy species. This is obviously the case for the higher altitude quadrats in which the ground cover and canopy (top stratum) categories are one and the same but for the middle and lower altitude quadrats there are several explanations. Group 1b, composed of quadrats 5-9 does not coincide well with the four separate groupings apparent in the quantitative canopy (top stratum) classification, however the difference is one of a qualitative versus a quantitative classification because in fact the same species are being recorded in different ways. The remainder of the groupings obtained at lower altitudes are ecologically meaningful in the sense that they parallel approximately the groupings obtained in the canopy (top stratum) classification and there appear to be good reasons for this. The *Podocarpus-Griselinia-Weinmannia* canopy grouping identified between 897m and 1,087m has its equivalent in the ground cover stratum between 897m and 1,145m in which important species include *A. nervosa, P. colorata, B. fluviatile, Cardamine sp., Uncinia spp.,* and *P. vestitum.* Although not common to all quadrats most quadrats exhibit a range of the canopy species seedlings in the ground cover and this in part could account for the similarity of the groupings identified. Further to this it is possible that the canopy influences ground cover composition because it imposes in part the environmental conditions under which the ground cover species must live. Thus it would be expected that the *Podocarpus-Griselinia-Weinmannia* canopy would affect ground cover composition differently to the *Senecio-Dracophyllum-Coprosma* canopy and the ground cover composition would to some extent parallel that of the canopy. The *Senecio-Dracophyllum-Coprosma* canopy grouping identified between 1,100m and 1,325m has its equivalent in the ground cover stratum between 1,100m and 1,250m in which important ground cover species include

D. filifolium, G. littoralis, Coprosma sp.(unnamed), A. nervosa, B. capense, and Uncinia sp. The presence of seedlings of the canopy species in the ground cover stratum particularly D. filifolium and Coprosma spp. appears in part to account for the coincidence of the groupings identified in each of the classifications. The different conditions imposed on the ground cover stratum by the Senecio-Dracophyllum-Coprosma canopy may also contribute to this coincidence of groupings.

In summary the groupings identified at the level 50 percent similarity for the ground cover stratum are:

1. Group 1 consisting of quadrats 1,3, and 4 an upper altitude grouping of P. colensoi, Rhacomitrium spp. and a range of smaller herb species. Dominant species are Poa colensoi and Rhacomitrium spp.
2. Group 1a consisting of quadrat 2 an upper altitude group in which the special conditions of substrate and moisture availability apparent on a scree blow-out give rise to a different species composition. The dominant species is Helichrysum sp.(unnamed).
3. Group 1b consisting of quadrats 5 to 9 an upper to middle altitude group of C. pumila, P. colensoi, a range of smaller herb species, and the two Celmisias. The dominant species is C. pumila.
4. Group 2a consisting of quadrats 10 and 11 a middle altitude group composed of some of the herb species characteristic of higher altitudes, a range of shrub seedlings, and several larger ground cover species including Ourisia macrophylla, Coprosma depressa, Astelia nervosa and Blechnum capense. Blechnum capense is the dominant species.
5. Group 2b consisting of quadrats 12 to 14 a middle altitude group composed to a greater extent of shrub seedlings and the large ground cover species A. nervosa and B. capense. Astelia sp.

(unnamed) is the dominant species.

6. Group 3 consisting of quadrats 15 to 19 a lower altitude group with a greater range of ferns in the ground cover and the dominant species being P. colorata.

Subcanopy, Shrubs and Epiphytes Qualitative Classification.

A classification resulting from a similarity matrix (see Appendix 7) comparing quadrats 15-20 on the basis of species present (floristic similarity) in the categories subcanopy, shrubs and epiphytes is summarised on the dendrogram (Figure 37). The dendrogram was constructed using the average linkage clustering method of Sokal and Michener (1958) and the similarity index used was Sorensen's qualitative similarity index which has already been described.

At the 50 percent level of similarity four groups are apparent; the first consisting of quadrats 15 and 16, the second consisting of quadrats 17 and 18, the third the single quadrat 19, and the fourth the single quadrat 20. Inspection at the 40 percent level of similarity reveals only two groupings; the first of quadrats 15 and 16 as before, and the second resulting from the fusion of quadrats 17-20. The important species in each of the groupings identified and the total number of species recorded in the groups is summarised in Tables 18 and 19 and enables clarification and explanation of the resulting classification.

Important species in this case means those species present in all the quadrats fused to form a single group. Thus in Group 1, formed by the fusing of quadrats 15 and 16 at 50 percent similarity, three subcanopy species P. hallii, P. colorata, and C. australis are found in both quadrats. It is the number of species common to both quadrats which determines the degree of similarity between them. Inspection of the raw data, the summarised data, and the resulting classification at level 50 percent similarity and level 40 percent similarity reveals a discontinuity in the distribution of the subcanopy, shrub

Table 16. York Road Track Ridge Ground Cover Qualitative Classification
Similarity Level 50 percent

Quadrat Groups, Species Present, Dominant Species and Mean Altitude

| | Species in Common | Dominant Species ( 25% Relative Cover) | Mean Altitude |
|---|---|---|---|
| Group 1<br>Quadrats 1,3,4 | Poa colensoi<br>Rhacomitrium spp.<br>Anisotome aromatic<br>Forstera bidwillii<br>Gaultheria sp.unnamed<br>Drapetes dieffenbachii<br>Colobanthus sp.<br>Celmisia gracilenta var. | Poa colensoi<br>Rhacomitrium spp. | 1,770.66m |
| Group 1a<br>Quadrat 2 | Helichrysum sp. unnamed<br>Poa colensoi<br>Epilobium sp.<br>Montia sp. | Helichrysum sp.unnamed | 1,797m |
| Group 1b<br>Quadrats 5,6, 7,8,9 | Poa colensoi<br>Luzula sp.<br>Anistome aromatica<br>Forstera bidwilli<br>Gaultheria sp.unnamed<br>Celmisia gracilenta var.<br>Coprosma pumila<br>Celmisia glandulosa | Coprosma pumila | |
| Group 2a<br>Quadrats 10,11 | Anisotome aromatica<br>Gaultheria depressa<br>Celmisia gracilenta var.<br>Ourisia macrophylla<br>Uncinia sp.<br>Coprosma depressa<br>Dracophyllum filifolium<br>Myrsine divaricata<br>Astelia sp.unnamed<br>Blechnum capense<br>Muehlenbeckia australis | Blechnum capense<br>Astelia sp.unnamed | |
| Group 2b | Dracophyllum filifolium<br>Griselinia littoralis<br>Coprosma sp.unnamed<br>Astelia sp.unnamed<br>Blechnum capense | Astelia sp.unnamed<br>Blechnum capense | |
| Group 3<br>Quadrats 15,16 17,18 plus 19 regeneration. | Uncinia sp.<br>Astelia sp.unnamed<br>Polystichum vestitum<br>Blechnum fluviatile<br>Cardamine sp.<br>Pseudowintera colorata | Pseudowintera colorata | |

Table 17. York Road Track Ridge Ground Cover Quantitative Classification

Similarity Level 40 percent

| Quadrat Groups | Species in Common |
|---|---|
| Group 1<br>Quadrats 1,3,4<br>5,6,7,8, 9, | Poa colensoi<br>Forstera sp.<br>Anisotome aromatica<br>Gaultheria sp.unnamed<br>Celmisia gracilenta var. |
| Group 1a<br>Quadrat 2 | As above |
| Group 2<br>Quadrats 10,11,<br>12,13,14 | Drachophyllum filifolium<br>Astelia sp.unnamed<br>Blechnum capense<br>Unicinia sp. |
| Group 3 | As above |

Figure 37
SUBCANOPY, SHRUBS & EPIPHYTES

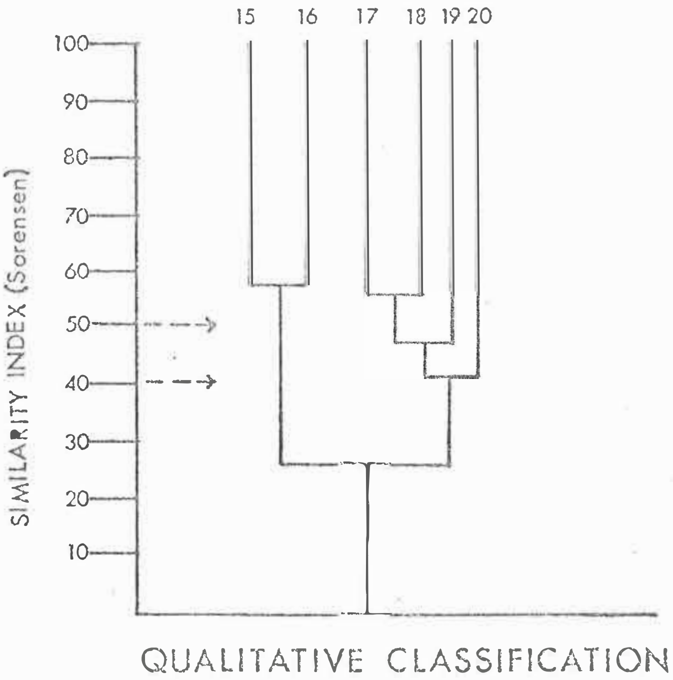
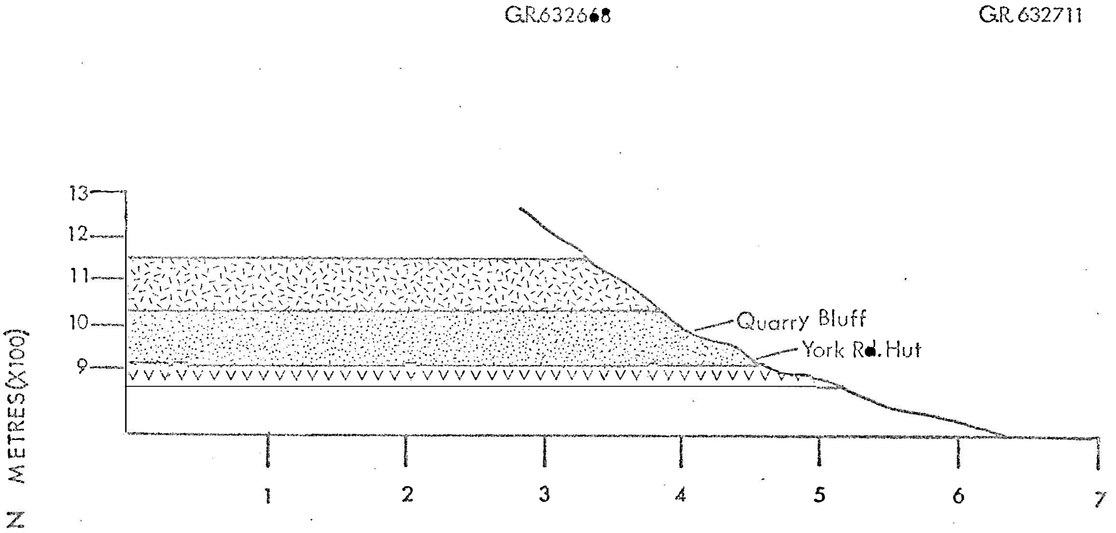


Figure 38

# YORK ROAD TRACK RIDGE

## Subcanopy, Shrubs & Epiphytes Qualitative

Similarity Level 50%



Similarity Level 40%

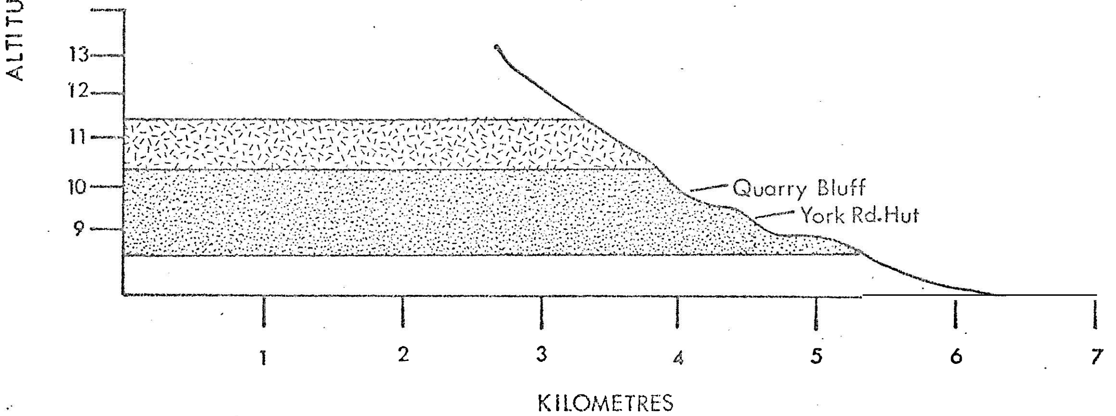


Figure 39

| Similarity Level 50% | | |
|---|---|---|
| ▨ | 1. | P.hallii, P.colorata, C.australis, Hymenophyllum sp., Grammitis sp. |
| ░ | 2a. | P.colorata, C.tenuifolia, M.divaricata, P.simplex, Coprosma sp., Hymenophyllum sp., A.flaccidum, Rubus sp. |
| V V | 2b. | P.colorata, C.tenuifolia, C.serratus, C.smithii, Hymenophyllum sp., A.flaccidum, Rubus sp., Clematis sp., M.diversifolium. |
| **Similarity Level 40%** | | |
| ▨ | 1. | P.hallii, P.colorata, C.australis, Hymenophyllum sp., Grammitis sp. |
| ░ | 2. | P.colorata, C.tenuifolia, Hymenophyllum sp., A.flaccidum, Rubus sp. |

and epiphyte species. The separation of quadrats 15 and 16 from quadrats 17-20 at level 40 percent similarity appears to be related to species diversity and the absence of a shrub layer in the former quadrats. The higher altitude quadrats 15 and 16 at 1143m and 1176m respectively exhibit many fewer species in the categories defined and in fact no shrub stratum could be distinguished in either. The discontinuity then is primarily one of number of species present with the lower altitude quadrats exhibiting a much greater range of species particularly in the epiphyte category. This discontinuity is further emphasised by the fact that P. hallii is an important component in the subcanopy of quadrats 15 and 16 but in quadrats 17-20 P. colorata is dominant. The altitudinal distributions of the quadrat groups recognised at 50 percent and 40 percent similarity levels are depicted on Figures 38 and 39.

The comparison of the canopy and ground cover classifications already described revealed similarities in the quadrat groupings identified and their altitudinal limits. This does not appear to be the case for this classification in that the groupings revealed at the 50 percent level of similarity between quadrats 16 and 17 and between quadrats 18 and 19 do not coincide with the groupings obtained in the other two classifications. Inspection of Figure 30 depicting the similarity indices for adjacent quadrats also supports the observation that the discontinuities evident in each vegetation stratum do not coincide. Thus although a degree of similarity is present when all of the classifications for the York Road Track Ridge are compared the groupings obtained in any given vegetation stratum do not necessarily apply to the other vegetation strata.

Table 18. York Road Track Ridge Subcanopy, Shrubs and Epiphytes
Qualitative Classification
Similarity Level 50 percent

Quadrat Groups, Total Number of Species, Important Species

| | Total No. Species | Important Species Subcanopy | Shrubs | Epiphytes |
|---|---|---|---|---|
| Group 1.<br>Quadrats 15,16 | 5 | P. hallii<br>P. colorata<br>C. australis | -<br>- | Hymenophyllum sp.<br>Grammitis sp. |
| Group 2.<br>Quadrats 17,18 | 26 | P. colorata<br>C. tenuifolia<br>M. divaricata<br>P. simplex | P. colorata<br>C. tenuifolia<br>Coprosma sp. (unnamed) | Hymenophyllum sp.<br>A. flaccidum<br>Rubus sp. |
| Group 3.<br>Quadrat 19 | 27 | P. colorata<br>C. tenuifolia<br>C. serratus | P. colorata<br>C. tenuifolia | Hymenophyllum sp.<br>A. flaccidum<br>Rubus sp.<br>Clematis sp.<br>M. diversifolium |
| Group 4. | 7 | P. colorata | P. colorata<br>C. tenuifolia | Hymenophyllum sp.<br>A. flaccidum<br>Rubus sp. |

Table 19. York Road Track Ridge Subcanopy, Shrubs and Epiphytes
Qualitative Classification
Similarity Level 40 percent

Quadrat Groups, Total Number of Species, Important Species

| | Total No. Species | Subcanopy | Important Species<br>Shrubs | <br>Epiphytes |
|---|---|---|---|---|
| Group 1.<br>Quadrats 15 & 16 | | Same as Similarity Level 50 percent | | |
| Group 2.<br>Quadrats 17-20 | 40 | P. colorata | P. colorata<br>C. tenuifolia | Hymenophyllum sp.<br>A. flaccidum<br>Rubus sp. |

## Chapter 7

## DISCUSSION

Just as the purpose of this study was twofold, so it logically follows that the conclusions fall into two main categories. Firstly the description and analysis of the vegetation of Mt Egmont must be compared directly with the research already described in Chapter 1 in order to confirm or refute the accepted notions of vegetation distribution and zonation on Mt. Egmont Secondly, and perhaps more importantly, the results and analysis of this study must be compared with those of other direct gradient analyses both within New Zealand and overseas. This will be attempted on two levels. At one level a comparison with regard to the more descriptive aspects, for example species composition, vegetation pattern and distribution, the "tree-line"and species altitudinal limits, the conclusions reached in each case with regard to the continuum and discrete community (association) hypothesis. At another level the direct gradient analyses will be compared on a theoretical basis, that is in terms of the methods of data collection, location of the study, and methods of data manipulation in order to determine whether or not the conclusions obtained in each study are comparable and whether or not they relate in any way to these theoretical considerations.

Finally an attempt will be made to amalgamate the contributions of this study with regard to the description of the vegetation of Mt Egmont, the description of other direct gradient analyses and their theoretical considerations, and to propose a tentative resolution of the continuum-discrete community controversy in terms of which of Whittakers (1970) hypotheses (listed in the introduction) appear tenable for the Mt Egmont vegetation data.

All of the research literature on Mt. Egmont's vegetation supports the view that the vegetation occurs in distinct zones or community types although in some instances (Schweinfurth (1962), Cockayne (1927) , and Druce (1964)) this belief is qualified by reference to transition zones or continuous variation from one vegetation type to another. Druce (1964) emphasises the continuity of the vegetation more than any of the other workers. The results and analysis of the present study support the view that distinct vegetation zones do occur, that is natural groupings of species sharing similar altitudinal distributions and distinct from other such groups. The boundaries of these vegetation zones are defined floristically, physiognomically, and structurally by discontinuities in the vegetation, in particular those occurring at the tree-shrub interface. However other discontinuities, for example the upper-lower altitude forest interface, are just as great, floristically at least. This study differs from others described in that the vegetation zones recognised and their altitudinal limits have a quantitative and objective basis. The vegetation zones recognised in this study are of equal relative status (they contain sites with at least 50 percent quantitative similarity) and they have been delimited according to an objective procedure in the sense that although a similarity level is chosen arbitrarily, once chosen it has been used throughout enabling direct comparisons to be made of data from different sites and with any future data collected. In The research work reviewed the zonation pattern delimited is based more on observation and n intuitive categorisation of the vegetation (except Druce (1964) who gives several **quantitative** values).

The quantitative classification provided by the present study for the York Road Track Ridge and the interface analyses generally support the zonation patterns described by previous workers in terms of species dominance but with minor differences in the altitudinal limits. There are however several important conflicting points of comparison. One major difference is the number of zones delimited for comparable areas and this probably results from the use of quantitative methods in that the zones identified in this study satisfy the criteria of equal status (equal internal homogeneity). Thus where Cockayne (1928), Mason (1951), Wilson (1961) and Druce (1964) simply list zones such as Herbfield or Fellfield, the quantitative classification recognises several categories which belong within the general title Herbfield or Fellfield and yet which have equal status with zones at lower altitudes. The inclusion of L. bidwillii by Mason (1951) and Wilson (1961) in the sub-antarctic and cold temperate zones respectively appears to be an overgeneralisation, particularly with reference to the tree-shrub interface data which clearly shows that the Libocedrus distribution is too scattered and complex to be grouped into such a zonation pattern. Libocedrus appears to distribute both as part of the upper altitude forest canopy in locations such as Lake Dive, Stratford and North Egmont, but also into the actual tree-shrub interface canopy at North Egmont. It is absent in the York Road Track Ridge canopy and poorly represented in the Dawson Falls canopy. Thus Cockayne's (1928) approach of describing actual associations from within a generalized zone, for example Stratford Mountain House in which Libocedrus forms a part, appears to be more realistic than including Libocedrus in a generalized zone. Unless this approach is adopted Libocedrus is grouped with species such as W. racemosa with which it very rarely associates. Schweinfurth's (1962, 7) note, confirmed by J. Hennessey, that Libocedrus is absent from the mountain forest above Dawson Falls is incorrect. A comparison of the quantitative values reported by Druce (1964) for the Stratford side of Mt. Egmont shows a good deal of agreement with a *Weinmannia* maximum value of 67 percentage point cover at 2,635 ft (802.80m) compared to Druce's 66 percent cover at 2,750 ft (837.83m). The *Senecio* maximum value of 45 percentage point cover at 4,200 ft (1279.60m) is low compared to Druce's 66 percent cover at 4,000 ft (1218.66m). Druce's point about *Weinmannia* and the other smaller trees making up the majority of cover in the lower altitude forest with *Dacrydium* forming only a small proportion of the cover (one eighth along with *Metrosideros*) is also well supported with *Weinmannia* alone achieving 50 percentage point cover at 2,100 ft (639.80m) in comparison to the 5 percentage point cover of *Dacrydium*. The obvious interrelationship between *P. hallii* and *G. littoralis* in the upper altitude forest is not mentioned in any of the literature reviewed and deserves more detailed investigation. In the majority of locations described *G. littoralis* appears to begin life as an epiphyte on *P. hallii*, eventually growing up into the canopy.

A most important difference in interpretation between this study and others, is the recognition that while there is obvious vegetation discontinuity, it is clear cut at some locations and less apparent at others. The tree-shrub interface data best illustrate this. The Lake Dive tree-shrub interface represents the extreme of discontinuity in which the vegetation zones are well defined with change from one zone to another occurring within an increase of 30m altitude. The York Road shrub-tussock interface represents the extreme of continuity, so that if the 40 percent level of similarity is accepted as the delimiting value for vegetation zones then the shrub and tussock dominated quadrats together may be considered as a single floristic vegetation zone. Druce (1964) claimed that the progression of species dominance through altitude gives the vegetation a large measure of continuity without any sudden changes. This is not supported at locations like Lake Dive and Razorback where change of dominants and subdominants is rapid. It is this interaction of dominant and subdominant species, and the rate of change in vegetation composition, which is critical in such an interpretation. If the dominant and subdominant species show a deal of coincidence in altitudinal limits (at the disjunction), and change from one dominant to another is rapid, there is little vegetation continuity. If, however, as is the case at the York Road shrub-tussock interface, the change from one dominant to another is gradual, and the degree of overlap in species distributions of both dominant and subdominants is much greater, there is a large measure of vegetation continuity. This continuity or discontinuity may be physiognomic and structural as well as floristic and in this respect Schweinfurth (1962) is perhaps the only previous worker to stress the point sufficiently. In addition, depending on whether the zonation pattern employed is floristically based only or physiognomically, floristically, and structurally based, the zones recognised may be different, for as noted previously, in the tree-shrub interface G. littoralis gives a degree of floristic continuity but changes in growth form.

All the previous literature discusses zonation on Egmont mainly in terms of the canopy stratum, although Cockayne (1928) and Druce (1964) do provide some species lists of the other vegetation strata. The implication is that a zonation pattern based on the canopy stratum holds for the other vegetation strata. This is not the case however according to the comparison of the classifications provided for the Canopy, Sub-canopy, Shrubs and Epiphytes and Ground Cover at York Road. In that location, if a given similarity level is accepted for all vegetation categories, the zones identified are not identical in terms of altitudinal limits or extent. They are similar for ground cover and canopy but very different for the other vegetation categories. Thus it does not necessarily follow that discontinuities in other vegetation strata will coincide with the canopy enabling a zonation scheme to emcompass the total vegetation pattern.

To summarise, the description and analysis of this vegetation data collected at various locations on Mt. Egmont permits a refinement of the accepted notions of vegetation zonation. This is based on quantitative data, floristic, physiognomic and structural, and this is not subject to the errors of judgment that may arise through observation of the vegetation pattern alone. The vegetation of Mt. Egmont for the most part exhibits discontinuities. These are critical points along the altitudinal gradient at which major changes, floristic, physiognomic, and structural, take place. This tendency towards discontinuity enables a classificatory strategy to be followed and vegetation zones or community types delimited at specific similarity levels giving dominant species and altitudinal limits. The zonation pattern thus obtained supports the accepted notions of zonation although altitudinal limits, dominant species, and the number of zones delimited varies to some extent. The data suggests that it is more realistic to recognise that the degree of discontinuity varies from ridge to ridge, as does species complement, and that the tendency towards zonation is therefore more clear cut at some locations than others. In view of this and the variation in species complement, extending a zonation pattern further than two or so very similar ridges causes such overgeneralization that the vegetation pattern thus described can only be superficial. Furthermore the complexity of the zonation pattern is increased when other vegetation categories, that is sub-canopy, shrubs, ground cover, are considered, for the zonation pattern delineated for one stratum does not necessarily hold for others. The variation of species complement and relative species composition amongst the five locations on Mt. Egmont examined appears to result from the past history of disturbance (including volcanic activity and animal effects), differences in slope and aspect, general climatic and substrate differences, and the probabilistic element of species distribution. The fact that quantitative species composition has been determined for sites which can be accurately located presents possibilities of future application of the data to remote sensing techniques and subsequent large scale vegetation mapping.

Schweinfurth's (1962) comment that Egmont should be considered in terms of the major variations in vegetation pattern latitudinally has already been noted in Chapter 2. The results of the present study may be compared with those of the other direct gradient analyses from New Zealand and overseas cited in Chapter 3. Fig.3, a location map of the New Zealand gradient analyses, gives the approximate latitude of each of the study locations ranging from Mt. Anglem $46^{o}43'$S to Mt. Egmont $39^{o}17'$S, a difference of some $7^{o}$ latitude. The "tree-line" has always been considered as a prime indicator of the different environmental conditions prevailing at any given location although its definition is often not clear cut. Using the definition already employed in this study, that is the altitude at which a change in growth form from the predominantly tree-like growth habit to the shrub growth habit occurs, the differences in tree-line for the relevant studies are summarised in Table 20 and Figure 40.

This data illustrates the generally accepted trend of the tree-line occurring at lower altitudes the higher the latitude. Thus at Mt. Anglem the tree-line occurs at only 640m while on Mt. Egmont at approximately 1,100m. The quantitative data on species composition collected in this study enables not only a simple comparison of tree-line,but rather an overall comparison of the performance of major canopy species common to the locations reviewed. (See Figure 41). The fact that Egmont lacks a number of species has already been mentioned in Chapter 2. The most notable absence is that of Nothofagus. In all the New Zealand

Figure 40

N.Z. GRADIENT ANALYSES Comparison of Tree-line

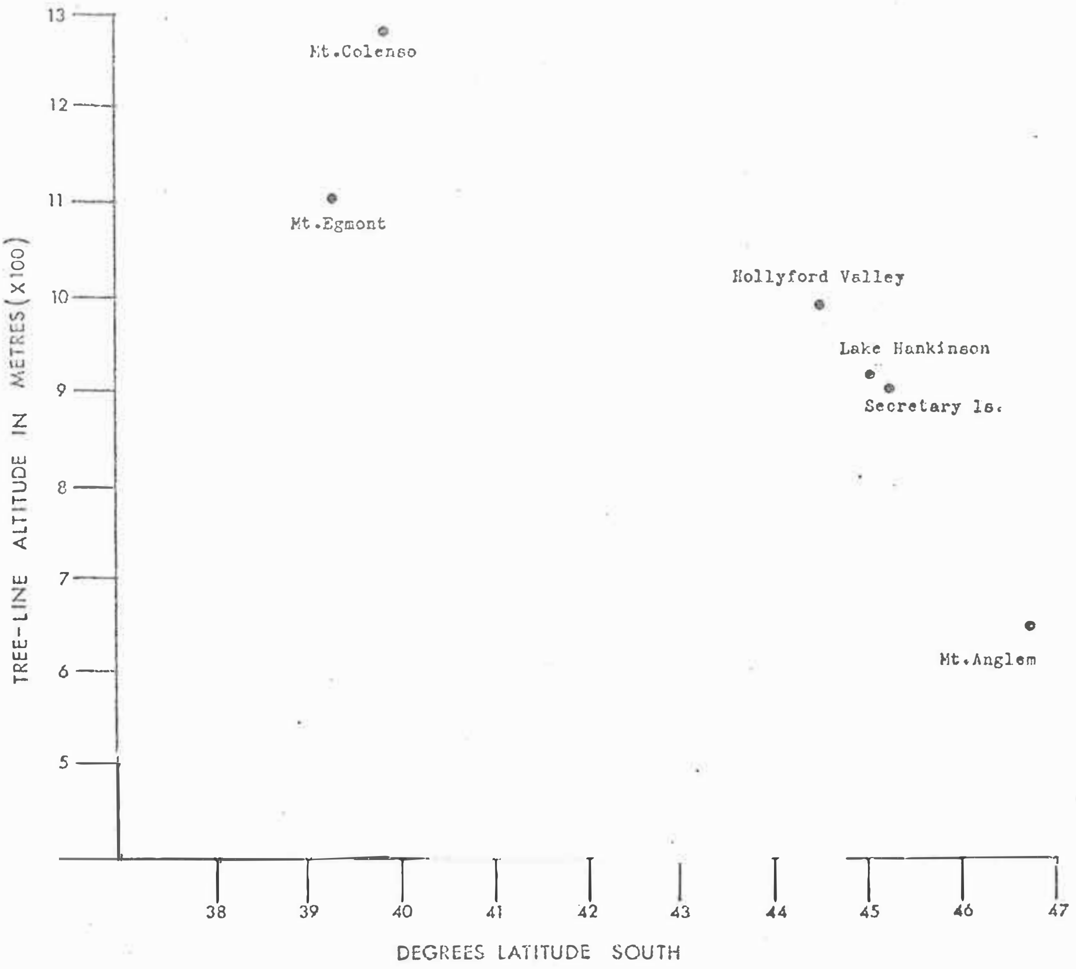


TABLE 20

New Zealand Gradient Analyses: Comparison of Tree Line.

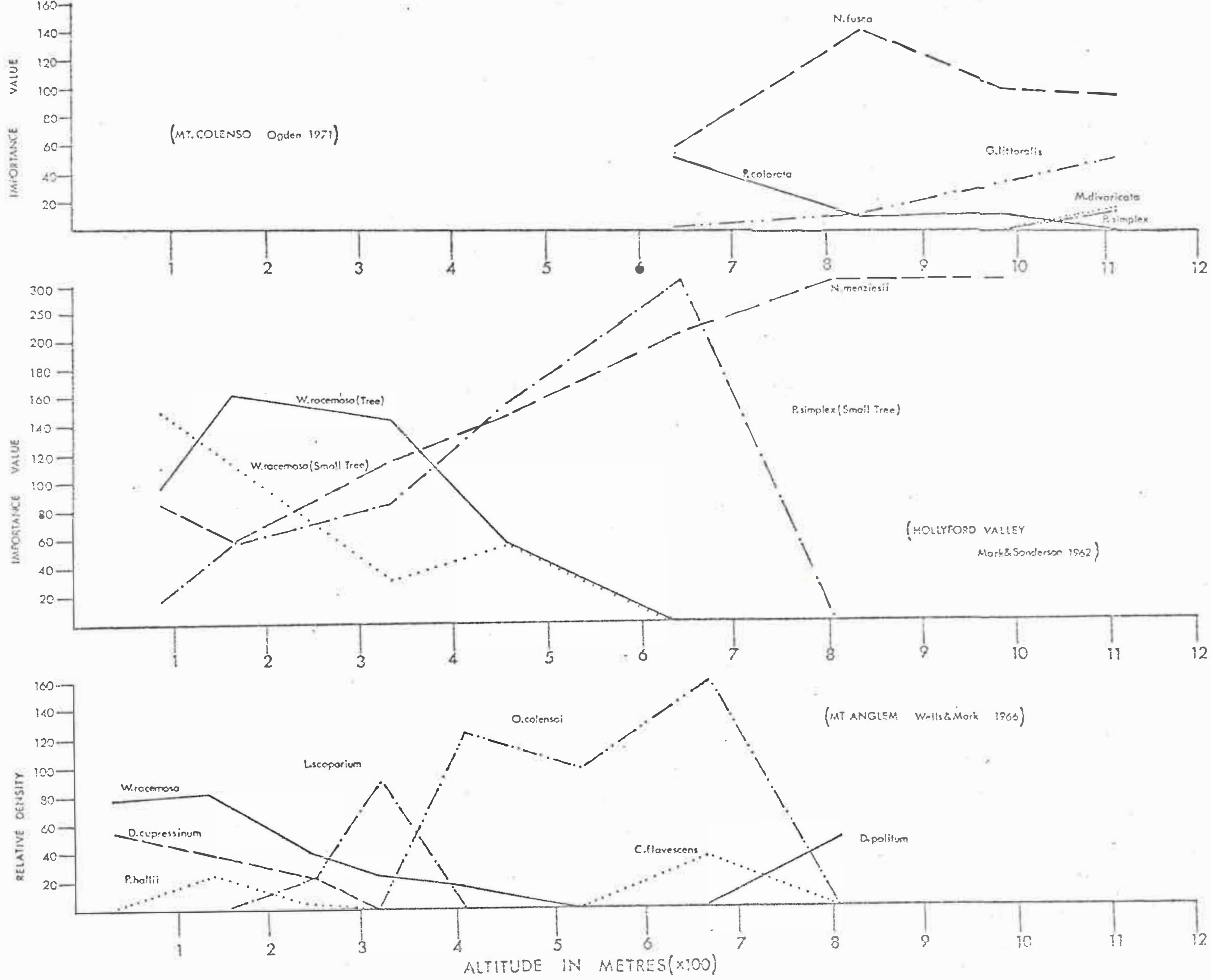
| Location | Latitude | Altitude Metres | Altitude Feet |
|---|---|---|---|
| Mt. Egmont | 39°17'S | 1,100 | 3,600 |
| Mt. Colenso | 39°44'S | 1,279 | 4,200 |
| Hollyford Valley | 44°30'S | 990 | 3,250 |
| Lake Hankinson | 45° 2'S | 914 | 3,000 |
| Secretary Island | 45°15'S | 898 | 2,950 |
| Mt. Anglem | 46°43'S | 640 | 2.100 |

gradient analyses reviewed except Mt. Anglem, Nothofagus species are an important component of the vegetation. This enables close examination of the performance and interaction of important canopy species such as G. littoralis, W. racemosa, L. bidwillii, and P. hallii in the absence of Nothofagus. It also enables a quantitative comparison of the tussock, herbfield, and fellfield communities which on Egmont are also lacking in a range of the so called "mountain" species. The absence of Nothofagus on Mt. Egmont appears to have major effects on the relative importance of other species throughout the lower part of the altitudinal gradient and on altitude of the tree-line. In the studies reviewed, where Nothofagus is present it tends to dominate and reduces other species such as G. littoralis and P. hallii to minor components of the canopy only.

On Mt. Colenso for example (Ogden, 1971), G. littoralis consistently remains subordinate to N. fusca reaching a maximum importance value (Relative Frequency plus Relative Basal Area) of 53 at 3,650 ft (1,112m) the highest altitude at which it was quantitatively recorded. Its altitudinal distribution is therefore similar to that on Mt. Egmont and it provides a degree of floristic continuity from the Nothofagus dominated Stand 3 (3,250 ft 990m) to Stand 4 (3,650 ft 1,112m) in which shrub species are beginning to be

Figure 41

SELECTED N.Z. GRADIENT ANALYSES Major Species Altitudinal Distributions



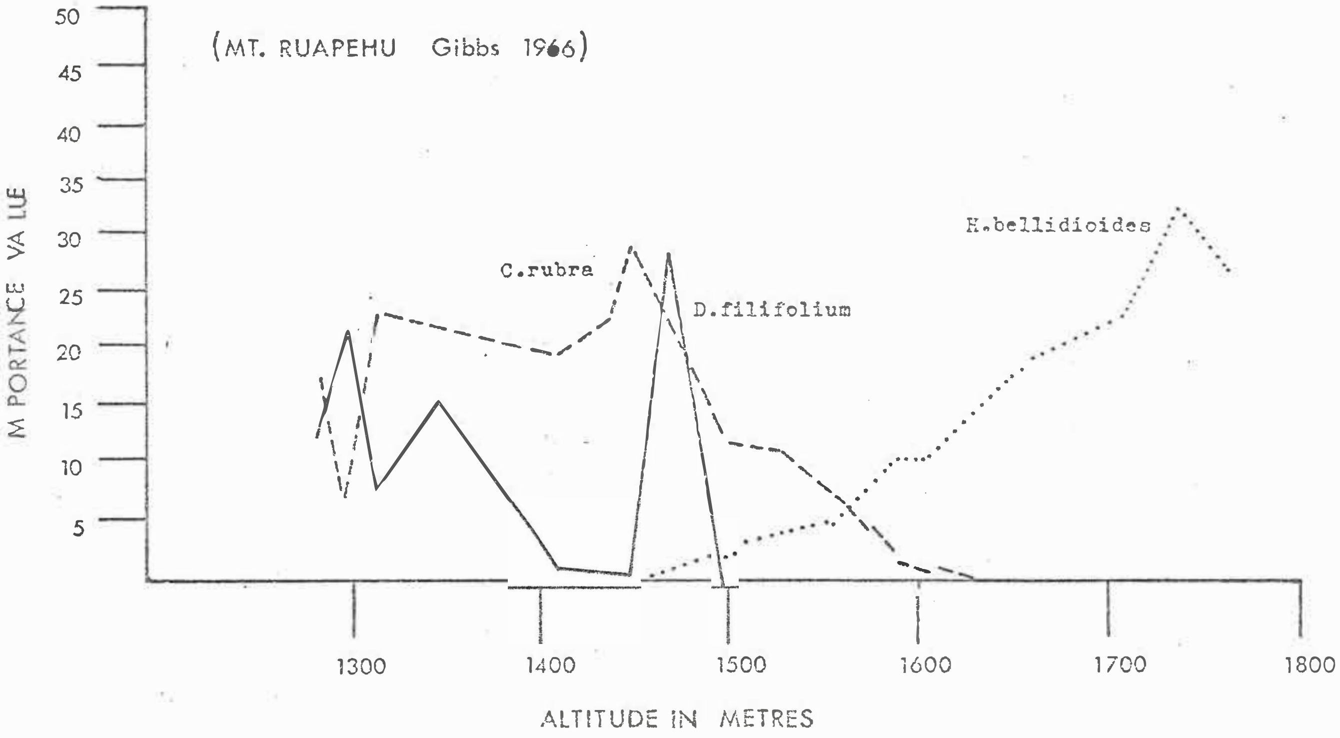
recorded in the canopy. In contrast to its distribution on Mt Egmont however, *G. littoralis* is not closely associated with *P. hallii* which is recorded once only with an importance value of 4 at 2,750 ft (837,). P. colorata, an important understorey tree on Mt. Colenso, has a similar role on the York Road Track Ridge of Mt Egmont but its upper altitudinal limit is some 400 ft (121m) higher on Mt Egmont.

The Hollyford Valley and Secretary Island gradient analyses both provide data enabling comparison of the distribution of *W. racemosa.* In both locations *Weinmannia* is the major component of a lower altitude forest in which it progressively gives way to *N. menziesii* with increasing altitude. As would be expected *Weinmannia's* upper altitudinal limit is much lower in these South Island locations than on Mt Egmont,where instead of giving way to *Nothofagus*,it is *P. hallii* and *G. littoralis* which assume dominance. The distribution of *P. hallii* at the Secretary Island location is also different to that on Mt Egmont,not only in altitudinal limits,but also in the way in which it tends to overshadow the *Weinmannia* distribution at its upper altitude,but never achieving dominance in its own right as it does on Mt Egmont. The greater competitive ability of *Nothofagus* may prevent this at Secretary Island whereas on Mt Egmont such competition does not exist. The Mt Anglem study also provides comparable data on the distribution of *W. racemosa, D. cupressinum.* *G. littoralis,* and P. *hallii* and further to this, *Nothofagus* is absent as is the case on Mt Egmont. *W. racemosa* records highest densities in the Lowland Podocarp-Broadleaved Forest Community where it is associated with *D. cupressinum* and *P. hallii. W. racemosa* and D. *cupressinum* interact in a similar manner to that recorded in the Stratford side of Mt Egmont, but again, *P. hallii* never achieves the dominance so characteristic of the upper-altitude forest on Mt Egmont. *G. littoralis* is also less important than on Mt Egmont and as well does not appear to be closely associated with *P. hallii. L. scoparium* appears to fill the role performed by say P. colorata on the York Road Track Ridge or P. colensoi at Dawson Falls on Mt Egmont, that is, an intermediate between the tree dominated and the shrub dominate communities. O. colensoi, dominant in the subalpine scrub of Mt Anglem, is the physiognomic equivalent of S. elaeagrifolius on Mt Egmont. Wells and Mark (1966) note that herb densities are quite low in the subalpine scrub, perhaps because of the dense canopy, and that they increase in the shorter more open scrub. This is also the case on Mt Egmont.

The main tussock, herbfield, and fellfield species distributions which are comparable with this study are those of H. bellidioides, C. rubra, and D. filifolium as described by Gibbs (1966) on Mt Ruapehu (see Figure 42). These species interact in a similar way to their counterparts on Mt Egmont, and as well, their altitudinal limits are very similar as would be expected because of the similar latitude. The difficulties of fluctuating species distributions through altitude as the result of differences in substrate and drainage factors noted by Gibbs (1966) have also been described earlier in this study. Near the Bruce Road on Mt Ruapehu C. rubra reaches its maximum importance value 30 at 4,550 ft (1386m), D. filifolium fluctuates markedly reaching a maximum importance value 29 at 4,600 ft (1401m), and H. bellidioides reaches its maximum importance value 33 at 5,500 ft (1675m). Comparable values on the York Road Track Ridge are 100 at 1410m for C. rubra, 75 at 1325m for D. filifolium, and 147 at 1797m for H. bellidioides. The large discrepancies in importance value may in part be due to the fact that the method of calculation is not exactly comparable, although a much greater range of species is recorded in the upper altitude Mt Ruapehu data. Few of the other tussock, herbfield and fellfield species distributions from the South Island gradient analyses are comparable with this study. The South Island examples exhibit a much greater range of species

Figure 42

Major Species Altitudinal Distribution



(MT. RUAPEHU Gibbs 1966)

from any given genus so that instead of the single Chionochloa species on Egmont, three species, each with different distributions, are recorded in the Humboldt Mt study of Mark and Burrell (1966), and again where two Celmisia species were recorded in the Egmont data, nine species are listed in the Humboldt Mt data. Overall then the impressions gained in comparing species altitudinal limits, relative importance or performance, and species interaction are firstly that the Mt Egmont data elucidates several major species distributions because of a unique species complement and the absence of Nothofagus and secondly a realisation that the range of species on Mt Egmont is considerably less.

Finally, the lower tree-line on Mt Egmont at 1100m when compared with that at similar latitude on Mt Colenso (1279m) may in part be explained by the lack of Nothofagus on Egmont. Additionally the major climatic differences imposed by Egmont's exposed coastal location must also be partly responsible.

The direct gradient analyses reviewed draw conclusions as to which type of interpretation of vegetation pattern is more appropriate. In fact several of those reviewed set out specifically to formulate conclusions regarding the continuum and discrete community hypotheses, for example Beals (1969) and Mark and Burrell (1966). In the majority of examples reviewed the continuum concept of Whittaker (1956) is favoured although most authors qualify their support for one or other of the hypotheses noting exceptions to otherwise continuous variation, transition zones, or even using a classification or community grouping as a convenience for vegetation description. The various conclusions drawn in the gradient analyses reviewed are summarized on Table 21. It must be borne in mind however, that such a summary necessarily categorizes and summarizes the conclusions and may in part be unfair to some, for example even Whittaker (1956) noted minor trends contrary to the continuum hypothesis.

## TABLE 21

### Direct Gradient Analyses : Summary of Conclusions.

| Author | Location | Continuum Favoured | Discrete Communities Favoured | Comments |
|---|---|---|---|---|
| Whittaker,R.H. | Great Smoky Mts.<br>Tennessee,U.S.A. | X | | A continuum of vegetation. |
| Beals,E.W. | Bati, Combolchia<br>Ethiopia | X | X | Capable of forming both. |
| Reeder,W.G. & Reichert,S.E. | Santa Cruz, Galapagos | X | X | Continuity however some discontinuity present in the form of zone separation by equally dominant species. |
| Mark,A.F. & Sanderson,F.R. | Hollyford Valley<br>Fiordland,N.Z. | X | | |
| Mark,A.F. | Secretary Island<br>Fiordland,N.Z. | X | | Still recognised an abrupt change at 475m enabling distinction of two forest types. |
| Scott,G.A.M. et.al. | Lake Hankinson<br>Fiordland,N.Z. | X | | Impractical to recognise discrete communities although two facies were apparent. |
| Wells,J.A. & Mark,A.F. | Mt Anglem<br>Stewart Is.N.Z. | | X | Four communities separated by discontinuities in physiognomy and floristics. |
| Mark,A.F. & Burrell,J. | Humboldt Mts.<br>Fiordland,N.Z. | | X | Abrupt changes in structure enabled recognition of separate communities. |
| Daly,G.T. | Otago, N.Z. | X | | A continuum of vegetation. |
| Gibbs,J.G. | Bruce Road,<br>Mt Ruapehu N.Z. | | X | Floristic discontinuities. |
| Clarkson,B.D. | Taranaki Falls<br>Mt Ruapehu N.Z. | | X | Floristic discontinuities. |
| Ogden, J. | Mt Colenso<br>Ruahine Range<br>N.Z. | X | | A continuum of species. |
| Clarkson,B.D. | Mt Egmont N.Z. | X | X | Capable of forming both but generally discrete communities. |

When the range of conclusions reached is considered it becomes apparent that there are several possible reasons for the conflict, and following on from this the controversy, between the continuum and discrete community hypotheses. The possibilities are:

1. that for each site the correct conclusion has been drawn; that is both hypotheses are tenable,
2. that the conclusions reached are influenced by the methods of data collection and data manipulation and thus have been prejudiced in favour of one or other of the hypotheses,
3. that only one of the hypotheses is correct and proponents of one or other have drawn invalid conclusions.

Before the first or third possibilities listed can be examined the gradient analyses reviewed must be compared in terms of the second possibility in order to decide whether or not the conclusions obtained have in any way been influenced by the methods of data collection and data manipulation. A range of data collection and data analysis procedures are used in the direct gradient analyses reviewed and several may be considered as possible influences. Under the heading data collection, altitudinal interval employed and altitudinal range encountered will be considered. Under the heading data analysis, amalgamation of data and classificatory versus ordination techniques will be considered. Examples of the possible effects of these theoretical considerations on the direct gradient analyses reviewed can easily be provided. The altitudinal interval employed may affect the conclusions reached if, for example, the interval is so great as to fail adequately to detect and thus describe a species distribution through altitude. Possible effects of an altitudinal interval that was too great could be a loss of the "tails" of species distributions, so that species which in fact associate over part of their respective ranges appear to distribute more separately than is actually the case. What hypotheses might be favoured by such an interval selection is questionable and would depend on whether the species concerned were dominants or relatively minor components of the vegetation. Large altitudinal intervals, as in the case of 243m (Daly, 1967) or 198m (Ogden, 1971), might possibly smooth out major species distributions and make associated species appear to be more individualistically distributed. The effect of the larger altitudinal interval employed for the Stratford data (140m) already described in Chapter 6 of this study was a smoothing of distributions, although in spite of this the vegetation pattern coincided well with sites where a smaller altitudinal interval was employed. It is possible that increasing the altitudinal interval could favour a discrete community interpretation if "tails" of species distributions are lost. However, whatever the effect, it is obvious that much greater consideration of the magnitude of the altitudinal interval should be made. A comparison of data collected from the same location employing different altitudinal intervals would be invaluable in this respect. The altitudinal range employed could be one of the underlying causes of the conflicting conclusions reached in the studies reviewed. Some of the altitudinal gradients considered encounter a much greater range of vegetation (forest through to herbfield) and environmental conditions than others. As well, the rate of change (deterioration) in environmental conditions along the altitudinal gradient varies. Thus the different altitudinal gradients described are not equivalent. It seems obvious, for example, that Ogden (1971) and Mark (1973), dealing with altitudinal ranges of 350 and 898 metres respectively, should conclude in favour of a continuum of vegetation, while the present study should lean more towards discrete community types in that the altitudinal range is nearly 1,000m and therefore a greater range of vegetation types and environmental change is to be described and analysed. A comparison of all the direct gradient analyses reviewed does not support this notion however, for example Gibbs (1966) and Mark and Burrell (1966), employing altitudinal ranges of 487 and 560m respectively, still favoured the discrete community approach, while Daly (1966), dealing with an altitudinal range of 1553m, concluded in favour of the continuum hypothesis.

Amalgamation of data, that is the grouping and averaging of data from spatially separated sites, is carried out by Whittaker (1956), Beals (1969), Reeder and Reichert (1975), and Gibbs (1966), although the actual procedure and effect is different in each of the studies. Beals, Reeder and Reichert, and Gibbs grouped and averaged data which was only slightly spatially separated since samples grouped and averaged came from single transects. Reeder and Reichert thus grouped and averaged the results of five linearly arranged contiguous 10 x 10m quadrats located altitudinally and along the contour. Beals grouped and averaged the results of five samples (each sample consisting of ten plots 20 x 10m) into segments representing fifty metres of altitude. Gibbs grouped and averaged the results of up to twenty-three quadrats 2 x 2m from any one altitude. In each of these cases however the data which was grouped and averaged still came from the same data transect or line along the altitudinal gradient. Whittaker (1956) on the other hand grouped and averaged data from spatially separated transects and into segments representing 200 or 300 ft (60.73m or 91.40m) of altitude. Most of the New Zealand gradient analyses reviewed are single transect altitudinal gradients as is the present study for the main part. The possible effects of this type of data amalgamation have already been noted in Chapter 6, that is, amalgamation tends to increase data heterogeneity in any segment of data, while the averaging procedure then smooths out the species distributions so that a generalised picture of species distributions is achieved; a distribution which cannot be located on the ground. The example given in Chapter 6 of this study supports the view that this data amalgamation may increase the apparent continuity in a given vegetation data set thus prejudicing the conclusions in favour of the continuum hypothesis. There may be cases where such data amalgamation could strengthen the view that there are discontinuities in the data, but whatever the effect of data amalgamation it is obvious that careful consideration should be given to such a practice. If a generalisation of species distributions from a range of spatially separated locations is required, amalgamation will do the job, but the resulting species distributions described are unreal since they cannot be located on the ground. It is also possible that quadrat size could have a similar influence on data interpretation. For example, if the quadrat homogeneity constraints of quadrat size noted in Chapter 4 are not met the results obtained are in effect an average of species representation over a greater or lesser environmental range at any given altitude.

The fact that the strategy adopted in analysing vegetation data may influence the conclusions drawn, that is, whether or not a classificatory or ordinatory approach is employed, has also already been noted in Chapter 6. In general it appears that the approach employed in part determines the conclusions reached with regard to the continuum and discrete community hypotheses. An attempt was made in this study to avoid this problem although it seems likely that particularly in some of the earlier gradient analyses described this may not have been the case. Overall it appears likely that the processes of data selection and data analysis influence the conclusions drawn in any given direct gradient analysis, however this still only partly resolves the conflicting conclusions reached with regard to the continuum and discrete community hypotheses.

It is therefore obvious that the conflicting conclusions result from fundamental differences in the vegetation patterns described by various researchers. Thus species distributions may be considered to form a spectrum ranging from species distributions which are essentially individualistic (forming continua) through to species distributions which exhibit association and marked discontinuity. Therefore in reference to the hypotheses listed by Whittaker (1970), hypotheses two, three, and four appear tenable on Mt Egmont at least. Hypothesis one, the extreme of discontinuity, appears to be too precise to be met by the Egmont data. Although major discontinuities (floristic and physiognomic) were recognised in the vegetation strata on Mt Egmont, the discontinuities in each stratum do not coincide to the extent required to satisfy the first hypothesis. Hypotheses two, three, and four all appear tenable for the Egmont data although the support provided by the data can only be general because the sampling was not designed specifically to test each individual hypothesis. If hypotheses two, three, and four are viewed as a spectrum of possibilities for species distributions ranging from a continuum through to discontinuity then several examples have been determined in the Egmont data. The Lake Dive and Razorback locations represent species distributions with marked discontinuities and a rapid rate of change from one group of dominant and subdominant species to another. The York Road Track Ridge shrub-tussock interface, the Dawson Falls tree-shrub interface, and the York Road Track Ridge tree-shrub interface represent locations at which there is greater continuity in vegetation pattern with centres and boundaries of species populations scattered along the altitudinal gradient.

In the perspective of the various altitudinal gradient analyses examined however it is obvious that overall the species distributions on Mt Egmont show a greater tendency towards discontinuity than is apparent at many other locations.

# APPENDIX 1

## York Road Track Ridge
## Species encountered in Canopy (Top Stratum) quadrats

Astelia sp. (unnamed)
Aporostylis biflora
Blechnum capense
Carmichaelia arborea var.
Carpodetus serratus
Cassinia vauvilliersii
Celmisia glandulosa
var. latifolia
Celmisia gracilenta var.
Chionochloa rubra
Colobanthus sp.
Coprosma sp. (unnamed)
Coprosma depressa
Coprosma pseudocuneata
Coprosma tenuifolia
Coriaria plumosa
Coriaria pteridioides
Drapetes dieffenbachii
Dracophyllum filifolium
Epilobium sp.
Epilobium brunnescens s.s.
Epilobium nerteroides
Euphrasia cuneata
Festuca rubra
subsp. commutata
Forstera bidwillii
var. densifolia
Gahnia procera
Gaultheria sp. (unnamed)
Geranium microphyllum
Griselinia littoralis
Hebe odora
Hebe stricta
Helichrysum sp. (unnamed)
Luzula sp.
Lycopodium fastigatum
Montia sp.
Myrsine divaricata
Olearia ilicifolia
Oreobolus pectinatus
Oreomyrrhis colensoi
Ourisia macrophylla
Pentachondra pumila
Poa anceps var. anceps
Poa colensoi
Poa laevis
Podocarpus hallii
Prasophyllum colensoi
Pseudopanax colensoi
Pseudopanax simplex
var. sinclairii
Pseudowintera colorata
Ranunculus nivicola
Rhacomitrium lanuginosum
var. pruniosum
Rhacomitrium ptychophyllum
Senecio elaeagnifolius
Uncinia spp.
Wahlenbergia albo-marginata var.
Weinmannia racemosa

# APPENDIX 2

## York Road Track Ridge
## Canopy Species Correlation (Significance Levels p=0.005 to p=0.001)
## Pearsons Product Moment Correlation Coefficient (unmodified data)

### Cluster 1

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| W. racemosa | C. serratus | 0.8812 | p=0.001 |

### Cluster 2

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| G. littoralis | P. hallii | 0.9340 | 0.001 |
| G. littoralis | P. colorata | 0.6290 | 0.004 |
| P. colorata | C. tenuifolia | 0.9536 | 0.001 |
| P. colorata | Coprosma sp. | 0.9378 | 0.001 |
| Coprosma sp. | H. stricta | 0.6228 | 0.004 |
| H. stricta | P. simplex var. sinclairii | 0.6819 | 0.001 |
| P. simplex | M. divaricata | 0.9315 | 0.001 |
| P. simplex | S. elaeagnifolius | 0.7337 | 0.001 |
| M. divaricata | S. elaeagnifolius | 0.8477 | 0.001 |
| M. divaricata | C. pseudocuneata | 0.7221 | 0.001 |
| S. elaeagnifolius | C. pseudocuneata | 0.9589 | 0.001 |

### Cluster 3

Species

| | | | |
|---|---|---|---|
| D. filifolium | C. vauvillersii | 0.8205 | 0.001 |
| D. filifolium | P. colensoi | 0.6927 | 0.001 |
| C. vauvilliersii | H. odora | 0.7284 | 0.001 |
| C. rubra | P. laevis | 0.6927 | 0.001 |
| C. rubra | H. odora | 0.6230 | 0.004 |

### Cluster 4

Species

| | | | |
|---|---|---|---|
| P. colensoi | D. dieffenbachii | 0.9431 | 0.001 |
| F. bidwillii var. densifolia | Gaultheria sp. | 0.9161 | 0.001 |

## APPENDIX 2 Contd.

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| Luzula sp. | C. pumila | 0.8605 | 0.001 |
| Gaultheria sp. | D. dieffenbachii | 0.8211 | 0.001 |
| A. aromatica | Gaultheria sp. | 0.7486 | 0.001 |
| A. aromatica | F. bidwillii var. densifolia | 0.7480 | 0.001 |
| P. colensoi | Gaultheria sp. | 0.7124 | 0.001 |
| Gaultheria sp. | C. gracilenta var. | 0.6885 | 0.001 |
| A. aromatica | D. dieffenbachii | 0.6881 | 0.001 |
| A. aromatica | Rhacomitrium spp. | 0.6817 | 0.001 |
| F. bidwillii var. densifolia | D. dieffenbachii | 0.6745 | 0.001 |
| C. pumila | C. gracilenta | 0.6333 | 0.004 |
| C. glandulosa var. latifolia | A. aromatica | 0.7158 | 0.001 |

# APPENDIX 3

## York Road Canopy Species Correlations
(Significance Level p=0.009 to p=0.001
Pearsons Correlation Coefficient (logarithmic transformation)

### Cluster 1

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| P. hallii | G. littoralis | 0.9809 | p=0.001 |

### Cluster 2

| Species | | | |
|---|---|---|---|
| P. laevis | H. odora | 0.6455 | 0.003 |
| C. rubra | H. odora | 0.7618 | 0.001 |
| C. rubra | P. laevis | 0.7455 | 0.001 |
| C.vauvilliersii | H. odora | 0.6542 | 0.002 |
| C.vauvilliersii | C. rubra | 0.8007 | 0.001 |
| C.vauvilliersii | D. filifolium | 0.7682 | 0.001 |
| S. elaeagnifolius | D. filifolium | 0.8459 | 0.002 |
| C. pseudocuneata | D. filifolium | 0.7569 | 0.001 |
| C. pseudocuneata | S. eleagnifolius | 0.8647 | 0.001 |
| P. colensoi | H. stricta | 0.8392 | 0.001 |
| Coprosma sp. | H. stricta | 0.6689 | 0.002 |
| Coprosma sp. | P. simplex var. sinclairii | 0.7614 | 0.001 |
| M. divaricata | S. eleagnifolius | 0.6957 | 0.001 |
| M. divaricata | C. pseudocuneata | 0.7962 | 0.001 |
| M. divaricata | H. stricta | 0.6748 | 0.002 |
| M. divaricata | P. simplex var. sinclairii | 0.7919 | 0.001 |
| W. racemosa | G. littoralis | 0.6277 | 0.004 |
| W. racemosa | P. hallii | 0.6217 | 0.004 |
| W. racemosa | C. serratus | 0.7254 | 0.001 |
| P. colorata | G. littoralis | 0.6247 | 0.004 |
| P. colorata | Coprosma sp. | 0.7746 | 0.001 |
| C. tenuifolia | G. littoralis | 0.6678 | 0.002 |
| C. tenuifolia | P. simplex var. sinclairii | 0.6223 | 0.004 |
| C. tenuifolia | Coprosma sp. | 0.6329 | 0.004 |
| C. tenuifolia | P. hallii | 0.6507 | 0.003 |
| C. tenuifolia | P. colorata | 0.8555 | 0.001 |

## APPENDIX 3 contd

Cluster 3

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| Helichrysum sp. | P. colensoi | 0.6974 | 0.001 |
| Helichrysum sp. | Luzula sp. | 0.6275 | 0.004 |
| Montia sp. | Helichrysum sp. | 0.7285 | 0.001 |
| A. aromatica | P. colensoi | 0.8599 | 0.001 |
| F. bidwillii var. densifolia | P. colensoi | 0.8410 | 0.001 |
| F. bidwillii var. densifolia | A. aromatica | 0.9692 | 0.001 |
| Gaultheria sp. | P. colensoi | 0.8744 | 0.001 |
| Gaultheria sp. | A. aromatica | 0.9390 | 0.001 |
| Gaultheria sp. | F. bidwillii var. densifolia | 0.9816 | 0.001 |
| D. dieffenbachii | P. colensoi | 0.8399 | 0.001 |
| D. dieffenbachii | A. aromatica | 0.9667 | 0.001 |
| D. dieffenbachii | F. bidwillii var. densifolia | 0.9487 | 0.001 |
| D. dieffenbachii | Gaultheria sp. | 0.9777 | 0.001 |
| C. gracilenta var. | P. colensoi | 0.8382 | 0.001 |
| C. gracilenta var. | Luzula sp. | 0.6439 | 0.003 |
| C. gracilenta var. | A. aromatica | 0.9709 | 0.001 |
| C. gracilenta var. | F. bidwillii var. densifolia | 0.9478 | 0.001 |
| C. gracilenta var. | Gaultheria sp. | 0.9770 | 0.001 |
| C. gracilenta var. | D. dieffenbachii | 0.9252 | 0.001 |
| Coprosma sp. | Luzula sp. | 0.6556 | 0.002 |
| Coprosma sp. | A. aromatica | 0.6413 | 0.003 |
| Coprosma sp. | C. gracilenta var. | 0.6669 | 0.002 |
| C. glandulosa var. | A. aromatica | 0.6469 | 0.003 |
| C. glandulosa var. | C. gracilenta var. | 0.6570 | 0.002 |
| C. glandulosa var. | C. pumila | 0.9820 | 0.001 |
| Rhacomitrium spp. | A. aromatica | 0.6411 | 0.003 |
| Rhacomitrium spp. | C. gracilenta var. | 0.6472 | 0.003 |
| Rhacomitrium spp. | C. glandulosa var. | 0.9965 | 0.001 |
| S. elaeagnifolius | P. colensoi | -0.6655 | 0.002 |

# APPENDIX 4

## York Road Track Ridge
## Canopy Species Correlation (Significance Levels p = 0.005 to p = 0.001
## Spearmans Rank Correlation Coefficient

**Cluster 1**

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| 28 | 29 | 0.7265 | 0.001 |

**Cluster 2**

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| 14 | 15 | 0.6910 | 0.002 |
| 14 | 16 | 0.7925 | 0.001 |
| 14 | 17 | 0.6613 | 0.003 |
| 14 | 18 | 0.7462 | 0.001 |
| 14 | 20 | 0.6363 | 0.004 |
| 15 | 16 | 0.9306 | 0.001 |
| 15 | 18 | 0.7640 | 0.001 |
| 16 | 18 | 0.7923 | 0.001 |
| 17 | 18 | 0.7734 | 0.001 |
| 17 | 19 | 0.8320 | 0.001 |
| 17 | 20 | 0.9048 | 0.001 |
| 19 | 22 | 0.6383 | 0.004 |
| 19 | 24 | 0.6645 | 0.002 |
| 19 | 26 | 0.7686 | 0.001 |
| 20 | 26 | 0.7095 | 0.001 |
| 22 | 24 | 0.8437 | 0.001 |
| 22 | 25 | 0.6759 | 0.002 |
| 23 | 27 | 0.9368 | 0.001 |
| 23 | 28 | 0.6410 | 0.004 |
| 24 | 25 | 0.7513 | 0.001 |
| 24 | 26 | 0.8168 | 0.001 |
| 24 | 31 | 0.7721 | 0.001 |
| 25 | 30 | 0.7474 | 0.001 |
| 25 | 31 | 0.7483 | 0.001 |
| 27 | 31 | 0.7006 | 0.001 |
| 30 | 31 | 0.7474 | 0.001 |
| 19 | 20 | 0.9254 | 0.001 |

## APPENDIX 4 contd.

**Cluster 3**

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| 1 | 2 | 0.7701 | 0.001 |
| 1 | 3 | 0.7026 | 0.001 |
| 1 | 4 | 0.6969 | 0.001 |
| 1 | 5 | 0.6908 | 0.002 |
| 1 | 6 | 0.8476 | 0.001 |
| 1 | 7 | 0.8476 | 0.001 |
| 1 | 8 | 0.8771 | 0.001 |
| 1 | 9 | 0.8918 | 0.001 |
| 1 | 10 | 0.8107 | 0.001 |
| 3 | 4 | 0.7056 | 0.001 |
| 3 | 6 | 0.8359 | 0.001 |
| 3 | 7 | 0.7645 | 0.001 |
| 3 | 8 | 0.7837 | 0.001 |
| 3 | 9 | 0.8071 | 0.001 |
| 3 | 10 | 0.8743 | 0.001 |
| 3 | 11 | 0.7354 | 0.001 |
| 3 | 12 | 0.7158 | 0.001 |
| 3 | 13 | 0.7158 | 0.001 |
| 6 | 8 | 0.9459 | 0.001 |
| 6 | 9 | 0.9716 | 0.001 |
| 6 | 10 | 0.9715 | 0.001 |
| 6 | 11 | 0.6394 | 0.004 |
| 6 | 12 | 0.6461 | 0.003 |
| 6 | 13 | 0.6461 | 0.003 |
| 7 | 8 | 0.9371 | 0.001 |
| 7 | 9 | 0.9613 | 0.001 |
| 7 | 10 | 0.9639 | 0.001 |
| 8 | 9 | 0.9794 | 0.001 |
| 8 | 10 | 0.9510 | 0.001 |
| 9 | 10 | 0.9253 | 0.001 |

APPENDIX 4 contd.

Cluster 3

| Species | | Correlation Coefficient | Significance Level |
|---|---|---|---|
| 10 | 11 | 0.6645 | 0.002 |
| 10 | 12 | 0.6645 | 0.002 |
| 10 | 13 | 0.6645 | 0.002 |
| 11 | 12 | 0.9870 | 0.001 |
| 11 | 13 | 0.9870 | 0.001 |
| 12 | 13 | 1.000 | 0.000 |

Key to Species

| | |
|---|---|
| 1 | P. colensoi |
| 3 | Luzula sp. |
| 4 | Holichrysum sp. (unnamed) |
| 5 | Montia sp. |
| 6 | A. aromatica |
| 7 | F. bidwillii var. densifolia |
| 8 | Gaultheria sp. (unamed) |
| 9 | D. dieffenbachii |
| 10 | C. gracilenta var. |
| 11 | C. pumila |
| 12 | C. glandulosa var. latifolia |
| 13 | Rhacomitrium spp. |
| 14 | H. odora |
| 15 | P. laevis |
| 16 | C. rubra |
| 17 | D. filifolium |
| 18 | C. vauvilliersii |
| 19 | S. elaeagnifolius |
| 20 | C. pseudocuneata |
| 21 | P. colensoi |
| 22 | H. stricta |
| 23 | G. littoralis |
| 24 | P. simplex var. sinclairii |
| 25 | Coprosma sp. (unnamed) |
| 26 | M. divaricata |
| 27 | P. hallii |
| 28 | W. racemosa |
| 29 | C. serratus |
| 30 | P. colorata |
| 31 | C. tenuifolia |

# APPENDIX 5

## SIMILARITY MATRIX (Sorensen's Similarity Index)

## York Road Track Ridge Canopy Quantitative

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | | | | | | | | | | | | | | | | | |
| 2 | 38 | | | | | | | | | | | | | | | | | | | |
| 3 | 54 | 14 | | | | | | | | | | | | | | | | | | |
| 4 | 46 | 14 | 74 | | | | | | | | | | | | | | | | | |
| 5 | 26 | 7 | 35 | 52 | | | | | | | | | | | | | | | | |
| 6 | 22 | 7 | 27 | 26 | 39 | | | | | | | | | | | | | | | |
| 7 | 20 | 7 | 16 | 20 | 40 | 51 | | | | | | | | | | | | | | |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | | | | | | | | | | | | | |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 73 | | | | | | | | | | | | |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 39 | 64 | | | | | | | | | | | |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 51 | 63 | | | | | | | | | | |
| 12 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 28 | 45 | 51 | 74 | | | | | | | | | |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 22 | 22 | 61 | 76 | | | | | | | | |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 10 | 17 | 22 | 58 | 79 | | | | | | | |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 22 | 28 | 60 | 65 | 86 | 80 | | | | | | |
| 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 6 | 6 | 7 | 17 | 26 | 22 | | | | | |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 5 | 7 | 10 | 76 | | | | |
| 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 5 | 46 | 63 | | | |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 5 | 43 | 44 | 65 | | |
| 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 5 | 6 | 8 | 53 | 61 | 45 | 25 | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |

Quadrat Number

# APPENDIX 6

## SIMILARITY MATRIX (Sorensen's Similarity Index)

## ~~York Road Track Ridge~~ Ground Cover Qualitative

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | | | | | | | | | | | | | | | | |
| 2 | 40 | | | | | | | | | | | | | | | | | | |
| 3 | 36 | 29 | | | | | | | | | | | | | | | | | |
| 4 | 76 | 14 | 80 | | | | | | | | | | | | | | | | |
| 5 | 74 | 20 | 62 | 62 | | | | | | | | | | | | | | | |
| 6 | 57 | 19 | 44 | 52 | 73 | | | | | | | | | | | | | | |
| 7 | 53 | 17 | 41 | 48 | 63 | 83 | | | | | | | | | | | | | |
| 8 | 53 | 15 | 42 | 42 | 56 | 65 | 67 | | | | | | | | | | | | |
| 9 | 44 | 16 | 32 | 39 | 59 | 68 | 65 | 77 | | | | | | | | | | | |
| 10 | 24 | 0 | 24 | 24 | 36 | 46 | 48 | 52 | 36 | | | | | | | | | | |
| 11 | 25 | 0 | 26 | 26 | 21 | 34 | 31 | 44 | 36 | 61 | | | | | | | | | |
| 12 | 8 | 0 | 8 | 8 | 6 | 19 | 18 | 21 | 22 | 47 | 57 | | | | | | | | |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 | 15 | 35 | 30 | 63 | | | | | | | |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 | 11 | 27 | 30 | 49 | 65 | | | | | | |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 6 | 24 | 26 | 40 | 40 | 50 | | | | | |
| 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 5 | 20 | 13 | 31 | 49 | 45 | 52 | | | | |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 5 | 22 | 11 | 37 | 42 | 27 | 36 | 55 | | | |
| 18 | 0 | 0 | [illegible] | 0 | 0 | 0 | 0 | 5 | 5 | 9 | 12 | 22 | 29 | 23 | 39 | 47 | 59 | | |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 6 | 16 | 14 | 33 | 51 | 41 | 56 | 75 | 63 | 56 | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |

Quadrat Number

## APPENDIX 7

## SIMILARITY MATRIX (Sorensen's Similarity Index)

### York Road Track Ridge Subcanopy, Shrubs, and Epiphytes Qualitative

| | 15 | 16 | 17 | 18 | 19 | 20 |
|---|---|---|---|---|---|---|
| 15 | | | | | | |
| 16 | 57 | | | | | |
| 17 | 14 | 36 | | | | |
| 18 | 14 | 20 | 55 | | | |
| 19 | 13 | 19 | 42 | 53 | | |
| 20 | 40 | 36 | 44 | 43 | 41 | |

Quadrat Number

# APPENDIX 8

## Canopy Species Present in Tree - Shrub Interface Quadrats

### North Egmont

S. elaeagnifolius
P. colensoi
G. littoralis
P. simplex
C. pseudocuneata
P. hallii
Coprosma sp. (unnamed)
D. filifolium
H. stricta
C. tenuifolia
M. divaricata
L. bidwillii
P. colorata
W. racemosa
C. serratus
Carmichaelia sp.
P. tenuifolium
M. salicina
P. crassifolium

### Dawson Falls

P. colensoi
P. hallii
Coprosma sp. (unnamed)
S. elaeagnifolius
G. littoralis
P. simplex
C. pseudocuneata
H. stricta
W. racemosa

### York Road Track Ridge

D. filifolium
G. littoralis
S. elaeagnifolius
P. hallii
C. pseudocuneata
P. simplex
C. tenuifolia
H. stricta
Coprosma sp. (unnamed)
P. colorata
P. colensoi
M. divaricata
W. racemosa
C. serratus

### Lake Dive Track Ridge

S. elaeagnifolius
C. pseudocuneata
Coprosma sp. (unnamed)
C. tenuifolia
P. simplex
H. stricta
G. littoralis
P. colensoi
P. hallii
M. divaricata
L. bidwillii
O. ilicifolia

## REFERENCES CITED

Allan, H.H. 1961: Flora of New-Zealand. Government Printer, Wellington. Vol. 1.

Beals, E.W. 1965: Species Patterns in a Lebanese poterietum. Vegetatio, 13: 69-87.

Beals, E.W. 1969: Vegetational Change Along Altitudinal Gradients. Science, 165: 981-985.

Bray, J.R. and Curtis, J.T. 1957: An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monog. 27: 325-349.

Brown, R.T. and Curtis, J.T. 1952: The upland conifer-hardwood forests of Northern Wisconsin. Ecol. Monog. 22: 217-234.

Buchanan, J. 1869: Notes on the botany of Mount Egmont and neighbourhood, New- Zealand, February, 1867. J. Proc. Linn. Soc. Bot. 10: 57-62.

Clarkson, B.D. 1973: A description and analysis of the vegetation near Taranaki Falls Mt. Ruapehu. University of Waikato, unpublished.

Cockayne, L. 1909: Report on a botanical survey of Stewart Island. Append. J. House Repres. N.Z. C 12 Wellington.

Cockayne, L. 1927: New-Zealand Plants and their story. Government Printer, Wellington. (Third Edition)

Cockayne, L. 1928: The Vegetation of New -Zealand Engelmann, Leipzig. (Second Edition)

Cottam, G. and Curtis, J.T. 1956: The use of distance measures in phytosociological sampling. Ecol. 37: 451-46P.

Coulter, J.D. 1967: Mountain Climate. Proc. N.Z. Ecol. Soc. 14: 40-57.

Coulter, J.D. 1976: Weather in Egmont National Park, In Fullarton, 1976: 51-55.

Curtis, J.T. 1955: A prairie continuum in Wisconsin. Ecol. 36: 558-566.

Curtis, J.T. 1959: The Vegetation of Wisconsin: An Ordination of Plant Communities. Univ. Wisconsin, Madison.

Curtis, J.T. and Mc Intosh, R.P. 1951: An upland forest continuum in the prairie-forest border region of Wisconsin. Ecol. 32: 476-496.

Daly, G.T. 1967: Ordination of Grassland and Related Communities in Otago. Proc. N.Z. Ecol. Soc. 14: 63-70.

Daubenmire, R.F. 1966: Vegetation: Identification of Typal Communities. Science 151: 291-298.

Daubenmire, R.F. 1968: Plant communities A textbook of plant synecology. Harper and Row, New York.

Dieffenbach, H. 1843: Travels in New-Zealand, with contributions to the geography, geology and natural history of that country. John Murry, London. Vol. 1.

Druce, A.P. 1961: Mountain Vegetation of the North Island. N.Z. Soil News 3: 95-107.

Druce, A.P. 1964: The Vegetation, In Scanlan, 1964: 41-56.

Druce A.P. 1966: Tree ring dating of recent Volcanic Ash and Lapilli, Mt Egmont. N.Z. J. Bot. 6: 3-41.

Druce, A.P. 1973: Checklist of the Higher Plants of Mount Egmont including Pouakai and Kaitake Ranges. Third Approximation Nov. 1973, Corrections Aug. 74, Oct. 74, Jul. 75, Apr. 76. A.P. Druce Botany Division, D.S.I.R. Taita, Hutt Valley, unpublished.

Druce, A.P. 1974: Some notes on the flora of Mt Egmont. Auckland Botanical Newsletter 31 (2), 1-4.

Druce, A.P. 1976: The Vegetation, In Fullarton, 1976. 39-50

Elder, N.L. 1965: Vegetation of the Ruahine Range: an introduction. Trans. of the Royal Soc. of N.Z. (Botany) 3 (3), 13-66.

Ellenberg. H. 1948: Unkrautgesellschaften als Mass fur den Sauregrad, die Verdichtung und andere Eigenschaften des Ackerbodens. Ber. Landtech. 4: 130-146.

Ellenberg, H. 1950: Landwirtschaftliche Pflanzensoziologie 1 Unkrautgemeinschaften als Zeiger fur Klima und Boden. Ulmer, Stuttgart.

Ellenberg, H. 1952: Landwirtschaftliche Pflanzensoziologie 11 Wiesn und Weiden und ihre standortliche Bewertung. Ulmer, Stuttgart.

Everitt, B. 1974: Cluster Analysis. Heinmann.

Flenley, J.R. (editor) Altitudinal Zonation in Malesia: being the Transactions of the Third Aberdeen-Hull Symposium in Malesian Ecology Hull 1973. Dept. of Geography, University of Hull.

Fosberg, F.R. 1961: A classification of vegetation for general purposes. Trop. Ecol. 2: 1-28.

Fullarton, J.H. (editor) 1976: Egmont National Park. Egmont National Park Board. (Third Edition)

Gauch, Jr. H.G. and Chase, G.B. 1974: Fitting the Gaussian Curve to Ecological Data. Ecol. 55 (6), 1377-1381.

Gauch, Jr. H.G. and Whittaker, R.H. 1974: Ordination of Vegetation Samples by Gaussian Species Distributions. *Ecol.* 55 (6), 1382-1390.

George, H. 1967: Egmont: the Vegetation Belts. *N.Z. Plants and Gardens.* 7: 61-69.

Gibbs, J.G. 1966: Studies of the Importance of Plant Species in Vegetation. Above Timber-line on North-West Slopes adjoining Bruce Road, Mt Ruapehu, Tongariro National Park. *Tuatara 14* (1), 19-29.

Gleason, H.A. 1926: The individualistic concept of the plant association. *Bull. Torrey Bot. Club 53*: 7-26.

Gleason, H.A. 1939: The Individualistic concept of the plant association. *Am. Midl. Nat.* 21: 92-110.

Goodall, D.W. 1963: The Continuum and the Individualistic Association. *Vegetatio* 2: 297-316.

Goodall, D.W. 1973: Sample Similarity and Species Correlation, In Whittaker, 1973: 107-156.

Hall, J.B. 1973: Vegetational Zones on the Southern Slopes of Mount Cameroon. *Vegetatio* 27 (1-3), 49-69.

Imp, P. and van Groenwoud, H. 1975: A multivariate ordering of Vegetation data based on Gaussian type gradient response curves. *J. Ecol.* 63 (3), 767-777.

Kohn, B.P. and Neall, V.E. 1973: Identification of Late Quaternary Tephras for dating Taranaki Lahar Deposits. *N.Z. J. Geol. and Geophys.* 16: 781-792.

Kellman, M.C. 1975: *Plant Geography.* Methuen and Co. London.

Langford, A.N. and Buell, M.F. 1969: Integration and stability in the plant association. *Adv. Ecol. Res.* 6: 83-135.

Lenoble, F. 1926: À propos des associations végétales. *Bull. Soc. Bot. Fr.* 73: 873-893.

Lenoble, F. 1928: Associations végétales et espèces. *Archs Bot. Caen, Bull. mens.* 2 (1), 1-14.

Looman, J. and Campbell, J.B. 1960: Adaptation of Sorensen's K. (1948) for estimating unit affinities in prairie vegetation. *Ecol.* 41: 409-415.

Mark, A.F. 1963: Vegetation studies on Secretary Island, Fiordland Pt. 3: The altitudinal gradient in forest composition, structure, and regeneration. *N.Z.J. Bot.* 1: 188-202.

Mark, A.F. and Burrell, J. 1966. Vegetation studies in the Humboldt Mountains, Fiordland, Part 1. The Alpine Tussock Grasslands. *Proc. N.Z. Ecol. Soc.* 13: 12-19.

Moore, L.B. and Edgar, E. 1970. *Flora of New-Zealand.* Government Printer, Wellington. Vol.11.

Mark, A.F. and Sanderson, F.R. 1962: The Altitudinal gradient in forest composition, structure, and regeneration in the Hollyford Valley, Fiordland. *Proc. N.Z. Ecol. Soc.* 9: 17-26.

Mason. G.M. 1951: A note on the Vegetation of Mount Egmont. *Tane* 4: 23-25.

Mc Intosh, R.P. 1967: The continuum concept of vegetation. *Bot. Rev.* 33: 130-187.

Mc Quitty, L.L. 1957. Elementary orthogonal amd oblique types and typal relevancies. *Educational and psychological measurement.* 17: 207-229.

Mueller-Dombois, D. and Ellenberg, H. 1974: *Aims and Methods of Vegetation Ecology.* John Wiley and Sons.

Neall, V.E. 1972: Tephrochronology and tephrostatigraphy of Western Taranaki. *N.Z. J. Geol. and Geophys.* 15: 507-557.

Neall, V.E. 1976: Volcanology of Egmont National Park. In Fullarton, 1976. 56-62.

Noy-Meir, I. 1974: Multivariate Analysis of the Semi Arid Vegetation in south-eastern Australia 11: Vegetation Catenae and Environmental Gradients. *Aust. J. Bot.* 22: 115-140.

Ogden, J. 1971: Studies on the Vegetation of Mount Colenso N.Z. 1. The Forest Continuum. *Proc. N.Z. Ecol. Soc.* 18: 58-65.

Orloci, Laszlo. 1975: *Multivariate Analysis in Vegetation Research.* Dr. W. Junk b.v. Publishers, The Hague.

Petrie, D. 1912a. On the slopes of Mt Egmont: A botanical visit - (1) *Taranaki Herald,* 18 October 1912.

Petrie, D. 1912b. On the slopes of Mt Egmont: A botanical visit - (2) *Taranaki Herald*, 23 October 1912.

Poole, M.A. and O'Farrell, P.N. 1970: The assumptions of the linear regression model. *Institute British Geography Transactions Reprint Publication* 52: 45-158.

Ramensky, L.G. 1924: Die Grundgesetzmässigaeiten im Aufbau der Vegetationsdecke. Wjestn. opytn. djela Woronesch. 37 s. (Bot. Centbl., N.F. 7: 453-455, 1926.)

Ramensky, L.G. 1930: Zur Methodik der vergleichenden Bearbeitung und Ordnung von Pflanzenlisten und anderen Objekten, die durch mehrere, verschiedenartig wirkende Faktoren bestimmt werden. Beitr. z. Biol. der Pflanz. 18: 269-304.

Reeder, W.G. and Reichert, S.E. 1975: Vegetational Change along an Altitudinal Gradient, Santa Cruz Island, Galapagos. *Biotropica* 7 (3), 162-175.

Rice, E.L. 1967: A statistical method of determining quadrat size and adequacy of sampling. *Ecol.* 48: 1047-1049.

Robbins, R.G. 1942: The Pouakai ranges. *J. Royal N.Z. Inst. Hort.* 12: 37-41.

Schweinfurth, U. 1962: Mount Egmont Taranaki, and a contribution to the study of the vertical arrangement of the vegetation. *Erdkunde* 16 (1), 34-38.

Scanlan, A.B. 1961: *Egmont - The Story of a Mountain.* A.H. and A.W. Reed, Wellington.

Scanlan, A.B. (editor) 1964: *Egmont National Park.* Egmont National Park Board.

Scott, G.A.M. et. al. 1964: Altitudinal variation in forest composition near Lake Hankinson, Fiordland. *N.Z.J. Bot.* 2: 310-323.

Seal, H. 1964: *Multivariate Statistical Analysis for Biology.* Methuen, London.

Shimwell, D.W. 1971: *Description and Classification of Vegetation.* Sidgwick and Jackson.

Siccama, T.G. 1974: Vegetation, Soil, and Climate on the Green Mts of Vermont. *Ecol. Monog.* 144(3), 325-349.

Sneath, P.H.A. 1966: A Method for Curve Seeking from scattered points. *Computer Journal* 8: 383-391.

Sokal, R.R. and Michener, C.D. 1958: A statistical method for evaluating systematic relationships. *Univ. Kansas Sc. Bull.* 38: 1409-1438.

Sokal, R.R. and Sneath, P.H.A. 1963: *Principles of Numerical Taxonomy.* Freeman, SanFrancisco.

Sorensen, H. 1948: A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Det Kong. Danske Videnske. Biol. Skr.* 5(4), 1-34.

Strain, B.R. and Billings, W.D. 1974: *Vegetation and Environment.* Dr. W. Junk b.v. Hague.

Symes, R.E. and Wells, N. 1973: Mineral content of topsoils on coastal terraces from Mt Egmont to Palmerston North. *N.Z.J. Geol. and Geophys.* 16(3), 651-656.

Thomson, G.M. 1917: A ramble on Mt Egmont. *Otago Daily Times*, 6 Jan. 1917.

Tonkin, P.J. 1970: The soils of the south eastern sector of Egmont National Park. *Earth Sc. J.* 4: 36:57.

Topping, W.W. 1972: The Burrell Lapilli eruptions, Mt Egmont, N.Z. *N.Z. J. Geol. and Geophys.* 15: 476-490.

Topping, W.W. 1974: A Maori oven from Mount Egmont, New-Zealand. *N.Z. J. of Science.* 17: 119-122.

Wardle, P. 1964: Facets of the distribution of forest vegetation in New-Zealand. *N.Z.J. Bot.* 2: 352-366.

Wardle, P. 1971: An explanation for Alpine Timberlines. *N.Z.J. Bot.* 9 (3), 371-402.

Wells, J.A. 1972: Ecology of Podocarpus hallii. *N.Z.J. Bot.* 10 (3), 399-426.

Wells, J.A. and Mark, A.F. 1966: The altitudinal sequence of climax vegetation on Mt Anglem, Stewart Island Pt. 1 The principal strata. *N.Z.J. Bot.* 4: 267-282.

Whitmore, T.C. 1975: *Tropical Rain Forests of the Far East.* Clarendon Press. Oxford.

Whittaker, R.H. 1948: A vegetation analysis of the Great Smoky Mountains. Ph.D. Thesis, Univ. of Ill., Urbana, unpublished.

Whittaker, R.H. 1956: Vegetation of the Great Smoky Mountains. *Ecol. Monog.* 26: 1-80.

Whittaker, R.H. 1962: Classification of natural communities. *Bot. Rev.* 28 (1), 1-239.

Whittaker, R.H. 1967: Gradient Analysis of Vegetation. *Biol. Rev.* 42 (2), 207-264.

Whittaker, R.H. 1970: *Communities and Ecosystems.* Macmillan.

Whittaker, R.H. (editor) 1973a. *Ordination and Classification of Communities.* Dr. W. Junk b.v. - Hague.

Whittaker, R.H. 1973b. Direct Gradient:Analysis Techniques, In Whittaker, 1973: 9-30.

Whittaker, R.H. 1973c. Direct Gradient Analysis: Results, In Whittaker, 1973. 35-46.

Whittaker, R.H. and Woodwell, G.M. 1973: Retrogression and Coenocline Distance, In Whittaker, 1973: 55-69.

Wilson, P.T. 1961: The Vegetation of Mount Egmont: an ecological study of the Sub-polar Vegetation. Palmerston North Teachers College, unpublished.

Zotov, V.D. 1938: Some Correlations between Vegetation and Climate in New-Zealand. *N.Z.J. of Science and Technology* 19: 474-487.