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Secondary Succession In The High-Alpine of Central Otago, New Zealand, 25 Years Following Anthropogenic Disturbance

by

Charles Stewart Brown ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science

Department of Earth and Atmospheric Sciences

Edmonton, Alberta

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ABSTRACT

Secondary succession and soil development were investigated 25years following anthropogenic disturbance in the high-alpine of Central Otago, N.Z. Species cover, soil properties and microclimatic variables were collected from disturbed and adjacent undisturbed sites. Species richness and average plant cover in disturbed sites were equal to undisturbed areas but were different structurally and compositionally. Cushion plants dominated undisturbed treatments while graminoid species characterized disturbed sites. Revegetation did not support either the intermediate disturbance hypothesis or the initial floristic composition model. Extensive modification of microtopography and complete removal of plant cover produced warmer, drier, more basic soils, which had lower organic matter content and higher ammonium levels than undisturbed soils. Variation in community species composition could not be explained by selected environmental variables through indirect ordination. Plant communities continue to respond to the initial disturbance with no indication of when a 'stable' community will occur and what species will characterize it.

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Secondary succession in the high-alpine of Central Otago, New Zealand, 25 years following anthropogenic disturbance** submitted by **Charles Stewart Brown** in partial fulfillment of the requirements for the degree of **Master of Science.**

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I also owe a great deal of thanks to Prof. A.F. Mark from the University of Otago who initiated this study and had the foresight to establish the monitoring of the disturbance for a long-term study. Without his support and unrestricted access to all of the archived data this study would not have been possible. His help with identifying what was for me an entirely foreign flora was greatly appreciated. Dr. K. Dickinson also provided help in the field and was always available for comments. My committee members, Drs. R.B. Rains and A. Sanchez also provided well-appreciated comments and ideas on my thesis.

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Chapter 1: Introduction, Site Description and Thesis Objectives

Introduction:

Since the 1970s, terrain disturbances in arctic and alpine environments have become more widespread and frequent (Reynolds and Tenhunen 1996) as a result of a dramatic increase in resource exploration and development. Increased access to the alpine has resulted in a variety of anthropogenic disturbances which originate from a number of localized sources: agricultural uses involving grazing and associated management (e.g., tilling, fertilizing, seeding, burning, stocking); industrial uses such as mining and transport facilities (e.g., airstrips) as well as linear disturbances including pipelines and seasonal and all-weather roads (Pomeroy 1985; Roxburgh et al. 1988; Rikhari et al. 1993; Harper and Kershaw 1996). It is, therefore, necessary to pay special attention to the natural response of plant communities to disturbances in these susceptible regions.

Natural disturbances in alpine environments result from geomorphological processes such as frost action and cryoturbation on a highly localized scale to wildland fire on a regional scale. Disturbances clearly play an important role in maintaining species and community composition differences within and between alpine vegetation types (Fox 1981). Plant communities' responses to disturbances have resulted in both, decreased species richness or diversity (Chapin and Shaver 1981; Truett and Kertell 1992) and increases in richness (Rikhari *et al.* 1993; Harper and Kershaw 1996). Total cover has generally been less within disturbed sites than undisturbed sites (Bliss and Wein 1972; Felix and Raynolds 1989).

Primary and secondary succession in low Arctic environments are predominantly slow processes owing to cold climates which slow and restrict biological activity to such an extent that plant community recovery is minimal even decades after the initial disturbance (Kershaw 1984, Harper and Kershaw 1996). It is, therefore, desirable to conduct disturbance studies in alpine environments (similar climatic conditions to the low Arctic) over a longer time frame than similar studies in temperate environments. Longer growing seasons in New Zealand's alpine communities offer an opportunity to observe disturbance-induced changes in species richness and diversity of plant communities on a shorter time-scale than in northern environments (Bliss and Mark 1974).

New Zealand's alpine ecosystems also provide an opportunity to study the effects and natural revegetation of recent disturbances in a region that has undergone considerable alteration due to the cumulative effects of Polynesian burning and European pastoral activities for the past

800 years. These activities have resulted in a naturalized vegetation type, which cannot be easily difined due to rampant invasion of introduced species and the continual pressure of inducing early successional stages by cultural interference (Molloy 1969). Such interference has produced induced, undisturbed plant communities, which complicates attempts at the prediction of successive plant communities following contemporary disturbances.

Literature Review:

Evolution of New Zealand Alpine Plant Communities

Prior to the Polynesian colonization of New Zealand (C. 1000 yrs BP), alpine vegetation of the South Island was characterized by scrub and grassland communities (Molloy 1969). Investigations of palaeo investigations have found that, while past alpine snow-tussock grasslands (*Chionochloa* spp.) composition and structure were comparable to present communities, the contemporary distribution of this vegetation type is much more restricted and only exists at lower altitudes. The change in vegetation throughout New Zealand has been attributed to anthropogenic interference, predominantly Polynesian burning and later European agronomic practices.

Although fire played an important role in central Otago throughout the Holocene and Pleistocene, it is only since the arrival of Polynesians in the region (about 800 yrs BP) (Anderson 1991) that the plant communities were substantially transformed. Fire-induced disturbances have resulted in the replacement of lowland scrub and forest with tussock grasslands (McGlone *et al.* 1997), a process that has also affected alpine communities. Polynesian burning destroyed competing and fire-intolerant grasses and forbs, allowing for the expansion of fire-adapted tussocks. Regeneration of burned alpine environments was dependent on the severity of soil erosion. Snow-tussocks regained dominance except on exposed sites (plateaus) where a progressive deterioration occurred (Molloy 1969).

Modification of the native vegetation also occurred as a result of pastoral activities from the 1850s onwards, during which time large flocks of sheep were introduced to central Otago, along with weeds such as *Rumex acetosella*. Grazing also included the earlier practice of regular burning to remove scrub and increase the palatability of tussocks (Molloy *et al.* 1963). Burning also led to an increase in sward grasses, *Celmisia* spp. and *Aciphylla* spp. and a decrease in cover and stature of native grasses (Molloy 1969, McGlone *et al.* 1997). As a result, European pasture replaced native tussock grasslands up to an elevation of about 700 m. New Zealand's tussock grasslands have also been modified by rabbit grazing pressures following their introduction to New Zealand (Rose and Platt 1992, Norbury and Norbury 1996, Moller *et al.* 1997).

Repeated burning since Polynesian colonization, and high densities of stock accompanying the European era, have eliminated large areas of secondary scrub, red-tussock and snow-tussock grasslands, promoting the spread of fire-adapted and grazing-resistant short tussock plants (Molloy 1969). Successive invasions by introduced, sward-forming grasses, coupled with maintained grazing, resulted in conditions too hostile to permit early germination and growth of native shrubs and taller herbs. These activities have produced widespread invasion of introduced species, to produce plant communities that have little similarity to the pre-agricultural native vegetation. Contemporary short-tussock grasslands in alpine regions of the South Island have a large portion of their plant cover resulting from these factors (Connor 1965) and they are in a state of retrogressive succession, initiated and controlled primarily by cultural interference (Molloy 1969). Cessation of pastoral burning activities, and recovery of Maori land holdings used for grazing in high altitudes has, however, resulted in shrub invasion, especially on plateaus (Rogers and Leathwick 1994).

Successional Theories for Plant Communities

Perhaps the most fundamental and least understood theory of plant ecology is that of succession, a model, which still entails heated debate. Since succession was first described by Warming (1895) as a universal and unceasing process, a multitude of theories and interpretations of successional processes have been hypothesized. Early in the development of succession theory schools of thought developed around the work of Clements and Gleason. The Clementian school views succession as being deterministic, while those following Gleason envision it as a stochastic process.

Clements (1916) viewed succession as the movement of populations through waves of invasion, which rise and fall from initiation to climax in the habitat, which also corresponds with an associated progression of vegetation forms. This occurs in an ordered process of (1) nudation, (2) migration, (3) ecesis, (4) competition, (5) reaction and (6) stabilization. Succession will progress from one state to another until the highest state possible under present climatic conditions is attained. Clements found that succession was largely dependent upon the interaction of habitat, life-forms and species, in the progressive development of a formation. In this development, habitat and population act and react against each other until equilibrium is attained. Succession, therefore, is regarded as the life-history of the climax species. Gleason,

(1927) however took an individualistic approach to plants and regarded succession as all types of change in time, whether they were fluctuating or resulting in a fundamental change in the association.

Since these initial definitions, multiple definitions for succession have been put forward by a number of researchers including Grime (1979) who described it as 'a progressive alteration in the structure and species composition of the vegetation'. Miles (1979) claimed that succession was a 'directional change away from an initial state...changes which markedly alter the appearance of the patch such that it can be considered to have changed into a different type'.

Plant community succession is either primary or secondary. The difference between the two is dependent upon the substrate that is being vegetated. Primary succession occurs on undifferentiated and usually unweathered soils (Miles 1984) while secondary succession occurs on soils, which have previously supported plant cover that was removed or significantly altered (Clements 1904). Primary succession occurs on sites free of seeds or other propagules (Odum 1969). Secondary succession and the later stages of primary succession, however, may just reflect changing patterns of dominance of species that were always present throughout the successional episode but in minor 'roles' (Miles 1984).

In Miles' (1984) review of vegetation succession which included studies by Clements (1916), Egler (1954), Horn (1976), Connel and Slatyer (1977) and Whittaker and Levin (1977) he concluded that succession models relate to particular species in particular situations and not vegetation types. This is even more apparent in tundra environments where direct succession may occur through direct recolonization by earlier species due to the absence of later successional species (Shreve 1942, Mueller 1952, Babb and Bliss 1974). The idea of succession is an increasingly complex process that often may be site-specific and is continually evolving with the availability of new data. A better understanding of the successional model will only occur through continued research in a variety of environmental settings for extended time periods.

Due to the overwhelming number of definitions for the term 'succession', throughout this thesis it will refer to the continual evolution in plant community composition with time. The term will not be used in the context of a single theory, but instead will be considered as a general ecological process, the definition of which is constantly being expanded and altered with increasing knowledge.

Intermediate Disturbance Hypothesis and Initial Floristic Composition Model:

Studies concerned with vegetation responses to disturbances have found that changes in species richness are dependent upon frequency and severity of disturbance. This condition is embodied in the intermediate disturbance hypothesis (Connell 1978) and the initial floristic composition model of succession (Egler 1954).

The intermediate disturbance hypothesis predicts maximum species richness at intermediate levels of disturbance in which a tradeoff exists between specie's ability to endure disturbances and its ability to compete (Collins *et al.* 1995). Infrequent disturbances result in a decrease in species richness because dominant species monopolize resources and eliminate less adapted competitors. Species richness also decreases with higher frequency of disturbance when intolerant species are eventually out-competed. Therefore, species richness should be highest at intermediate frequencies of disturbance when conditions favour competitive and disturbance-tolerating species. Intensity of the disturbance also determines the species richness following disturbance. Species diversity will be greatest for a disturbance of intermediate intensity, allowing for the maximum colonization from both species that are more adept at dispersal as well as species, which are able to establish and grow in the presence of other species. Species richness is further favoured at intermediate time spans during post-disturbance succession. This is a result of late successional species displacing early successional species through competition producing species richness declines with time (Collins *et al.* 1995).

The initial floristic composition model of succession asserts that species found early and late in the successional sequence are present at the beginning of the sequence (Egler 1954). Therefore, succession can be considered a function of differential growth rates and survivorship among early and late successional species (Pickett *et al.* 1987). Species richness would therefore be expected to be highest early during succession and to decrease with time.

Markovian Model of Succession

The Markovian model of succession (van Hulst 1979) is the only model that is able to incorporate the two dichotomous views of succession expressed by Clements (1916) and Gleason (1926). Clements' concepts, which are viewed as deterministic, predict that succession will occur in an orderly manner, resulting in a self-sustaining climax state. This theory can be incorporated into the Markovian model, allowing for the estimation of the probabilities of transition from one state to another. The model may also be used to test Gleason's stochastic ideas and individualistic view towards plant species if each individual is treated as an entity, permitting an estimation of a series of probabilities that define all of the possible outcomes for the fate of the individual.

The Markovian model provides the opportunity to mathematically investigate the successional trends and predict plant community development. Species distribution data may further allow for the determination of the validity of the initial disturbance hypothesis according to the Markovian model predictions of species composition.

Constraints on Secondary Succession in Alpine Environments:

Secondary succession, considered to occur on developed soils is not thought of as being soil-driven. Rather it may be related to the life histories of species, their maximum growth rates, colonization abilities and interactions (Horn 1971, Tilman 1985). However, a secondary succession starting on nutrient-poor soils can be more similar to primary succession (Gleeson and Tilman 1990). Different morphology and physiology of dominant plants occurring at different times can be interpreted in the context of the resource ratio hypothesis of succession (Tilman 1985) which assumes that the dynamics in primary succession are caused by slow changes in soil quality as measured by the supply of N. According to the resource ratio hypothesis, initial dominants on nutrient-poor soils are predicted to have high-root to low-stem and leaf biomass ratios (Gleeson and Tilman 1990).

Secondary succession in alpine and arctic environments can result from abiotic factors (van Andel *et al.* 1993, Zobel *et al.* 1997). During the early stages of secondary succession, abiotic factors exert a more important influence than biotic factors such as competition (Bliss 1962). It is not until plant establishment is well advanced that biological constraints begin to be more influential than the physical environment on the development of a plant community (Billings 1987).

Objectives:

The purpose of the study was to ascertain the long-term response of plant communities to anthropogenic disturbances in high-alpine environments. The primary objective of the study was to determine how plant species composition, cover, and community structure change on disturbed and undisturbed, vegetation types 25 years after the initial disturbance. This was done by examining the environmental context of the sites, including microclimate and soil characteristics. Environmental factors were evaluated to determine their effect on processes within the site. The vegetation characteristics during first, second, third, fourth, and twelfth growing season (Mark

1978, Roxburgh *et al.* 1988) were compared to the 25th to assess the degree of recovery in comparison to the undisturbed. Vegetation differences between disturbed and undisturbed sites were investigated by field sampling of their botanical and environmental characteristics. Vegetation response models, including the intermediate disturbance hypothesis, initial floristic composition model and the Markovian model of succession, were assessed using changes in species richness and diversity.

Study Site:

The study was undertaken in the high-alpine cushionfield environment of the Old Man Range, in the Central Otago region of the South Island, New Zealand (Figure 1.1).

In the spring of 1974 an access road was constructed across the plateau summit of the Old Man Range, through a high-alpine cushionfield (Figure 1.2). The road was built for the installation and servicing of a television translator for the Broadcasting Corporation of New Zealand at Obelisk (1695 m a.s.l.) (Figure 1.3). Clearing of surficial material for the establishment of the road resulted in deposition of a 50-mm-deep layer of topsoil in 20-m-wide strips adjacent and parallel to the road edge (Mark 1978). Immediately following the disturbance, nine permanent transects were established in disturbed and undisturbed plant community types (Figure 1.4), all at altitudes above 1500 m. Plant species and cover conditions were recorded for 1975, 1976, 1977, 1978 and 1986, the 1st, 2nd, 3rd, 4th, and 12th growing season and made available by Prof. A.F. Mark, Botany Department, University of Otago, New Zealand.

Geology and Soils:

The study area was located between 1550 - 1690 m a.s.l. along the summit of the Old Man Range, composed of Upper Paleozoic and Lower Mesozoic Otago Schist (Billings and Mark 1961). The Old Man Range comprises part of the largest area of block mountains in Central Otago. Topographically, the range is dominated by broad, tectonically warped ridges and depressions, which are dotted with schist tors often exceeding 10 m in height (Stirling 1991). Microtopography of the Old Man Range in the high-alpine area varies with wind exposure and slope. Ridge crests and exposed sites are predominantly flat with exposed sections of the underlying schist. Earth hummocks, ranging from 20-40 cm in height and had basal diameters of 1-1.5 m, on relatively flat areas while stripes were confined to low-relief slopes of 4° to 7° (Billings and Mark 1961). Solifluction terraces were also present on slopes >7°.

The alpine soils of the Old Man Rangehave been classified as semiarid Obelisk-type soil (Upland brown earth) (Molloy 1993). They originated from loess and colluvium parent materials producing shallow, poorly-developed, deflated soils that are sandy with fragments of unweathered schist throughout (McGlone *et al.* 1997).

Climate:

The severe climate of the Old Man Range is mainly influenced by Antarctic air masses, which have strong winds and cool temperatures. Severity of climatic conditions in the Central Otago region is further increased owing to the semiarid conditions which result due to its positioning in the lee of the Southern Alps. This positioning has resulted in Central Otago being the driest and most continental region in New Zealand (Meurk and Blaschile 1990). The Old Man Range summit, however, experiences cooler temperatures with higher precipitation and lower evapotranspiration due to its increased elevation.

Mean daily temperatures on the Old Man Range; vary between 6.5° C and 6.0° C with a mean annual temperature of 0° C resulting in a poor growing season with only 986 degree days (0° C) annually (Meurk 1978). Air temperature extremes range between 24° and -19° C. Lapse rates determined for the Old Man Range are similar to those determined by Kidson (1931) for other New Zealand conditions. Lapse rates varied both with altitude and season, and were greater at higher altitudes (Mark 1965). Daily freeze-thaw cycles occur during 50% of the days of the year while 31% are below freezing and 20% are frost-free (Mark 1994). During a five-year period the longest frost-free period varied between 8 and 13 days. On an annual basis, soil temperatures at a depth of 10 cm had 38% frost-free days, 20% freeze-thaw and 42% continually frozen days. On average, soils remain unfrozen for 4 months during the summer and are continuously frozen for 3 months of the year (Mark and Bliss 1970).

The Old Man Range receives 1600 mm of precipitation annually with the majority being deposited as snow during the winter (Mark and Bliss 1970). Summer precipitation is typically low but still exceeds potential evapotranspiration, resulting in soil moisture values that remain greater than field capacity throughout the snow-free period (Mark and Bliss 1970). Snow cover remains 3-6 months and semi-permanent snow patches only completely melt 1 year in 10 (McGlone *et al.* 1997, Mark 1994). Additional precipitation inputs can also be attributed to fog, which enshrouds the Old Man Range 60% of the days in the year (Mark and Bliss 1970).

Winds on the Old Man Range increase in velocity with altitude (Mark 1965) and average 5.7 m s^{-1} at a gauge height of 1.25 m on the summit. These relatively high velocities have been attributed to the location of the range, which lies perpendicular to the prevailing winds (Mark and Bliss 1970). Seasonal variation in wind velocity is minimal (Mark and Bliss 1970) and winds are predominantly westerly (Mark and Bliss 1970).

Vegetation:

The vegetation of the Old Man Range study area can be classified into three distinct high-alpine plant community types: cushionfield, herbfield and soil hummocks/soil stripes (Mark and Bliss 1970). Cushionfield communities predominantly occur on the most exposed sites in the high-alpine, especially along the plateau summit where the most severe winds are experienced. Cushionfields are dominated by up to 15 species of cushion, mat or prostrate plant growth forms including *Dracophyllum muscoides* and *Raoulia hectorii* and vagrant lichens and dwarfed grasses (Figure 1.5). *D. muscoides* normally dominates cushionfield habitats and is considered to be the only important species. Community structure and composition change gradually in response to wind with cover inversely related to exposure.

Herbfield communities are characterized by herbs 10-20 cm tall, and are dominated by *Celmisia viscosa* and *Poa colensoi*. Although limited in extent, herbfield communities are also present in the study area where less severe winds are experienced and the greatest soil development occurs. This is usually associated with depressions between soil hummocks and stripes or in the lee of solifluction terraces and in and around tors.

The least prominent plant community found in the study area is that associated with soil hummocks and stripes. Variation in topography has resulted in a change in community pattern, which is closely associated with microtopographic setting. *Dracophyllum muscoides* can be found dominating the tops and sides of the features while *Celmisia viscosa* is typically associated with sheltered sites. Deep hollows between hummocks and stripes are predominantly characterized by snow species including *Celmisia haastii* and *Caltha obtusa* while *Poa colensoi* and *Luzula pumila* do not exhibit any preference for any of the available microhabitats.

Following road construction, disturbance sites on the Old Man Range summit were dominated by *Poa colensoi* and *Luzula pumila*, up to and including the 1986 sampling period. During the early successional period a distinct absence of pioneer species was observed throughout the study transects (Roxburgh *et al.* 1988).

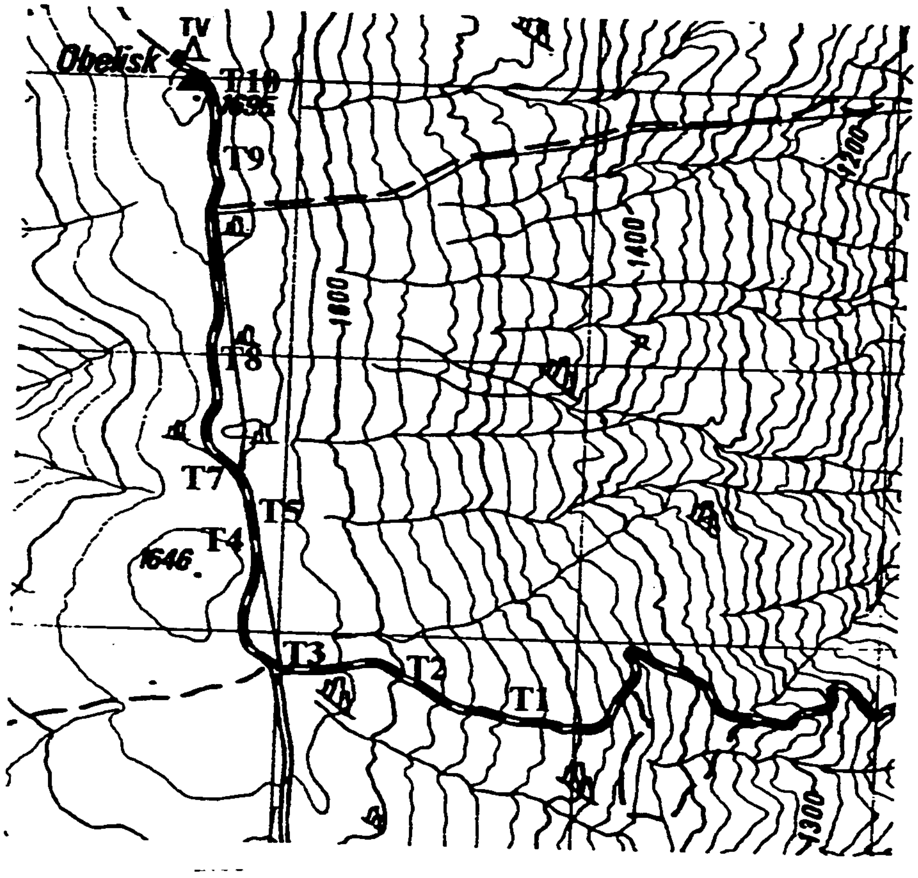

Figure 1.1 Location of study site on the Old Man Range, South Island, New Zealand. Numbers refer to location of permanent transects.

Figure 1.2 Example of the extent of disturbance immediately following road construction, 1975. Complete removal of organic material occurred in 20 m-wide strips parallel to the access road.

Figure 1.3 Installation of the B.C.N.Z. transmitter required the construction of the road along the summit of the Old Man Range, which resulted in the studied associated disturbances.

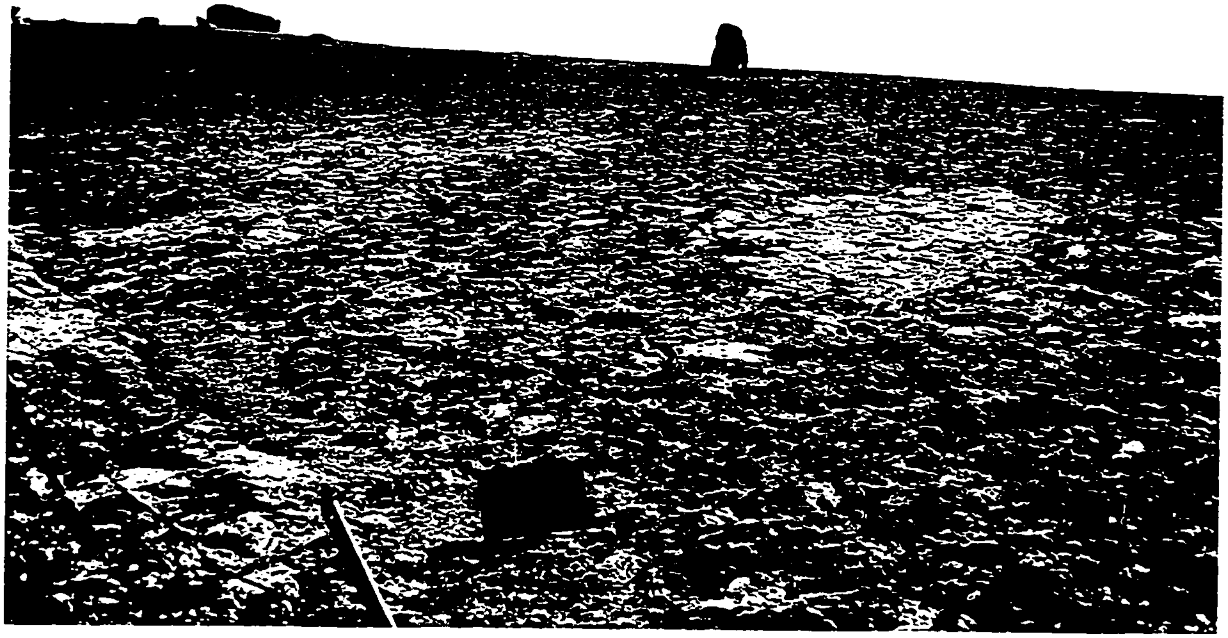

Figure 1.4 *Dracophyllum muscoides* cushionfield, which is the characteristic plant cover of the Old Man Range.

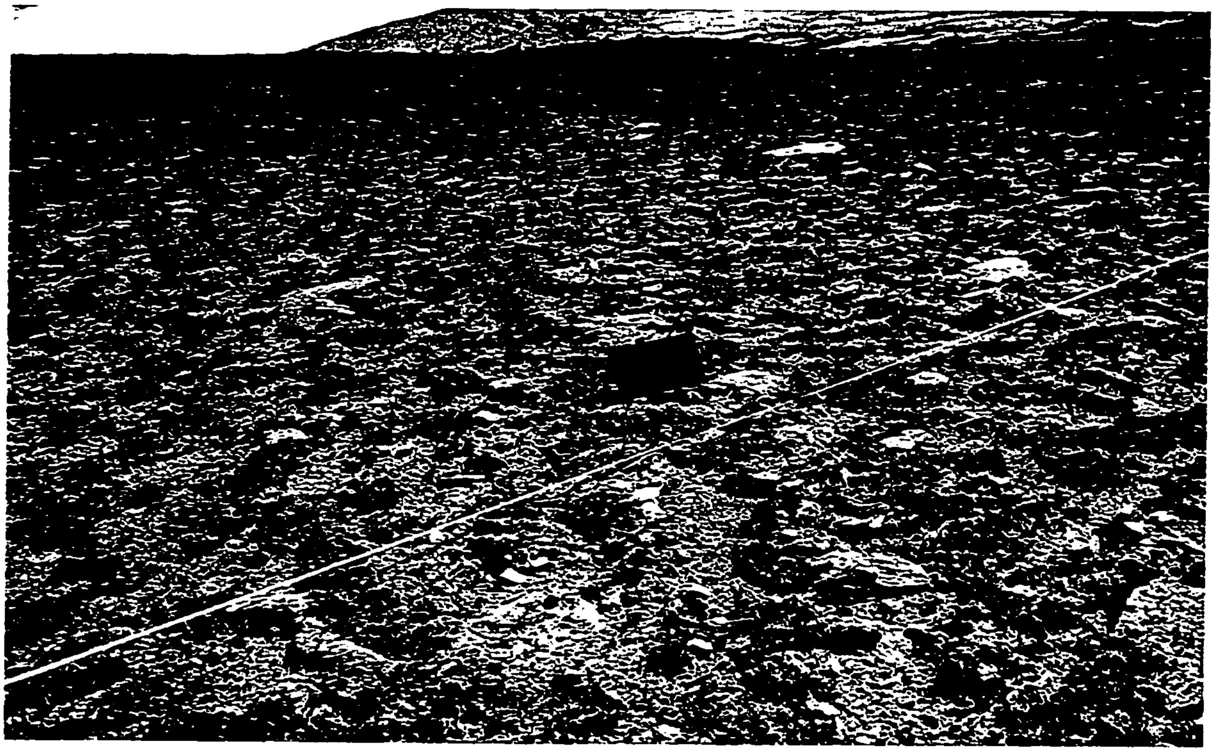

Figure 1.5 Example of permanent transects established by A.F. Mark.

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Chapter 2: Disturbances in the High-alpine of Central Otago, New Zealand: Microclimatic and Soil Property Responses

Introduction:

Plant community composition and its structure in alpine environments are frequently accentuated by complex topographic diversity and corresponding changes in environmental gradients (Douglas and Bliss 1977). The harsh conditions of alpine environments have been further shown to determine the status of a plant community. This has been attributed to: low temperatures, low infrared and solar irradiance and high wind velocities. These conditions restrict microbial decomposition, nutrient availability, soil fauna activity, plant growth, development and composition (Bliss 1956, Billings and Mooney 1968, McCown 1973). Inducing changes in environmental characteristics, including soil moisture, wind velocity and temperature, could further alter alpine vegetation (Nielson *et al.* 1981). A common means of altering environmental characteristics is by the disturbance of the vegetation and soil. Soil temperature, moisture and particle size will all experience change following disturbance, the degree though is dependent on the extent of the removal of overlying vegetation and/or organic horizons, and the amount of soil compaction. Loss of topsoil through deflation and erosion may also reduce soil nutrient levels.

By altering environmental characteristics, the recovery of the alpine community will be dependent upon the degree and type of change experienced by the soil and microclimate variables as well as specific vegetation characteristics (seed source, germination potential). The low productivity and slow revegetation rate observed in alpine environments has been ascribed to a variety of environmental factors such as low air and soil temperatures (Bliss 1962, Dennis and Johnson 1970), short growing season (Miller *et al.* 1976), low nutrient availability (Chapin *et al.* 1975, McKendrick *et al.* 1978) and low soil moisture (Billings and Bliss 1959, Douglas and Bliss 1977). Whether recovery is impeded or facilitated is dependent upon the nature of the environmental alterations and the environmental variables that are affected.

Objectives:

The objective of the study was to describe the microclimate and soil properties of undisturbed and disturbed treatments in the high-alpine of New Zealand, 25 years after initial disturbance.

Factors affecting environmental variables following disturbance:

-Effects of the removal of vegetation and organic horizon on alpine soils

Surface organic layers buffer the soil from near-surface energy exchanges and atmospheric energy inputs. Removal of vegetation or the organic horizon in tundra and alpine environments will result in higher soil temperatures (Bliss and Wein 1972, Hernandez 1973, Chapin and Shaver 1981, Kershaw 1983, Truett and Kertell 1992). Higher temperatures originate from the loss of insulation afforded by organic matter and a higher thermal conductivity that is observed in exposed mineral soils. Removal of the organic material will also result in a reduction in soil moisture due to enhanced evaporation (Haag and Bliss 1974, Gartner *et al.* 1983, Johnson 1987), resulting in warming of soils and a reduction of water available for plant uptake. Decomposition rates that are strongly dependent on soil temperature (Douglas and Tedrow 1959) will also rise, increasing the nutrient pool size and nutrient availability.

-Effects of nutrient status on plant community recovery

Succession following disturbance in the nutrient-poor alpine has been linked to nutrient availability, which affects recovery and successional rates (Huston 1979, 1980), community composition (Bowman *et al.* 1993) and the abundance of plant species (Chapin and Shaver 1985) on disturbed terrain. Reduced nutrient levels will result in less species diversity (Fox 1992, Jonasson 1992, Theodore and Bowman 1997) due to changes in species richness and eveness (Tillman 1984, 1987, Fox 1992, Jonasson 1992). An increase in nutrients will produce an increase in species diversity due to the release of subordinate species from nutrient limitation (Grime 1979, Tilman 1982). Therefore, a decrease in nutrients should cause a reduction in diversity due to the exclusion of additional species as a result of nutrient limitations. Dominant growth form is also related to soil nutrient status, which, in turn, affects above ground productivity (Webber 1978, Miller 1982, Chapin and Shaver 1985).

Perhaps the most important and limiting nutrient in alpine environments is nitrogen (N). Its availability is largely determined by soil microbial biomass through mineralization of soil organic matter, and by nitrogen immobilization and re-mineralization from biomass (Paul and Juma 1981). Low soil temperatures in alpine environments limit the amount of available nitrogen by impeding the decomposition and microbial transformation of organic nitrogen into nitrate (Haag 1974) resulting in low nitrification rates (Stutz 1973). Nitrogen levels experience a seasonal high below alpine snowpacks prior to and during snowmelt (Brooks *et al.* 1996). Nitrogen uptake in low-temperature soils has been slow (Dadykin 1958). Low plant community productivity in cold environments is due more to a low cycling rate of nitrogen than to low nitrogen levels.

The characteristically low growth rate of alpine plants could further be related to their efficiency of nitrogen use (Atkin *et al.* 1996a). Alpine plants have much lower photosynthetic nitrogen efficiency than lowland species (Korner and Diemer 1987). Atkin *et al.* (1996a) found that alpine *Poa* spp. had substantially higher rates of root and shoot respiration, using a greater proportion of daily fixed carbon in respiration (Atkin *et al.* 1996b).

Fluctuations in N levels have also been linked to community succession. During primary succession an increase in nitrate levels with age occurs until the last stage of the sere (Robertson and Vitousek 1981). Mineralization and nitrification should increase throughout the early phases of revegetation, as succession generally begins on nitrogen-poor substrates, but progressively increases the N pool due to fixation (Stevens and Walker 1970). Changes in nitrogen levels through secondary succession, however, are in dispute. Robertson and Vitousek (1981) found no consistent pattern in nitrate production except that the oldest sites had the greatest amount of nitrate. McLendon and Redente (1992) however, found that available N decreased during the early stages of secondary succession due to immobilization, which produced compositional changes associated with successional dynamics. This resulted from N depletion by rapidly growing individuals at the beginning of the chronosequence. As N resources were depleted, early seral species were replaced by less resource-demanding species.

Phosphorous limitations may also be relatively important to vegetation success and dynamics (Saebo 1968). Extractable phosphorous is low in alpine soils, likely due to cold soil temperatures (Chapin 1981, Clarkson 1985). Cold soil temperatures have also been found to reduce phosphorous uptake for oats, rye and potatoes (Zhurbitsky and Shtrausberg 1954, 1958) and may potentially be the same for alpine vegetation.

Methods:

Microclimate

A microclimate station, consisting of a Campbell Scientific CR10X datalogger and sensors, was established on the Old Man Range adjacent to Transect 7 (Figure 2.1) in November 1998. Environmental conditions were monitored on a continual basis until the station's removal in May 1999. The location for the microclimate station was chosen for its proximity to all of the dominant vegetation and microtopographic types observed within the study area, therefore, permitting the monitoring of conditions typifying the study area.

Thermal conditions were monitored for 8 sites that were representative of the dominant plant communities: 1. *Poa* tussock, 2. *Poa* tussock gap, 3. *Celmisia* clump (herbfield), 4. Road ditch top, 5. Cushion plant hummock top and 6. Cushion plant hummock hollow. Sites 1-4 were located in disturbed conditions originating from the 1974 roadway construction while sites 5-6 were in undisturbed locations. All monitored sites were <35 m apart. Additionally, wind speed was monitored in the *Poa* sites, while volumetric soil moisture was monitored in the *Poa* and cushionfield sites.

Soil and air temperatures were measured using 24 ga. type-T (copper constantan) thermocouples mounted on wooden doweling. Soil temperatures were measured at depths of 5 cm and 10 cm while the near-surface air temperature profile was monitored by sensors at 0 and 15 cm. These sensors were fitted with radiation shields made of 3.5-cm-diameter by 10 cm long white plastic tubing vented from the bottom and sides. All temperature sensors were connected to a multiplexer (CSI AM416) with a thermistor reference junction mounted on the center of the panel. Both the datalogger and multiplexer were in the same enclosure with the 32 Ah gel-cell battery that acted as a heat sink to moderate enclosure temperatures.

Wind speed was monitored by MetOne 014 anemometers with an offset of 0.447 m s^{-1} in the *Poa* site. The anemometer was placed 25 cm above the surface to allow for the measurement of near-surface winds that were more representative of wind conditions experienced by the low-lying high-alpine vegetation than the standard height of 150 cm. Based on a lack of structural and surface roughness difference and given the close proximity (<15 m apart) of the disturbed and undisturbed sites, it was felt that the one anemometer was sufficient to describe wind speed for both surface types.

Soil moisture probes (Time Domain Reflectometry method) were used to monitor volumetric soil moisture in the *Poa* and cushionfield. To install the probes, a soil block was excavated and the probe was inserted in the undisturbed soil of the pit wall at 10 cm depth parallel to the surface. The soil block was then replaced. Calibration of the soil moisture probes was not required as the soil properties which affect measurement, high clay content (> 30%), high organic matter content and high quartz content were not a factor in the monitored soils (Campbell Scientific 1996).

The measurement interval was 60 s for each sensor except those measuring soil moisture where it was hourly. The 60 values accumulated each hour were averaged with maximum and minimum values output each hour. The 1440 values stored daily for each sensor were then processed to provide mean, maximum and minimum daily values. Soil moisture values were output hourly with daily mean, maximum and minimum values derived from the 24 daily measurements.

Soils

Soil samples and soil pit descriptions were collected over a two-day-period in February 1999 from each of the disturbed and undisturbed portions of the permanent transects, for a total of 22 samples. Soil pits were excavated adjacent to the fifth, randomly-located cover plot sampled in the vegetation survey.

Soil pits were dug to the depth of the rooting zone. Horizons were identified and their thickness recorded. Special attention was given to pits in disturbed terrain to determine if the pre-disturbance, buried soil profile could be identified.

Undisturbed soil samples were taken prior to the excavation of soil pits. A thick-walled cylindrical tube (d = 6.9 cm, h = 12.8 cm) of 478.6 cm^3 was hammered into the ground until flush with the surface (Figure 2.2). This depth adequately sampled the rooting zone. After extraction, samples were double bagged and transferred to University of Otago's Botany Department lab within two days.

Laboratory analysis was carried out at both the University of Otago and the University of Alberta. While at the University of Otago, soil samples were weighed, air-dried and measured for: bulk density, volumetric water content, colour, and gravel (> 2mm) fraction. At the University of Alberta soil samples were further analyzed for: pH, organic matter content, partial nutrient analysis and determination of particle size distribution for the <2 mm fraction. Bulk density was determined from the dry weight of the 478.6 cm^3 (expressed as kg m^{-3}) sample. Volumetric water content was expressed as a percentage of wet soil on a wet weight basis. Soil colour was determined on dry soils with the use of a Munsell color chart. The gravel fraction was separated by dry sieving while the <2 mm fraction was determined using the Boyocous Hydrometer Method (Kalra and Maynard 1991). Particle size was expressed as a percentage of the dry weight. The Fisher Accumet pH Meter was used to determine the pH of a soil paste.

Organic matter content was derived by the loss-on-ignition method (LOI) and expressed as a percentage of the <2 mm soil fraction. Partial nutrient analysis included the measurement of total N, P, K, NO_3 and NO_4. Total N and P were determined by the Standard Kjeldhal digestion method (McGill and Figueiredo 1993), while a KCl extraction and Technicon Autoanalyzer II were used to calculate NO_3 and NH_4 values (Kalra and Maynard 1991).

Statistical Analysis

Microclimate

Near-surface (15 and 0 cm) and soil (-5 and -10 cm) temperatures were statistically tested to determine if temperatures differed significantly between sites due to varying vegetation and microtopographic characteristics. Non-normal distribution of the data made it necessary to use the Kruskal-Wallis one-way analysis of variance based on ranks (Zar 1999). To further isolate the significantly different group or groups, a multiple comparison procedure (Tukey Test) was used.

Soils

Statistical analyses were performed on all the measured physical and chemical properties of the soil samples. Significant differences of these properties between disturbed and undisturbed sites were determined through the use of t-tests with the SigmaStat 2.03 program.

Degree Day Calculations

Degree days are the cumulative number of degrees above or below a particular threshold for a particular period. Thaw degree days (TDD) (> 0° C) and freezing degree days (FDD) (< 0° C) were calculated for all sampled sites at each sampled height (-10, -5, 0, and 15 cm) based on daily pure averages.

Results:

Microclimate

Near-surface Air Temperature

Mean and minimum air temperatures, 15 cm above the surface varied little between vegetation and microtopographic types (Figure 2.3). However, there were significant differences in maximum temperatures (Table 2.1). The *Poa* gap had higher temperatures than the *Poa* tussock, hummock, *Celmisia*, and ditch. The hollow also had higher temperatures than the ditch at 15 cm above the surface.

Surface temperatures (0 cm) (Figure 2.4) were more widely influenced by varying vegetation and microtopography than temperatures at 15 cm had been. Mean temperatures were significantly lower in the hummock (Table 2.1) than the *Poa* gap, *Poa* tussock, and hollow. Vegetation and microtopography had a greater influence on maximum and minimum temperatures at the surface resulting in a greater number of significant differences in temperature among treatments. On average, maximum temperatures in the *Poa* gap were the highest of all the treatments, significantly higher than the hollow, ditch, *Celmisia,* and hummock. The *Poa* tussock was also significantly higher than the hollow, ditch, and *Celmisia*. Maximum temperatures in the hummock were higher than the hollow and ditch, while, *Celmisia* was higher than the hollow. Minimum temperatures in the *Poa* gap were significantly lower than the hollow, *Celmisia,* Hummock and ditch. Additionally, the *Poa* tussock had significantly lower minimum temperatures than the *Celmisia*, hummock, hollow and ditch. The hollow was also higher than the ditch and hummock.

A greater number of freeze-thaw episodes (minimum temperature < - 0.5 °C, maximum temperature > 0.5 °C during a 24 h period) (Table 2.2) were observed in disturbance-associated treatments than undisturbed sites. The *Poa* gap and *Poa* tussock had 93 and 86 episodes each, respectively, while only 22 and 45 episodes occurred for the Hollow and *Celmisia* respectively, less than half of that experienced in disturbed conditions. The Ditch treatment that was void of vegetation had 58 freeze-thaw cycles, approximately 30 fewer cycles than other disturbance sites.

Soil Temperatures

Mean temperatures, 5 and 10 cm below the surface did not vary significantly with vegetation type and microtopography (Table 2.1). Maximum temperatures 5 cm below the surface were generally significantly higher in sites which experienced significantly higher maximum temperatures at the surface (0 cm). The hummock, *Poa* tussock and gap were all significantly higher than the hollow, while the hummock and *Poa* tussock were significantly higher than the *Celmisia* site. Maximum temperatures 10 cm below the surface were higher under exposed and topographic high features (*Poa* tussock, hummock and ditch) than the hollow, *Celmisia* and *Poa* gap.

The *Poa* gap and hollow experienced significantly higher minimum temperatures 5 cm below the surface than the hummock and *Poa* tussock (Figure 2.5). Temperature was not recorded at 5 cm below the surface at the ditch site. Minimum temperatures at 10 cm below the surface did not respond in the same manner as was experienced at the surface (Figure 2.6). Much less variation between treatments was observed and treatments responded differently than at the surface. The ditch was significantly cooler than every treatment except for the hummock sample (Table 2.1).

Diurnal soil and near-surface temperature

Magnitude and extent of diurnal temperature change increased from December to February for all sites and rapidly decreased from March to May. The *Poa* tussock (Figure 2.7) experienced the greatest daily range in temperature, attaining the highest surface temperatures of all the sites. Surface temperatures were higher than all other measured temperatures until April, after which surface temperatures and temperatures at 15 cm were similar. Little diurnal change in temperature was observed at 10 cm below the surface and did not increase noticeably during the summer. Temperatures at 5 cm below the surface also varied little but became more pronounced during the peak of the summer, January and February. Daily fluctuations in surface temperatures at the ditch (Figure 2.8) were greatest from November to January, after which surface temperatures were similar to temperatures at 15 cm. Temperatures 10 cm below the surface were similar to temperatures at the surface and at 15 cm throughout the study. Temperatures at -10 cm also experienced the greatest diurnal range, usually in excess of 5 °C, the highest observed difference in all of the sites at this depth. The hummock site (Figure 2.9) experienced higher temperatures at the surface until May after which it was the same as at 15 cm. Temperatures at depth increased with progression of the summer, resulting in a more prominent diurnal change. The difference between surface and soil temperatures also increased as the summer progressed and decreased with the onset of autumn.

Peak daily temperatures 10 cm below the surface (Table 2.3) occurred first in the ditch treatment during the early afternoon (16:00) followed by the hummock and *Poa* sites after a 2-hour delay. All three of the measured sites at 5 cm below the surface experienced a peak temperature at approximately 16:00. Diurnal temperature peaks at the surface occurred first in the ditch (13:00-14:00) followed by the hummock and *Poa* environments after a 1-2 hour delay.

Diurnal temperatures at 10 cm below the surface reached highs during mid-growing season in the ditch but were delayed by a month in the hummock and *Poa* sites (Table 2.3). Temperatures at 10 cm below the surface were greatest in the ditch treatment throughout the entire growing season, followed by the *Poa* and hummock sites. During the early-growing season, temperatures 5 cm below the surface were the highest in the hummock site but were higher in the *Poa* for the mid- and late-growing season. The *Poa* site also experienced the highest surface temperatures throughout the study. During the first part of the late-growing season the ditch had the highest temperature while the *Poa* treatment had the highest temperature at 15 cm during the latter part of the late-growing season.

Degree Day Calculations

Change in TDD values with height was characterized by a decrease in values from 15 cm above the surface to the soil surface (Figure 2.10), after which values increased to a depth of 5 cm into the soil followed by a decrease with depth. The Hollow site, however, experienced an increase in TDD values at the soil surface, after which the values changed little with depth. The ditch site which experienced the highest TDD values at heights > 0cm, did not experience a warming at a depth of 5 cm but instead cooled further, to one of the lowest values of all of the sites. Topographic lows (*Poa* gap, Hollow) typically had lower TDD values 15 cm above the surface while topographic highs (*Poa* tussock, Hummock) had lower TDD values at the soil surface (0 cm).

FDD values decreased with height above the soil surface to a value of 0 at a depth of 10 cm (Figure 2.11). FDD values approached similar levels 15 cm above the surface with the Hummock site experiencing the greatest FDD values at heights > 0 cm while the vegetation-free ditch site had the lowest values. Differences in FDD values were most pronounced at the soil surface and were only a consideration for topographic highs at a depth of 5 cm.

Soil Moisture

Soil moisture values (Figure 2.12) generally decreased through the mid-growing season to the lowest recorded values for all three treatments on Julian day 67, prior to which time soil moisture values in all three treatments were nearly identical and had been so for the preceding 10 days. Julian day 68 experienced a substantial input of moisture resulting in a rapid recharge of soil moisture to early-growing season levels. Following the recharge a slight increase in soil moisture levels was observed for the remainder of the monitoring period.

The soil moisture values found in the cushionfield after intermediate moisture input events remained high for brief periods of time (~5 days) except during a 35-day-period occurring at the height of the summer drought during which soil moisture values were at their lowest.

Small moisture inputs and losses, which were characteristic of the soil moisture record, had a much more subtle difference between treatments than the three major input events. During the major inputs, a substantial difference in soil moisture values between treatments was observed. The cushionfield was subjected to a much greater increase than *Poa*.

Although the magnitude of soil moisture inputs and losses varied between treatments, a delay in soil moisture fluctuation was not observed except during moderate moisture inputs. During these events moisture input as snow was likely the norm, while the other inputs were typically in the form of rain

Soil Moisture and Air Temperature

On four occasions, soil moisture values in the cushionfield were greater than the *Poa* site following intermediate moisture input events. All four of these periods were also associated with a preceding period during which surface temperatures were near, or more often less than 0°C, and were immediately followed by rapid increases in temperature (Figure 2.13). The increase in temperature occurred in conjunction with an increase in soil moisture that was most noticeable in the cushionfield. Although smaller and greater observed moisture inputs during which tussock moisture values were greatest were often associated with a decrease in temperature the temperature usually remained above 0 °C

Wind velocity

Mean wind velocity, 25 cm above the surface in the cushionfield environment, varied between 0 m s^{-1} and 10 m s^{-1} (Figure 2.14). Maximum wind velocity values for the cushionfield were usually twice that of the mean velocities and peaked at 23 m s^{-1}.

No wind activity in the cushionfield was observed during two periods, Julian days 335-358 and 80-138. The latter period, however, experienced two brief pulses on day 88 and 98. The inactivity in the cushionfield may be attributed to equipment malfunction or another factor that may have impeded proper functioning of the anemometer. It is highly unlikely that no appreciable amount of wind occurred during these periods as the study site is characterized by continuous, strong winds (Mark and Bliss 1970). It is possible that the winds were the threshold speed (0.447 m s^{-1}) of the anemometer.

Soils

Soil profiles did not vary much among the undisturbed and disturbed sites. Soils were classified as semi-arid Obelisk soil (Upland brown earth) (Molloy 1993). The sampling sites commonly had two horizons, an Ah and Bw horizon of varying depths (Figure 2.15). Although effort was taken to locate a third horizon indicative of the deposition of extra soil in disturbance areas no such layer was identified. Soil pits were dominated by a thick platy schist gravel lag found on the surface and occurring within the uppermost portions of the profiles that rapidly declined with depth. Gravel concentrations were usually found closer to the surface in undisturbed soils. Both the undisturbed and disturbed soils lacked a substantial O horizon; instead, a distinct break between plants and underlying mineral horizons was found, with little litter present. Soils had good structure and friability below the gravel-dominated surface.

Disturbance and deposition of additional soil in disturbance sites did not leave any significant effects on soil physical properties within the rooting zone, 25 years after the initial disturbance. Bulk density values were found to be moderate and slightly, but not statistically higher in disturbance areas (Table 2.4). Moderate moisture values were observed, however, they were lower in disturbed sites. There was almost a 10% greater stone fraction in undisturbed soils. Sand, silt and clay averages, however, were not statistically different between treatments, with slightly higher sand contents found in disturbance sites.

Soil organic matter was significantly lower in the disturbed soils (Table 2.4). K concentrations and total N also decreased in disturbed soils. A significant increase in pH and NO_3 occurred in the disturbed soils. NH_4 also increased while P remained almost exactly the same as in the undisturbed soils.

Discussion:

Near-surface temperature

Air temperatures 15 cm above the surface were not significantly influenced by whether they occurred in an undisturbed or disturbed environment. The significantly lower maximum temperatures found in the ditch, hummock, *Celmisia* and *Poa* tussock sites that are the most prone to wind suggests that wind is the most important factor in regulating temperatures above the surface.

Surface temperatures (0 cm) appear to be closely associated with a number of factors including topography and vegetative cover, and are not specifically related to whether it was disturbed or not. The significantly lower mean surface temperatures in the hummock site were primarily the result of wind. The influence of wind was greater in the hummock site owing to increased exposure and the characteristic low-lying vegetation that didn't afford protection from wind, nor retain much longwave radiation. Although the ditch site lacked vegetation and therefore was exposed to the full effects of wind, resulting in lower maximum temperatures, the mean temperature was not lower than the hummock site, likely due to dryer soils resulting from the absence of overlying vegetation. Dryer soils would result from enhanced evaporation and no transpiration owing to the complete plant cover removal thereby enhancing exposure, facilitating rapid drying of surface soils. Once the surface dried, less energy would be required for evaporation releasing radiation to sensible heat, resulting in an increase in soil surface temperature.

Diurnal variation at the surface was inversely related to soil moisture. Sites that had the greatest soil moisture levels attained the lowest temperatures on a daily basis. Higher moisture contents result in high specific heat that causes lower thermal conductivity, decreasing the susceptibility of wet sites to variation in temperature (Davey *et al.* 1992). Diurnal variation in the moist sites would also be reduced due to lower extreme temperatures resulting from the consumption of energy during evapotranspiration. The absence of vegetation in the ditch site would prevent the interception and retention of radiation at the surface, resulting in an increase in solar heat flux. Maximum surface temperatures in the ditch, therefore, occur when incoming radiation is greatest and are not dependent on the retention of outgoing radiation as the other sites were for attaining maximum surficial warming.

Soil Temperature

Soil temperatures 5 cm below the surface were substantially altered by disturbances. Changes originated from the removal of vegetation, replacement with different vegetation types and structural alterations. Variation was also observed due to microtopographic differences. Topographic highs (hummock, *Poa* tussock) had lower minimum and higher maximum temperatures than topographic lows (hollow, *Poa* gap) and experienced greater FDD values. The greater temperature extremes observed in the topographic highs result from higher exposure to wind, causing greater heat dissipation and enhanced radiative losses associated with a higher sky view factor (Oke 1987).

Although differences in peak diurnal temperatures at the surface and 5 cm below the surface were not significantly different, surface temperatures in the *Poa* environment attained higher maximums than the hummock environment. Temperatures 5 cm below the surface were greater in the hummock site than the *Poa* tussocks for the first half of the growing season. During the period in which the hummock's subsurface temperatures were higher, their soil moisture levels were also higher than in the *Poa* tussocks. The temperature differences could be due to the influence of soil moisture. The effect of higher surface temperatures in the *Poa* environment was offset by the dry soil conditions that offered greater resistance to soil heat flux. Once soil moisture values in the *Poa* and hummock environments approach the same level, with the progression of the growing season, the difference in subsurface temperatures would not be offset by the influence of varying soil moisture between sites.

Removal of the vegetation and organic matter in the ditch site had a substantial effect in raising soil temperatures down to 10 cm depth. Absence of an insulating plant cover resulted in significantly lower minimum and significantly higher maximum temperatures. The greatest effect, however, was the substantially higher diurnal temperatures recorded for the ditch subsurface. There was also greater diurnal variation at the surface and 15 cm above ground. Removal of vegetation also led to a drying out of the soil thereby preventing the buffering effects of soil moisture that might have otherwise better controlled seasonal and diurnal variation measured within and among sites. Patterns observed 5 cm below the surface did not extend to greater depths. While topography appeared to largely influence subsurface temperatures at -5 cm, temperatures 10 cm below the surface were more influenced by soil moisture levels.

Soil Moisture

Although there was no appreciable distance between TDR units in the study area (all units occurred within a 10 m radius) the *Poa* treatment continually had significantly lower amounts of soil moisture than the Cushionfield, which was considered to be representative of undisturbed conditions. Soil texture and bulk density in the disturbed and undisturbed treatments did not differ significantly and therefore should not have been the cause of soil moisture differences. The differences must therefore be attributed to variation in vegetation and microtopography.

Moisture values in the cushionfield and *Poa colensoi* were low during all precipitation events except during moderate events that were additionally characterized by a drop in temperature to below freezing, followed by a rapid increase in temperature. Such events can be attributed to mid-growing season snowfall events which are common at high altitudes on the Old Man Range (Mark 1965), in which snow preferentially accumulates in cushionfield environments. Snow in the cushionfield could readily collect amongst the depressions that characterize the microtopography of the undisturbed sites. Snow collecting in the depressions would then be less prone to removal by wind action, allowing for the retention of snow for a prolonged period. Retention of snow in the disturbed sites would be hindered by the lack of microtopography, resulting from the uniform blading of the disturbed areas during road construction. The relatively flat surfaces found in the disturbed where microtopographic variation was limited to *Poa* tussocks would be more efficiently scoured by the severe winds that continually blow across the Old Man summit, preventing accumulation of snow.

Accumulated snow would remain until air temperatures increased sufficiently to melt the snow thereby increasing soil moisture. The increase in soil moisture coincided with an increase in temperature after a period of <0°C. Disturbed sites were not completely devoid of snow during these events, less snow just happened to accumulate.

Observed differences in soil moisture among treatments did not result from differences in plant cover (51% vs 56% for disturbed and undisturbed respectively). The influence of plant cover was mainly due to structure. The erect graminoids of the disturbed sites extend further into the wind profile and likely experience a greater deal of evapotranspirative loss than the low lying species found in the undisturbed sites. Although differences in ability to control moisture loss (stomata, cuticle, mesophyll resistance, etc.) may have existed between graminoids and non-graminoids, erect graminoid species would experience greater potential evapotranspiration due to the greater depth into the atmosphere that they extend, areas of greater wind speed.

Differences found in soil moisture between disturbed and undisturbed sites can be attributed to both differences in vegetation type and microtopography that originated from the initial disturbance. Type of precipitation is also midsummer snowfalls and fog can be important during drought years when rainfall input is low.

Soil Nutrients

Following vegetation and organic matter removal, available nutrients from the uppermost portion of the soil during road construction were lost, resulting in nutrient-poor soils immediately following disturbance as observed by Roxburgh *et al.*'s (1986) bioassay experiments. Soil fertility would have been low following organic matter removal and soil deflation due to the direct loss of nutrients and the reduction of nutrient cycling that would have occurred with organic matter removal. The increase in soil temperature observed in the disturbed areas, however, would have favoured an increase in decomposition rates (Douglas and Tedrow 1959) due to increased microbial activity and chemical decomposition, thus enhancing the soil nutrient pool. Increased nutrient levels coupled with the absence of competitors would have made the disturbed areas more prone to colonization by graminoids (Bliss and Wein 1972, Chapin and Chapin 1980, Chapin and Shaver 1981, May and Webber 1982, Shaver and Chapin 1986). The increase in graminoid cover would result in enhanced organic matter accumulation on the disturbed soils due to annual shoot senescence. Carbon and nitrogen mineralization rates would also increase under a graminoid-dominated community (Miles 1985). The combined effect of an increase in soil temperature and addition of organic matter would result in increased decomposition rates and nitrate production resulting in significantly higher ammonium levels in the disturbed soils than in the undisturbed soils. The high potential frequency of frost activity observed in the disturbed treatments could additionally result in higher levels of cations and nitrogen (Jonasson 1986).

Disturbance and removal of organic material should have resulted in accelerated soil weathering resulting in a decrease in pH (Bollen *et al.* 1969, Miles 1985). Average pH values in the disturbed treatments, however, were significantly higher. The higher pH values may potentially be attributed to the dominance of graminoids, which have been found to produce less acidic soils in North American grasslands (Jenny 1980, Ugoloni and Edmonds 1983). While change in plant cover has been observed to affect soil pH on the Old Man Range summit (Mark and Bliss 1970), it is also probable that the increase in pH found in disturbed soils could be due to exposure of underlying soils. Deflation, following disturbance would have exposed the higher pH horizons, which were originally found lower in the profile (Mark and Bliss 1970, Mark 1994). An increase in soil pH would also result in higher phosphate availability (Barel and Barsdate 1978). The increase in pH would also improve the litter quality, increasing the cycling rates of nutrients (Chapin 1981). Nutrient levels have currently achieved levels similar to those of the undisturbed soils. Further increases in organic matter should result in a decrease in pH to levels found in the undisturbed soils.

Addition of soil, and the removal and gradual replacement of vegetation, appear to have resulted in a more significant modification of the soil chemistry than the physical properties.

Soil Loss

Initial disturbance during road construction included deposition of a 50-mm-deep layer of topsoil from the road onto the adjacent surfaces (Roxburgh *et al.* 1988). While topsoil additions would be viewed as being beneficial due to the addition of limited soil nutrients, any benefits that may have aided a speedier vegetation recovery were lost as a result of deflation. Following the disturbance, the vegetation-free areas were exposed to the intense winds found on the summit of the Old Man Range, resulting in rapid deflation of disturbed soils. Loss of soil recorded in 1975 and 1977 was significantly greater following road construction in the disturbed sites than in undisturbed sites (Table 2.5), producing a net loss of 15.28 cm of soil during the initial three years following disturbance (Mark 1978). Removal of plant cover resulted in the loss of the buffering and binding ability of soil by root networks against the influence of wind. This caused enhanced deflation of deposited soil as well as 10 cm of the original soil. Wind-induced soil loss would be further enhanced by the lack of microtopography in the disturbed areas, allowing for lower surface resistance and a thinner laminar layer. The reduced ability of the ground surface to lower near-surface winds would likely result in a slower recovery of the disturbed areas since the substrate would be too instable to permit seedling survival.

Soil loss and prevention of establishment of plant cover may have been further enhanced by the formation of needle ice. This phenomenon loosens the surface particles producing conditions more prone to wind erosion (Kind 1981). During spring and fall months the frequency and areal extent of needle ice may be high, thereby hindering the development of plant cover in the disturbed areas. Soil surfaces would be further jeopardized during the thaw and melting of needle ice that produces a fine, highly erodable surface that can be acted upon by rain and wind (Brink 1964, Soons 1967), resulting in an ongoing loss of soil. Characteristic 'raked ground', associated with needle ice development was observed throughout the disturbed portions of the study area, confirms that needle ice is a common phenomenon on the Old Man Range (Billings and Mark 1961). Plant disturbance associated with needle ice has been observed by Soons and Greenland (1970), Hastenrath (1977) and Johnson and Billings (1962) and has been linked to mechanical stresses in the rooting zone (Brink *et al.* 1967).

Needle ice development relies on the correct combination of microclimate, soil water and soil physical properties. A specific radiative-evaporative atmospheric heat sink is required to produce a strong temperature gradient to undercool the soil surface (Outcalt 1969). Needle ice development is further dependent on a gradual rate of cooling; otherwise soil water freezes *in situ* rather than migrating to form segregation ice (Soons and Greenland 1970). Although Outcalt (1971) found that ice segregation should occur at a soil moisture volume of 27% for sandy loams, soils in the study area were able to form needle ice due to the higher proportion of fines found in the soils. Needle ice formation is more likely to occur either early or late in the growing season when higher soil moisture values and cooler, more conducive temperatures may occur.

Summary:

Following the road construction disturbance on the Old Man Range summit in 1974, abiotic factors were substantially altered through the removal of overlying vegetation, loss of topsoil and removal of microtopographic variation. Loss of topsoil during construction and subsequent deflation enhanced by prevailing strong winds and surface modification by needle ice further resulted in the loss of soil mass, nutrients and organic matter.

Disturbance of the high-alpine environment resulted in a significant increase in soil temperature and decrease in moisture. The increase in soil temperature was due to the removal of vegetation and subsequent re-colonization by a plant community and structure unlike that of the undisturbed sites. Establishment of a graminoid-dominated community resulted in a decrease in soil moisture owing to an increase in evapotranspirational losses due to increased wind exposure. Minimal microtopographic variation in the disturbed sites resulted in an inability to retain snow during summer while in undisturbed hummocky sites, snowmelt collected in the hollows to enhance soil moisture content. Soil nutrient levels initially decreased following disturbance but after 25 years, appear to have returned to undisturbed levels. This can be attributed to the observed increase in soil temperatures that would enhance biological activity and chemical decomposition. The greater concentration of ammonium in the disturbed soil is likely due to increased nitrogen mineralization and nitrification rates in disturbed soils.

Disturbances associated with road construction in the high-alpine of the Old Man Range produced significant changes in environmental parameters that have persisted for 25 years. The landscape was substantially altered during the initial clearing, re-deposition of topsoil, and following natural disturbances, which have since operated in these areas to produce soil and microclimatic conditions that remain distinct from adjacent undisturbed areas. Soils of disturbed sites are warmer, drier, more basic, have less organic matter but higher ammonium content. Recovery of the disturbed sites, as in other alpine environments globally, has been a slow process, which is still not yet fully realized.

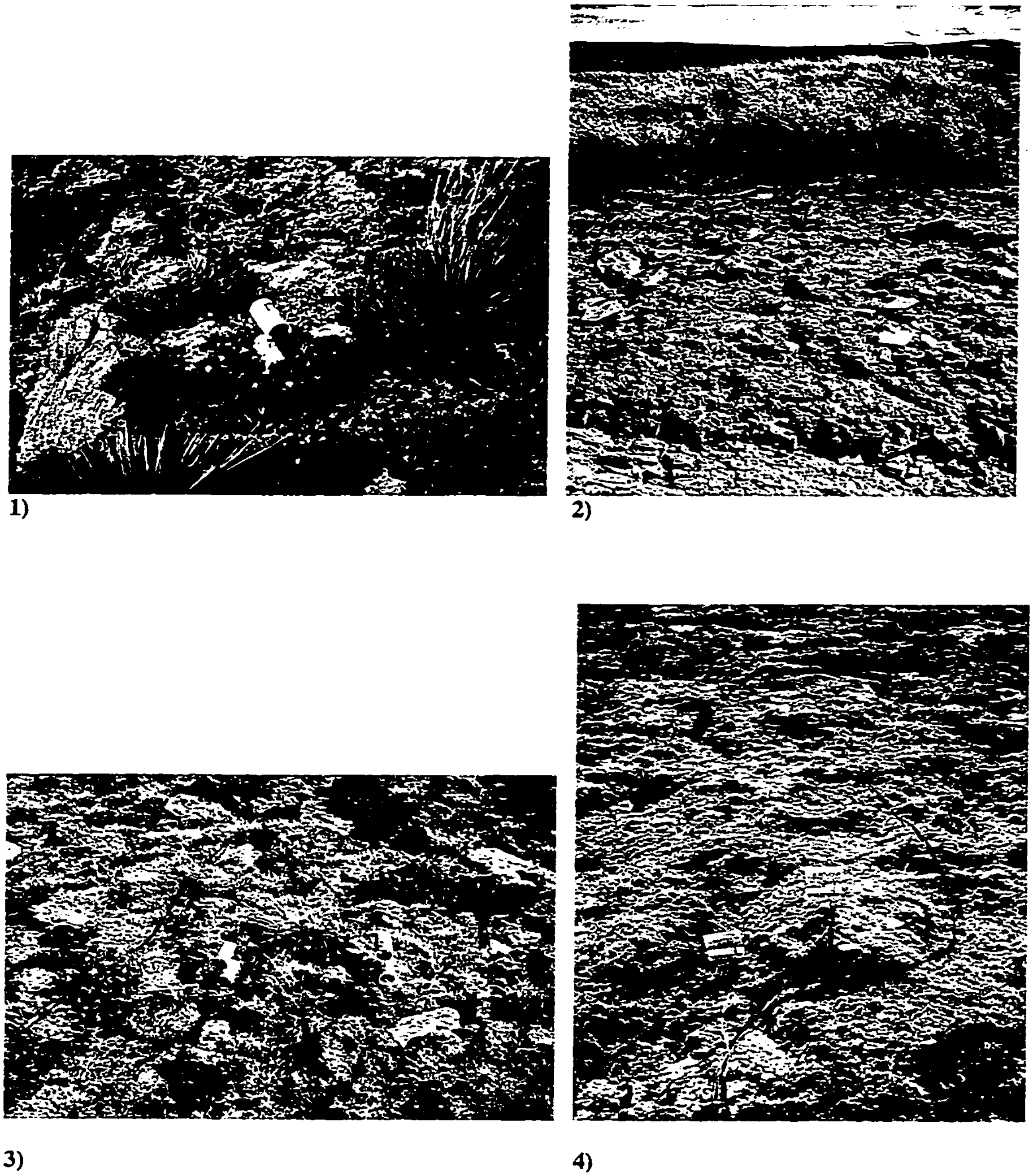

Figure 2.1 location of microclimate sensors in the 1) *Celmisia*, 2) ditch, 3) *Poa* gap and *Poa* tussock and 4) hummock and hollow sites. Sites 1-3 are classified as disturbed treatments, while site 4 is undisturbed.

Figure 2.2 Example of soil bulk density tin, which was used to collect soil from the rooting zone.

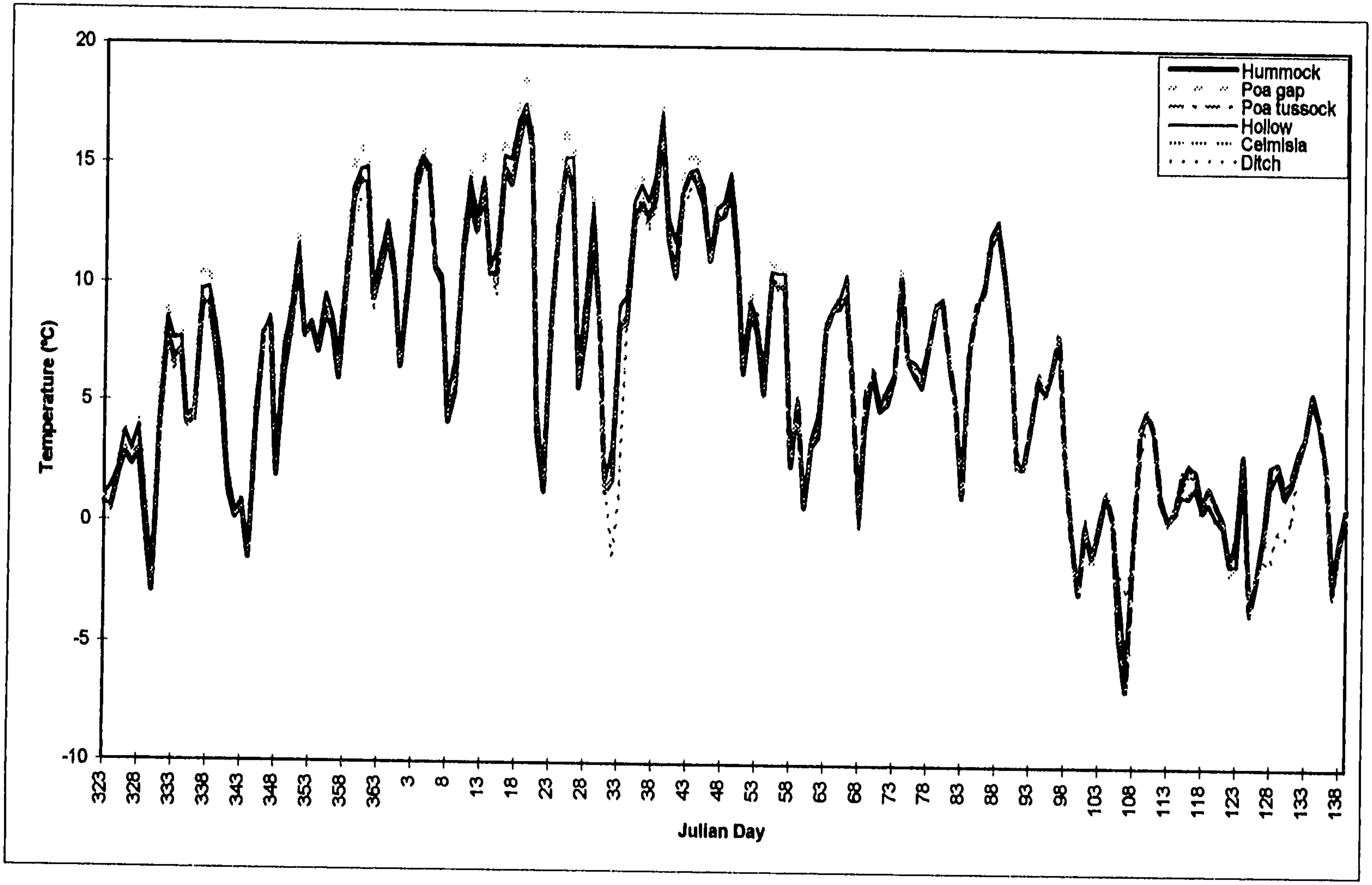

Figure 2.3 Air temperature 15 cm above the surface for the Julian Day period 322-139

		Minimum	Mean	Maximum
15 cm				
Celmisia	A			
Hummock	B			
Hollow	C			F
Poa tussock	D			
Poa gap	E			F,B,A,D
Ditch	F			
0 cm				
Celmisia	A	E,D,		C
Hummock	B	E,D,		C,F
Hollow	C	E,D,F,B	B	
Poa tussock	D		B	C,F,A
Poa gap	E		B	C,F,A,B
Ditch	F	E,D		
5 cm below				
Celmisia	A			
Hummock	B			C,A
Hollow	C	B,D		
Poa tussock	D			C,A
Poa gap	E	B,D		C
10 cm below				
Celmisia	A	F		
Hummock	B			C,A,E
Hollow	C	F		
Poa tussock	D	F		C,A
Poa gap	E	F		
Ditch	F			C,A,E

Table 2.1 Results of an ANOVA test for minimum, mean and maximum temperatures between sites. Letters in each column refer to sites which are significantly lower than the selected site at $p>0.05$.

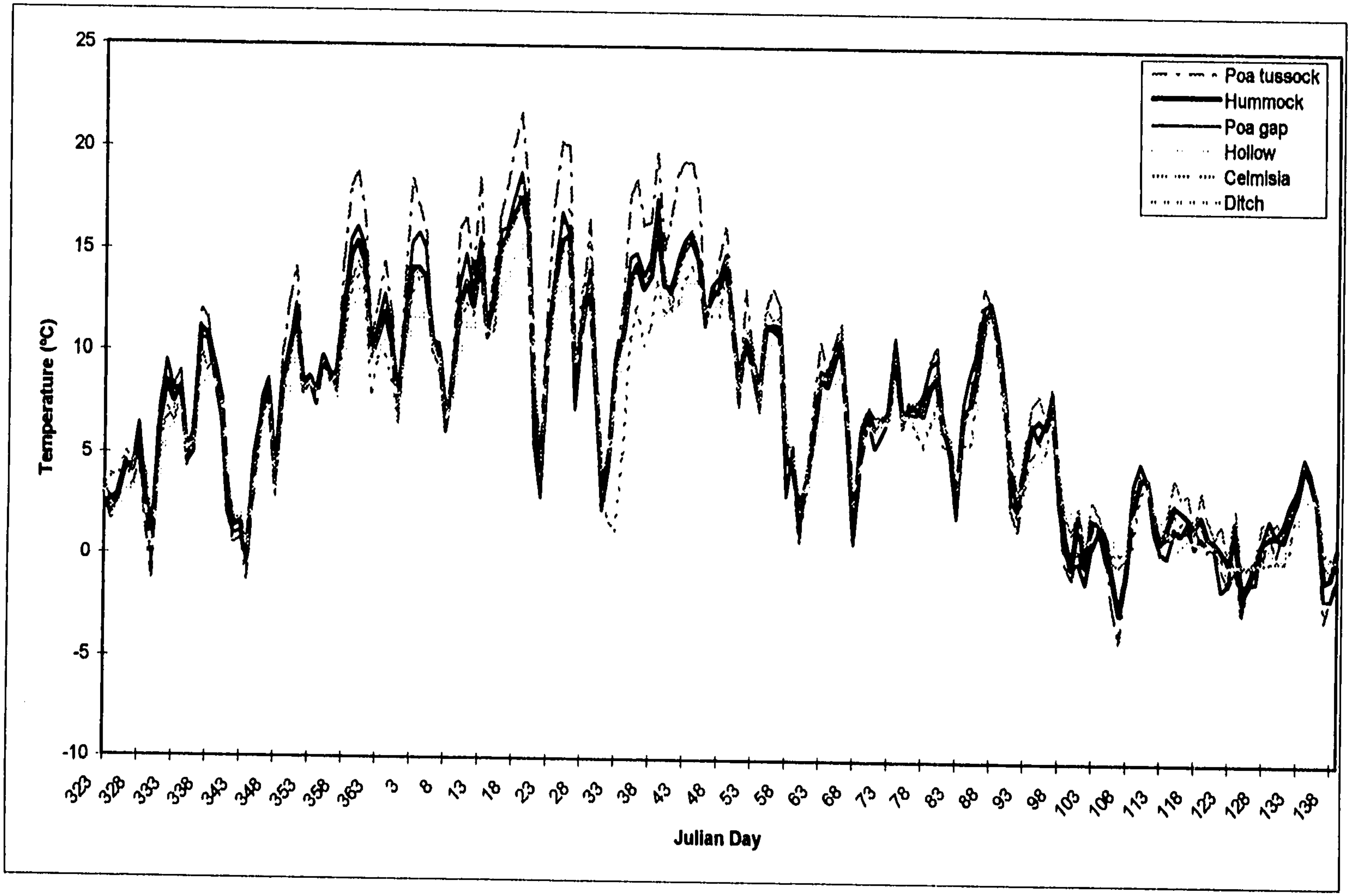

Figure 2.4 Mean air temperature at the soil surface (0 cm) for the Julian Day period 322-139.

	Undisturbed			Disturbed		
	Celmisia	Hollow	Hummock	*Poa* tussock	*Poa* gap	Ditch
Number of freeze-thaw cycles	45	22	59	86	93	58

Table 2.2 Number of potential freeze-thaw cycles (-1°C to 1°C during 24-hr period) in undisturbed and disturbed habitats during microclimate monitoring (November 1998-May 1999).

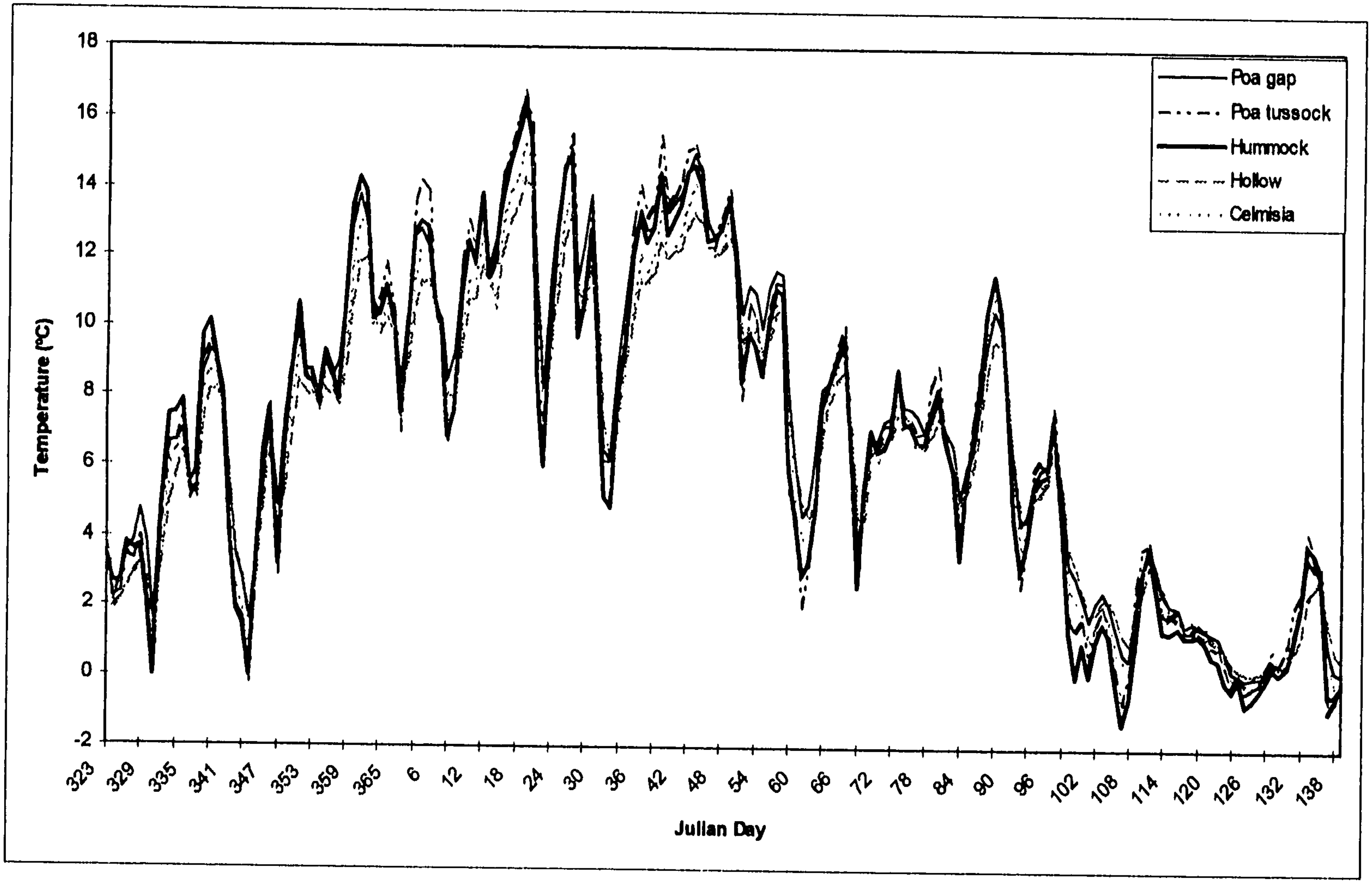

Figure 2.5 Mean soil temperature at 5 cm below the surface for the Julian Day period 322-139.

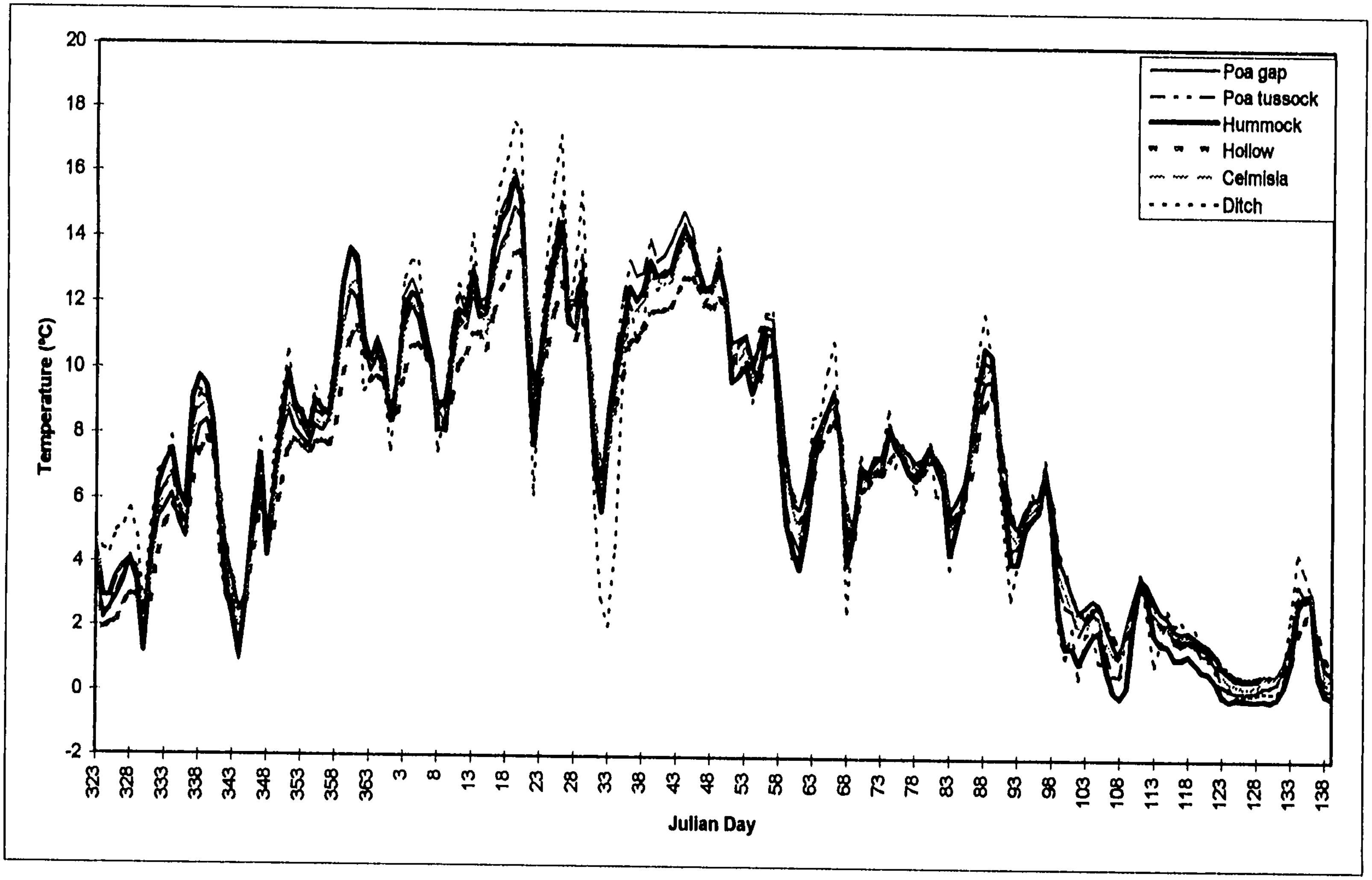

Figure 2.6 Mean soil temperature 10 cm below the surface for the Julian day period 323-138.

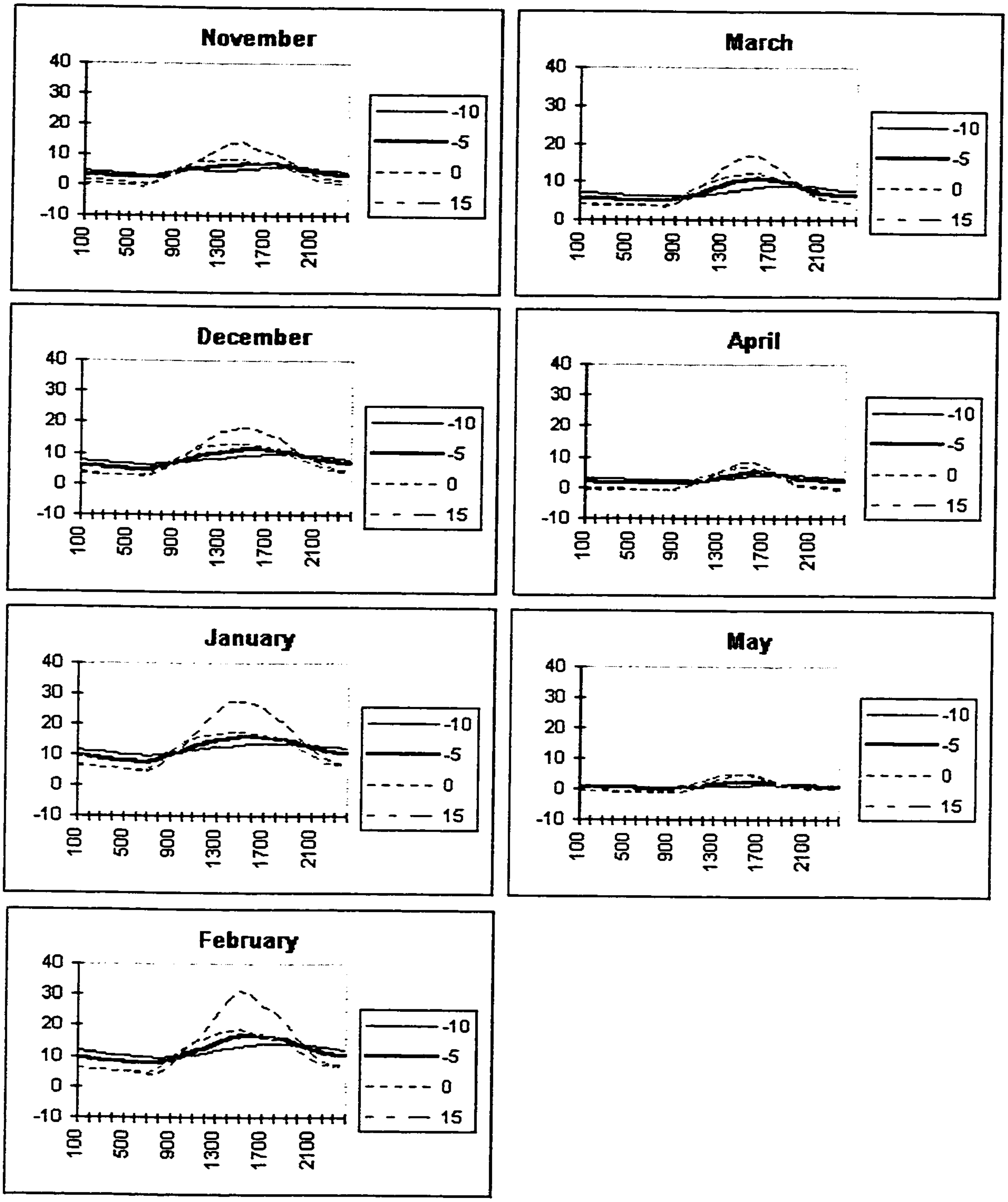

Figure 2.7 Mean diurnal temperatures at heights of 15, 0, -5 and -10 cm for the *Poa* tussock on a monthly basis for the duration of the monitoring period.

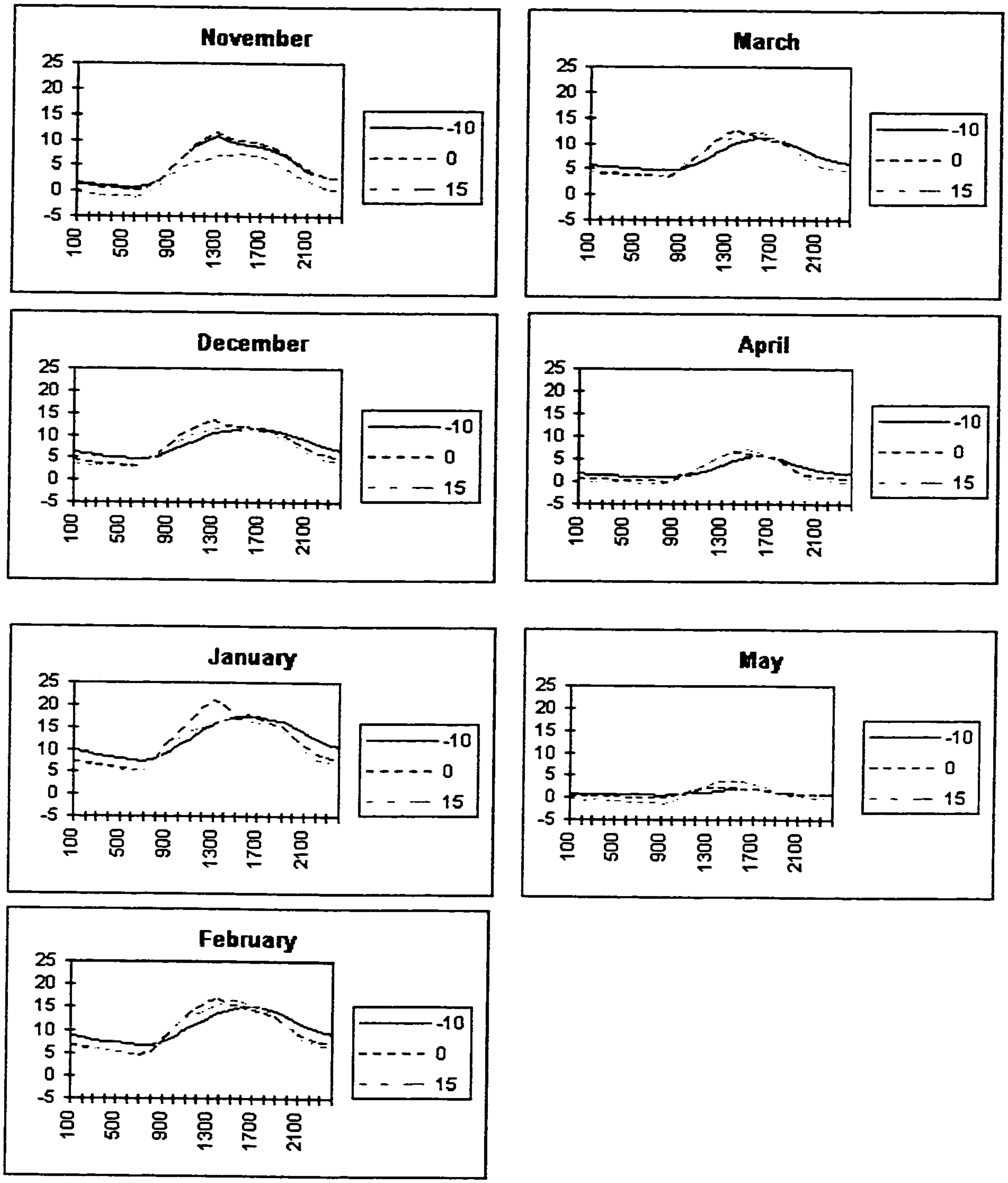

Figure 2.8 Mean diurnal temperatures at heights of 15, 0, -5, -10 cm for the ditch on a monthly basis for the duration of the monitoring period.

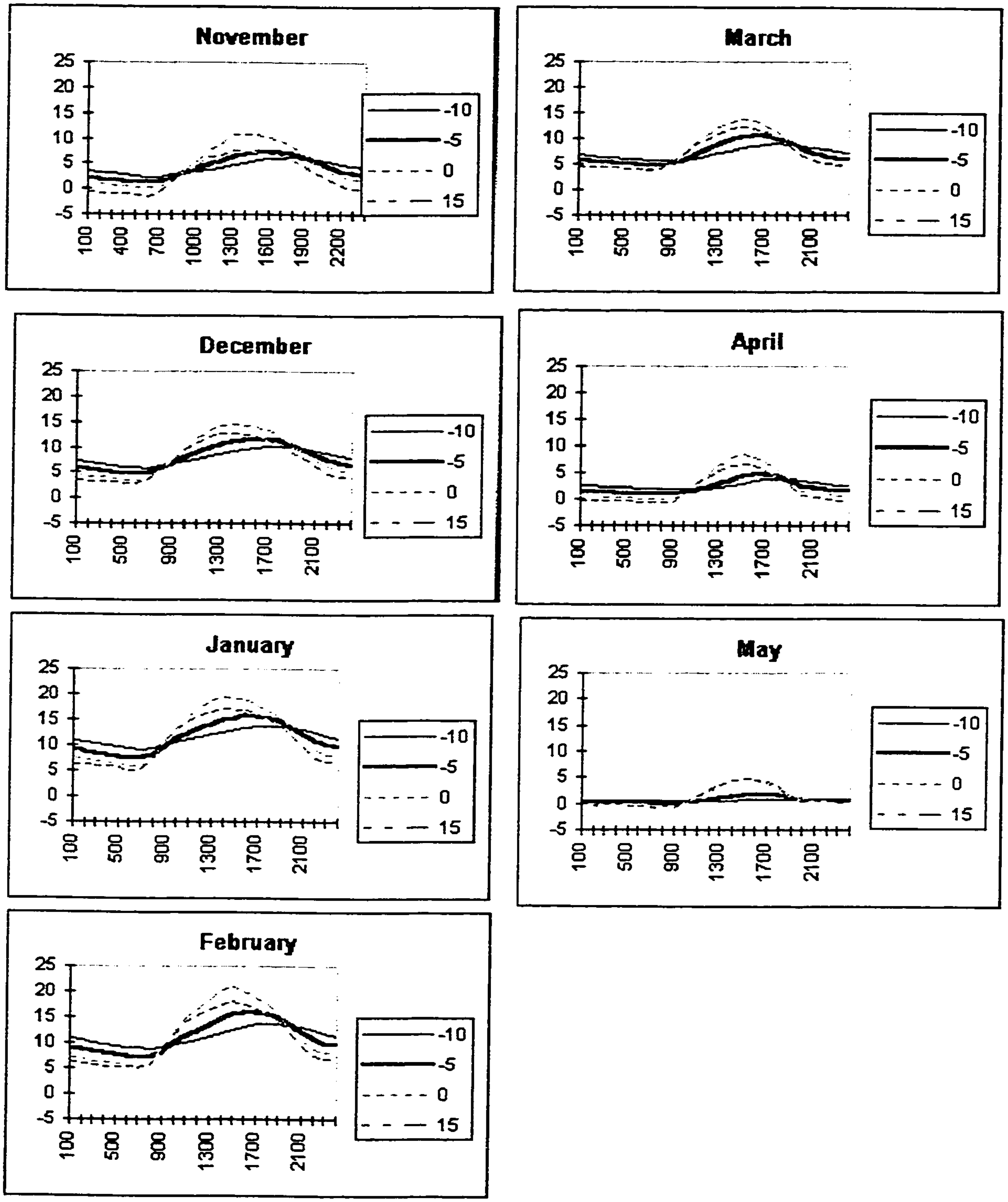

Figure 2.9 Mean diurnal temperatures at heights of 15, 0, -5 and –10 cm for the hummock site on a monthly basis for the duration of the monitoring period.

A)
Ditch

	-10		0		15	
	Temp	Time	Temp	Time	Temp	Time
November	10.9	13:00	11.4	13:00	7.27	15:00
December	11.57	16:00	13.44	13:00	11.49	14:00
January	17.36	16:00	20.87	13:00	16.73	16:00
February	15.05	16:00	16.99	14:00	16.45	15:00
March	11.16	16:00	11.86	15:00	12.13	15:00
April	5.61	16:00	6.56	14:00	7.01	15:00
May	1.86	16:00	2.3	14:00	3.68	15:00

B)
Hummock

	-10		-5		0		15	
	Temp	Time	Temp	Time	Temp	Time	Temp	Time
November	6.2	18:00	7.4	16:00	10.92	14:00	7.5	13:00
December	10.16	17:00	11.63	16:00	14.56	14:00	12.6	13:00
January	13.78	18:00	15.8	16:00	19.4	14:00	17.06	14:00
February	13.82	18:00	16.02	16:00	20.91	15:00	18	15:00
March	8.97	18:00	10.57	16:00	13.62	15:00	12.04	15:00
April	3.71	18:00	4.78	16:00	8.39	16:00	6.61	16:00
May	0.91	18:00	1.85	16:00	4.85	15:00	4.68	15:00

C)
Poa

	-10		-5		0		15	
	Temp	Time	Temp	Time	Temp	Time	Temp	Time
November	5.82	18:00	7.04	15:00	14.38	15:00	8.67	15:00
December	9.67	18:00	11.27	16:00	17.98	15:00	12.94	14:00
January	13.94	18:00	16.26	16:00	27.6	15:00	17.43	14:00
February	14.2	19:00	16.65	16:00	31.06	15:00	18.41	15:00
March	8.99	18:00	10.77	16:00	16.98	15:00	12.25	15:00
April	4.21	18:00	4.97	16:00	8.32	15:00	6.58	15:00
May	1.38	18:00	2.22	16:00	4.76	15:00	4.71	15:00

Table 2.3 Average maximum temperatures (° C) and average time of occurrence at -10, -5, 0, and 15 cm for A) Ditch, B) Hummock and C) Poa sites.

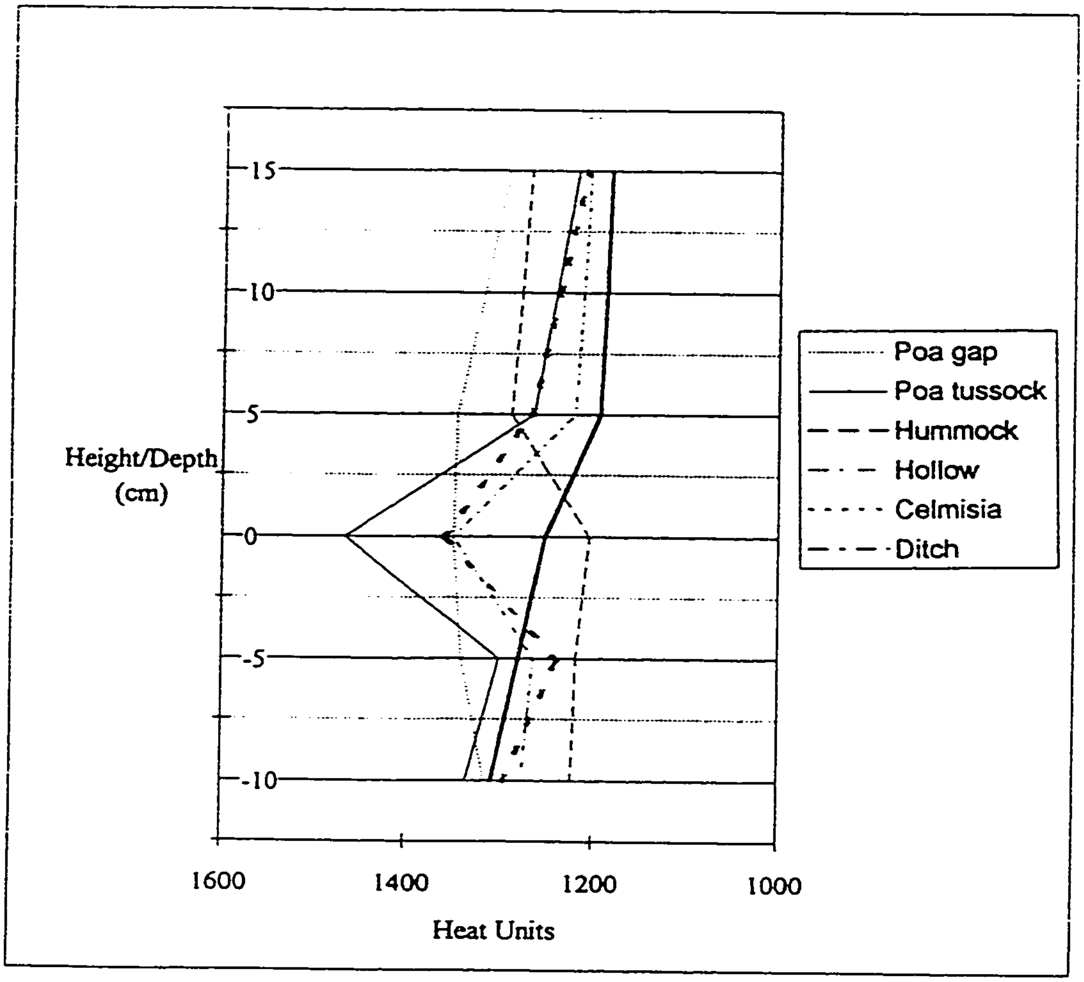

Figure 2.10 Thaw degree day values based on daily averages for the Julian Day period 322-139, for each site at heights of 15, 5, 0, -5 and -10 cm.

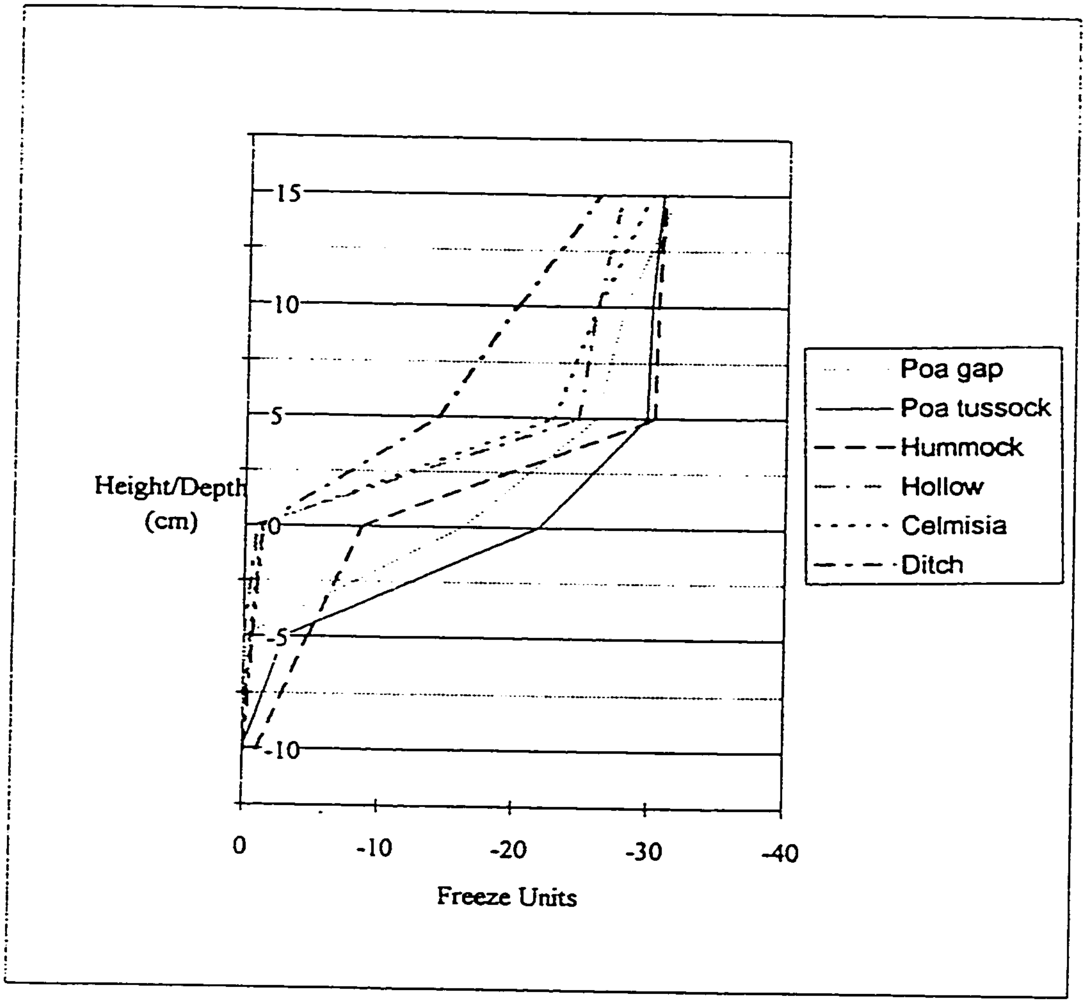

Figure 2.11 Freeze degree day values based on daily averages for the Julian Day period 322-139, for each site at heights of 15, 5, 0, -5 and -10 cm.

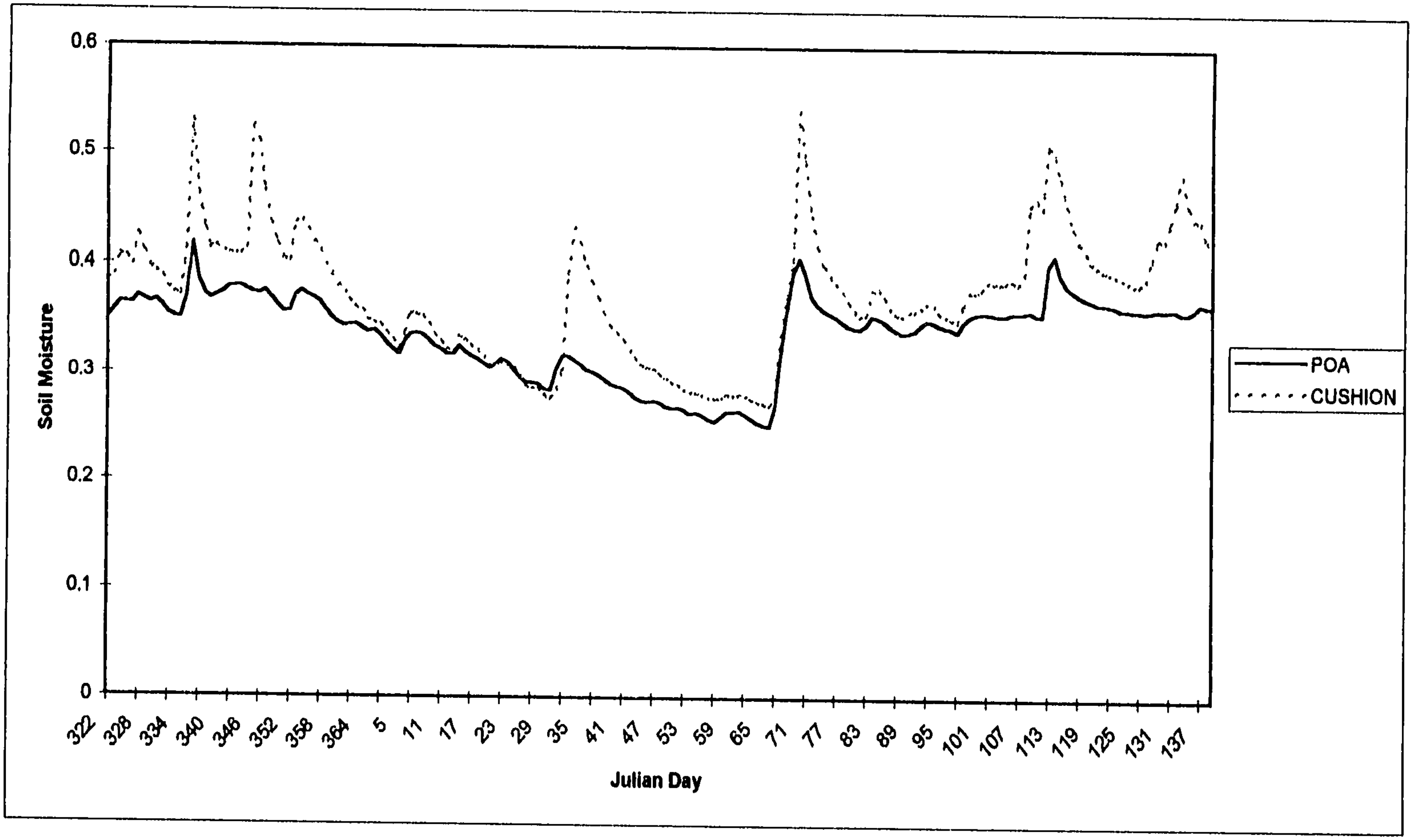

Figure 2.12 Soil moisture values for the *Poa* site (disturbed) and cushion site (undisturbed) for the sampling period (Julian day 322-138).

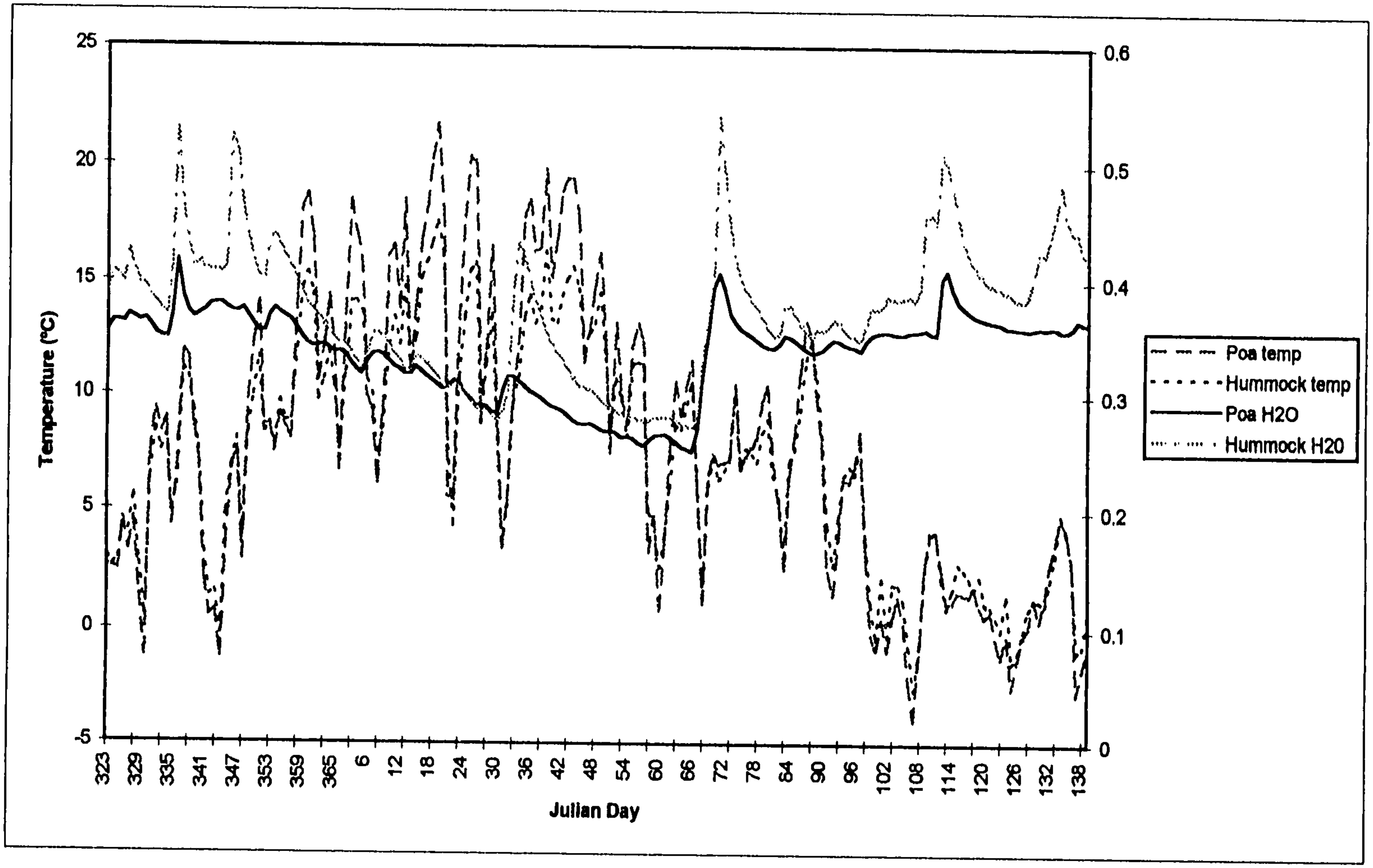

Figure 2.13 Comparison of relationship between soil moisture values and soil surface temperatures for the sampling period (Julian day 323-138) for the *Poa* site (disturbed) and hummock site (undisturbed).

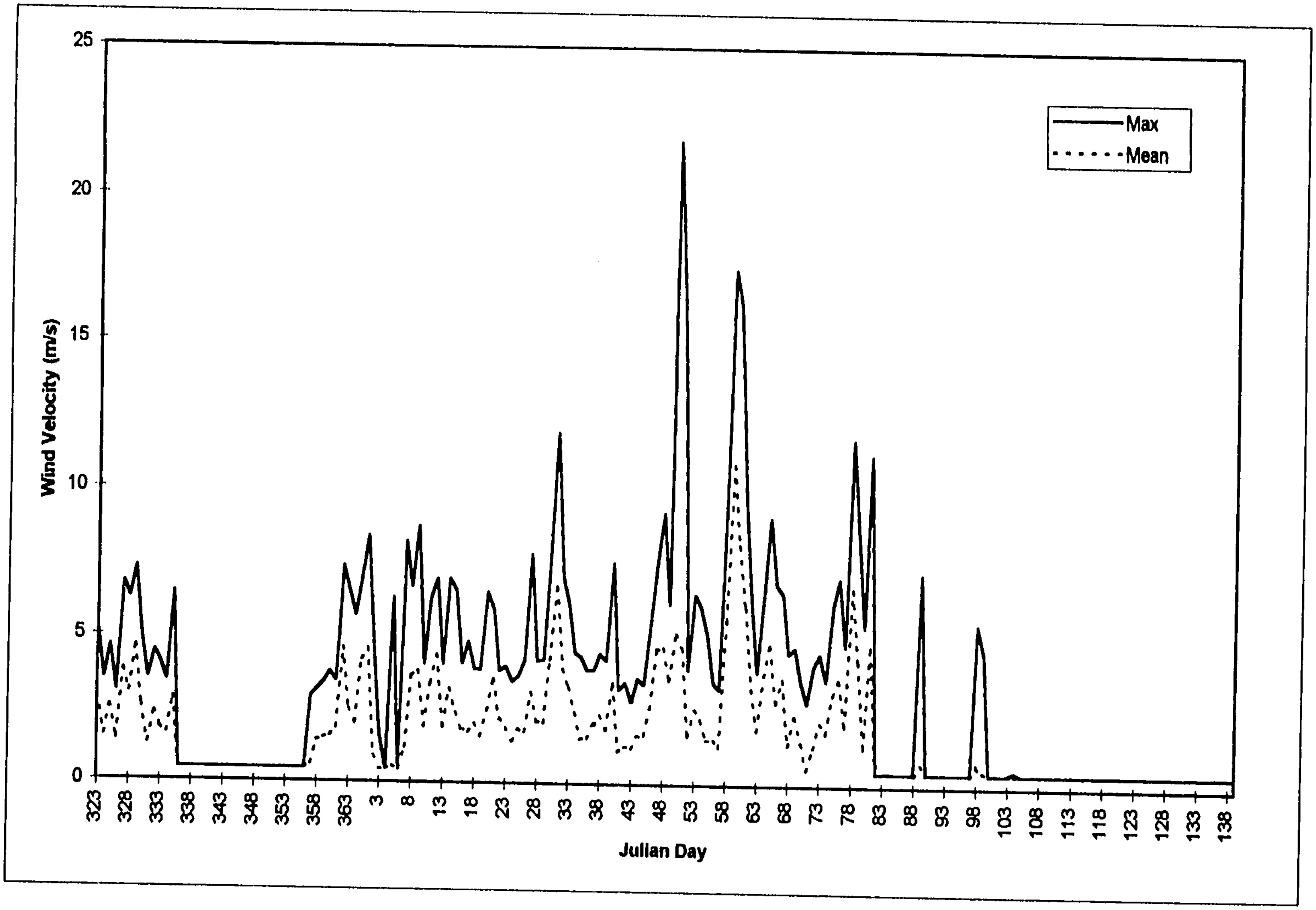

Figure 2.14 Maximum and mean wind speed values for the sampling period (Julian day 323-138).

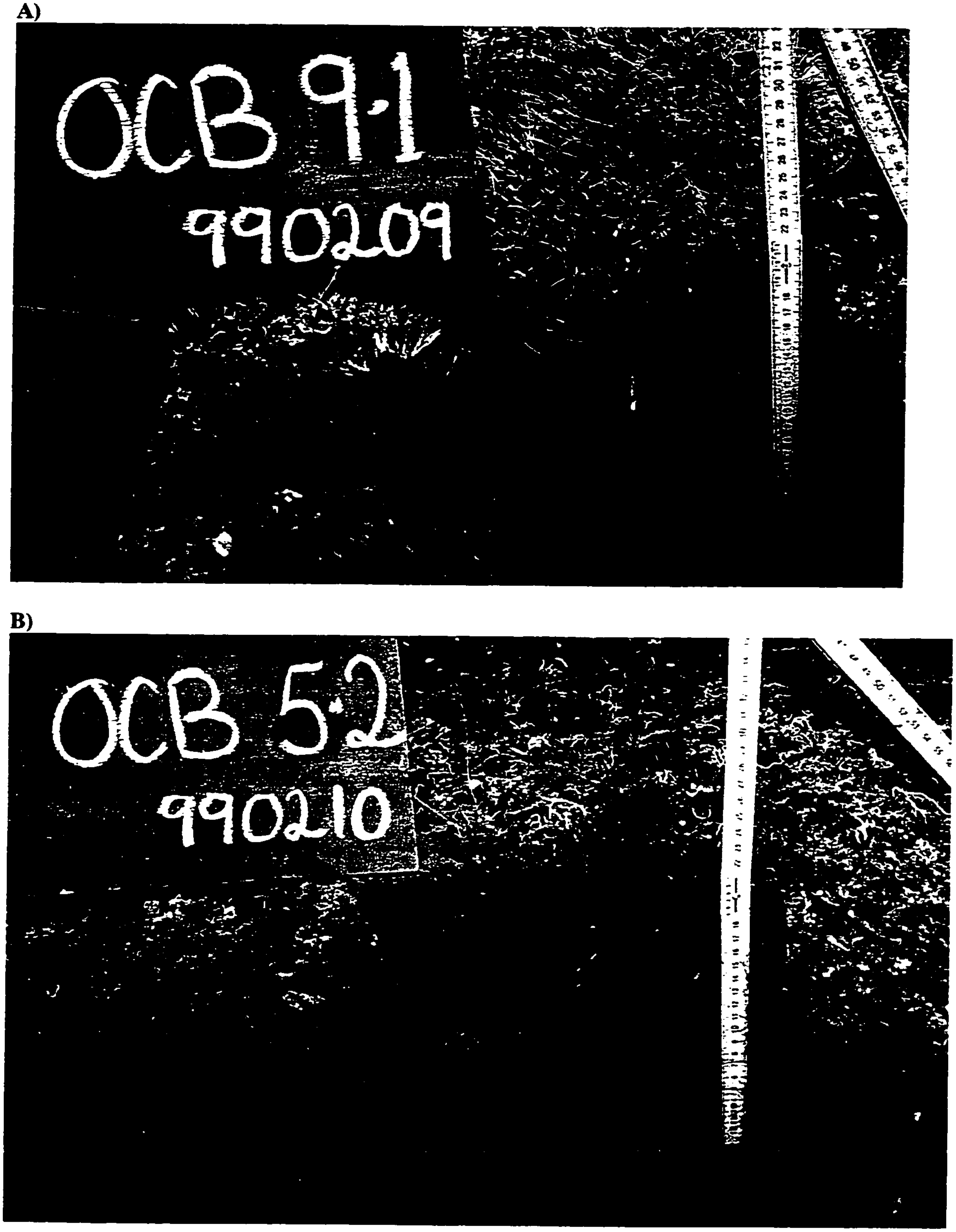

Figure 2.15 a) Disturbed and b) undisturbed soil pit profiles.

	Disturbed n=11		Undisturbed n=11					
Soil parameter	Mean	Std. Dev.	Mean	Std. Dev.	t	D.F.	p	Sig Diff
Total %N	0.178	0.044	0.235	0.101	-1.709	20	0.103	no
Total %P	0.051	0.012	0.050	0.017	0.218	20	0.83	no
K ppm	74.107	37.101	87.662	63.169	-	-	-	no
N03-N ppm	0.979	0.499	0.284	0.176	4.356	20	<0.001	yes
NH4-N ppm	8.645	1.629	8.043	1.926	0.792	20	0.437	no
pH	4.935	0.109	4.692	0.153	4.283	20	<0.001	yes
OM	6.256	1.433	9.596	4.533	-2.33	20	0.03	yes
Bulk Density	1.206	0.148	1.136	0.216	0.882	20	0.388	no
% Moisture	13.102	3.025	13.360	5.964	-0.128	20	0.9	no
gravel (>2mm)	20.785	9.959	29.181	15.798	-1.491	20	0.152	no
sand	34.473	7.088	30.353	4.379	1.582	19	0.13	no
silt	29.700	4.031	29.194	6.319	0.221	19	0.828	no
clay	15.042	1.934	14.692	4.920	0.219	19	0.829	no

Table 2.4 Mean soil variables values for disturbed and undisturbed treatments and corresponding test for significant difference.

A)

	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	Mean	St. Dev.
U1975	-0.2	-0.18	-0.18	0	-0.2	-0.16	0.16	0.32	0.2	-0.04	-0.28	0.192
U1976	-0.78	-0.2	-0.92	-0.14	-0.48	-1.34	-2.18	0.02	-0.06	-0.06	-6.14	0.709
U1977	0.56	0.3	-0.04	0.54	-0.08	0.56	-0.86	0.04	0.08	0.28	1.38	0.428
D1975	-0.7	-0.66	-0.14	-0.2	-1.12	-	-1.22	-1.04	-0.34	-2.16	-7.58	0.633
D1976	-0.56	0.26	-0.54	-0.86	0.12	-	-0.92	-0.92	-0.02	-1.5	-4.94	0.576
D1977	-0.06	-0.3	-0.54	0.06	-0.46	-	-0.58	-0.18	-0.4	-0.3	-2.76	0.216

B)

	t	D.F.	P	Sig Diff
U1975 - D1975	3.884	17	0.001	yes
U1976 - D1976	-0.218	17	0.830	no
U1977 - D1977	2.804	17	0.012	yes
U1975 - U1976	2.521	18	0.021	yes
U1976 - U1977	-2.869	18	0.010	yes
D1975 - D1976	-1.028	16	0.319	no
D1976 - D1977	-1.181	16	0.255	no

Table 2.5 A) Changes in soil depth as determined by erosion markers during 1975-77 in undisturbed treatments (U) and disturbed treatments (D) on each of the permanent transects (T) (A.F. Mark 1978 unpublished data). B) Comparison of difference of mean soil loss values between treatments and between years in similar treatments.

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Chapter 3: Secondary Succession Following Human-induced Disturbances in the High-alpine of Central Otago, New Zealand.

Introduction:

Vegetation disturbances have been divided into two categories (Petraitis *et al.* 1989): 1) selective mortality (e.g. herbivory) and 2) catastrophic events which cause random, localized mass mortality. Mass mortality is the elimination of most of the species from an area, followed by plant recolonization with a delay of the competitive exclusion of species during the early period of plant reestablishment. Regardless of the disturbance type, it can be considered a discrete event that will initiate succession at some spatial scale (Pickett *et al.* 1989) to produce changes in community composition and species richness and diversity. Changes in community characteristics resulting from disturbances are not due to an interruption of competition but, rather, to a change in the relative supply rates of resources for which plants compete (Petraitis *et al.* 1989). Alteration of the resources results in a shift of the competitive hierarchies among patches in a manner more complex than the dichotomy occurring between colonizing species and competitively dominant species (Hibbs 1982, Tilman 1982, 1984). Increases in species diversity have been further attributed to the response of plant strategies (seed dispersal, germination) following disturbance (Collins *et al.* 1995). Under this theory, a disturbance event can result in the maintenance or a decrease in species richness but cannot result in an increase. The occurrence of an increase in species richness following disturbance, would not be due to the disturbance itself, but rather the favourable conditions which it created. The increase in species richness would, therefore, occur in response to the plant strategies of the colonizing species.

Control of species diversity by disturbance has been linked with the paradigm, which views a community as a mosaic of patches in various stages of recovery from disturbance (Griggs 1956, Horn 1975, Connell 1978, Pickett 1980). The post-disturbance point at which diversity will be highest is controversial. One of the competing schools of thought is the intermediate disturbance hypothesis (Connell 1978) where species richness is highest at intermediate intensities of disturbance and at intermediate time spans following the disturbance. It is hypothesized that at low and high rates of disturbance and recovery, patches composing the vegetation should be most similar and consequently species diversity of the community will be lower than at intermediate levels of disturbance and recovery where patches should be most dissimilar and achieve the greatest species diversity. Studies in alpine and tundra environments, however, have found mixed results where diversity after disturbance was higher (Fox 1981, Harper and Kershaw 1996) and lower (Chapin and Shaver 1981, Bishop and Chapin 1989, Truett and Kertell 1992, Zobel *et al.* 1997). Differences in findings, however, may be predominantly related to the length of time following disturbance in which the studies were carried out. This is an important consideration for alpine and tundra environments where plant growth and establishment processes are much slower.

A small number of numerically dominant species and a larger middle class of moderately important species and a small number of rare species characterize most plant communities. Changes in a community's species diversity, however, will be primarily dependent upon the abundance of the more inconspicuous intermediate and rare species, many of which are ecological specialists (Whittaker 1965).

Objectives:

The objectives of the study were to:

i) Quantitatively describe plant community composition and structure in undisturbed and disturbed treatments 25 years after disturbance.

ii) Using these data, assess two models of vegetation responses to disturbance: the Intermediate Disturbance Hypothesis and the Initial Floristic Composition Model.

iii) Ascertain whether succession is Markovian, and estimate plant community composition and time required to reach equilibrium.

Plant community responses to disturbance:

Two models of the post-disturbance responses of vegetation are the intermediate disturbance hypothesis (Connell 1978) and the initial floristic composition model (Egler 1954).

- *Intermediate Disturbance Hypothesis:*

The intermediate disturbance hypothesis predicts maximum species richness at intermediate levels of disturbance in which a trade-off exists between a species ability to endure disturbances and its ability to compete (Collins *et al.* 1995). Infrequent disturbances result in a decrease in species richness because dominant species occupy resources and eliminate less adaptable competitors. Species richness also decreases under a frequent disturbance regime where intolerant species are extirpated locally. Therefore, species richness should be highest at intermediate frequencies of disturbance when conditions favour competitive and disturbance-tolerating species. Species richness is further favoured at intermediate time spans between disturbance events. This is a result of late successional species displacing early successional species through competition resulting in a decline of species richness with time since disturbance (Collins *et al.* 1995).

- *Initial Floristic Model*:

The initial floristic composition model of succession asserts that species in the early and late stages of the successional sequence are present immediately following the disturbance (Egler 1954). Therefore, succession can be considered a function of differential growth rates and survivorship among early and late successional species (Pickett *et al.* 1987). Species richness would therefore be expected to be highest early in the successional process and lowest late in the sequence.

Analyzing plant community succession:

- *Markovian Model of Succession*

Attempts to reduce the highly complex interactions of successional processes to a simple process response model have been mixed. They usually involve a trade-off between ease of computation and amount of data required. To adequately model succession a plethora of data is required with considerations for both time and space. Compilation of the necessary data would be time consuming, and once collected the model itself may not be needed as the interactions and pathways will have already been identified. Modelling succession after the fact would therefore contribute little. Successional models, therefore, must be approached simply as a predictive tool of future trends. Such a predictive model is the Markovian model, which is concerned with the movement from one state to another state and forecasting future changes including the predominant direction and rate of change. Van Hulst (1979) found the predictive abilities of the Markovian model to be better suited for modeling succession than deterministic succession models like the differential equation models. This is due to the indeterminateness of some successions, successional models therefore require a stochastic description.

The Markovian model is based on the Markov process which Bartlett (1955) defined as 'a stochastic process for which the values of X_r at any set of times $t_r(r = 1, 2 \ldots n)$ depend on the values X_s at any set of previous times $t_s(s = 0, -1 \ldots -j)$ only through the last available value X_o.'

Therefore, the Markovian process is only dependent on the single and last value X_o, consideration of the plant community history is irrelevant when predicting future vegetational states. Basing a Markov model on a single transition matrix of cover change data results in a stationary or homogenous model. Therefore, if succession is Markovian it is stationary (Usher 1979, Childress *et al.* 1998) and experiences consistent transition probabilities and available states over time. Markovian models also include an erodic property whereby convergence towards a limiting probability distribution for the states will occur regardless of the initial state of the system (Usher 1979). This property allows for prediction of what a system will converge towards if left untampered with, a state similar to a plant community climax.

The Markovian model of succession (Van Hulst 1979) is the only model that is able to incorporate the two dichotomous views of succession expressed by Clements (1916) and Gleason (1926). Clements' concepts, which are viewed as deterministic, predict that succession will occur in an orderly manner, resulting in a self-sustaining climax state. This theory can be incorporated into the Markovian model, allowing for the estimation of the probabilities of transition from one state to another. The model may also be used to test Gleason's stochastic ideas and individualistic view towards plant species if each individual is treated as an entity, permitting an estimation of a series of probabilities, which define all of the possible outcomes for the fate of the individual. Usher (1981) found a number of disadvantages with Markovian models: i) states that are to be used in the model, which are defined by dominant species or genera are difficult to define, ii) collection of data is difficult and time consuming, iii) vegetation history is irrelevant and the model has only a single dependence (X_o), iv) transition probabilities may not remain constant with time, v) spatial effects and known patterns are averaged out, and vi) introduction of new arrivals are impossible to include. Additional problems identified with Markovian models have been with its predictive ability and determination of the erodic property, which for long-term changes have been found to be conservative (Hobbs 1983, Lough *et al.* 1987). The Markovian model, however, provides the opportunity to investigate mathematically, successional trends and predict plant community development. Concepts, which are expressed as descriptive or verbal, can also be tested with the Markovian model. This permits determination of the validity of the initial disturbance hypothesis according to Markovian model predictions.

Terminology:

There is ambiguity with the terms species richness and species diversity. Connell (1978) found that species richness, the number of species found within a patch regardless of their relative abundance (Alpha diversity as described by Osman and Whitlatch 1978), was the most appropriate measurement of species diversity. Species diversity however can also be measured by an index that is a function of the number of species and the eveness of their relative abundances (Fox 1981, Petraitis *et al.* 1989). Eveness refers to the homogeneity or relative diversity of the species abundances.

Methods:

Vegetation Sampling

Line Intercept Transects

Transects used for line intercept vegetation sampling were those established by Prof. A.F. Mark immediately following the construction of the access road in February 1975 (Figure 3.1a and b). Although 10 permanent transects were laid out, only 9 were included in the study as transect 6 extended through introduced plantings of *Chionochloa rigida*. Transects were laid perpendicular to the road in two sections, extending 20 m from the disturbance margin towards the road edge (Figure 3.2a) and 20 m into the undisturbed cushionfield (Figure 3.2b). Shorter transect lengths (19 m), however, were used in the disturbance portions of transects 5 and 9 due to the limited extent of disturbance.

Vegetation surveys along the transects followed Mark's point intercept method (1978), where at a 0.20 m interval, plants at the point intercept were recorded to provide species and frequency data for a total of 1780 points. Aside from plant species, additional cover categories included, soil, dead, litter, pavement and rock. Soil was considered to be any fine-textured mineral sediment other than pebbles and rock. Dead differed from litter since it was still attached to the substrate and was usually recorded by species. Pavement was considered to be any clast larger than soil particles that was likely to be moved under the influence of strong wind. Any clast larger than this was considered to be 'rock'.

Initial plant field identification was made following Mark and Adams (1995). A voucher collection was made for comparison with specimens at the University of Otago's Department of Botany's herbarium. Prof. A.F. Mark verified ecological collections of all taxa.

Cover Plots

Five 50 x 50 cm quadrats were randomly positioned adjacent to the undisturbed and disturbed portions of each of the 9 transect for a total of 90 plots. Each quadrat was partitioned into 25, 10 x 10 cm cells, which were individually sampled to estimate percent on a species basis.

Cover was estimated to the nearest 5% for cover >10% and to the nearest 1% for cover <0%. The number of cells occupied by each species was used to calculate frequency. These values were used as an indicator of abundance. Classification of a species as 'common' was dependent upon an average cover >1%, or an average frequency >10%.

Biomass

Above and below ground biomass samples were collected over a two-day-period from randomly-placed locations along the undisturbed and disturbed portions of the transects for a total of 22 samples. Difficulties associated with defining and separating cushion plants into separate individuals made it necessary to determine biomass in 10 x 10 cm plots. Samples were excavated to a depth of 20 cm (Figure 3.3).

Initial laboratory analysis was conducted at the University of Otago. Soil was separated from the biomass samples using a fine wire mesh (2mm) and water. After the removal of soil, biomass samples were further separated into three categories before being air-dried: live aboveground biomass, dead aboveground biomass and belowground biomass. Following separation, biomass samples were oven-dried and weighed at the University of Alberta. Dead aboveground biomass and belowground biomass were weighed as single samples while alive aboveground biomass samples were weighed on a species basis. Following initial weighing, belowground biomass samples were ashed to determine the weight of remaining sediment in the material, thereby allowing an accurate measurement of the weight of belowground biomass.

Statistical Analysis

Plant Community Determination

Determination of plant communities and indicator species associated with different disturbance treatments was done through the use of the CANOCO 4.0 for Windows program (ter Braak and Šmilauer 1998). Species cover and site data were analyzed using Detrended Correspondence Analysis (DCA).

Markovian Model

Vegetation data collected by the line intercept method were used to construct Markovian models to determine rate and direction of change of surface cover in undisturbed and disturbed treatments on the Old Man Range. Cover data were separated into 7 distinct cover states for the undisturbed and disturbed treatments (Mark 1978). Both treatments included the states: dead, pavement, rock, litter, soil and other species. The undisturbed treatment also included a *Dracophyllum muscoides* state while the disturbed treatment included a *Poa colensoi* state. Low frequency occurrences of many species made it necessary to combine all species with a frequency <5% into a single 'other species' class. Inclusion of these species as independent classes would have resulted in a matrix dominated by zeroes. Cover data from 1999 were compared to 1986 data supplied by Prof. A.F. Mark to create tally matrices of cover state change for the undisturbed and disturbed sites to determine the frequency and type of transitions that have occurred since 1986. A transition is considered to be a change in cover state between two sampling periods. Autotransitions, in which a change in cover state does not occur, were also included. Tally matrices were converted into transition matrices by dividing the number of times cover state A changed to cover state B, etc., by the number of times cover state A was observed at the first sampling time.

Transition matrices were used to calculate transition probabilities (P), which quantify the probability that any cover state will change to another cover state or remain the same from one sampling period to another (Collins 1975). The initial state (1986) was determined by converting the value of each of the cover classes to a percentage of the whole, allowing the initial state to be expressed as a probability vector p(^{0}), which refers to the cover state in 1986. The cover state in 1999 is referred to as p(^{1}). Using algebraic theorems, transition probabilities and the initial state probability vector were multiplied together to produce p(^{1}) and predict future cover characteristics at discrete time intervals (13 years in this study) (Collins 1975).

$$p^{(0)}\,P = p^{(1)} \quad (1)$$

Example:

$$p^{(0)} = (a, b, c)$$

$$(a, b, c,) \times \begin{array}{ccc} A & B & C \\ D & E & F \\ G & H & I \end{array}$$

$$a \times A = aAa \times B = aBa \times C = aC$$
$$b \times D = bDb \times E = bEb \times F = bF$$
$$\underline{c \times G = cG} \qquad \underline{c \times H = cH} \qquad \underline{c \times I = cI}$$
$$aA + bD + cG \qquad aB + bE + cH \qquad aC + bF + cI$$

$$p^{(1)} = (aA + bD + cG,\ \ aB + bE + cH,\ \ aC + bF + cI)$$

If transition probabilities from 1986-1999 are considered to remain constant for the period 1999-2012, then the cover distribution for 2012 can be determined by multiplying the 1999 cover state $p^{(1)}$ by P.

$$p^{(2)} = p^{(1)}\, P \ (2)$$

The vector-matrix multiplication procedure was used to determine successive cover states until the limiting matrix was found, at which point equilibrium within the cover states occurred if the system was to go on unhampered.

$$p^{(n)} = p^{(n-1)}\, P \ (3)$$

Valid application of the Markov model was dependent upon the identification of its specific order property. Partial dependence (Markovity property) of a Markov chain would render it unsuitable for analysis of an independent series of events. Prior to determining the specific order of the Markov model it was necessary to test the validity of the Markov property assumption that it is a stochastic process (Collins 1975). This was accomplished using the Maximum Likelihood Ratio Criterion, a procedure based on asymptotic distribution theory and Chi-square tests. The tally matrix was used to test the null hypothesis that change from one cover state to another cover state was statistically independent (zero-order) as opposed to the alternative hypothesis that it was partially dependent (first-order).

Application of the Maximum Likelihood Ratio Criterion involved the construction of an N log P matrix that was achieved by multiplying each element of the tally matrix by the equation:

$$\lambda = 120 \log_e (p_j/p_{ij}) \ (4)$$

The p_j values were obtained by summing columns for each state and converting them to a percentage, while p_{ij} values were determined by dividing each matrix element by its corresponding marginal row total. Matrix elements were summed algebraically to produce an N log P matrix. Matrix elements were doubled and compared to Chi-square values for the selected level of significance and $(n-1)^2$ degrees of freedom.

Sensitivity Analysis

The importance of each of the components of the Markov analysis (class types) on influencing equilibrium outcome was determined by sensitivity analysis. The probability of each class type was individually increased by a constant 10% and the Markov Analysis was run until equilibrium was attained. Differences in equilibrium cover composition were statistically determined to identify which cover types the Markov analysis was the most sensitive to.

Species Diversity

Change in species diversity through succession was analyzed by dominance-diversity curves (importance-value curves) based on species average cover values from disturbance sites for 1975, 1976, 1977, 1978, 1986 and 1999. Average covers on a species basis for undisturbed sites for 1999 were also included as a reference point for 'climax' conditions. Species were assigned a species number based on cover. Species were then plotted by cover against species number in sequence from highest to lowest cover. In each curve the highest point represents the species with the highest cover value while the lowest point corresponds to the lowest cover. Curves have been arbitrarily spaced with origins being separated by five units along the x-axis for clarity.

Species richness was expressed as a total number of species observed in each of the treatments. Species diversity was quantitatively expressed by Shannon-Wiener diversity (H') using point intercept data. Eveness (J') was expressed using the diversity data as a proportion of the maximum possible diversity (Zar 1999).

$$H' = \frac{n \log n - \Sigma f_i \log_i}{n} \quad (5)$$

$$H'_{\max} = \log k \quad (6)$$

$$J' = \frac{H'}{H'_{\max}} \quad (7)$$

Results:

Plant Communities

Differences between plant communities in the undisturbed and disturbed treatments were readily evident in both composition and structure. Analysis of the vegetation cover (Table 3.1) data by Detrended Correspondence Analysis (DCA) permitted distinct grouping of sites (Figure 3.4 and 3.5) and site affiliation with specific species (Figure 3.6). The high eigenvalue (Table 3.2) observed with the primary axis of variation (0.748) indicates that there is a large degree of niche separation of the species occurring along the axis. DCA runs of undisturbed and disturbed data on a separate basis additionally indicated the similarity in species cover based on treatment (Figure 3.5). This is evident by the large degree of separation between the grouping of undisturbed and disturbed sites. The high length of gradient (3.304) indicates a modest amount of unimodality in the cover data.

Although there does not appear to be a substantial amount of clustering of species, certain species are associated with particular site conditions in compliance with the Distance Rule. According to the Distance Rule, an extension of the Centroid Principle, a sample that is near a species point is more likely to have that species than another sample, which is not near the species point. Undisturbed treatments, therefore, can be characterized by *Dracophyllum muscoides*, and lichen species (*Thamnolia vermicularis, Siphula* spp. and *Cetraria islandica*) (Figure 3.6), while disturbed treatments are dominated by *Poa colensoi*. The remainder of the species do not have a particularly strong affiliation with either treatment.

Undisturbed Vegetation Change

The total number of plants observed in the undisturbed treatments declined on a survey basis (Table 3.3). While the decline was marginal in the first 13 years of observation, a substantial drop in richness was found in the last 12 years resulting in 7 fewer species being observed in 1999 than in 1975. Mean values for the number of species per transect (Table 3.4) however, were not significantly different between sampling years. While diversity means were substantially lower on a transect basis there was little variation from one survey to the next.

Cover values of classes used for Markov projections varied little in undisturbed areas throughout the 25-year record (Table 3.5). Following a noticeable change in cover up until 1986, the 1999 covers returned to levels of the 1975-78 sampling periods. The most noticeable change in cover between 1986 and 1999 was an increase in *Dracophyllum muscoides* and a decrease in litter cover. Throughout the sampling period inverse relationships between 'other species' and dead, as well as between *Dracophyllum muscoides* and soil occurred (Figure 3.7). This was most evident between 1976 and 1978.

Transitional pathways occurring in the undisturbed sites did not change much between the 1975-1986 and 1986-1999 periods (Figure 3.8). The main difference was the increased probability transition from litter to 'other species' in the 1986-1999 period. Transitions occurring between 1986 and 1999 (Table 3.6) produced minimal change to the overall cover of the 7 cover classes, although most of the pathways (change from one state to another) were in the direction of *Dracophyllum muscoides* and other species. While total cover changed little (Table 3.7) and the probability of the occurrence of autotransitions was high in the soil, rock, other species and *Dracophyllum muscoides* classes (Table 3.8), the undisturbed areas were still quite dynamic with only 38% of the transitions being autotransitions. The importance and longevity of the dominant species *Dracophyllum muscoides*, is evident in its high rate of self-replacement and the high probability of transition to *Dracophyllum muscoides* from an uncolonized space (soil, dead, pavement). Although most classes remained relatively stable in the undisturbed treatments, an increase of 6.2% in soil cover (Table 3.7) and a decrease of 7.4% in pavement did occur during the 13-year period. Sensitivity analysis found that the Markov analysis was not significantly sensitive to any of the classes.

According to Markov projections for the undisturbed sites (Table 3.9), equilibrium under current conditions could be attained after 2 transitions of 13 years each (i.e. 2025 AD).

Disturbed Vegetation Change

Species diversity and richness (Table 3.3) decreased after the first year following the disturbance to between 3 and 5 species per transect, and did not increase substantially until the 1986 sampling period. Species diversity continued to increase to the 1999 sampling (27 species) and was greater than the undisturbed treatments in 1999 (21 species) and was similar to levels observed in the undisturbed areas in 1975-76 (27 species) when the greatest diversity was observed. The increases in species richness and diversity were predominantly associated with the increase in vascular plants, especially within the *Magnoliopsida* class. Little or no change in the number of species per transect (Table 3.4) in the disturbed areas was observed during the first 4 years following the disturbance. Average species richness per transect, however, nearly doubled in each of the following 1986 and 1999 sampling periods to 6 and 11 species respectively, resulting in significant increases in diversity from each of the preceding sampling periods.

Since the initial disturbance, cover values for the disturbed treatments (Table 3.5) changed substantially, resulting in an increase of 44% in plant cover in 1999. Pavement cover also increased at the expense of soil cover. Since the 1986 sampling though, pavement cover decreased by 26% while soil cover remained stable at levels similar to those observed under undisturbed conditions (14%). Percent cover values, were approaching those of the undisturbed sites. Cover values in the undisturbed treatments were observed to deviate from the relatively stable averages in 1986 but have since returned to average levels. A glaring difference between the disturbed and undisturbed environments is the relative importance of *Dracophyllum muscoides* in the undisturbed sites and *Poa colensoi* in the disturbed sites.

Comparison of 1975-1986 and 1986-1999 transitions in disturbed sites (Figure 3.9) shifted transition probabilities dominance from *Poa colensoi* to 'other species'. Transition probabilities originating from dead and litter also decreased during the 1986-1999 period (Table 3.10) while the dominant movement towards pavement during the 1975-1986 period was no longer the case. Although, fewer autotransitions (29%) (Table 3.11) occurred in the disturbed treatments, their importance increased substantially since the 1986 sampling (Roxburgh *et al.* 1986), and were currently dominated by pavement. The high amount of self-replacement observed in the 'other species' class is somewhat misleading as it was likely largely due to replacement by another species as species richness increased. The inclusion of all other species aside from *Poa colensoi* in the 'other species' class makes it impossible to indicate whether the autotransitions observed in the 'other species' class is a result of self-replacement or replacement due to competition or death of the individual. A large number of transition types between classes in the disturbed sites were experienced during the 1986-99 period in which a 28% decrease in pavement cover (Table 3.12) and 12.5% increase in other species cover was observed. The latter part of the chronosequence was characterized by a slight decrease in *Poa colensoi* (Figure 3.10), the dominant plant species of the disturbed treatments and a general transition to 'other species' (Figure 3.9) as observed in the transitional pathways. Also of interest was the moderate increase in soil and dead cover values during the 1986-99 period.

Cover equilibrium (Table 3.13), based on Markov projections in disturbed areas should occur by 2064 based on 13-year intervals. Sensitivity analysis of the cover class' eigenvalues indicates that no class significantly influenced the outcome of the following transitions. The model was therefore not sensitive to any of the cover states included in the Markov analysis.

Species Richness and Diversity

Species richness (Table 3.3) was moderate and varied insignificantly with time in the undisturbed treatments. 28 species were found during the 1975 sampling period declining to the 1999 low of 21. Species richness in the disturbed treatments decreased during the first three years and increased to a maximum of 27 species in 1999.

Species diversity (Table 3.3), as measured by the Shannon-Wiener index, in the undisturbed treatments varied between 0.79 and 0.86 until the 1999 sampling when it decreased to 0.73. Eveness (Table 3.3), however, stayed relatively stable, fluctuating between 0.54 and 0.62, even during periods of low diversity and richness. Eveness values (Table 3.3) were kept low due to the dominance of *Dracophyllum muscoides*. Species diversity in the disturbed sites increased to 0.86 in 1999, a higher species diversity than observed in the undisturbed treatments. Eveness also increased but was kept low due to the dominance of *Poa colensoi*.

Dominance-diversity curves for the disturbed treatments (Figure 3.11) exhibit a gradual increase in number of species and a gradual change in slope from a linear geometric line to a more sigmoid lognormal shape. Although the slope of the 1999 dominance-diversity curve decreased, and was similar to that of the 1999 undisturbed community, the slopes were still relatively linear due to high cover values contributed by only a few species and a high number of rare species.

The number of species and total cover increased with time in the disturbed treatments to a peak in 1999 similar to that of the undisturbed treatments (Figure 3.12). A peak in species numbers occurring at an intermediate time similar to that observed by Connell (1978) in tropical forests and coral reefs was, however, not observed in these data.

Biomass

Above ground biomass (Table 3.14), alive and dead, was not significantly higher in undisturbed areas than in disturbed sites. Below ground biomass, however, was marginally higher in disturbed environments. Comparison of biomass values yielded on a species basis was not possible due to the dissimilarity in species composition between disturbed and undisturbed treatments.

Discussion:

Post disturbance succession

Throughout the 25 years that vegetation data have been collected, plant cover and species richness in the undisturbed treatments varied little. Analysis of the successional pathways indicates that the undisturbed areas are in a state of equilibrium where *Dracophyllum muscoides* and pavement are the dominant cover states. Undisturbed areas, therefore, may be stable communities where the vegetation is dominated by the cushion plants; *Dracophyllum muscoides*, *Raoulia hectorii* and the herb *Celmisia viscosa* where wind exposure is low. Additional indicator species of undisturbed conditions are the lichens *Thamnolia vermicularis*, *Cetraria islandica* and *Siphula* species. Disturbance treatments were still in the midst of recovery as evidenced by the continued increase in plant cover and species richness. Re-establishment of vegetation has been a slow process and during the first 4 yrs was restricted to only 5 species, resulting in a cover of 3%. Contemporary cover and species richness values in the disturbed treatments were similar to those of the adjacent undisturbed cushionfield. Differences, however, existed with respect to the structure and composition of the respective plant communities. While low-lying cushionfield plants and lichens characterized the undisturbed vegetation, disturbance treatments were dominated by the graminoids *Poa colensoi* and *Luzula pumila* (Figure 3.13).

During the first 12 yrs (1975-1986) that the disturbance treatments were monitored, the successional pathways were characterized by a rapid decrease in soil cover with a corresponding increase in pavement. This relationship resulted from the removal of plant cover and exposure of a highly wind-prone surface, which experienced significant deflation and soil loss, producing a pavement lag. The following 13 yrs have had stable soil cover and decrease in pavement cover, with increasing plant cover. During this period a gradual increase in *Poa colensoi* and other species occurred. Of interest, however, is the unexpected increase in soil cover and decrease in pavement as well as a smaller decrease in dead and increase in litter cover during 1978. The undisturbed treatments also had unexpected changes in cover the previous year (1977). Other species cover was found to increase while dead cover decreased. Smaller decreases in litter and pavement, as well as an increase in soil were observed.

The importance of *Poa colensoi* in disturbance sites may be waning. Cover values for *Poa colensoi* determined from the transition matrices decreased marginally between 1986 and 1999 however, a high proportion of the *Poa* tussocks had dead centres. The reduction of *Poa colensoi*, and increase in transitions from *Poa colensoi* to dead, therefore, may be caused by tussock mortality. Tussock mortality may originate from two sources; natural tiller turnover and desiccation/ice blast associated with increased exposure. Death of the centre of a tussock is a normal occurrence and in this situation the original tillers may die after 20-25 yrs. Additionally, tussock mortality may result from the erosive effects of the severe wind that characterizes the Old Man Range. The detrimental effect of wind on the Old Man Range vegetation has been previously documented by Billings and Mark (1961) and Mark and Bliss (1970). As the largely soil-based tussock mounds grow and increase in height, they are no longer protected within the internal boundary layer determined by the upstream (undisturbed) wind profile, which is a result of the mean height of the vegetation. As the tussock tops increase surface roughness, the internal boundary layer thickens (Figure 3.14), which effectively alters the momentum exchange to the height of the fully adjusted portion of the internal boundary layer (Oke 1987). Prior to being fully adjusted, tussock tops occurring within the transition zone are higher than the adjusted wind profile and experience increased shearing stresses due to increased exposure. Increased exposure would enhance erosion as was observed on hummocks on the Old Man Range by Billings and Mark (1961). The resulting wind scour leads to shoot mortality and deflation (Figure 3.15). The substantial degree of *Poa* tussock mortality is further related to tussock form when considering morphological characteristics of additional tussock types found in the study area. Other tussock types found in the undisturbed sites, including *Chionochloa rigida* (Mark 1965), were largely plant material based and, therefore, readily bend and deform with wind and are more tolerant to wind. The poor responses of the *Poa* tussocks may be due to the unnatural form in which it occurs in the disturbed sites. *Poa colensoi* predominantly occur as small patches of sward in high-alpine settings (Roxburgh *et al.* 1988), not as large soil-based tussock mounds which extend well into the wind profile and do not yield to wind. While the effect of wind scour on the *Poa colensoi* coverage does not appear to be great, ~~the~~ dead *Poa colensoi* compose relatively high cover, supporting the thesis that *Poa colensoi* is slowly dying out. Following the 1986 sampling, it is likely that the *Poa colensoi* cover continued to increase for a period of time but at some point began to be influenced by wind and possibly by snowblast during the winter. After death of *Poa* shoots, lichen species have begun to overtake the available substrates once inhabited by the *Poa* and one species seems specific to *Poa* litter..

Establishment of a dominant *Poa colensoi* community may be considered an intermediate phase of succession in New Zealand's high-alpine. Following the initial disturbance, successful establishment of plant species was very poor during the first four years. During this period, the only species to effectively establish themselves on the disturbed treatments were *Dracophyllum muscoides* and two graminoid species, *Poa colensoi* and *Luzula pumila*. With further recovery, *Dracophyllum muscoides* was not able to take advantage of the disturbed treatments as *Luzula pumila* and most noticeably *Poa colensoi* were able to. Once *Poa colensoi* could become successfully established on the vegetation-free surfaces the plants began to slowly accumulate wind-blown soil amongst their shoots (Roxburgh *et al.* 1988). The accumulated soil became incorporated into the *Poa colensoi* tussocks (Figure 3.16) and effectively altered the microtopography of the disturbed treatments by covering the once bladed flat surface into one with small hummocks/tussocks the latter being biogenic. The resulting alteration of the microtopography resulted in a modification of the environmental parameters of the disturbed treatments and allowed for an increase in the boundary layer depth, which afforded extra protection from the severe winds. Lower surface wind speeds and breaks in the microtopography would permit trapping of wind-blown seeds and the recruitment of less wind-tolerant species. Although all the newly recruited species were present in the undisturbed sites throughout the recovery period it was only once *Poa colensoi* became established and began to alter the surface that these species began to colonize the site and their importance values increased. Dependence of late establishing species on environmental conditions created by *Poa colensoi* conforms to the precepts of the facilitation model (Connell and Slayter 1977). The effect of the altered micro-topography is most noticeable when considering the importance of lichen species. Lichen species are relatively important in the undisturbed treatments yet were almost completely absent from the disturbed treatments until recently. It was only once topographic highs and lows formed that lichen cover started to increase in the disturbed areas. The increase in cover was largely due to the occurrence of 'vagrant' lichen species such as *Thamnolia vermicularis* and *Alectoria nigricans*, which were observed to preferentially accumulate in topographic lows where they were more protected from the wind and less likely to be removed.

The absence of pioneer species during succession may be due to severe conditions on the summit, predominantly due to extreme wind conditions, resulting in 'direct succession'. Urbanska and Schutz (1986) found that while disturbances can result in higher resource availability, the risks associated with snowblast and desiccating winds were greater than potential gains from increased resource availability. Selection of colonizing species and succession on the Old Man Range, therefore, would have been greatly influenced by wind exposure. The dominance of *Poa colensoi,* under conditions, which may be best described, as primary succession was likely due to the ready supply of *Poa colensoi* seed in the adjacent undisturbed areas and its ability to readily disperse by wind. Seeds and fruit of most species often fall near the parent plant (Miles 1979); therefore, wind dispersal of seed would be an advantageous attribute for colonizing the extensive disturbances on the Old Man Range summit. Establishment of *Poa colensoi* primarily through clonal growth from tillers surviving the initial disturbance was unlikely due to the complete removal of plant cover and subsequent significant loss of soil. The low occurrence and cover of *Poa colensoi* in the undisturbed sites (~ 2%) compared with its widespread and high cover (24%) on the disturbed sites suggests predominance of colonization mechanisms other than tiller regeneration. Establishment of *Poa colensoi* primarily from the seed bank was unlikely, due to the extensive removal of the organic mat and significant loss of soil through deflation. The seed bank would have been removed with the soil and initial seeding onto the disturbed sites would be entirely dependent on seed rain (Gartner *et al.* 1983). Dominance of *Poa colensoi* during the early succession can also be attributed to its ability to persevere, once established, under harsh environmental conditions.

If current trends continue with *Poa colensoi* cover decreasing and other species, dominated by *Dracophyllum muscoides*, *Raoulia hectorii* and *Celmisia brevefolia* increasing, then the disturbance areas are presently still in an intermediate state of succession. Eventually the plant community dominating disturbed sites will evolve to one the same species structure and composition of that characterizing the current undisturbed cushionfield.

Species Diversity and its Relation to Disturbance Hypotheses

Species diversity and richness continued to increase within the disturbed treatments while they decreased in the undisturbed treatments. Although species richness was similar to the average values found in the undisturbed treatments, the composition of the two treatments were not overly similar, especially for dominant species. The plant community of the disturbed treatment was dominated by the grass *Poa colensoi* and had a greater number of species of moderate importance (greater than 1% cover)(n = 15) than the undisturbed treatments (n = 11). Perhaps the best example of this was grass species in the two treatments. While the same grass species were found in both treatments, they were much more important in the disturbed treatment where they composed 32 % of the cover, compared to 5 % in the undisturbed. The relatively high occurrence of grasses in the disturbed treatment was likely due to the modification of the environment during the disturbance. Disturbances often result in an increase in soil nutrients due to increased nutrient cycling. Removal of the overlying vegetation and organic horizon would result in increased nutrient cycling from modification of the soil environment. Increased nutrient availability, coupled with the absence of competitors would greatly favour graminoid establishment as has been observed in other studies (Bliss and Wein 1972, Chapin and Chapin 1980, Chapin and Shaver 1981, May and Webber 1982, Shaver and Chapin 1986).

- *Intermediate Disturbance Hypothesis*

According to the intermediate disturbance hypothesis (Connell 1978), species richness should have progressively increased throughout post-disturbance recovery to a peak at an intermediate time following the initial disturbance. The limited literature on long-term disturbances in alpine environments makes it difficult to determine what point after the disturbance should be considered as an intermediate time. The amount of time required to reach this point is further prolonged in high-alpine environments by the harsh environmental conditions encountered and the limited growing season.

Species richness on the Old Man Range generally increased following disturbance and after 25 years was characterized by species richness and average cover similar to the undisturbed treatments. According to the intermediate disturbance hypothesis, the disturbed treatment should have achieved higher species richness values with lower average cover than the undisturbed treatment. The absence of a peak may be attributed to one or several possible explanations. The first may be that the peak has not yet occurred, 25 years after the disturbance may still be early in the recovery period. The substantial decrease in cover of the single pioneer species *Epilobium alsinoides* and decrease of *Poa colensoi*, however, suggest that succession is no longer at an early stage. The peak in species richness may have also been missed due to the long interval between the 1986 and 1999 sampling periods. Finally, as asserted by the intermediate disturbance hypothesis species richness should be highest under an intermediate frequency of disturbance. Higher or lower frequencies will result in lower species richness. Although there was only a single initial disturbance during the construction of the road, additional disturbances have been influencing the disturbed treatments on a continual basis in the form of wind erosion and needle ice activity. While the impact of these activities may not be as great as the initial disturbance, their high frequency could result in their cumulative effects limiting species richness. The effect of wind erosion can be observed in the significant loss of soil in the first three years following disturbance (Chapter 2). The potential for a high frequency of needle ice episodes suggests the possibility for a high disturbance frequency. A high disturbance frequency, according to the intermediate disturbance hypothesis, would result in lower species richness, therefore, offsetting the effect of the intermediate recovery time and maintaining lower species richness than expected.

- *Initial Floristic Composition Model*

Plant recovery on the Old Man Range did not conform with that proposed by the initial floristic composition model. According to the initial floristic composition model, species richness should have been highest immediately following disturbance, decreasing with time. These predictions were not met in this study where species richness was significantly lower during the first few years following disturbance compared to conditions observed 25-yrs later, in 1999. Perhaps the most important reason for the discrepancy between the theory and actual conditions observed in the study can be attributed to the magnitude and intensity of the disturbance. Under natural disturbances it is not common for all of the plant cover and the soil organic layer to be completely removed, nor would the seed bank be as adversely affected under a natural disturbance regime. Road construction, however, has disrupted the seed-containing soil in alpine environments (McGraw and Vavrek 1989) resulting in lower seed quantities. Removal of the top 10 cm of soil, in which the majority of the seed bank is located, is also unlikely to occur under natural conditions. The complete loss of both of these seed sources makes it highly improbable that species richness would be able to be highest immediately following disturbance as predicted by Egler (1954).

Removal of the organic layer and underlying soil would also decrease initial species diversity through the removal of rhizomes and other perennating organs that Egler (1954) found to be present at the outset and which contributed to plant colonization. Since the initial floristic composition model claims that any species, which may occur at any point during succession, are present at the beginning of succession it is impossible for the observed successional sequence to conform to these principles with the near-complete removal of potential propagule sources from the disturbed areas. Revegetation, therefore, would be dependent upon seed rain and vegetation encroachment of established plants from the adjacent undisturbed areas.

The total area of the disturbance included the bladed sections abutting the road top and ditch for an estimated width of 50m. Seed sources, therefore, were not readily available within the disturbances, hindering a rapid establishment of species following the initial disturbance. However, the disturbed corridor was relatively narrow given the influence of the wind. A disturbance of similar intensity, but impacting a smaller area would likely be revegetated more effectively and quickly due to close proximity of potential propagule sources, which could possibly result in the predicted outcome of the initial floristic composition model.

Markovian Succession and Predictions

Analysis of the transition matrices found that the plant replacement occurring in the undisturbed and disturbed sites during the 1986-1999 period was a first-order process (Markovian), rather than a zero-order process (random). The present community composition

(1999), therefore, was dependent on the 1986 community composition. The first-order behaviour exhibited in the disturbed sites, therefore, could be an indication that *Poa colensoi* promoted establishment of wind-intolerant species, which would be evidence in support of the Connell and Slayter's facilitation model (1977).

Effective use of the Markovian approach to predicting succession in this study can only be done with the undisturbed treatment data due to the general stability of transition probabilities and cover states there. Transition probabilities calculated for the disturbed treatments varied from one sampling period to another and therefore the succession experienced on the Old Man Range could not be classified as Markovian. Use of the Markovian approach was confounded by the increasing importance of *Dracophyllum muscoides* and *Rytidosperma pumilum* whose cover values were nearly great enough to warrant the inclusion of their own classes in the transition tables. The disturbed treatments could not be modeled under Markovian principles, as the system cannot experience changing transition probabilities, or the introduction of new species classes (Li 1996). The inability of the Markovian model to incorporate new species and classes after initiation of the chronosequence during later stages of succession invalidates it in this application. The increase in importance of additional species, which are currently included under the 'other species' classification, also prevents valid predictions based the Markovian process. Continual use of the 'other species' classification with species which are no longer considered rare would give an inaccurate view of the successional trends occurring on the Old Man Range as well as a disproportionate view of the importance of the rare species. An increase in 'other species' would indicate that rare species coverage and number of species is increasing substantially when it may only be the result of two species, which are becoming more dominant. The importance and role of the new dominants would, therefore, be lost under these conditions. These problems would be further compounded when predicting further cover changes as many of these transitions are occurring in the later stages of succession and cannot be included in the model. Such problems were encountered by Hobbs (1983) whose model predicted too early an equilibrium. Childress *et al.* (1998) also found that using Markov models for successional studies on Mt. St. Helens was inappropriate because species colonized the site at different times during the observation period. Therefore, all types of vegetation cannot occur throughout the simulation period. New species originally considered to be rare become more abundant with time, resulting in unstable transition probabilities.

The predictive abilities of the Markovian model results, however, could be used for determining any long-term trends for the undisturbed treatments, which in this case show a continued stability within the community. These predictions can be used as long as environmental conditions remain stable. Use of the predictions for the disturbed treatments for non-vegetation related classes, which should not be as greatly affected by the introduction of new species, did generate some interesting predictions. The continual increase in plant cover predicts that pavement coverage should decrease with time from 18.0 % to 7.7 %, which is similar to that found in the undisturbed treatments (8.5 %). Increases in plant cover should also result in decreased soil cover. The higher litter values observed in the disturbed treatments was likely due to the relatively high abundance of *Poa colensoi*, a grass which should experience high annual turnover of plant material compared to the dominant *Dracophyllum muscoides* of the undisturbed treatments. With a predicted decrease in *Poa colensoi* in the disturbed treatments it is unlikely that the predicted increase in litter cover would be as great as the Markovian predictions since most of the litter encountered during sampling originated from *Poa colensoi*. Therefore, the predictions based on non-vegetation classes may not be completely reliable due to their reliance on vegetation characteristics.

Summary:

Succession on the Old Man Range has been a slow process, which after 25 years has not attained vegetation conditions similar to those of the undisturbed treatment. Although species richness and average plant cover values were equivalent in both treatments, the species composition and structure were quite different. While low-lying cushionfield plants dominated the undisturbed treatments, the disturbed treatments were dominated by graminoid species.

Following road · construction, disturbed areas were devoid of vegetation and available for colonization but only *Poa colensoi* was able to exploit the conditions. The *Poa* structure also enabled *Poa colensoi* to retain wind-blown soil which promote development of tussock mounds that effectively altered the microtopography and increased the boundary layer thickness. Alteration of the microtopography and boundary layer permitted retention and establishment of species less tolerant to wind exposure than *Poa colensoi*. The decrease in *Poa colensoi* cover, widespread tussock mortality and increasing importance of other species indicates that the *Poa colensoi*-dominated community may be considered as an intermediate successional phase.

While a continual increase in species richness was observed with recovery, species richness values have not become greater than those observed in the undisturbed treatments. If succession on the Old Man Range conforms to the intermediate disturbance hypothesis then the peak in species richness has been missed, has yet to occur, or is prevented from occurring by the high frequency of low-impact disturbances associated with deflation and needle ice events.

The observed successional trends did not agree with those predicted by the initial floristic composition model. Species richness was not highest right after disturbance but increased with time. The low species richness immediately following disturbance resulted from the near complete loss of propagule sources and removal of the overlying vegetation and seed/propagule bank.

The Markov model was inappropriate due to the inability of the model to account for non-stationary transition probabilities and the introduction of additional classes with succession. While the predictive capabilities of the model may be used to determine general trends within the immediate future, results should not be considered for long-term predictions.

Secondary succession in the high-alpine of New Zealand is a slow process that is heavily influenced by environmental conditions. Succession has been further hindered by the removal of microtopographic variation whose influence on recolonization has been largely underestimated in alpine environments. Succession was also delayed due to the manner in which the disturbance was caused. Under natural disturbances it is unlikely that the entire overlying vegetation and seed/propagule bank would be removed on such a large scale. Further exploitation and development of alpine environments must attempt to preserve or recreate microtopographic variation and limit the amount of removal of seed bearing sources if the site is to be left to revegetate naturally.

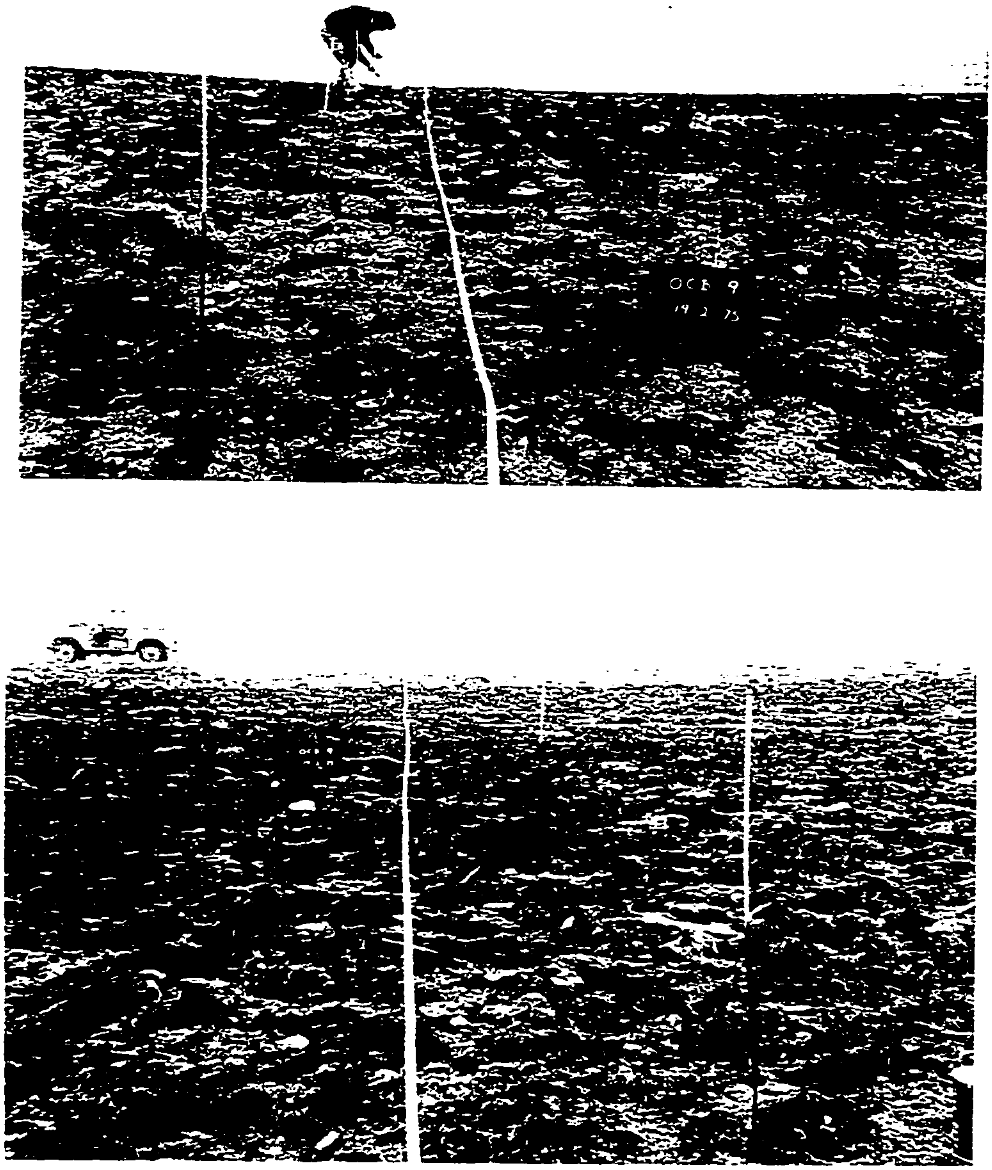


Figure 3.1 a) Overview of characteristic plant cover immediately following disturbance in 1975 (Transect 9). b) Overview of characteristic plant cover in 1975 of undisturbed sites (Transect 9). (Photos courtesy of A.F. Mark)

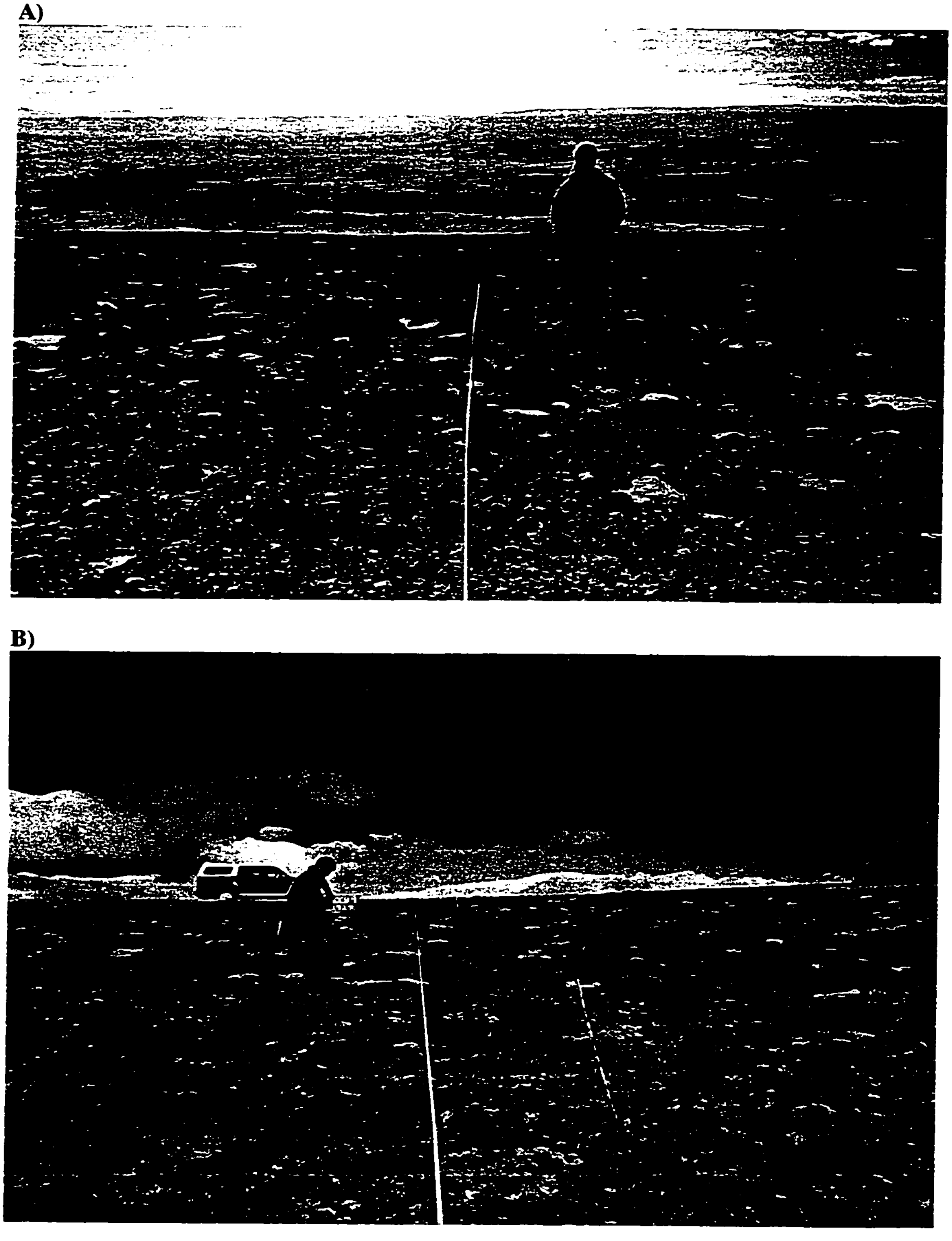


Figure 3.2 Plant cover in 1999 of transect 9 for A) disturbed and B) undisturbed treatments.

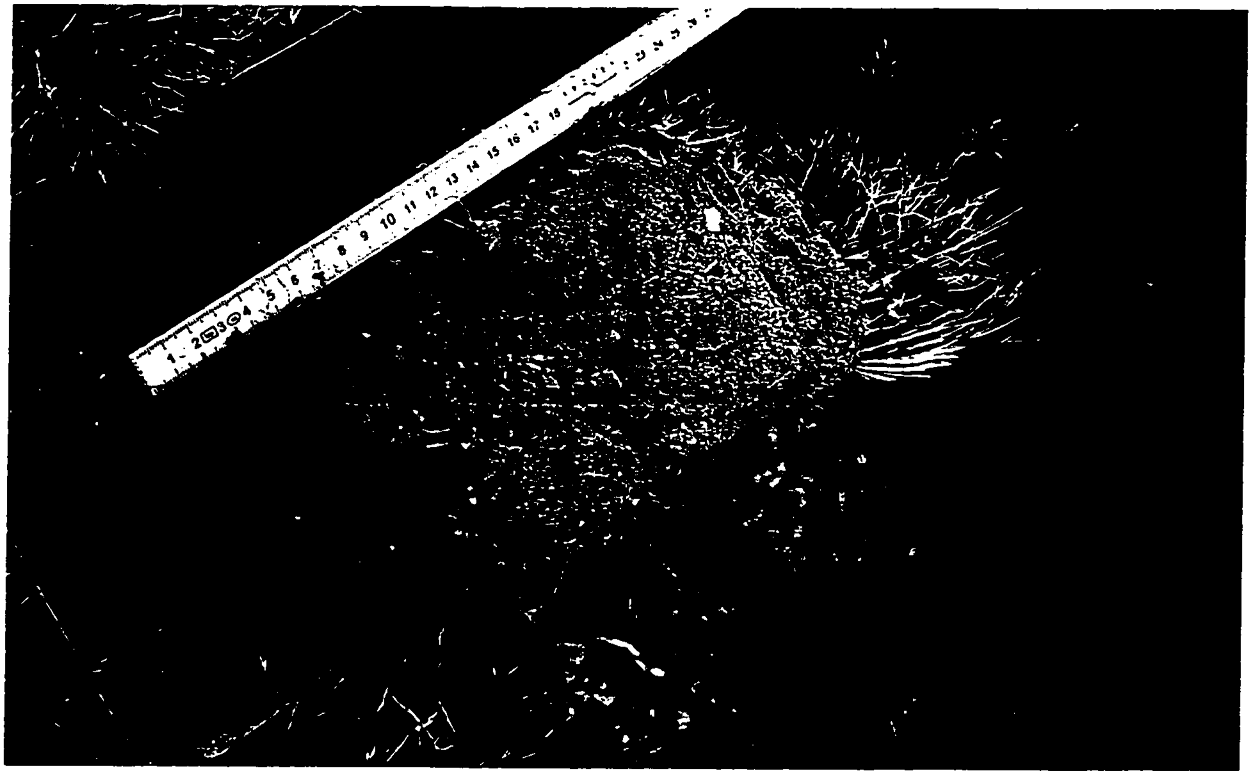


Figure 3.3 Example of sample taken to determine aboveground dead and alive and belowground biomass.

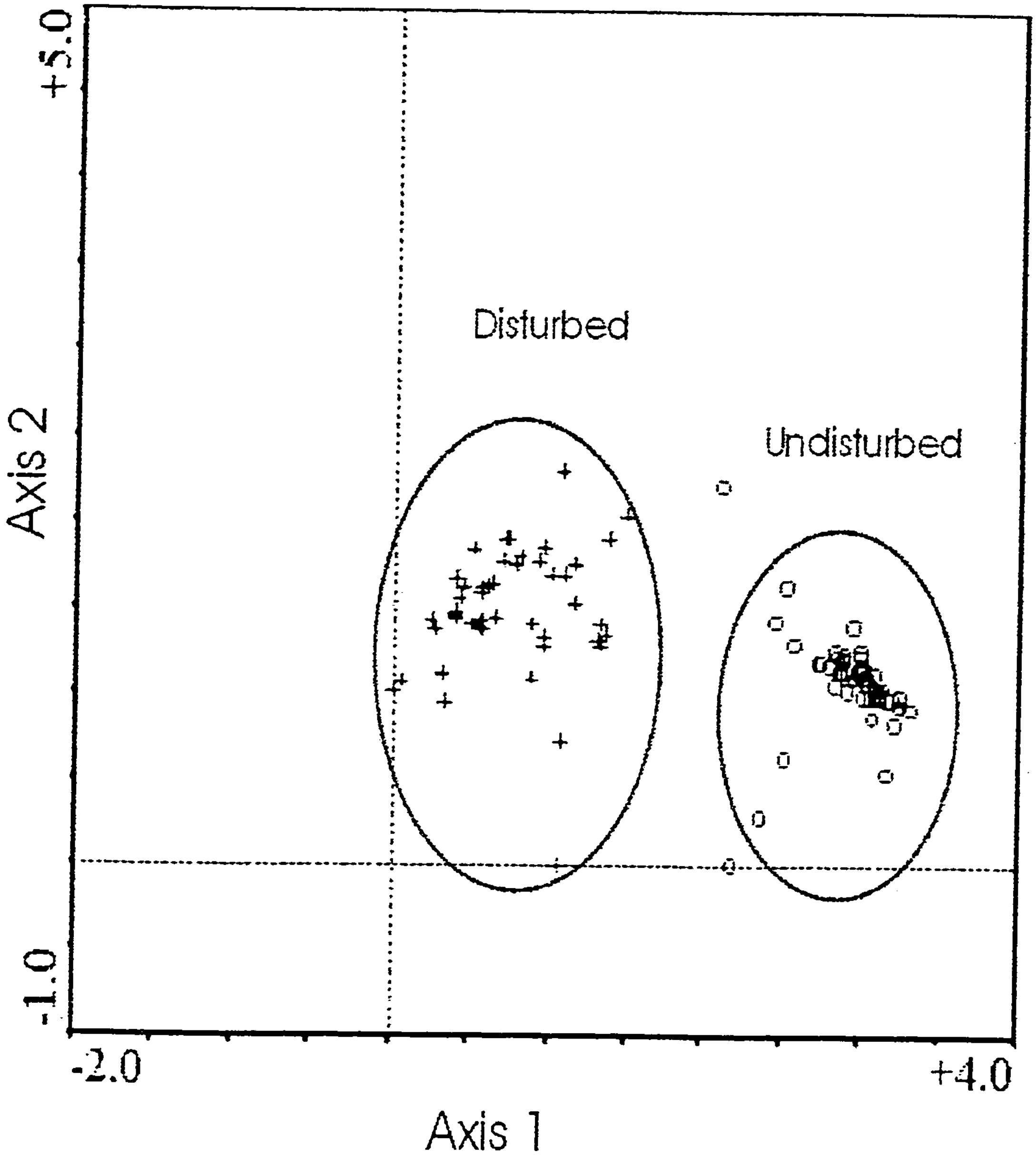


Figure 3.4 Detrended Correspondence Analysis (DCA) of disturbed (+) and undisturbed site (o) locations.

		% Frequency		% Cover	
Taxonomic Group	Species	Undisturbed	Disturbed	Undisturbed	Disturbed
	soil	41	31	12	9
	litter	7	26	1	4
	pavement	51	55	12	15
	rock	8	10	3	3
	dead	81	29	21	6
Magnoliopsida	*Abrotanella inconspicua*	0	1	0	0
	Anisotome imbricata	3	1	0	0
	Anisotome lanuginosa	1	0	0	0
	Celmisia brevifolia	2	10	0	3
	Celmisia laricifolia	4	1	0	0
	Celmisia sessiliflora	2	0	0	0
	Celmisia viscosa	6	1	2	0
	Chionogentia bellidifolia	0	7	0	2
	Chionohebe densifolia	0	2	0	0
	Chionohebe thomsonii	0	0	0	0
	Dracophyllum muscoides	87	5	33	0
	Epilobium alsinoides	0	6	0	0
	Euphrasia zealandica	3	2	0	0
	Hectorella caespitosa	6	3	0	0
	Kellaria chilpia	2	0	1	0
	Leptinella goyenii	1	6	0	1
	Myosotis pulvinaris	0	1	0	0
	Phyllachne rubra	4	0	1	0
	Raoulia grandiflora	4	2	0	0
	Raoulia hectorii	14	12	4	5
	Raoulia subsericea	0	6	0	2
Liliopsida	*Agrostis muelleriana*	3	9	0	0
	Carex pterocarpa	1	0	0	0
	Luzula pumila	22	34	1	2
	Poa colensoi	22	72	1	26
	Dead *Poa col*	0	41	0	15
	Trisetum spicatum	3	12	0	0
Pteridophyte	*Lycopodium fastigiatum*	3	0	0	0
Bryophyte	*Psilopilum australe*	11	25	0	2
Lichens	*Alectoria nigricans*	23	22	1	1
	Cetraria islandica	32	41	4	2
	Cladina				
	Hypogymis lugubis	2	4	0	0
	Siphula sp	10	1	0	0
	Thamnolia vermicularis	66	46	1	0

Table 3.1 Average 1999 percent cover and percent frequency data for disturbed and undisturbed treatments (> 10% frequency and/or > 1% cover).

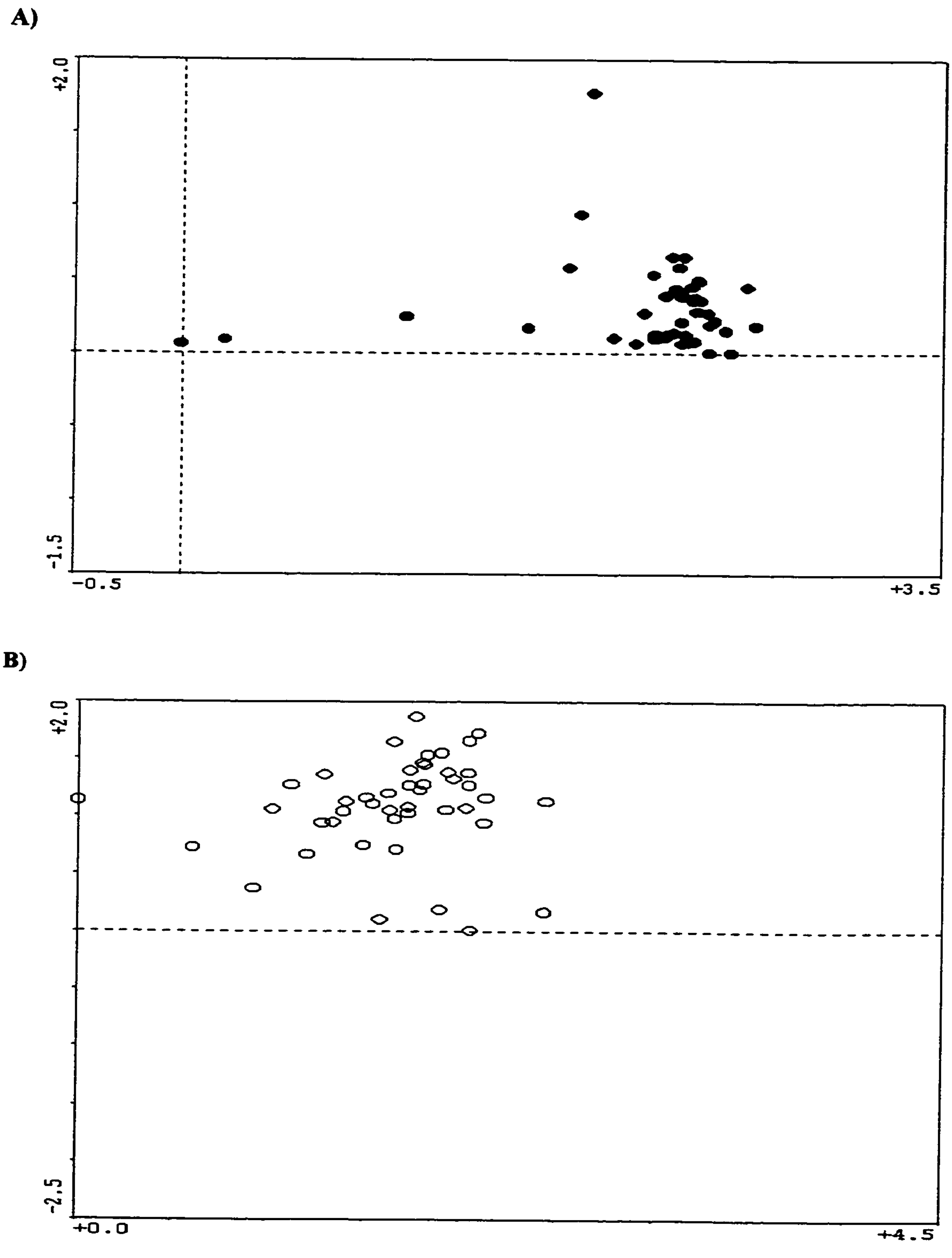


Figure 3.5 Ordination diagram of DCA site distribution for 1999 vegetation data for A) disturbed and B) undisturbed treatments.

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.748	0.351	0.173	0.122	3.662
Lengths of gradient:	3.304	2.312	2.849	2.431	
Cumulative percentage variance of species data:	20.4	30	34.7	38.1	
Sum of all unconstrained eigenvalues					3.662

Table 3.2 Eigenvalues and percent variance for the first four axes of the DCA based on 1999 undisturbed and disturbed vegetation data.

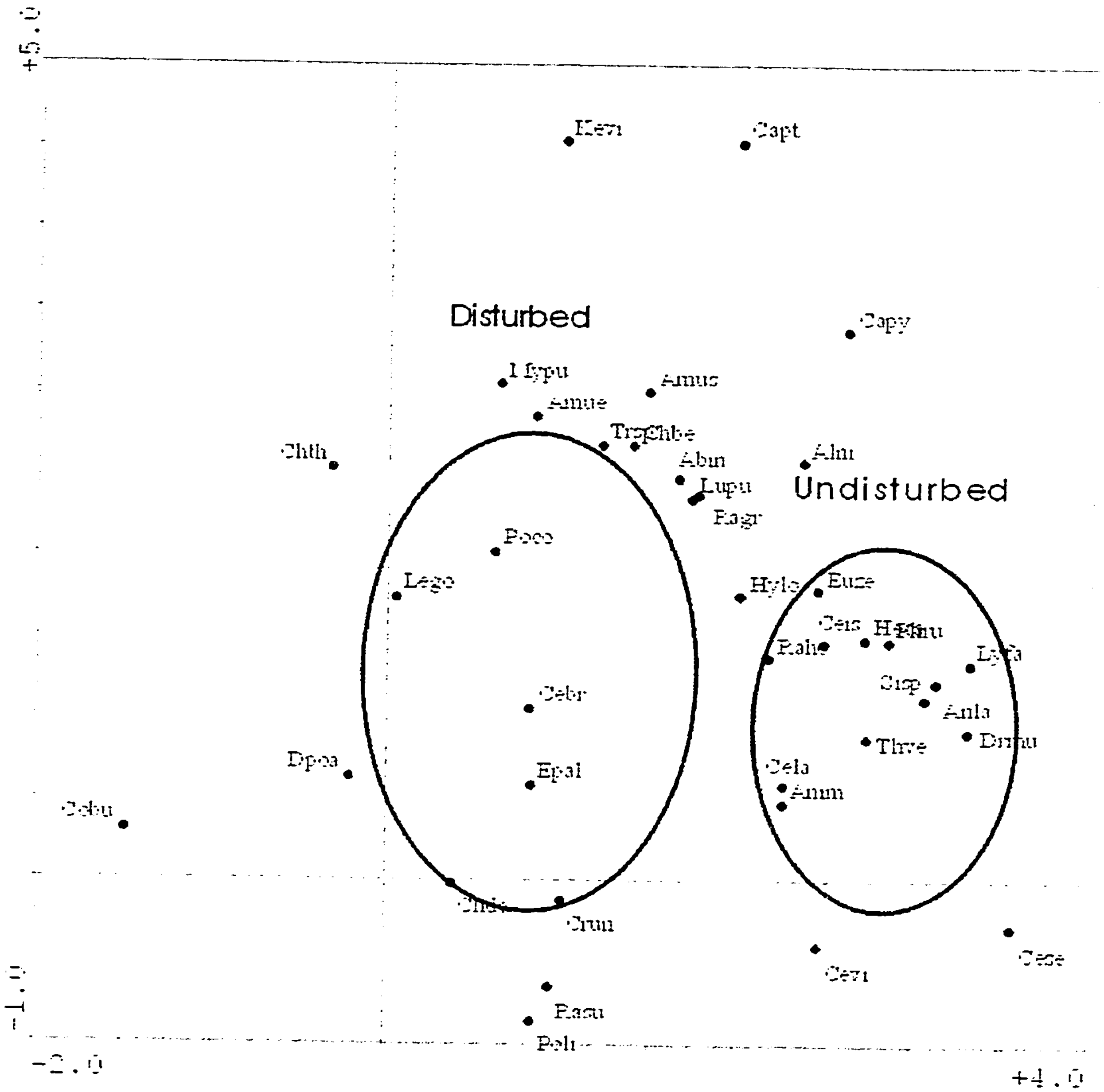


Figure 3.6 Species association with site type (disturbed and undisturbed) determined by DCA ordination based on 1999 cover estimates.

Species	Undisturbed						Disturbed					
	1975	1976	1977	1978	1986	1999	1975	1976	1977	1978	1986	1999
Magnoliopsida												
Abrotanella inconspicua	+	1	5	+	+	+					+	+
Anisotome imbricata				+								
Anisotome lanuginosa	+		+	+	1							
Celmisia brevifolia	+	+	+	+	1	+					+	3
Celmisia laricifolia	1	+	1	+			+					+
Celmisia sessiliflora	+	+	+	+	1	+					+	+
Celmisia viscosa	2	2	2	2	3	4					+	1
Chionogentia bellidifolia					+							
Chionohebe denrifolia			+									
Chionohebe thomsonii	+	+			+							
Colobanthus buchananii	+	+	+	+							+	+
Craspedia uniflora												
Dracophyllum muscoides	28	27	27	26	31	31	+	1	+	+	1	4
Epilobium alsinoides					1						4	+
Euphrasia zelandica	+											
Hebe haastii												+
Hectorella caespitosa	+	1	1	1	1	1	+				1	+
Kellaria childii	1	1	1	1	1	2	+					1
Leptinella goyenii	1	+	1	+	+							+
Myosotis pulvinaris	+	+	+	+	+	+						+
Neopakia australasia												+
Phyllachne rubra	+	1	+	1	1	+	+	+			+	
Raoulia grandiflora	+	+	1	+								
Raoulia hectorii	3	2	2	3	5	4					+	2
Raoulia subsericea											+	1
Liliopsida												
Agrostis muelleriana	1	+	+	2	2	1				+	+	1
Carex pterocarpa		+		+							+	
Carex pyrenaica	+											
Luzula pumila	1	+	1	1	1	2	+	+	+	+	4	2
Poa colensoi	2	2	3	1	3	2	+	+	1	1	17	24
Poa lindsayi											+	
Rytidospermin pumilum						+						4
Trisetum spicatum		+				+					+	1
Pteridophyte												
Lycopodium fastigiatum	1	+	+	+	1							+
Bryophyte												
Psilopilum australe	+	1	1	+	1	+					2	1
Lichens												

Alectoria nigricans	2	3	1	1	2	2					+	1
Cetraria islandica	4	4	5	4	1	3						2
Cladina						+						
Hypogymis lugubis	+	+		+	+							
Siphula sp	+	1	+	1	+	+						+
Thamnolia vermicularis	3	3	3	3	3	2				+	+	1
Total Cover (%)	51	51	54	47	59	56	1	1	1	2	34	51
Species Richness	28	27	25	27	25	21	7	4	3	5	20	27
Species Diversity	0.79	0.79	0.86	0.79	0.87	0.73	0.85	0.23	0.16	0.3	0.61	0.86
Eveness	0.54	0.55	0.62	0.55	0.62	0.55	1	0.38	0.33	0.42	0.47	0.6

Table 3.3 Average species cover of undisturbed and disturbed treatments during six sampling periods and corresponding species richness, diversity, and eveness values. Cover is based on 1000 (undisturbed) and 870 (disturbed) points collected from line intercept transects.

A)

		Mean	Std. Dev
Undisturbed	1975	9.6	2.6
	1976	9.3	3
	1977	8.3	3.1
	1978	9.3	2.9
	1986	9.4	2.4
	1999	8.7	3.3
Disturbed	1975	2	2.9
	1976	2	2.9
	1977	2	2.4
	1978	3	2.8
	1986	6	2.1
	1999	11	4.2

B)

		t	D. F.	P	Statistically Significant
Undisturbed	1975-76	0.171	16	0.867	no
	1976-77	0.697	16	0.496	no
	1977-78	-0.702	16	0.493	no
	1978-86	-0.089	16	0.93	no
	1986-99	0.574	16	0.574	no
Disturbed	1975-76*	-	-	0.691	no
	1976-77*	-	-	0.965	no
	1977-78	-0.0449	16	0.659	no
	1978-86	-3.234	16	0.005	yes
	1986-99	-3.048	16	0.008	yes

Table 3.4 A) Average number of species per transect in the undisturbed and disturbed treatments and B) significance of change in treatments from one sampling period to the next.

Cover state	% Cover											
	Undisturbed						Disturbed					
	1975	1976	1977	1978	1986	1999	1975	1976	1977	1978	1986	1999
soil	12	12	13	14	8	15	77	61	48	51	10	14
dead	18	19	16	18	13	16	3	3	8	4	4	12
litter	5	5	4	6	2	1	3	4	2	4	2	3
pavement	11	11	10	11	14	10	10	24	32	30	45	19
rock	3	3	4	3	4	2	3	3	5	4	3	4
Dmus/Pcol	28	27	27	26	31	32	0.5	0.5	1	1	17	24
other spp.	23	23	26	22	28	24	3.5	4.5	4	6	19	24

Table 3.5 Average percent cover of selected cover states used for transition analysis in undisturbed and disturbed treatments for six sampling periods.

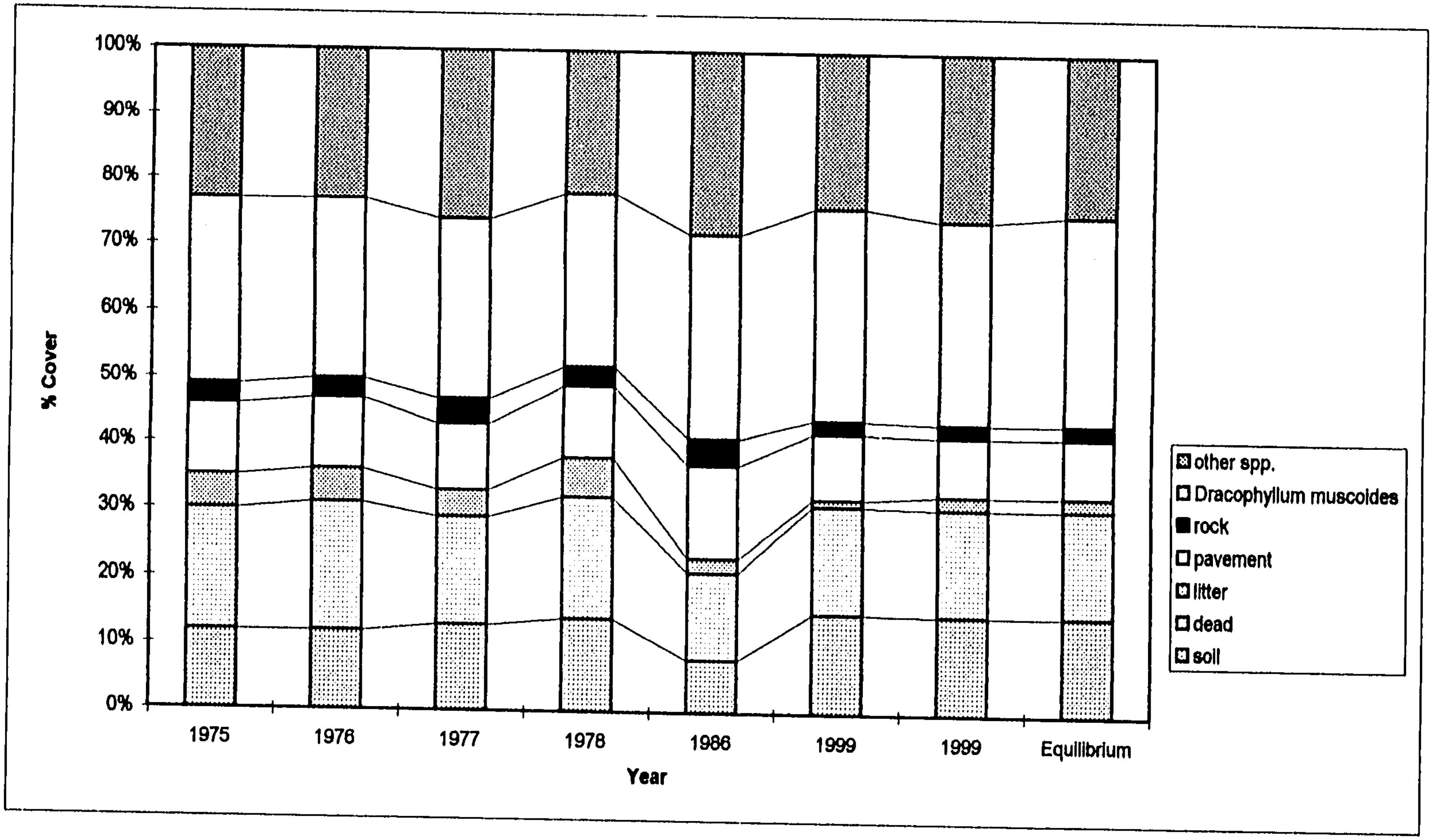
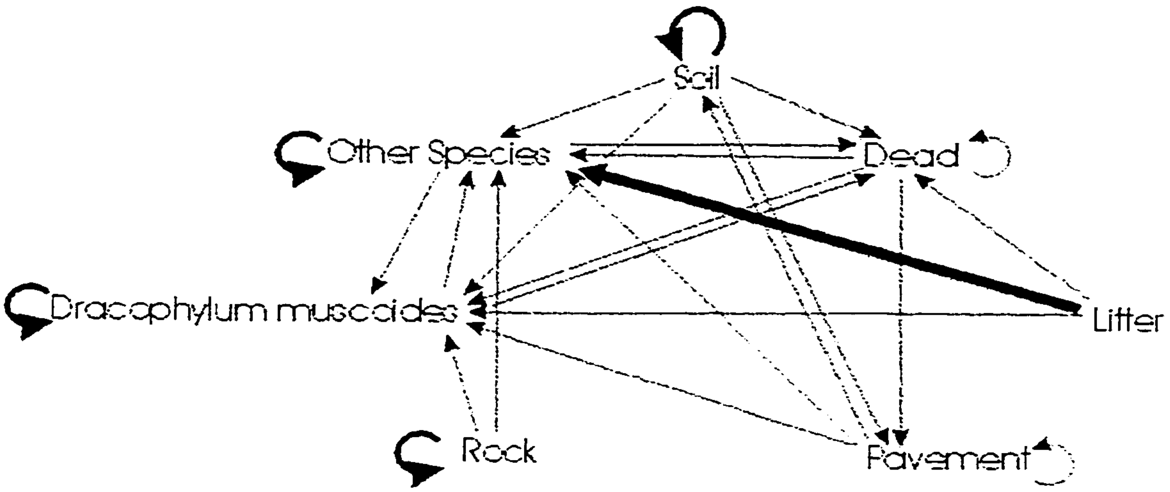


Figure 3.7 Change in cover state in undisturbed habitats based on transects data from 1975, 1976, 1977, 1978, 1986, 1999 and the projected equilibrium distribution predicted by Markov analysis. Cover states are based on those of Roxburgh *et al.* (1988).

Transition probabilities in undisturbed sites 1977-1986



Transition probabilities in undisturbed sites 1986-1999

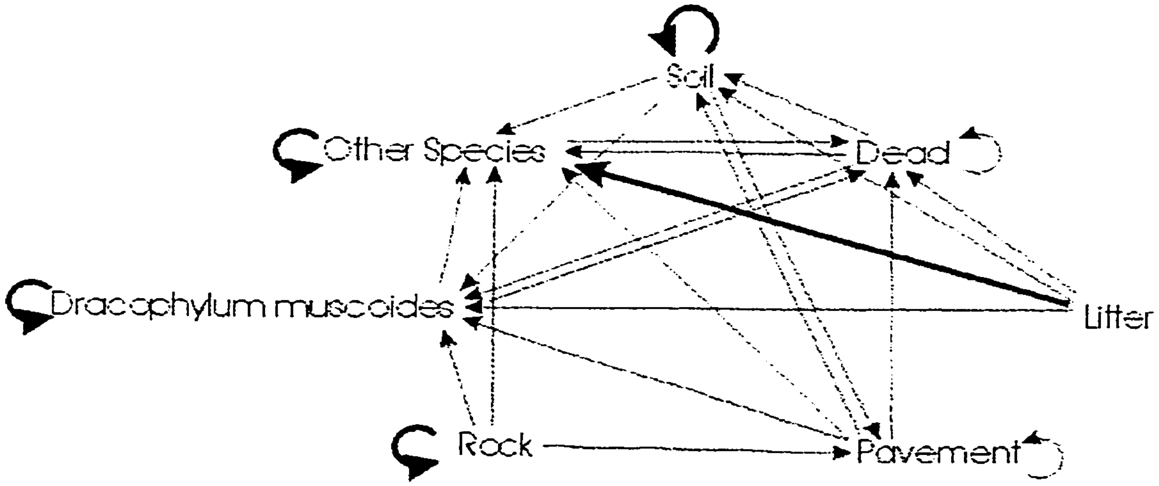


Figure 3.8 Transition probabilities from 1986 and 1999 for undisturbed treatments. Transitions with a frequency >0.1 are not shown. Thin lines correspond to frequencies >0.3 while thick lines indicate frequencies $\leq$0.3.

	Cover in 1999							
Cover in 1986	soil	dead	litter	pavement	rock	Dmus	other spp	Total
soil	25	5	0	12	1	17	15	75
dead	18	29	1	10	4	34	18	114
litter	2	2	1	0	0	4	9	18
pavement	34	16	10	25	0	30	29	144
rock	2	0	0	5	11	7	4	29
Dmus	26	53	2	16	0	133	42	272
other spp	24	35	5	10	3	53	115	245
Total	131	140	19	78	19	278	232	897

Table 3.6 Tally matrix of change in cover state in the undisturbed treatments (1986 - 1999).

Cover Type	1986	1999	Change	Cover change (% of total change)
soil	75	131	56	6.2
dead	114	140	26	2.9
litter	18	19	1	0.1
pavement	144	78	-66	-7.4
rock	29	19	-10	-1.1
Dracophyllum muscoides	272	278	6	0.7
other spp	245	232	-13	-1.4

Table 3.7 Percent change of cover states in undisturbed treatments between 1986 and 1999.

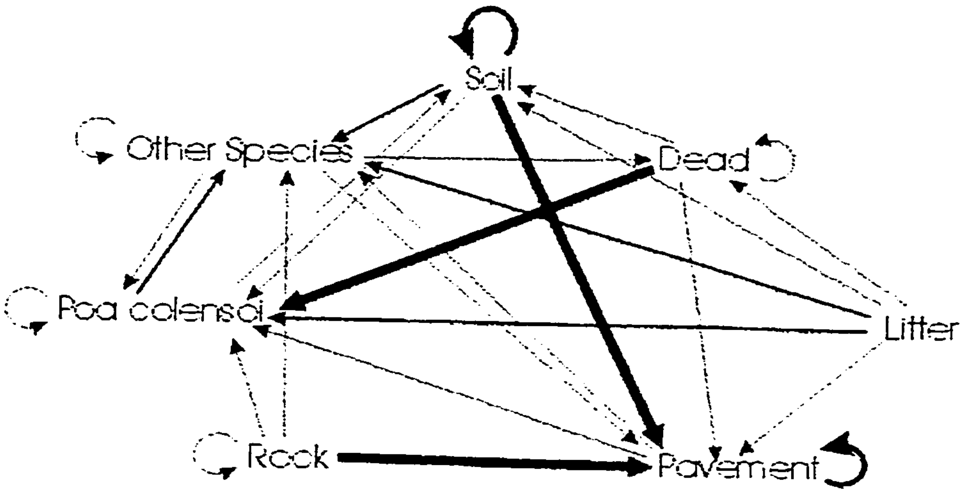
	soil	dead	litter	pavement	rock	Dmus	other spp
soil	0.333	0.067	0	0.16	0.013	0.227	0.2
dead	0.158	0.254	0.009	0.088	0.035	0.298	0.158
litter	0.111	0.111	0.056	0	0	0.222	0.5
pavement	0.236	0.111	0.069	0.174	0	0.208	0.201
rock	0.069	0	0	0.172	0.38	0.241	0.138
Dracophyllum muscoides	0.096	0.195	0.007	0.059	0	0.49	0.154
other spp	0.098	0.143	0.02	0.041	0.012	0.216	0.469

Table 3.8 Probability of transition between states for the undisturbed treatment based on 1986 and 1999 values.

No. of transitions Year	1 1999	2 2012	3 2025	4 2038	5 2051	6 2064	7 2077
soil	0.1463	0.1528	0.1537	0.1543	0.1544	0.1545	0.1545
dead	0.1561	0.1588	0.1593	0.1594	0.1594	0.1594	0.1594
litter	0.0210	0.0159	0.0153	0.0154	0.0154	0.0154	0.0154
pavement	0.0872	0.0828	0.0850	0.0854	0.0854	0.0855	0.0855
rock	0.0210	0.0184	0.0176	0.0173	0.0171	0.0171	0.0171
Dracophyllum muscoides	0.3100	0.3153	0.3165	0.3169	0.3170	0.3170	0.3170
other spp	0.2583	0.2537	0.2504	0.2492	0.2490	0.2489	0.2489

Table 3.9 Projected changes in cover values in the undisturbed treatment based on Markov predictions.

Transition probabilities in disturbed sites 1977-1986



Transition probabilities in disturbed sites 1986-1999

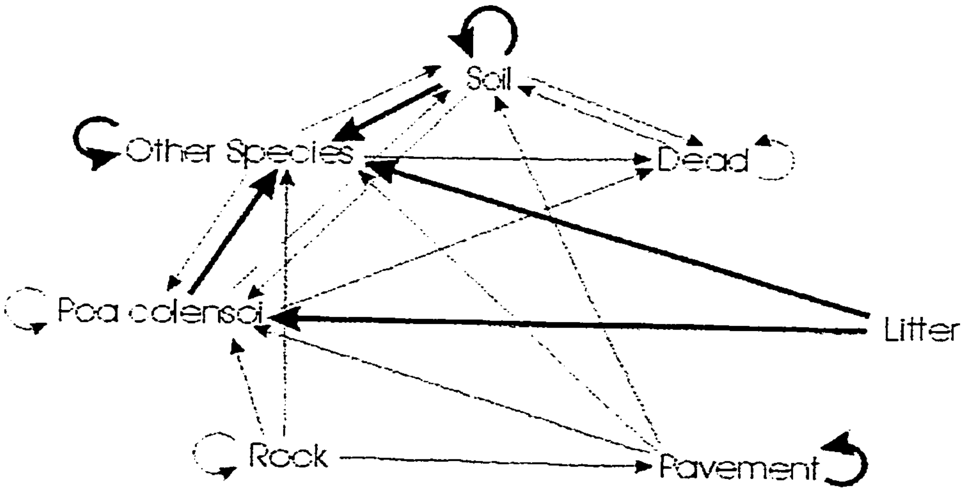


Figure 3.9 Transition probabilities from 1986 and 1999 for disturbed treatments. Transitions with a frequency >0.1 are not shown. Thin lines correspond to frequencies >0.3 while thick lines indicate frequencies ≤ 0.3.

	Soil	Dead	Litter	Pavement	Rock	P.col	Other spp
Soil	0.304	0.13	0.054	0.054	0.011	0.109	0.337
Dead	0.111	0.194	0.083	0.028	0	0.083	0.5
Litter	0	0	0.071	0.071	0	0.357	0.5
Pavement	0.188	0.071	0.023	0.305	0.058	0.155	0.201
Rock	0.037	0.074	0	0.259	0.185	0.148	0.296
Poa colensoi	0.103	0.231	0.045	0.045	0.013	0.231	0.333
Other spp.	0.139	0.131	0.051	0.095	0.007	0.219	0.358

Table 3.10 Probability of transition between states for the disturbed treatment based on 1986 and 1999 values.

	Cover in 1999							
Cover in 1986	Soil	Dead	Litter	Pavement	Rock	P.col	Other spp	Total
Soil	28	12	5	5	1	10	31	92
Dead	4	7	3	1	0	3	18	36
Litter	0	0	1	1	0	5	7	14
Pavement	74	28	9	120	23	61	79	394
Rock	1	2		7	5	4	8	27
Poa colensoi	16	36	7	7	2	36	52	156
Other spp.	19	18	7	13	1	30	49	137
Total	142	103	32	154	32	149	244	856

Table 3.11 Tally matrix of change in cover states in the disturbed treatments (1986 - 1999).

Cover Type	1986	Cover 1999	Change	Cover change (% of total cover)
Soil	92	142	50	5.84
Dead	36	103	67	7.82
Litter	14	32	18	2.10
Pavement	394	154	-240	-28.04
Rock	27	32	5	0.58
Poa colensoi	156	149	-7	-0.82
Other spp.	137	244	107	12.50

Table 3.12 Change in percent cover of states in disturbed treatments between 1986 and 1999.

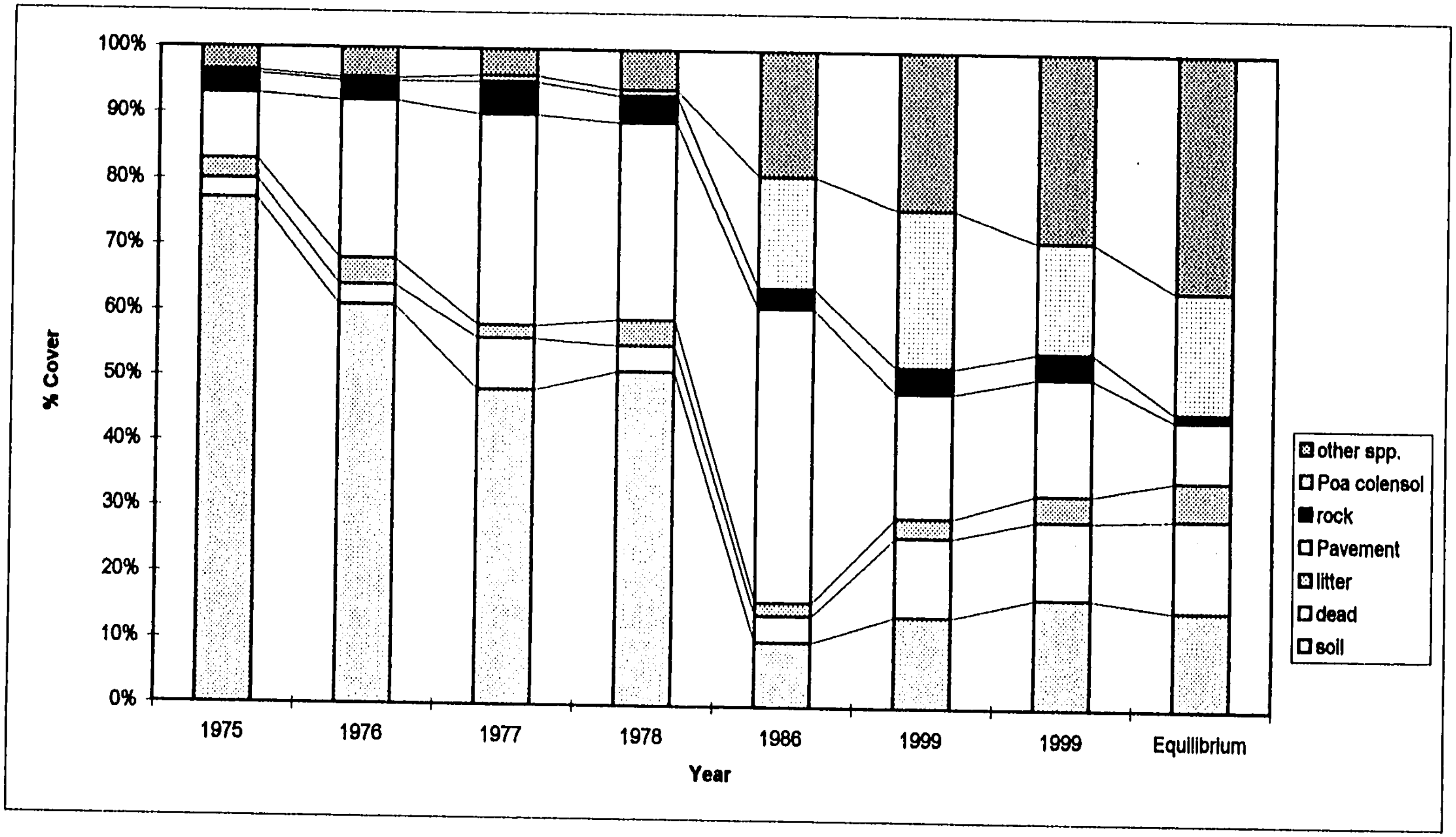


Figure 3.10 Change in cover state in disturbed habitats based on transects data from 1975, 1976, 1977, 1978, 1986, 1999 and the projected equilibrium distribution predicted by Markov analysis. Cover states are based on those of Roxburgh *et al.* (1988).

No. of transitions Year	1 1999	2 2012	3 2025	4 2038	5 2051	6 2064	7 2077
soil	0.166	0.156	0.151	0.149	0.148	0.148	0.148
dead	0.120	0.138	0.143	0.144	0.145	0.145	0.145
litter	0.037	0.048	0.051	0.052	0.053	0.053	0.053
pavement	0.180	0.114	0.097	0.092	0.091	0.090	0.090
rock	0.037	0.023	0.017	0.015	0.015	0.015	0.014
Poa colensoi	0.174	0.177	0.183	0.185	0.185	0.185	0.185
other spp	0.285	0.342	0.357	0.361	0.363	0.363	0.363

Table 3.13 Projected changes in cover values in the disturbed treatments based on Markov predictions.

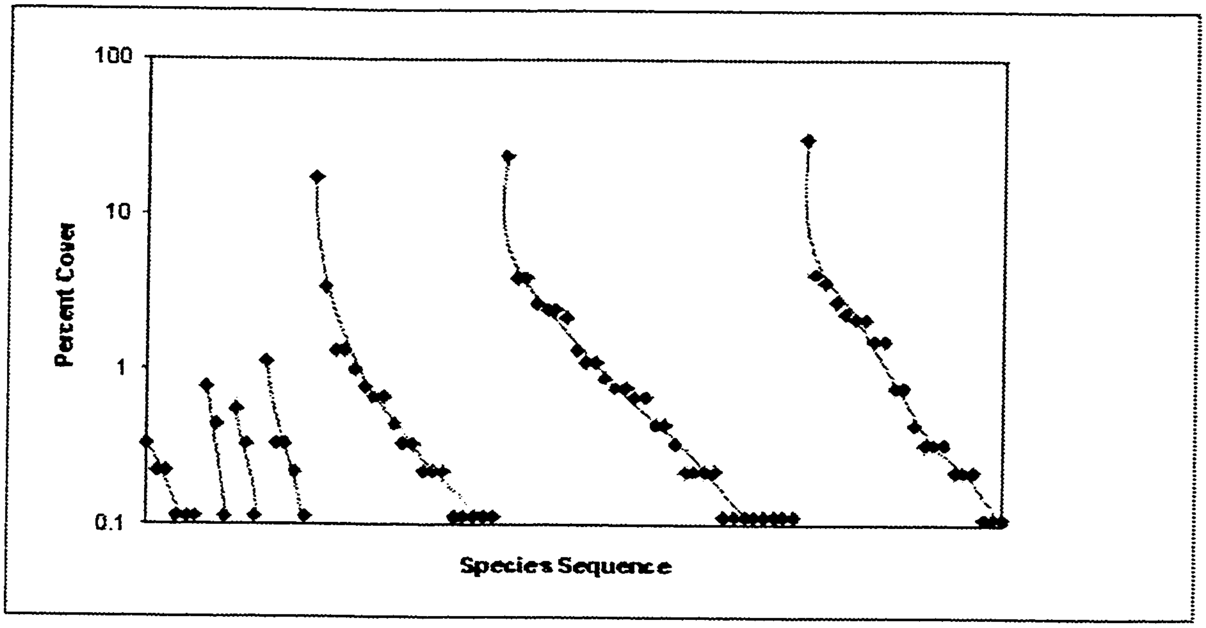


Figure 3.11 Importance-value curves for succession on disturbance treatments on the Old Man Range, New Zealand. Values are based on percent plant cover collected in 1975, 1976, 1977, 1978, 1986 and 1999.

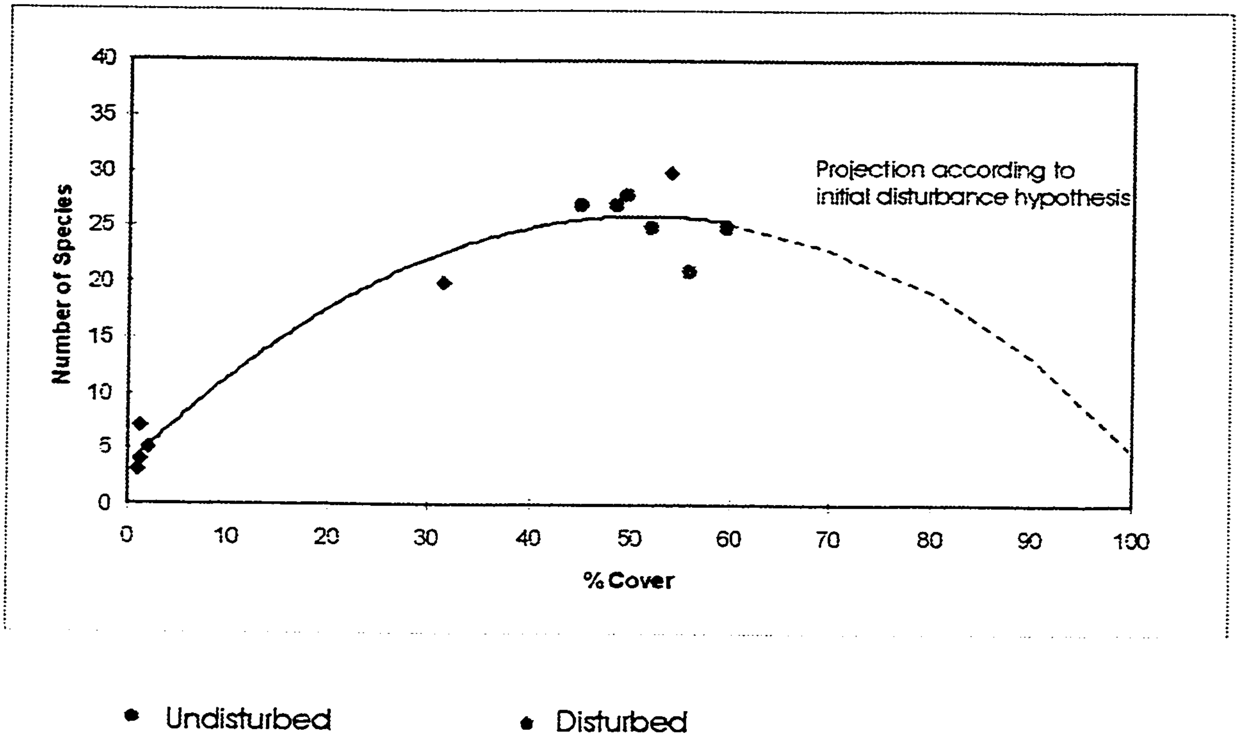


Figure 3.12 Change in species richness with time based on species cover values derived from line intercept transects. Blue diamonds indicate data collected from disturbed treatments while red circles correspond to data from undisturbed treatments. Graph is based on data collected from 1975, 1976, 1977, 1978, 1986 and 1999.

	Undisturbed		Disturbed					
	Mean	Std. Dev.	Mean	Std.Dev	t	D.F.	P	Sig Diff
Above ground biomass (alive)	26.027	21.335	17.011	15.250	1.14	20	0.268	no
Above ground biomass (dead)	11.405	7.858	8.985	7.826	0.724	20	0.478	no
Below ground biomass	31.175	31.175	34.473	35.349	-	-	0.844	no

Table 3.14 Mean biomass values for undisturbed and disturbed treatments based on alive and dead above ground biomass and below ground biomass and test of significant difference.

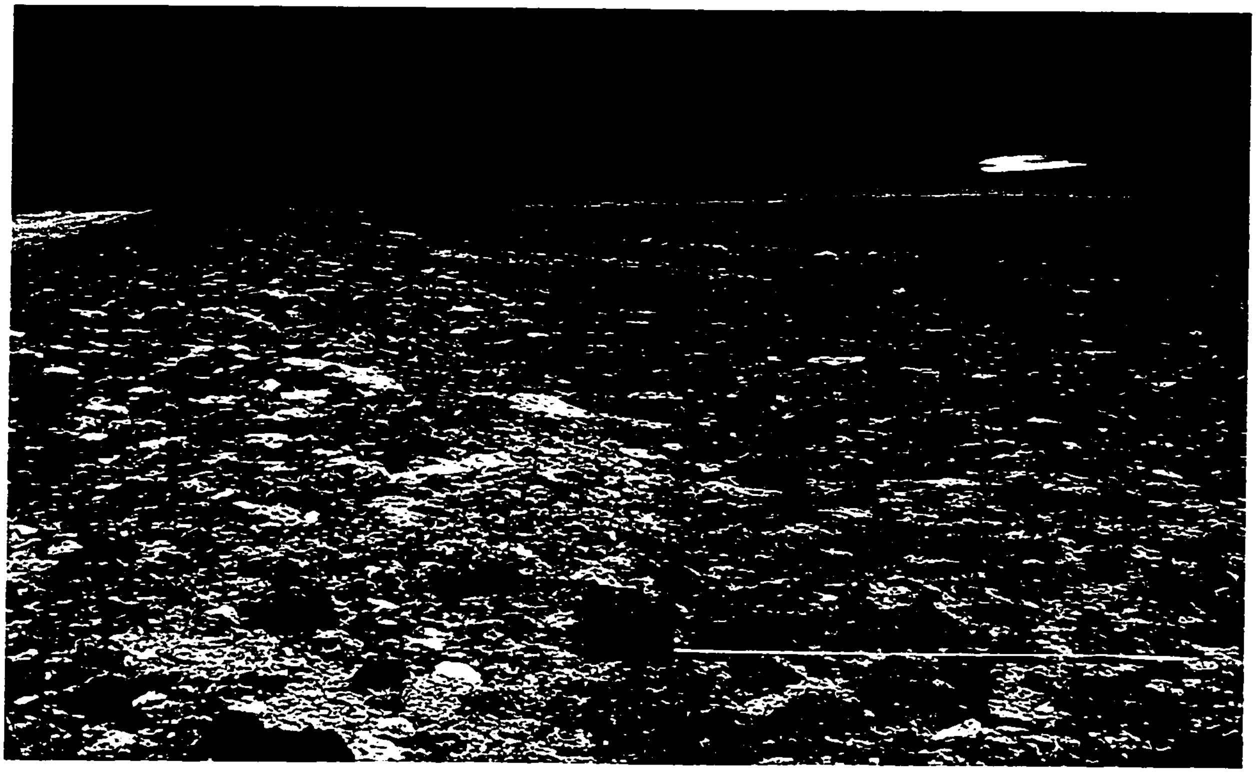


Figure 3.13 Example of the dramatic difference in community species composition and structure still persisting 25 years following disturbance.

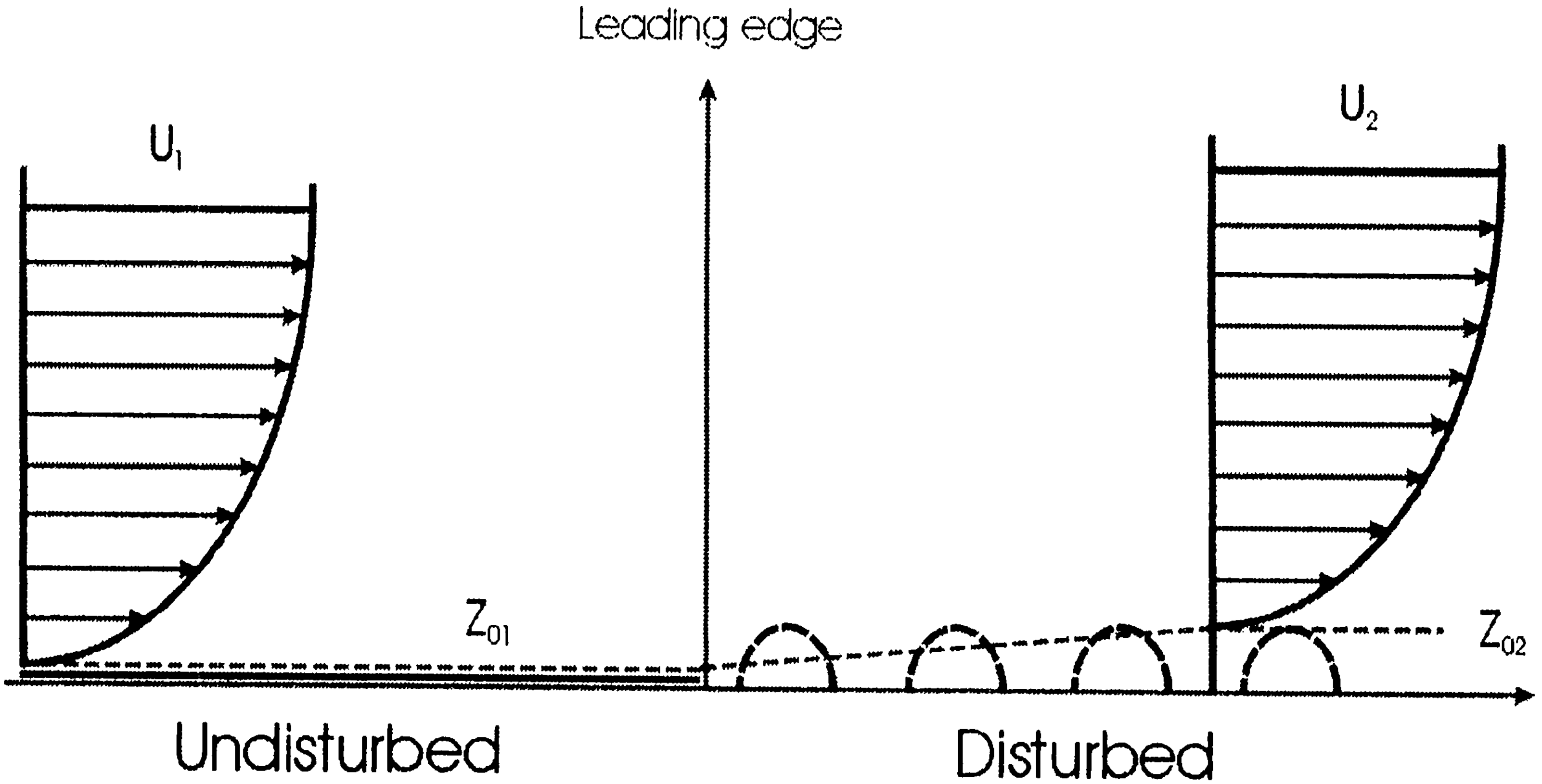


Figure 3.14 Diagram of the potential change in wind profile from undisturbed to disturbed sites due to change in microtopography and its potential for tussock mortality.

Figure 3.15 Example of tussock top mortality, which was observed throughout the study site

Figure 3.16 Example of soil incorporation in *Poa* tussocks (photo courtesy of A. F. Mark).

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Chapter 4: Image Processing of Conventional, Sequential, Ground Photography: A Tool for Evaluating Plant Recovery Following Anthropogenic Disturbance

Introduction:

The importance of monitoring revegetation, following direct or indirect anthropogenic disturbance, has been identified by Forbes and Jefferies (1999). Of specific concern are the rates of establishment, patterns of growth and longevity of colonizing species. It is only once the mechanisms of natural succession are understood that restoration practices will be most effective (Cargill and Chapin 1987). Without this knowledge, prediction of recovery patterns and long-term results will be unsuccessful.

Assessing changes in plant community type and distribution has become an increasingly important objective for expanding our understanding of plant community ecology. Distributional patterns of species are exceedingly complex, both spatially and temporally (Nagendra and Gadgil 1999a), and therefore require a means of quantitatively monitoring changes within plant communities. The advent of remote sensing has permitted a greater ability to monitor these changes through time and space. Remote sensing has been used to compare deforestation and fragmentation rates (Sanchez *et al.* 1999), to map wildfire severity (Patterson and Yool 1998) and to monitor biodiversity (Nagendra and Gadgil 1999a). Monitoring the location, extent and changes in major vegetation assemblages and ecological units is dependent on land cover data (Moody 1998). This monitoring is currently supporting a wide-range of research concerned with modeling and understanding the response of vegetation to natural and anthropogenic forcing factors (Vitousek 1994). While previous monitoring of the effect of disturbance on plant communities has been concerned with landscape-scale responses, it has become increasingly important to consider the interactions and responses experienced on an individual plant basis. Once we have determined these conditions we will have a better understanding of the successional responses, which are expressed on a landscape scale.

Objectives:

The objectives of the study were to:

i) At a large scale, determine the rate of change in selected cover classes that are fine enough to track individual plants or cushion/tussocks.

ii) Using these data, quantitatively describe the successional trend and rate of succession in the disturbed treatments as well as determine the stability of the undisturbed treatment.

Monitoring change in cover:

- Cover Classification

Classification of an image for previously selected class types is best facilitated through the use of supervised classification, which automatically categorizes all of the pixels within the image into land cover classes selected by the operator. This is possible due to the different combinations of DNs (digital number) based on spectral reflectance and emittance properties. The supervised classification process is based on three stages: training, classification and output. During the training stage, representative samples of known cover types are sampled to compile a numerical interpretation key that describes the spectral attributes for the selected classes. Each pixel in the data set is then compared to each category in the interpretation key and labeled with the name that is most similar to it. The classified data can then be used to create a thematic map (Lillesand and Kiefer 1994).

Methods:

Image Collection

Fixed benchmarks used for vertically photographing permanent 0.75 m x 1 m plots were established in 1984 at the 10 m mark along the line intercept transects in the undisturbed and disturbed portions of the 10 transects (excluding transect 6) established by Prof. A.F. Mark immediately following disturbance on the Old Man Range, New Zealand. Plots were re-photographed in 1986, 1991, 1993 and 1999 using a tripod with a horizontally-mounted camera 0.98 cm above the ground with a 28 mm lens (Figure 4.1). The peripheral margin of the images was delimitated by permanent pegs and comparisons to previous photographs. Cover content of the 1999 photographs was determined in the field to permit ground truthing and allow for positive identification of the species present. Based on a visual analysis of the photos it was decided that there was insufficient change between 1984 and 1986 and between 1991 and 1993 so the 1986 and 1991 photos were not included for analysis.

Image Classification

Images from a representative sample of the undisturbed and disturbed treatments from 1984 and 1993 were digitized at 300 dpi while 1999 images were digitized at 600 dpi. The images were then referenced and geometrically corrected to the 1984 image. Images were processed by supervised classification based on species and cover type (soil, pavement, rock) basis with the ERDAS 8.4 software. Cover types were not selected on a spectral and statistical basis but instead were chosen based on presence. The amount of fragmentation on a cover type basis was determined using the Fragstats program. Given the time constraints, a single pair of sites was used from the set of 9-paired plots. Thus, a disturbed and its associated undisturbed plot were used in the initial analysis of the time series 1984, 1993 and 1999 photos for a total of 6 images.

Results:

Undisturbed Treatment

Overall cover varied little during the 15-year period in the undisturbed treatment (Table 4.1a). Species composition within the photo plot was especially low, dominated by *Dracophyllum muscoides* (Figure 4.2), with limited *Raoulia hectorii* cover. Rock cover remained constant while soil cover increased or decreased inversely with *Dracophyllum muscoides* cover.

Comparison of the degree of fragmentation was only possible between the 1984 and 1993 images owing to the higher resolution of the 1999 images. Plant-based cover classes varied little between images (Table 4.1b), while soil and rock classes substantially increased in fragmentation from 2705 to 6576 and 3484 to 5724 fragments respectively.

Disturbed Treatment

Number of species present within the disturbed treatment photo plot increased throughout the 1984-1999 period from 3 to 4 species (Table 4.2a). Change in species composition however varied greatly during this period. While *Poa colensoi* persisted throughout the sampling period, the cushion species *Kelleria childii* and *Phyllachne rubra*, which were present and increased in cover from 1984 to 1993 were no longer present in the 1999 sampling. *Raoulia hectorii*, another cushion species that did not establish until after 1984 continued to expand. Species composition in 1999 diversified by the addition of two more graminoid species, *Luzula pumila* and *Trisetum spicatum*.

Although much of the change in cover resulted from colonization of soil and rock (specifically pavement) (Table 4.1), increases in species cover also came at the expense of other species (loss of cushion species to *Poa colensoi*). As well as displacement of species, substantial mortality was observed within the plots warranting the inclusion of 'dead *Poa colensoi*' and 'dead cushion' classes. As observed from line intercept data (Table 3.5) revegetation of the disturbed treatment was characterized by an initial and then persistent colonization of *Poa colensoi* in tussock form as well as other grasses. Mortality and deflation of *Poa colensoi* was largely restricted to tussock tops to the extent that much of the tussock top became classified as soil (Figure 4.3).

While *Dracophyllum muscoides* was not observed in the disturbed treatment, *Raoulia hectorii*, a characteristic species found in the undisturbed treatments had established by 1993 and continued to increase in cover up to 1999.

Discussion:

Change in plant cover observed in the photo plots was similar to that found using the line transects data. Photo plot data, however, provided the opportunity to monitor the exact replacement and transitions in plant cover. This allowed for a more quantitative assessment of *Poa colensoi* tussock top mortality. Dead *Poa colensoi* values derived from the supervised classification were somewhat inflated compared to those from the line transect methods due to the inclusion of *Poa colensoi* litter in the dead *Poa colensoi* class. Perhaps the most important aspect of the supervised classification was the opportunity to monitor the development and decline of the *Poa colensoi* tussock on an individual basis. This allowed for a compelling illustration of the eventual mortality of the tussocks once their height became too great, which was observed by the extensive shoot loss, which was followed by deflation. The continuing change in plant cover, best characterized by tussock mortality, was a good indicator that the revegetation of the disturbed sites was not yet complete and that the *Poa colensoi*-dominated community was likely an intermediate successional stage.

Cover composition values in the undisturbed treatment varied little between 1984 and 1999. The undisturbed treatments, however, were quite dynamic, characterized by widespread transitions between the dominant cover types. This supports the transition findings of Chapter 3, which indicated that a lot of mortality and replacement occurred during the 1986-1999 period. Much of the replacement was due to a loss/gain of *Dracophyllum muscoides* at the gain/expense of the soil and rock classes.

Comparison of change in fragmentation occurring between the 1984 and 1993 images and the 1999 image was impossible due to the higher scanning resolution used for the 1999 images. The higher degree of fragmentation observed in the 1999 images were a result of the greater number of pixels which composed the images. Change in fragmentation in the undisturbed treatments was predominantly limited to the non-biotic classes. The greater increase and amount of fragmentation was likely the result of wind. The soil, and rock material, which was predominantly characterized by small clasts were highly mobile under the influence of wind and therefore would be subjected to a substantial amount of redistribution. Redistribution of material would increase the scatter and therefore, the number of small fragments and reduce the probability of the occurrence of large fragments.

The smaller number of rock class fragments observed in the disturbed treatments compared to the undisturbed treatments was due to the greater occurrence of large clasts and lesser extent of pavement-sized material. Plant structure also played a role in the extent of fragmentation observed in the disturbed treatments. Cushion species (*Kelleria childii*, *Phyllachne rubra*, and *Raoulia hectorii*) typically had a lower amount of fragments due in part to low cover values but also as a result of their dense cushion growth form.

Overall, the use of supervised classification techniques on such a large scale proved to be quite effective. It allowed for a more quantitative measure of changes in community composition, as well as the opportunity to accurately follow the successional pathways in the high-alpine of Old Man Range. Image analysis also provided a more objective and quantitative means of monitoring changes in plant community than previously available using methods provided by Roxburgh *et al.* (1988). Use of a supervised classification also allowed for the computation of precise area coverage of selected class types, permitting the calculation of rates of expansion and loss of cover types and the degree of fragmentation of each class. This provides a better understanding of rates of succession on an individual and species population basis.

Summary:

Supervised classification of sequential images form the permanent photoplots proved to be an effective means of monitoring change in surface cover. The minimal stratification of the plant community enabled detailed observations of the successional sequence following the initial disturbance, thereby providing a unique means of documenting the successional pathways. Time-series supervised classification also allows for the qualitative measurement of *Poa colensoi* tussock mortality, further supplementing the line intercept findings. Changes in plant distribution in the undisturbed treatments also confirm the dynamic nature of the cushionfield-dominated communities suggested by the transition matrices results in Chapter 3.

Figure 4.1 Method used to collect aerial photographs of permanent photoplots.

A)

	1984	1993	1999
Raoulia hectorii	2.5	1.5	3.4
Soil	32.9	16.7	35.6
Dracophyllum muscoides	32.6	40.1	19.3
Rock	12.7	11.8	14.0

B)

	1984	1993	1999
Raoulia hectorii	572	730	1788
Soil	2705	6576	14913
Dracophyllum muscoides	2603	2306	14145
Rock	3484	5724	33225

Table 4.1 A) Percent cover and B) number of fragments of selected classes for undisturbed treatments based on supervised classification for 1984, 1993 and 1999.

A)

	1984	1993	1999
Poa colensoi	17.4	20.8	42.5
Rock	19.2	8.2	9.9
Kellaria childii	1.4	0.4	-
Phyllachne rubra	0.2	2.3	-
Soil	47.5	15.4	19.5
Dead *Poa colensoi*	-	11.2	9.7
Raoulia hectorii	-	1.8	1.6
Luzula pumila	-	-	0.4
Dead *P. rubra*	-	-	0.6
Trisetum spicatum	-	-	2.2

B)

	1984	1993	1999
Poa colensoi	2189	3754	13778
Rock	3439	3194	8408
Kellaria childii	14	21	-
Phyllachne rubra	24	191	-
Soil	946	4443	23775
Dead *Poa colensoi*	-	2214	19447
Raoulia hectorii	-	7	229
Luzula pumila	-	-	3654
Dead *P. rubra*	-	-	52
Trisetum spicatum	-	-	177

Table 4.2 A) Percent cover and B) number of fragments of selected classes for disturbed treatments based on supervised classification for 1984, 1993 and 1999.

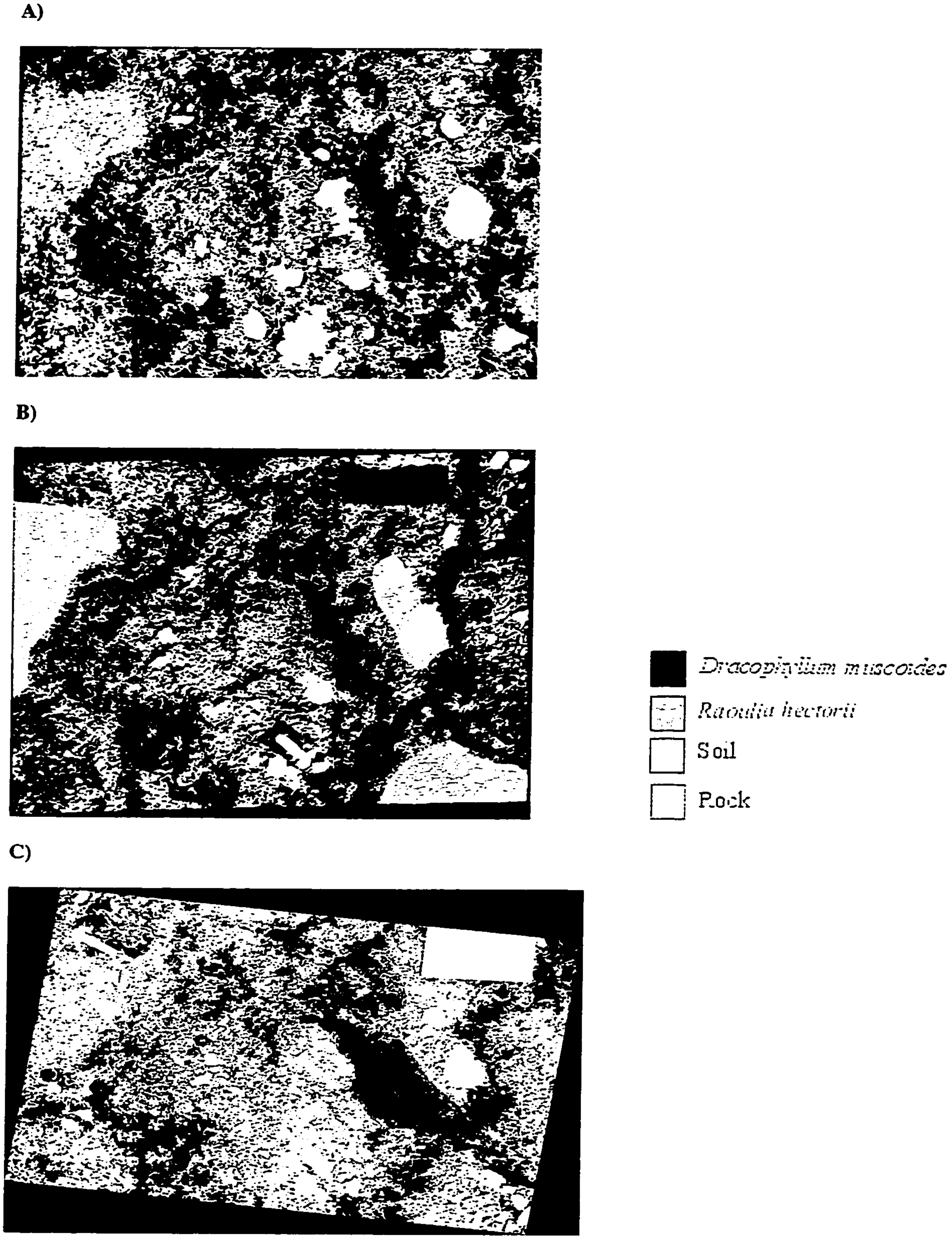

Figure 4.2 Change in cover in undisturbed permanent photoplot from A) 1984, B) 1993 and C) 1999.

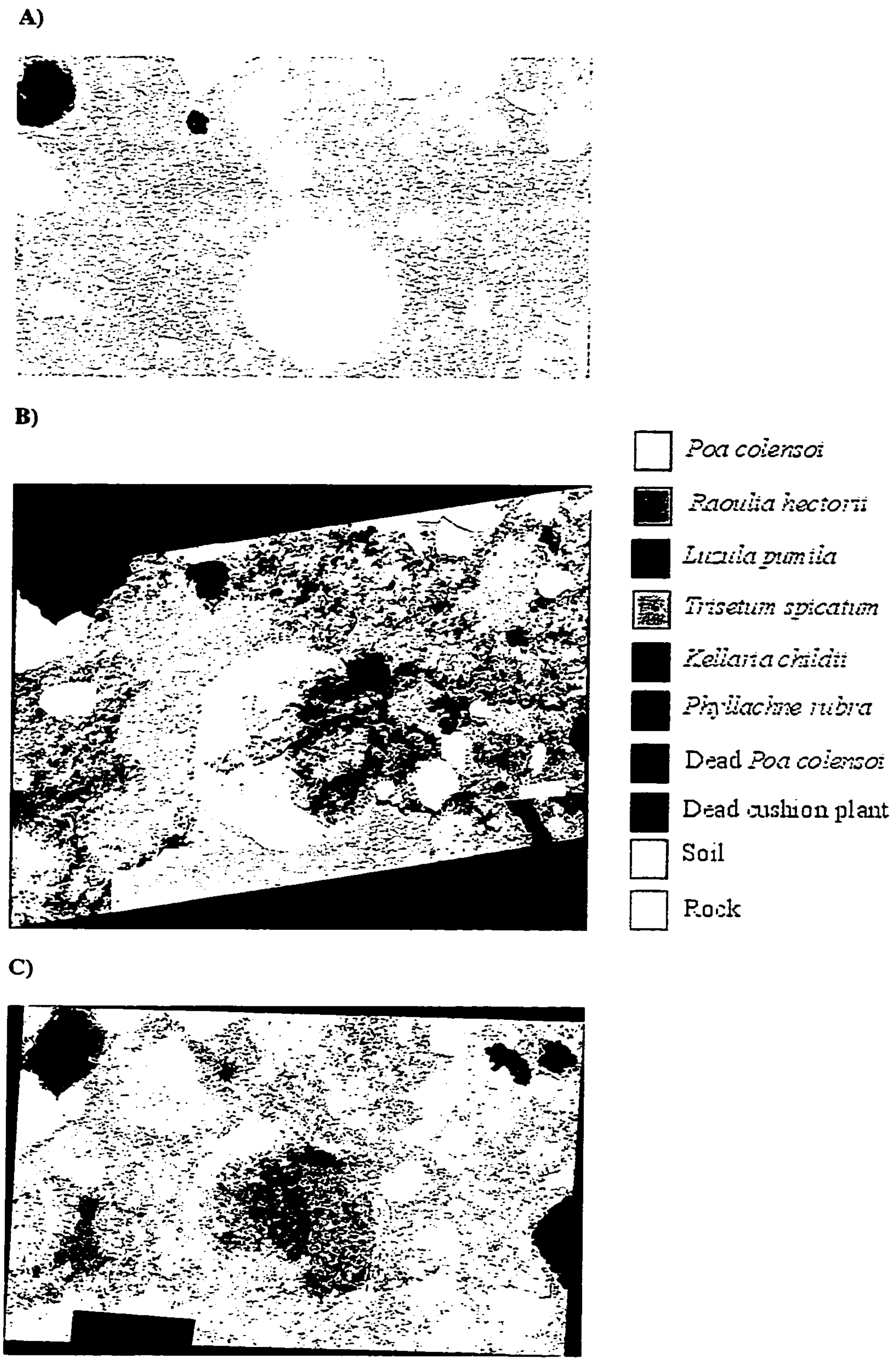

Figure 4.3 Change in cover in disturbed permanent photoplot from 1984, 1993, and 1999.

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Chapter 5: Correlations Between Plant Species Composition and Environmental Variables

Introduction:

A substantial body of laboratory and field research has demonstrated that the limited growth and primary production of alpine and tundra vegetation results from: low temperature, high winds, short growing seasons, low nutrient availability and soil moisture limitations (Billings and Bliss 1959, Savile 1972, Rehder 1976 a,b, Rehder and Schäfer 1978, Weber 1978, Bliss 1985, Chapin and Shaver 1985, Sundriyal 1992). However, the influence of these environmental variables on determining plant community composition and structure in alpine settings has been little studied.

While species occurrence and distribution in many environments is largely dependent upon competition, competition in severe settings, including alpine environments, is largely absent (Savile 1960, Grime 1977). This predominantly results from the absence of canopy stratification (Walker *et al.* 1994) and the overbearing importance of physical factors (Savile 1960). The adverse conditions produce a reduction in the number of competing taxa and weaken competitive pressures, thereby making stress tolerance the prime survival concern (Svoboda and Henry 1987). Species establishment and maintenance are therefore of greater importance in alpine environments than species replacement (Svoboda and Henry 1987). Chapin and Shaver (1985), however, suggested that competition would occur due to the less than optimal supply of available resources or when fast-growing, highly competitive exotic species are introduced (Cargill and Chapin 1987).

Although Savile (1960) and Whittaker (1975) have suggested that species within alpine and arctic communities are essentially random in their distribution, and patterns at the meso-scale are nonexistent, other researchers have found that communities can be largely dependent upon the complex interaction among a number of environmental variables and gradients. These include: snow depth, snow cover duration, length of growing season, soil moisture, soil properties, soil temperature, wind, disturbance, dispersal and interactions among plant species (May and Weber 1982, Billings 1988). The relative importance of these variables on community composition is further affected by the exclusion of high levels of competition in extreme environments (Savile 1960, Svoboda and Henry 1976).

Since the cumulative effects of a number of environmental variables imposed on plant species is considered to be the primary factor determining plant species distribution, except at the small spatial and temporal scale (ter Braak 1994), it may be best to analyze their joint effects (ter Braak 1987). Evaluating species-environment relationships based on community composition data and associated environmental measurements may be assessed through direct gradient analysis and ordination. Direct gradient analysis permits the study of the variation in community composition, which can be attributed to a particular set of environmental variables (ter Braak and Prentice 1988), in this manner the environmental factors underlying the ordination can be evaluated (ter Braak 1994).

Through the analysis of species and environmental data from the Old Man Range, it should be possible to evaluate the role of the selected environmental variables in the creation and maintenance of differences between the community composition of undisturbed and disturbed sites, 25 yrs following initial disturbance.

Relating species presence to environmental variables:

- Ordination

Relating species presence or abundance to environmental variables can be best achieved through the use of canonical correspondence analysis (CCA), an algorithm based on correspondence analysis (CA) (Palmer 1993). CA, an indirect gradient analysis technique, however, does not include environmental variables in the analysis of species presence; rather environmental gradients are inferred from the species composition data. CA is an ordination technique that is based on reciprocal averaging, thereby, minimizing community composition variation to the scatter diagram of samples and species (ter Braak and Smilauer 1998).

CCA is based on direct gradient analysis and relates species presence to environmental variables based on species and environmental data collected from the same data plot (Gauch 1982). The analysis is a direct gradient because of the use of supplemental environmental variables data. CCA is a weighted averaging ordination technique and models relative abundance rather than absolute abundance. CCA will visualize both, a pattern of species variation as in CA, and the main features of species distributions with environmental variables, thereby identifying an environmental basis for community ordination by determining patterns in community composition variation, which are best explained by environmental variables (ter Braak 1986, ter Braak 1987). This is achieved by selecting the environmental variables to maximize the dispersion of species scores. The underlying statistical model of CCA is that species abundance or presence is a unimodal function of position along environmental gradients (Palmer 1993).

Problems identified for detrended correspondence analysis (DCA) which are not a concern of CCA include 1) occasional poor performance with skewed species distribution, 2) instability of the detrending algorithm, 3) compression of one end of the gradient, 4) removal of true arch in data and 5) on occasion, it is unable to handle complex sampling designs. Additional advantages of the analysis include 1) simultaneous ordering of sites and species, 2) rapid computation, 3) good performance when species have a nonlinear and unimodal relationship to environmental gradients and 4) its ability to deal with species-poor sites containing rare species which could place such sites at the extreme ends of the first ordination axes (Gauch 1982, Palmer 1993).

Objectives:

The objectives of the study were to:

i) Determine whether significant correlations exist between plant species composition on disturbed and undisturbed sites and environmental variables on the sites.

ii) Ascertain whether the differences in plant community composition and structure observed between the undisturbed and disturbed sites could be explained by the observed environmental variables.

Methods:

Field Data Collection

Relative abundance data for plants in disturbed and undisturbed treatments were collected during February 1999. Cover data of individual species were collected from 92 randomly-placed quadrats (46 quadrats per treatment). Environmental variables sampled from 11 sites per treatment included (refer to Chapter 2): 1) total percent soil nitrogen, 2) total percent soil phosphorous, 3) soil potassium, 4) soil nitrate, 5) soil ammonium, 6) soil pH, 7) percent soil carbon, 8) bulk density, 9) percent soil moisture, 10) percent clay, 11) percent silt, 12) percent sand and 13) percent gravel.

Canonical Analysis

Vegetation-environmental relationships were analyzed by Canonical Correspondence Analysis (CCA) with the CANOCO 4.0 program (ter Braak, 1998). CCA was selected for its ability to rapidly analyze relationships between species and environmental variables through the use of a direct gradient analysis technique (Palmer 1993, ter Braak and Smilauer 1998). The CANOCO program was selected for its ability to handle sparse data sets, characterized by data containing many zero values as was the case in this study.

Species and environmental data were transformed from a spreadsheet into CANOCO format using WCanoImp 1.0. CCA was based on inter-sample distances and used biplot scaling. Data were not transformed and statistical significance was determined with the Monte Carlo test after 199 permutations. Data were then graphed using Canodraw 3.1 and Canopost 1.0. Significant relationships of individual environmental variables on species distribution were determined by manual forward selection.

Results:

Canonical Correspondence Analysis

Both of the eigenvalues for the first and second axes (Table 5.1) of the CCA were relatively low. Eigenvalues measure variance or dispersion of species distribution accounted for by the axis (ter Braak 1987, 1988). The eigenvalue associated with the first axis maximizes dispersion of species scores and is the correlation coefficient between species and site scores (Gauch 1982, Pielou 1984). Therefore, as the eigenvalue approaches a value of 1, it will reflect a high degree of correspondence between species and sites (Palmer 1993). The eigenvalue of the second axis is an index of the linear combinations of environmental variables that maximize dispersion of the species scores. The cumulative sum of all of the canonical eigenvalues measures the variance accounted for by the selected environmental variables. Species-environment correlations, which explain the strength of the relationship between species and selected environmental variables, were quite high for the first two axes. Eigenvalues are a much better measure of the quality of ordination than species-environment correlations because even ordination axes, which explain little of the species data, can have a high species-environment correlation (ter Braak 1986). This is evident when comparing the high species-environment correlations to the low percentage variance of the species-environment relationship. The first two axes only account for 29.4% of the variation in species composition as explained by the selected environmental variables.

CCA results revealed collinearity for the <2 mm soil fraction environmental variable and the remaining environmental variables (ter Braak and Smilauer 1998), which does not affect the ordination. Four univariate outliers were also detected, occurring when the sample was more than

5 times the average leverage (Montgomery and Peck 1982), indicating a standard deviation more than 3 times that of the mean. The bulk density variable was determined to have a variance inflation factor of 21.0255, which when >20 implies that the variable is nearly perfectly correlated with other variables and does not uniquely contribute to the regression equation. The statistical significance of the relationship between species and the entire set of environmental variables, as tested by the Monte Carlo permutation test for the first axis was not statistically significant (p 0.475). The relation between the species and selected physical and chemical soil properties (environmental variables) was not significant (p 0.345). Manual forward selection determined that the only environmental variable, which was statistically significant in explaining the species distributions, was pH (p 0.0450).

Canonical coefficients for the first axis were highest for pH, silt and P (Table 5.2), while the highest values for the second axis where bulk density, pH and NH_4. The significance of the contribution of an environmental variable to the regression is determined by its t-value and is only statistically significant when its absolute value exceeds the critical value of 2.1. The only variables to contribute significantly were pH on the first and second axes (Table 5.3) and bulk density on the second axis. Remaining variables with t-values < 2.1 did not contribute much to the overall fit of the species data when included with variables having t-values > 2.1 (ter Braak and Smilauer 1998). Based on t-values (Table 5.2), a subset of environmental variables including pH and bulk density explains the species data as well as the entire set. Inter-set correlations of environmental variables with axes are the correlation coefficients between environmental variables and species-derived sample scores. Inter-set correlations aid in determining the importance of environmental variables on species data and for this study the inter-set correlations were greatest for pH, silt and P for the first axis, while pH and N where the most strongly correlated for the second axis. Inter-set correlations, however, found NO_3 to be more important than NH_4 for the second axis, based on canonical coefficients. The difference in importance may result from the stability experienced by inter-set correlations when environmental variables are strongly correlated with each other, which canonical coefficients do not reflect (ter Braak and Smilauer 1998). This is because species axes in indirect gradient analyses do not depend on the environmental variables included in the analysis.

Ordination

Distribution of species and site points in an ordination diagram jointly represent dominant patterns in community composition as described by environmental variables. Species points and environmental gradients further reflect the species distribution with gradients in selected environmental variables (ter Braak 1986). The effects of environmental variables on species can therefore be reflected through the ordination axes.

Positioning of species is based on the centroid relation where species scores are a weighted average of the sample scores. Species position in the ordination occurs at the centroid of the sample points, therefore sites that contain the species are scattered around the point. Interpretation of the species-site diagram (Figure 5.1) using the centroid principle found that substantial differentiation of sites occurred, producing distinct separation between disturbed and undisturbed sites. The tight grouping of undisturbed and disturbed sites, observed in the biplot from the DCA ordination (Figure 3.4) indicates a strong similarity in species composition within each site type, while the distance between the undisturbed and disturbed groupings indicates dissimilarity in composition between the two site types.

Ordination of the CCA results allows for the graphical representation of the importance of measured environmental variables with respect to species and site distribution. This is done by the axes acting as response variables (dependent variables) and environmental variables as explanatory variables (independent variables) that are indicated as an arrow (ter Braak 1994). Increasing length of the arrow indicates a greater importance of the environmental variable in determining species occurrence; while direction indicates how well correlated the variable is with the species composition axes (Palmer 1993). Location of site scores relative to arrows indicates the environmental characteristics of the sites while the location of species scores indicates the environmental preferences of each species. Projection of the species points onto the axes indicates the strength of the relationship between the species and the environmental variable (ter Braak 1987). The weighted average will be higher if the species occurs on the same side of the origin as the arrowhead.

There was little correlation between environmental variables and the axes, silt was most strongly associated with the primary axis, while N, NH_4 and to a lesser degree, bulk density was associated with the secondary axis. The most important environmental variables sampled in the study, were pH and NO_3 (Figure 5.2), since they corresponded most strongly with disturbed and undisturbed environments respectively. Projection of species points onto the pH variable indicate that the occurrence of 'Poa lichen', *Celmisia viscosa* and *Raoulia subsericea* was influenced most by pH while *Celmisia sessiliflora* was influenced by it the least. Species points projected onto the NO_3 variable found that *Raoulia hectorii* and *Chionohebe densifolia* were the most influenced by NO_3, while *Chionogentia bellidifolia*, *Celmisia brevifolia* and *Anistome imbricata*, which are characteristic of the disturbed areas were the least influenced. Although most of the environmental variables were not correlated with a specific disturbance condition, clay, sand and bulk density were characteristic of disturbed sites.

Discussion:

Use of CCA allowed for an integrated description of species-environment relationships by assuming a response model common to all species, and by the selection of a single set of environmental variables which all species respond to (ter Braak 1986). Comparison of solutions derived by CCA to those found by DCA can be used to determine if the measured environmental variables are able to account for the main variation in species data (Hill and Gauch 1980). The substantial difference in the first eigenvalue observed between the CCA run with soil variables to those calculated by DCA indicate that the selected variables do not explain the variation in species composition between the undisturbed and disturbed sites. This does not exclude these variables from influencing community composition; however, they have minimal effect on the community. Their impact may be more substantial when combined with other variables not accounted for. Selected microclimate variables also exerted little impact on the composition of the communities. The problem with the microclimate data may be the choice of variables selected and the low number of sampling sites. Wind and surface roughness variables may be better suited for this type of analysis as they are potentially more important determining factors (Smith *et al.* 1995). Although soil moisture is not a limiting factor in most alpine areas in New Zealand (Talbot *et al.* 1992), it may have been an important variable in this study due to the change in the soil moisture regime following disturbance produced by increased evaporation.

The only tested environmental variable that was significantly correlated with the species composition was pH. The actual influence of pH on species composition however is unclear. Whether the species characterizing the disturbed treatments occurred due to altered pH levels associated with the disturbance, or if the species themselves altered the soil pH remains to be determined. It must be ascertained whether the significantly higher pH values observed in the disturbed sites were due to the higher pH found at depth (Mark and Bliss 1970, Mark 1994), or to the high pH leaf litter of *Poa colensoi* (Jenny 1980, Ugoloni and Edmonds 1983). The relationship between species composition and pH requires further investigation to determine whether the increase in pH caused the change in species composition or whether it came as a result of habitat variability, or topographic variation in this study as observed by Gould and Walker (1997).

Soil characteristics, as in other studies (Ratcliffe and Turkington 1987, Harper 1994), were not found to produce an obvious species-environment relationship and, therefore, the observed variation in community composition was due to one or a number of other variables not sampled in the study. The insignificant relationship between soil characteristics and species composition may be the result of the manner in which soil data were collected. Researchers have typically employed an averaging technique where a single soil pit is dug for *n* plant cover plots, which likely does not produce a representative view of the soil characteristics or the species-soil environment relationship. Possible environmental parameters that could have accounted for the main variation in species composition are wind and snow depth and duration, which are all correlated to microtopographical differences found between the undisturbed and disturbed sites. Exposure, snowpack duration and slope have all previously been correlated to determining the vegetation mosaic on the Rock and Pillar Range in Central Otago (Weir and Wilson 1987), while snow depth has been related to species composition by Smith *et al.* (1995) on the Old Man Range.

The extreme wind conditions, which characterize the summit of the Old Man Range, have previously been determined to be the main influence on species composition and structure, primarily selecting for cushion-plant species. This was most evident in the undisturbed sites, which were dominated by the low-lying, aerodynamic, wind-tolerant *Dracophyllum muscoides*. The dominance of the more erect graminoids *Poa colensoi* and *Luzula pumila* on the disturbed sites indicated that the influence of wind in these sites was not as important as in the undisturbed sites. Since the disturbed and undisturbed sites both occurred on the flat exposed surface of the summit the differences in wind influence cannot be attributed to topographic variation, but more likely results from microtopographic differences.

Establishment of *Poa* tussocks in the disturbed sites increased surface roughness, thereby, allowing less wind-tolerant species to flourish, directly influencing the plant community composition as was observed by Smith et al. (1995) in their wind fence experiments. Ratcliffe and Turkington (1987) observed similar modifications of microsite conditions by *Festuca ovina* and *Silene acaulis*, which enhanced germination, establishment and growth of other species. Ratcliffe and Turkington (1987) also determined that the initial establishment and vegetative spread of the dominant species acted as a strong determinant of community composition much in the same manner as was observed with *Poa colensoi*. While it is likely that exposed sections in the disturbed sites will be colonized by *Dracophyllum muscoides* or another cushion-plant species, they will not likely dominate the community to the degree observed in the undisturbed sites primarily due to the variation in microtopography and associated increased soil moisture, snow depth and duration. The overall result of increased microtopography and the associated decrease in surface wind speeds could be a more species-rich, heterogenetic community than found in the undisturbed sites.

Wind also influenced the species composition in the disturbed sites through its potential role in causing tussock mortality through abrasion, as has been observed for *Dracophyllum muscoides* (Mark and Bliss 1970). The role of wind will likely directly or indirectly determine the future community composition of the disturbed sites.

The most important consideration, which could not be taken into account in the CCA, was the evolution of the disturbed plant communities from a state of almost primary succession, without anthropogenic interference. The ability for the community to develop without burning and grazing pressures would allow a species composition to develop wholly different from the undisturbed sites which evolved in response to decades of anthropogenic stresses coupled with extreme wind conditions. It is, therefore, likely that the present species composition in the disturbed sites is in part, dependent upon the environmental conditions encountered during re-colonization, specifically the absence of anthropogenic disturbances. Cargill and Chapin (1987) found that natural revegetation following a disturbance, which drastically altered the physical characteristics of a site, alone would not restore the original community. Physical disturbances have also been attributed with favouring establishment of basicole flora at the expense of plants characteristic of acidic soils, while fertilizer addition often permanently alters plant species abundances (Forbes and Jefferies 1999).

The extent and intensity of the disturbance may also be a key factor in explaining the differences in community composition and structure. Through the complete removal of vegetation cover and microtopography, *Poa colensoi* was permitted to alter the surface characteristics in a manner not observed in the undisturbed sites. *Poa colensoi* is traditionally observed to occur as small swards in the high-alpine of the Old Man Range (Roxburgh *et al.* 1988) and does not form the large mineral-based tussocks which characterize the disturbed sites. It was the creation of these features that led to the alteration of the seemingly more important environmental variables of microtopography and wind. Therefore, extent and intensity of the disturbance may be quite an important variable in determining the eventual differences in species composition of the undisturbed and disturbed sites. The importance of disturbance type and intensity have been further supported by Vavrek *et al.* (1999) who found that community recovery in two tundra disturbance sites, characterized by similar recovery periods, environmental variables and pre-disturbance plant composition varied greatly in post-disturbance community composition. This, they attributed to the nature of the disturbance, blading compared to fire. There however is no means of incorporating this variable into the CCA to determine if it indeed explains the observed variation in species composition. If other disturbance types occurred in the area it may have been possible to classify the disturbances and treat them as nominal variables, thereby allowing for the transformation to a dummy variable, which could be used in CCA.

Summary:

The differences in plant community composition and structure observed between the undisturbed and disturbed sites on the Old Man Range cannot be adequately explained by the selected soil and microclimate variables. Although these variables may influence the community development, other site attributes not sampled are of greater importance in determining the community composition. Such variables likely arise from the extreme nature of the environment in which the sites occur, especially where wind conditions are concerned. Differences in communities may also arise from the extensive modification of the disturbed sites during the initial disturbance, as well as the opportunity for the sites to revegetate and develop without the pressures of anthropogenic interference.

A)

Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.367	0.236	0.199	0.138	2.056
Species-environment correlations	:	0.933	0.823	0.865	0.798	
Cummulative percentage variance						
of species data	:	17.8	29.3	39	45.7	
of species-environment relation	:	28.8	47.3	63	73.6	
Sum of all unconstrained eigenvalues						2.056
Sum of all canonical eigenvalues						1.274

B)

Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.748	0.351	0.173	0.122	3.662
Lengths of gradient	:	3.304	2.312	2.849	2.431	
Cumulative percentage variance						
of species data	:	20.4	30	34.7	38.1	
Sum of all unconstrained eigenvalues						3.662

Table 5.1 A) Summary of the canonical correspondence analysis (CCA) and B) comparison to DCA eigenvalues. Eigenvalues of the first two axes explain 29.4% of the variance of the species-environmental variables.

	Canonical Coefficient		t-values		inter-set correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Bulk Density	-0.1335	**-2.7424**	-0.2131	**-2.4518**	-0.0955	-0.2411
Moisture	-0.0965	-0.9258	-0.227	-1.2195	-0.1601	0.0615
C	0.3704	-0.8362	0.8708	-1.1009	-0.1883	0.1751
N	0.2407	-0.2149	0.4534	-0.2266	-0.0014	**0.2582**
P	**-0.5092**	1.0101	-1.7517	1.9461	-0.2360	0.1476
K	-0.0411	-0.8729	-1.4900	-1.7709	-0.1281	0.0747
NO3	0.2499	0.8057	0.8878	1.6030	**0.2961**	**0.2184**
NH4	0.0451	**-1.2297**	0.0800	-1.2219	0.0370	0.1753
pH	**0.9093**	**-1.2332**	**3.0390**	**-2.3083**	**0.5984**	**-0.2718**
Clay	-0.4336	-0.3332	-1.3424	-0.5777	-0.1819	-0.2081
Silt	**0.5526**	-0.0352	1.5014	-0.0536	**0.2594**	0.0418
Sand	0.0539	0.3871	0.2527	1.0172	0.1342	-0.0686
2 mm	0.0000	0.0000	0.0000	0.0000	-0.1533	0.0894

Table 5.2 Canonical coefficient, t-value and inter-set correlation values for environmental variables on the first two axes. t-values > 2.1 and high canonical coefficent and inter-set correlations are in bold.

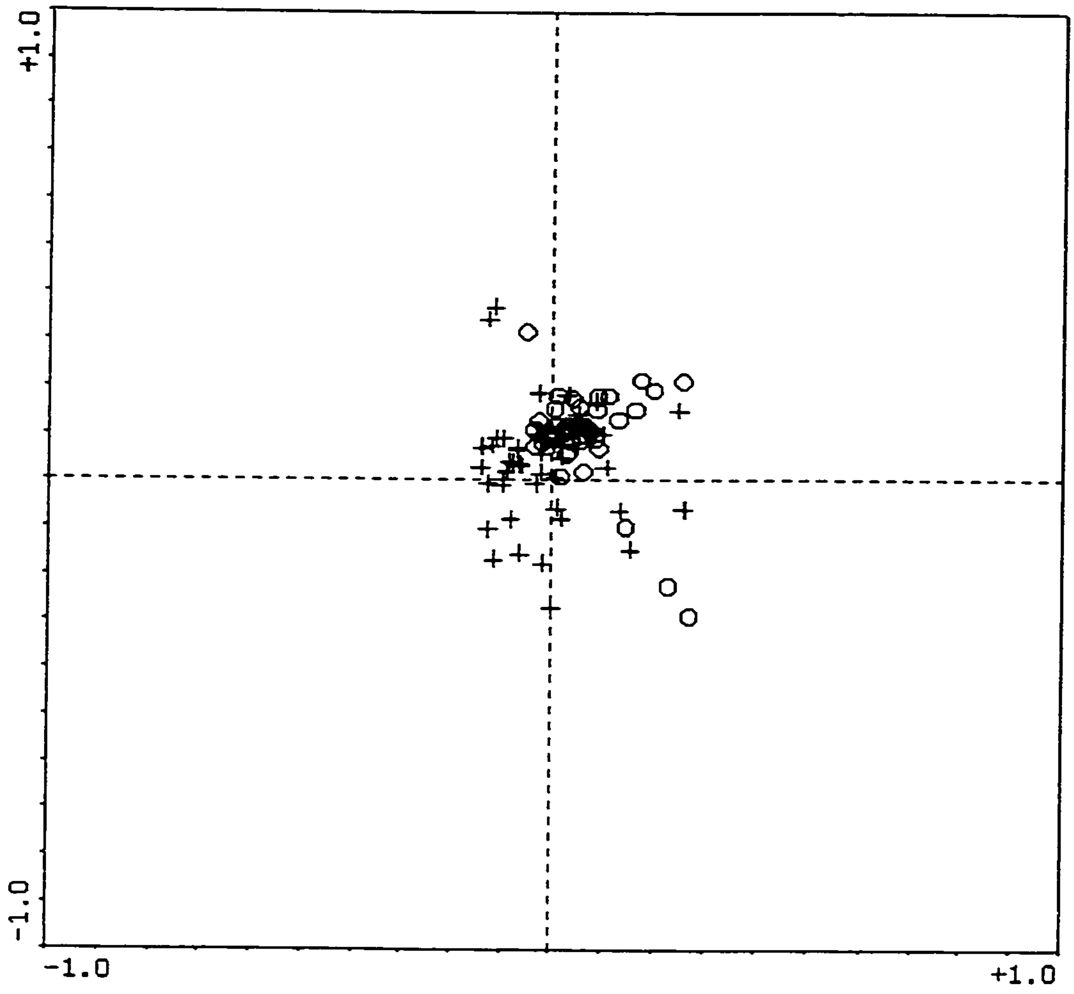

Figure 5.1 Ordination diagram of the CCA distribution of undisturbed (o) and disturbed (+) sites.

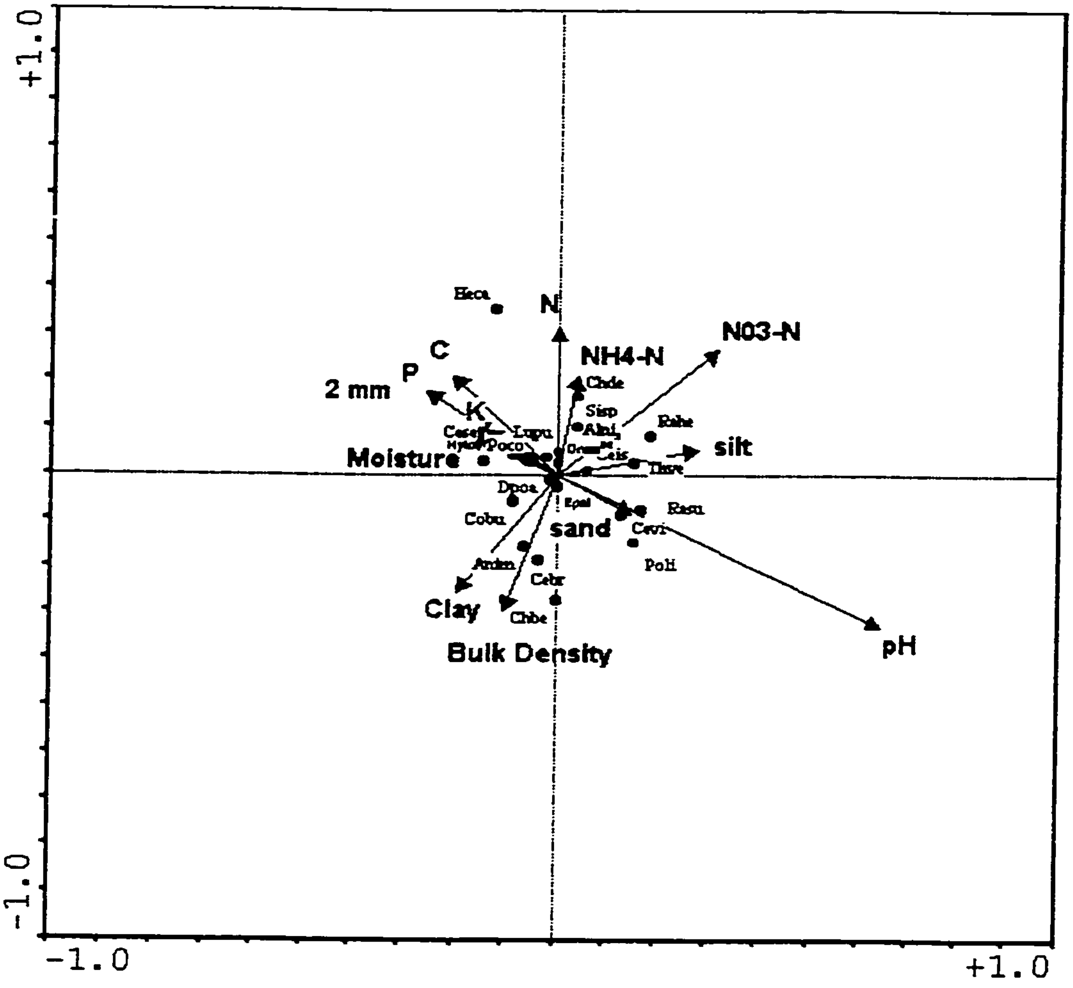

Figure 5.2 Ordination diagram of the CCA species-environmental variables relationship. Ordination diagrams explain species species distribution as explained by the selected environmental variables.

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Chapter 6: Conclusion

Anthropogenic disturbances in alpine environments have long-lasting impacts on the landscape that require long recovery periods, especially when recovering without any form of reclamation following disturbance (Kershaw 1984, Harper and Kershaw 1996). The means by which alpine/tundra communities recover naturally still remains poorly understood. While successional theories have been applied to a host of different ecosystems, especially tropical and temperate environments, alpine regions have been largely neglected. This study provided an opportunity to address this knowledge gap by building on the work initiated by Mark (1978) and Roxburgh *et al.* (1988) on the successional sequences during recovery of high-alpine environments by natural revegetation.

Soil and microclimate responses to disturbance

Following the road construction disturbance on the Old Man Range summit in 1974, abiotic factors were substantially altered through the removal of vegetation, loss of topsoil and removal of microtopographic variation. Loss of topsoil during construction and subsequent deflation and modification of the substrate by needle ice activity resulted in further loss of soil mass, nutrients and organic matter.

Disturbance of the high-alpine environment resulted in a significant increase in soil temperature and a decrease in soil moisture. The increase in soil temperature resulted from vegetation removal and the subsequent re-colonization by a plant community and vegetation structure unlike that of the undisturbed sites. Establishment of a graminoid-dominated community resulted in a decrease in soil moisture probably owing to an increase in evapotranspirational losses due to increased wind exposure. The loss of microtopographic variation in the disturbed sites resulted in reduced ability to retain snow while in undisturbed hummocky sites snowmelt water collected in the hollows to enhance the soil moisture content. The greater concentration of ammonium in the disturbed soil is evidence of increased nitrogen mineralization and nitrification rates in disturbed soils due to enhanced soil temperature.

Disturbances associated with road construction in the high-alpine of the Old Man Range initiated significant changes in environmental characteristics that are still quantifiable 25 years later. The landscape was altered during the initial clearing, and re-deposition of topsoil. A quarter of a century later, disturbed site soils are warmer, drier, more basic, have less organic matter but higher ammonium content. Recovery of the disturbed sites, as in other alpine environments around the world, has been a slow process, and edaphic characteristics on disturbed terrain remain different from adjacent undisturbed tundra.

Response of plant communities to disturbance

Natural revegetation on the Old Man Range after 25-yrs has not attained vegetation conditions similar to those of the undisturbed tundra. Although species richness and average plant cover values were equivalent in both disturbed and undisturbed treatments, the species composition and structure were quite different. While low-lying cushionfield plants dominated the undisturbed treatments, disturbances were dominated by graminoid species.

Following road construction, the disturbed areas were devoid of vegetation and available for colonization but only *Poa colensoi* was able to exploit the conditions. The *Poa* growth form enabled the retention of wind-blown soil and facilitated the creation of tussock mounds that effectively altered the microtopography and increased the depth of the internal boundary layer. Alteration of the microtopography and boundary layer permitted the retention and establishment of species less tolerant to wind exposure. The decrease in *Poa colensoi* cover, resulting from widespread tussock mortality and the coincident increase in importance of other species indicates that the *Poa colensoi*-dominated community was an intermediate successional phase.

While a continual increase in species richness was observed on disturbances over time, species richness values never exceeded those of the undisturbed tundra. If succession on the Old Man Range is similar to that predicted by the intermediate disturbance hypothesis then the peak in species richness has been missed, has yet to occur or has been prevented from occurring by the high frequency of low magnitude disturbances associated with wind and needle ice activity.

The observed successional trends did not agree with those predicted by the initial floristic composition model. Species richness was not highest right after disturbance but increased with time. Species richness was low immediately following disturbance because of the near complete removal of propagule sources from the disturbance at the time of the removal of the overlying vegetation and seed bank.

Use of the Markov model was not possible due to the inability of the model to account for non-stationary transition probabilities and the introduction of additional classes with succession. The predictive capabilities of the model may be useful for the short-term, but was less reliable for long-term predictions.

Secondary succession in the high-alpine of New Zealand is a slow process that is heavily influenced by environmental conditions. Succession has been further hindered by the removal of microtopographic variation whose influence on recolonization has been largely underestimated in alpine environments. Succession was also delayed due to the manner in which the disturbance was caused. Under natural disturbances it is unlikely that the entire overlying vegetation and seed bank would be removed on such a large scale. Further exploitation and development of alpine environments must attempt to preserve or recreate microtopographic variation and limit the amount of removal of propagule-bearing soil if the site is to be left to revegetate naturally. The differences in plant community composition and structure observed between the undisturbed and disturbed sites on the Old Man Range cannot be adequately explained by the selected soil and microclimate variables. Although these variables may influence the community development, other site attributes including wind and disturbance intensity and extent, which were not sampled may be of greater importance in determining the community composition. Such variables likely arise from the extreme nature of the environment in which the sites occur, especially where wind conditions are concerned. Differences in communities may also arise from the extensive modification of the disturbed sites during the initial disturbance, as well as the opportunity for the sites to revegetate and develop without the pressures of anthropogenic interference.

Development and Reclamation Considerations for Alpine Environments:

The importance of the New Zealand alpine has recently been highlighted by the New Zealand Department of Conservation, which has identified an ecological decline and loss of biodiversity occurring in its alpine environments. Depletion of ground cover has further been found to reduce site productivity and increase vulnerability to invasive species and wind erosion. The high occurrence of endemic species throughout New Zealand has fueled a conservation strategy to protect the species within the ecosystem.

The importance of wind in high-alpine environments was confirmed by the soil loss within disturbed sites and the consequent impediment of natural revegetation. The loss of soil was likely amplified by the reduction of surface microtopography when disturbance sites were bladed flat and left exposed. Future development in alpine environments must therefore take into consideration the potentially detrimental effects of microtopographic modification. Disturbances should therefore be limited in extent and consideration must be taken to create surface roughness or erect barriers to reduce the amount of deflation until plant cover is established.

Revegetation of the disturbed sites is still currently not complete 25-yrs following the initial disturbance. This is an indication of the susceptibility of alpine plant communities to anthropogenic disturbances. Natural revegetation has produced a plant community composition, which differs greatly from the undisturbed sites. The potential for invasion by exotic species following disturbance is a concern when attempting to protect the integrity of the plant community following disturbance. Although there was little evidence of invasive species within this study, *Rumex acetosella*, was observed and would likely be of greater concern at lower elevations.

Use of natural recovery practices following anthropogenic disturbances can be problematic when trying to preserve natural ecosystems, especially in an environment where endemic species are prevalent. Seed production may be infrequent and unpredictable for many species, and this will influence the composition of the recovering community. The localized distribution of many endemic species makes them susceptible to disturbances within their range.

Development and reclamation of alpine environments therefore requires special consideration, owing to the susceptibility of these environments and the long recovery periods that appear to be required.

Future Research Considerations:

This study was a continuation of work initiated by Prof. A.F. Mark, which provided a unique foundation upon which to build a detailed investigation of secondary succession in high-alpine environments. Continued monitoring of the plant communities is recommended, based on the dramatic plant community changes since the last sampling conducted in 1986. Further study, is required to determine whether succession is still continuing or if the current community will persist. If succession is still continuing, it is important to ascertain whether the current community is simply an intermediate step in the successional sequence to a community similar in composition to the undisturbed sites. If the undisturbed communities are following a different successional pathway, as indicated by *Poa colensoi* mortality then it is important to monitor community composition, structure and species richness to get a better understanding of the effects of anthropogenic disturbances in alpine environments.

Expansion of the study's scope to include analysis of environmental variables provided an opportunity to investigate vegetation-environmental correlations to better understand the affect of the disturbance on the plant communities. While soil nutrient and physical properties were included in the analysis, their effect was found not to be influential. Therefore, the environmental variables included in the analysis need to be expanded to include other environmental variables such as microclimatic and microtopographic data.

The role of microtopography needs to be given special consideration for future research on the study site. Development of surface roughness through tussock growth on the predominantly flat surface has an important role in influencing species recruitment and modification of the wind profile. A detailed wind profile needs to be constructed to determine whether an edge effect occurs along the transition from undisturbed to disturbed sites, to better understand whether this is the cause of tussock top mortality. A detailed microtopographic survey of both undisturbed and disturbed sites would also be useful, as well as a species distribution with respect to microtopographic position.

In order to determine whether the significantly higher pH values observed in the disturbed sites resulted from the disturbance or from the plant community that established on the disturbed sites needs further work. Such an analysis could be done to determine if the significant differences originate from leaf litter or exposure of higher pH soil horizons from lower in the soil profile.

Plant communities on the Old Man Range continue to respond to the initial disturbance, 25-yrs following road construction with no indication when a 'stable' community will occur and what species will characterize it.

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Appendix A. Complete species list and four letter abbreviations used in ordination diagrams.

SOIL	soil
LITT	litter
PAVE	pavement
ROCK	rock
DEAD	dead

Magnoliopsida

Abin	*Abrotanella inconspicua*
Acfi	*Acaena fissistipula*
Acte	*Acaena tesca*
Anim	*Anisotome imbricata*
Anla	*Anisotome lanuginosa*
Cebr	*Celmisia brevifolia*
Cela	*Celmisia laricifolia*
Cese	*Celmisia sessiliflora*
Cevi	*Celmisia viscosa*
Chbe	*Chionogentia bellidifolia*
Chde	*Chionohebe densifolia*
Chth	*Chionohebe thomsonii*
Drmu	*Dracophyllum muscoides*
Epal	*Epilobium alsinoides*
Euze	*Euphrasia zealandica*
Heca	*Hectorella caespitosa*
Kech	*Kelleria chilpia*
Kevi	*Kelleria villosa*
Lego	*Leptinella goyenii*
Mypu	*Myosotis pulvinaris*
Phru	*Phyllachne rubra*
Plla	*Plantago lanigera*
Ragr	*Raoulia grandiflora*
Rahe	*Raoulia hectorii*
Rasu	*Raoulia subsericea*
Tama	*Taraxacum magellanicum*

Liliopsida

Agmu	*Agrostis muelleriana*
Agto	*Agrostis topularis*
Capt	*Carex pterocarpa*

Lupu	*Luzula pumila*
Lufu	*Luzula rufa*
Poco	*Poa colensoi*
Dpco	Dead *Poa col*
Trsp	*Trisetum spicatum*
	Pteridophyte
Lyfa	*Lycopodium fastigiatum*
	Bryophyte
Psau	*Psilopilum australe*
	Lichens
Alni	*Alectoria nigricans*
Ceis	*Cetraria islandica*
Clad	*Cladina*
Hylu	*Hypogymis lugubis*
Poli	*Poa lichen*
Sisp	*Siphula* sp
Thve	*Thamnolia vermicularis*
	Exotics
Brsy	*Brachicomii syntherii*
Hipi	*Hieracium pilosella*
Ruac	*Rumex acetosella*