THE EVOLUTIONARY ECOLOGY OF

FESTUCA NOVAE-ZELANDIAE

IN MID-CANTERBURY, NEW ZEALAND.

A thesis

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"A few miles from Christchurch . . . a great plain of tussock grass spreads out till it is lost in the south in blue haze, but is bounded, westwards at a great distance, by the Southern Alps. Ones first impression is that of strange loneliness, unlike the solitude of the mountain country. Not a companionable rock or tree, or even a hummock of earth, to break the monotonous expanse of yellow brown grass; and a still silence, for there is no sound of insect or bird life, no rustle of ground game, no trace of any wild animal . . ."

H. W. Harper (1914)

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Terms and Conventions

All values quoted as 000 $\pm$ 000 are mean with 95% confidence limit unless otherwise stated.

Nomenclature follows Cheeseman (1925) for indigenous grasses, Fitter *et al.* (1984) for adventive grasses, Allan (1961) for indigenous pteridophytes and dicotyledonous angiosperms and Webb *et al.* (1988) for adventive dicotyledonous angiosperms, with changes listed in Connor & Edgar (1987).

ABSTRACT

Festuca novae-zelandiae (Hack.) Cockayne is a long-lived, caesptiose grass indigneous to New Zealand. It has expanded dramatically in range in 1000 years of human settlement. This study was conducted to determine how generalist life-history attributes and 'adaptive' variation have enabled this species to adjust to environmental change.

A range of aspects of the biology of *F. novae-zelandiae* were investigated. Reproduction in 155 individuals over four seasons was monitored. Only 17.4% of individuals flowered every year and 36.1% did not flower at all. However, the reproductive output of the population was still relatively consistent between years.

Reproduction of individuals and the pre-dispersal fate of seeds was compared among eight sites. Differences existed among sites for most attributes measured. Site factors appeared to mask any effects of tussock density on culm production. Total seed predation was positively related to density and negatively to altitude. A flightless fly, *Diplotoxa moorei* (Diptera, Chloropidae) was found to be the most common identifiable seed predator, accounting for up to 8% of seeds produced in some populations.

Seed germination was compared for eight populations in laboratory trials and most seeds germinated easily. Mean final % germination across all populations was 86%. Seedlings were monitored in the field for 30 months. They commonly established on mat-vegetation, were very slow-growing (mean of 0.6 leaves yr^{-1}) and had a half-life of 12 months.

Tillers in 26 tussocks were tagged and monitored for 30 months. Tillering was concentrated in spring, tillers lived on average 15.2 months and the majority (64%) did not produce daughter tillers. Tillering rate was not affected by either position within a tussock or size of the tussock.

A stage-based approach was used to investigate population structure. Stages were defined using discriminant analysis. The discriminant function was then used to assign stages to 255 tussocks which had been measured at the begining and end of a two year period. Transition probabilities were calculated between stages. Transitions were distinctly non-linear and tussock size and condition could vary widely in the space of two years in response to environmental fluctuations.

The genetic identity of mapped tussocks was investigated using isozyme electrophoresis and it was found that clonal fragmentation did not contribute significantly to the maintenance of population densities.

Patterns of variation at different taxonomic levels were compared using three taxa: *F. novae-zelandiae s.s.,* a distinct high altitude form of *F. novae-zelandiae* and a closely related species, *F. matthewsii*. Vegetation composition was investigated using ordination and classification techiques. Environmental gradients in altitude, temperature and rainfall were important in explaining observed patterns. The vegetation composition at "high altitude" *F. novae-zelandiae* sites was more distinct from that of *F. novae-zelandiae s.s.* sites than the latter was from *F. matthewsii* sites.

Morphological variation in the same taxa was investigated using Principal Components Analysis. The same environmental factors were important to observed patterns of variation. Populations within

F. novae-zelandiae possessed some genetically-determined differentiation that related to habitat. A narrow zone of intermediacy was found between *F. novae-zelandiae s.s.* and *F. matthewsii*.

Plants from populations of the three taxa were grown in cultivation. Culms of *F. matthewsii* emerged four weeks prior to *F. novae-zelandiae s.s.* "High altitude" *F. novae-zelandiae* was more similar to *F. matthewsii* in flowering phenology.

Levels of biochemical variation in populations of all three taxa were investigated using isozyme electrophoresis. All populations were characterised by high within-population variation and relatively low between-population variation. The differences between the three taxa were small. Variation among populations related to environmental factors but not to the proximity of populations.

The adaptiveness of populations to their own environment was tested using reciprocal transplants. No 'home-site' advantage was found. All populations proved to be highly plastic in growth responses.

The findings of this study are discussed in terms of generalist versus specialist strategies in long-lived, polyploid, perennial grasses. I conclude that in environments characterised by unpredictable, short-term fluctuations, long-lived species will show adaptation to large-scale, long-term environmental trends only, and adopt a generalist strategy in the face of short-term fluctuations.

CHAPTER 1: INTRODUCTION

1.1 The Ecology of Populations and Evolution in Response to Environmental Change

Evolution occurs within the context of the demography and ecology of populations (Harper, 1977; Sewall, 1977; Solbrig, 1980; Bradshaw, 1984; Levin, 1988). This is because natural selection is a demographic process; the demographic characteristics of survival and reproduction are the fitness components of population genetics (Schaal, 1985). Evolution by natural selection is the product of individual genetically-based variation in these demographic attributes (Levin & Wilson, 1978; Solbrig, 1980; Stebbins, 1983).

Ecology in the broad sense is concerned with the interaction between plants and the biotic and edaphic environment. As plants are sessile organisms the local ecological environment, that is the environment as it affects an individual's reproductive value or contribution to population growth (Antonovics et al., 1988) is a major selective force.

Independent of how organisms experience it, the environment is characterised by dynamic periodic and aperiodic behaviour at all spatial and temporal scales. The nature of an organism's response to its ecological environment, or the ability of selective forces to bring about adaptation to the environment, is governed by a number of factors. The most important of these are the temporal and spatial scale of environmental heterogeneity with reference to the generation time and dispersal ability of the organism (Bradshaw, 1965; Wiens, 1976; Lloyd, 1984; Antonovics et al., 1988) and the constraints imposed by genetic and life-history attributes (Grant, 1971; Levin, 1978; Levin & Wilson, 1978; Lloyd, 1980a; Levin, 1988).

The temporal scale of environmental heterogeneity with reference to the generation time of the organism determines the ability of the organism to track changes in the environment through genetic adjustment (Bradshaw, 1965; Antonovics et al., 1988; Levin, 1988). The rate of response of a population to directional selection is inversely related to generation time (Levin, 1978).

When the direction of selection changes in a random or cyclic manner, populations with longer generation times are less able to track the changes. Long-lived species are more likely to be tuned to long-term environmental trends and retain a relatively high level of genetic polymorphism among individuals (Levin, 1978). Even if change is directional and sustained, long-lived species will still experience a lag in genetic adjustment to the changing selective environment (Levin & Wilson, 1984).

Longevity, as an attribute of 'K'-selected species (MacArthur, 1962) is associated with other characteristics such as delayed maturity and low or irregular seed output (Harper, 1977) that further limit the ability of the species to genetically track short-term variation in the environment (Levin & Wilson, 1978). In many cases phenotypic plasticity is more important in the response of long-lived species to changes in their ecological environment (Bradshaw, 1965; Harper, 1977; Lloyd, 1984;

Schlichting, 1986). Phenotypic plasticity and generalist strategies rather than genetic specialisation will also be favoured if spatial variation in the environment is coarse grained and unpredictable (MacArthur & Levins, 1964; Wiens, 1976; Lloyd, 1984; Levin, 1988).

Genetic constraints on the ability of organisms to adapt to environment change include the organisation of the genome, the distribution and abundance of genetic variation and the manner in which genetic variation is passed to the next generation. Genome duplication through polyploidy can function to store genetic variation. However it can also act to dilute the affects of gene mutations and increase the resistance of populations to both random and directional changes. (Lewis, 1980).

A relationship has been shown between extent of geographical distribution and breadth of ecological amplitude and the amount and organisation of genetic variation within and between populations. Widespread species tend to have higher total genetic variation and generalist species tend to have high within-population variation. In addition levels of genetic variation have often been associated with the ability of a species to invade new habitats and adapt to both spatial and temporal environmental variation (Babbel & Selander, 1973; Bradshaw, 1984; Levin, 1986; Karron, 1987).

Change is an on-going and integral component of the ecological environment experienced by plants however the human-induced environmental changes in the last thousand years in New Zealand have radically altered the selective environment faced by plant species.

Human-induced vegetation changes do not simply repeat natural processes but create new ones. Plants that have increased in abundance after human-induced disturbance are therefore worthy of special attention (Grubb, 1985). In light of the short-term adaptive limitations experienced by long-lived species it is of particular interest when a relatively long-lived, apparently 'K'-selected species has increased as a result of human activity. This is the case with *Festuca novae-zelandiae*, a common New Zealand grass which is widespread particularly in eastern South Island.

Human-induced environmental changes in New Zealand have allowed *F. novae-zelandiae* to dramatically expand its range. In less than 1000 years *F. novae-zelandiae* has expanded from scattered populations in a forested landscape to widespread cover throughout the drier eastern montane areas of South Island. Short tussock grassland, of which *F. novae-zelandiae* is a physiognomic dominant now occupies approximately 11% of the New Zealand land area (Newsome, 1986).

In the remainder of this chapter I will outline that which is already known about the ecology of *F. novae-zelandiae* and summarise the changes that have occurred in New Zealand over the last 20,000 years with particular reference to grassland vegetation.

1.2. *Festuca novae-zelandiae* (Hack.) Cockayne

Festuca novae-zelandiae is a perennial grass with rigid, tightly rolled leaves to 60 cm in height and culms to 80 cm. It tillers intra-vaginally to produce a tightly-packed erect tussock. The taxonomic history of *F. novae-zelandiae* is detailed in Appendix 1. Like many grasses *F. novae-zelandiae* is wind-pollinated and possesses no obvious seed dispersal mechanisms. Experimental work has shown it to be out-crossing and virtually self-incompatible (Connor & Cook, 1955). One chromosome count has been made for a plant from Tara Hills in Otago and it was hexaploid (2n = 6x = 42) (Beuzenberg & Hair, 1983).

Moore (1976), in a study of the vegetation on a South Island high country station, found that the same tussocks could be identified in photographs spanning twenty years. She estimated that the life-span of individual tussocks could exceed 50 years. However as is usually the case with clonal herbs, genets are potentially immortal and the concept of 'lifespan' and the question of what constitutes an individual are problematic. These issues will be addressed in Chapter 4.

F. novae-zelandiae appears to produce culms every year (Sewell, 1947; Moore, 1976; Espie, 1987). Seed viability appears to be high and seeds germinate easily (Dunbar, 1970; D. Scott, *pers. comm.*). However seedlings have been reported as rare particularly in grazed areas and clonal spread by fragmentation has been suggested as being more important for population maintenance (Sewell, 1947, 1952; Moore, 1976; Espie, 1987).

F. novae-zelandiae is relatively unpalatable to stock and has a low relative growth in comparison to pasture grasses (Scott, 1970; O'Connor, 1977). *F. novae-zelandiae* is tolerant of nutrient-deficient conditions however it shows a rapid growth response with the addition of nutrients, particularly phosphorus and nitrogen (Morrison, 1958; O'Connor, 1977; Espie, 1987). *F. novae-zelandiae* would appear to have the ability to respond to periodic disturbance as it occurs on young terraces formed in braided riverbeds (Calder, 1958, 1961; Espie, 1987).

Aspects of the ecology of *F. novae-zelandiae* to do with its role as a component of high country pasture and the effect of range management practices have been the most studied. The two most detailed studies to date have been those of Sewell (1947, 1952) who investigated the effects of burning and grazing, and Espie (1987) who investigated the edaphic ecology of *F. novae-zelandiae* with glasshouse fertiliser trials and field experiments.

F. novae-zelandiae presents an interesting case history. It appears to possess attributes such as slow growth rates and low recruitment that tend to limit the ability of species to invade new habitats and adapt to changing conditions. Its expansion in range as a result of human interference with the landscape is therefore remarkable.

1.3 Recent vegetation change in the central South Island

1.3.1 Pre-human New Zealand

Most of the existing information about New Zealand Quaternary vegetation history begins with events during the latter part of the Otiran Glaciation from 22,000 yrs BP onward (BP = before 1950 AD). In the latter part of the Otiran Glaciation either shrubland or grassland taxa were dominant at most sites and grasses were ubiquitous (Moar & Suggate, 1979; Moar, 1980; McGlone, 1988). Pollen diagrams show that inland and eastern South Island in particular had the highest values for grassland taxa of anywhere in New Zealand, with almost negligible amounts of tree pollen.

The late glacial, 14,000 to 10,000 yrs BP, began with a rapid retreat of ice from the Poulter advance (Suggate, 1965; Suggate & Moar, 1970). Between 13,000 and 12,000 yrs BP a wave of reafforestation took place in central areas on the west coast of the South Island. Over the rest of the South Island, grassland gave way to denser shrubland after about 12,000 yrs BP (Moar, 1971; Moar, 1973; Moar & Suggate, 1979; McGlone & Bathgate, 1983) and a slow increase in temperatures finally enabled forest to spread.

The late-glacial afforestation of South Island was complete by 9500 yrs BP at the latest and from then until the arrival of humans in New Zealand most pollen spectra from lowland and montane sites show only a trace of grass pollen. However there is evidence for the role of natural fire in creating open areas in the pre-human landscape particularly in drought-prone regions such as lowland Canterbury (Cox & Mead, 1963; Molloy et al., 1963; Molloy, 1977).

A considerable area of Central Otago and adjacent parts of Canterbury and Southland experienced repeated fire 2500 to 1600 yrs BP, which progressively reduced the forest cover to shrub and grassland (Molloy, 1969; McGlone, 1973; McGlone, 1983). On the Canterbury Plains, natural fire appears to have contributed to the maintenance of a kanuka - podocarp forest mosaic with kanuka also dominating on shallow, droughty soils (Cox & Mead, 1963; Molloy et al, 1963; Molloy, 1969). However apart from central Otago, there is no evidence for large areas of lowland grassland prior to Polynesian settlement (Molloy, 1969).

During this last period of forest domination, grassland species would have been confined to either alpine areas or scattered habitats within a forested landscape. These latter areas would have included rocky bluffs, river flood-plains, stream beds and other stony, well-drained sites, valley-floor frost flats, edges of active avalanche tracks, debris fans and other areas of young soils (Cockayne, 1928; Connor, 1964; Connor & MacCrae, 1969; Molloy, 1969). Some grasses and herbs characteristic of lowland grassland today may have colonised forest and shrubland clearings brought about by natural disturbances (Molloy, 1969; Molloy & Ives, 1972) and occurred as understorey plants in areas of low, open vegetation.

1.3.2 Maori settlement: 1200 BP to 1840 AD.

There is no firm date for the settlement of New Zealand by Polynesians, but it is generally agreed to have occurred sometime between 1200 and 1000 yrs BP (Davidson, 1981). Between then and the time of extensive European settlement, in the 1840's and 1850's, close to one half of the original forest cover of New Zealand was removed (McGlone, 1983).

Molloy et al (1963) summarized the available charcoal and wood radiocarbon dates from the eastern South Island and established that extensive forest throughout the region had been destroyed by fire during the Polynesian era. There is also evidence of large-scale soil instability (Molloy, 1969; Molloy, 1977; McGlone, 1983) indicating that the charcoal did not come from the burning of a few trees but that fire affected entire catchments and coastlines. Pollen spectra covering that period show the dramatic decline in forest species such as *Nothofagus* and *Dacrydium cupressinum* with a corresponding increase in bracken, shrubland and grassland pollen and spores (McGlone, 1983).

The main period of deforestation appears to have been around 600 to 500 years BP; by 400 years BP a balance had been achieved between cleared and forested land (McGlone, 1983). Repeated burning of podocarp forest and kanuka on the Canterbury Plains during the Polynesian era (Molloy et al, 1963; Molloy & Ives, 1972) in combination with periodic flood events (Cox & Mead, 1963), allowed for the expansion of grasses on the Plains. By 300 yrs BP the podocarps that had dominated younger, deeper soils during most of the interglacial were absent or rare. Kanuka was much reduced and kowhai (*Sophora microphylla*) was common, indicating perhaps the existence of an open shrubland-grassland community (Cox & Mead, 1963).

Most of montane and lowland Canterbury remained in grassland and regenerating shrubland or low forest until the arrival of European settlers (Connor & MacRae, 1969; Molloy, 1977).

In montane regions of Canterbury, the grassland that formed following forest fires was most probably dominated by *Chionochloa* species with smaller light-demanding species such as *Dichelachne crinita, Elymus rectisetus, Festuca novae-zelandiae* and *Poa colensoi* occurring as understorey plants or confined to exposed or drought-prone situations (Cockayne, 1928; Zotov, 1938; Connor & MacRae, 1969). Other components of these induced grasslands would have colonised relatively rapidly from adjacent river-beds and rock outcrops or descended from alpine habitats once the intervening forest had been removed (Cockayne, 1928; Burrows, 1960; Connor, 1964; Connor & MacRae, 1969). *F. novae-zelandiae* was undoubtedly of less importance than in present-day montane Canterbury grassland (Zotov, 1938). Although in drier parts of eastern South Island such as the Canterbury Plains and the MacKenzie Basin there may have been more *F. novae-zelandiae* in the pre-European grassland than there is today (Connor, 1964). However grasslands in pre-European New Zealand may not have borne

any great resemblance to present-day short tussock grassland. Even if *F. novae-zelandiae* had been a relatively dominant species, individual tussocks would have been less obvious in an ungrazed grassland with an abundance of other large clump-forming grasses, shrubs, inter-tussock herbaceous species and fine, sward-forming grasses (Zotov, 1938; O'Connor, 1986).

1.3.3 Early European settlement

Once settlement of New Zealand by people of European origin had begun the pastoral occupation of open country in both islands proceeded rapidly. Organised settlement of Canterbury began in 1850 with the arrival of the first four ships; however pastoral farming began as early as the 1830's. By the late 1850's most of the eastern South Island was taken up as large sheep or cattle runs (Johnson, 1969; O'Connor, 1986).

The arrival of European pastoralists with grazing mammals, exotic plants and the deliberate policy of burning, marked a dramatic new era in the history of New Zealand grassland. The initial eruption of domestic stock numbers (10.7 million by 1874) and a plague of rabbits, must have had an enormous impact on grassland species because these animals were being maintained primarily by the exploitation of indigenous grassland (O'Connor, 1986). In addition, extensive areas of lowland Canterbury were ploughed and used for cropping (Johnson, 1969). It is therefore very likely that by the time the Armstrongs described the vegetation of Canterbury (J.F.Armstrong, 1870; J.F. & J.B.Armstrong, 1872; J.B.Armstrong, 1880), many palatable indigenous species had already been severely reduced or banished from many areas. The density and diversity of shrubs would also have been reduced by fire, altering the whole physiognomy of lowland vegetation.

Detailed descriptions of grassland and shrubland at the time of European settlement are scarce. However comments on the vegetation of the Canterbury Plains and foothills give the impression of a dense tussock grassland / shrubland mosaic. For example, Torlesse described the Plains in 1851 as being covered mainly with manuka (this name was apparently applied to both *Leptospermum scoparium* and *Kunzea ericoides*), *Cassinia* species, *Discaria toumatou*, fern (*Pteridium esculentum*), scattered *Cordyline australis, Phormium tenax, Cortaderia* species and 'tussock' (Maling, 1958). Charlotte Godley, in a letter dated 5th February 1851, spoke of the grass growing in "large tufts, perhaps two feet high" and growing densely enough to obscure the ground between them (Godley, 1957). Judging from the present-day distribution of remnant tussocks on the Canterbury Plains these tussocks were probably *Poa cita* and, to a lesser extent, *F. novae-zelandiae* (*pers. obs.*).

Although it was noted as early as 1857 that fire was eliminating them from some areas (Paul, 1857), the tussocks appeared fairly resilient to the initial pastoral onslaught. This was not the case with the shrubby component of lowland grassland. It was apparently sufficiently reduced after twenty years of pastoral occupation that in

1860, Samuel Butler could describe the Plains as being dominated by "brown tussocks of grass" with occasional individuals of *Cordyline australis* and *Phormium tenax* (Jones & Bartholomew, 1968). By 1880, pastoralisation on the Canterbury Plains had resulted in a vegetation "remarkably poor in plants" and "very uniform in character" with grasses predominant (Armstrong, 1880).

1.4 Aims

F. novae-zelandiae presents an opportunity to examine the importance of generalist strategies versus specialisations or 'adaptations' in a species response to environmental change over both recent and geological time-scales.

The aims of this dissertation are: (1) to investigate in detail a range of aspects of the biology of *F. novae-zelandiae*; (2) examine patterns of variation in different attributes within *F. novae-zelandiae s.l.* with reference to a sibling species and (3) using *F. novae-zelandiae* as an example, combine evolutionary and ecological thinking to address the issue of adaptation in long-lived, polyploid, perennial grasses occupying complex, heterogeneous environments.

1.5 Dissertation Structure

The body of the dissertation will be divided into three sections, each of which has a separate discussion. The first section deals with aspects of the regeneration of *F. novae-zelandiae* from seed. The second section deals with vegetative growth and regeneration and the structure of populations and the third section deals with patterns of variation in a range of characters at different taxonomic scales within New Zealand tussock-forming *Festuca*. Each section contains chapters dealing with different experiments. Each chapter is divided into methods and results sections with a discussion of the relevance of the specific findings of the chapter. A final section summarises and brings together the themes from the discussions at the end of each section and draws overall conclusions.

CHAPTER 2: STUDY AREA

2.1 Location of Study Area and Study Sites

This study was carried out mainly in the catchment of the Waimakariri River, South Island, New Zealand, with additional study sites on the lower Canterbury Plains (Bankside Scientific Reserve) and in the catchment of the Rakaia River. A total of 42 study sites was utilised in the course of the study; experiments were conducted using a hierarchy of subsamples of these sites.

Manipulative and monitoring work for sections 3.2, 3.3, 3.5, 4.2, 4.3 and 4.5 was carried out on Sugarloaf Fan in the University of Canterbury experimental area at the Cass Biological Field Station (Fig. 2.1). A core of eight sites in the Cass Basin and on the Plains was used for comparative work in sections 3.2, 3.4, 4.4 and 5.5 with the addition of other sites in the Waimakariri catchment relevant to the comparison in question. All 42 sites were used for the work described in sections 5.2 and 5.3.

In this chapter I will outline the geomorphology, climate and broad vegetation types that characterise the study areas. In doing so I will draw largely from volumes edited by Knox (1969) on the natural history of Canterbury and by Burrows (1977a) on history and science in the Cass district.

2.2 Geomorphology

Interaction and uplift at the margins of the Pacific and Indian-Australian plates has created the backbone of South Island in the form of the Southern Alps, which run roughly north-east to south-west down the western side of the Island (Stevens, 1980). The study areas lie mainly among the ranges east of the Main Divide; some study sites are on or just west of the Main Divide (Fig. 2.1, Table 2.1). Grid references to all sites are given in Appendix 2.

The topography of the study area is characterised by ranges extending from the Main Divide, large inland basins and high foothill ranges separating the montane zone from the Plains. The landscape was formed mainly from the poorly structured, easily fractured, hard sandstones and mudstones of the Torlesse terrain (Bradshaw, 1977). A history of faulting and differential uplift, combined with the ease with which the Torlesse rocks fracture to produce vast amounts of rock debris, has created the broad outlines of the landscape in the study area (Soons, 1977). The detailed landforms originate from the activity of glaciers during the Pleistocene (especially the last, Otiran glaciation) and from post-glacial fluvial and colluvial processes.

The montane portion of the Waimakariri valley was well filled with ice during all the early advances of the Otiran glaciation and later advances filled the upper valley regions. A large part of the gravel apron that forms

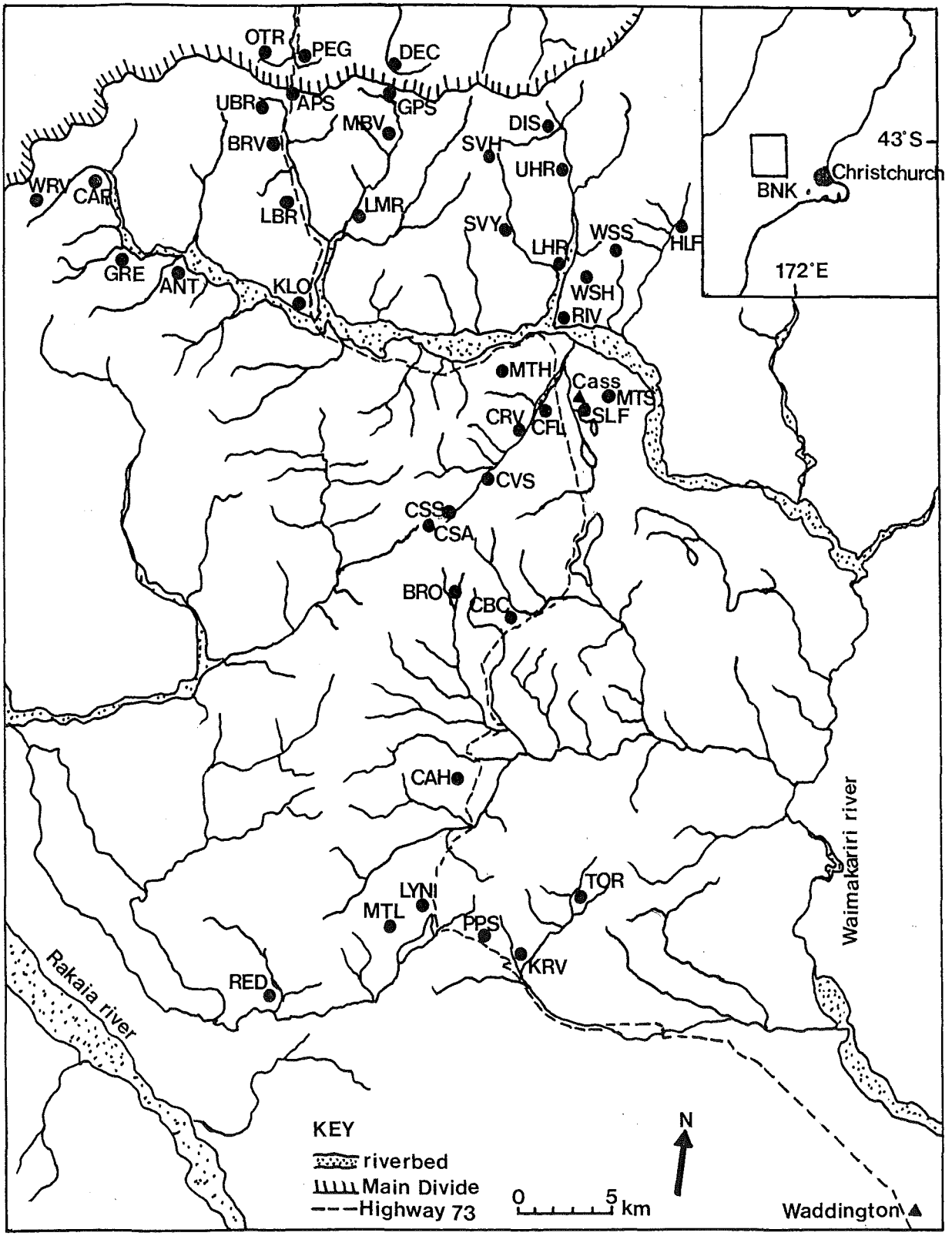


Figure 2.1: Location map of study area and study sites. See Table 2.1 for site details.

Table 2.1: Details of study sites. Type refers to landform: 1 = terrace, 2 = fan, 3 = debris slope, 4 = hill slope, 5 = stream channel. Tussock density is m^{-2}. Alt is altitude from topographic maps. Aspect is degrees from north. Slope was read using an Abney level. Rain is mean annual rainfall from isohyet map (Greenland, 1977) or climate station (New Zealand Met. Service, 1982). Min and max temp are mean annual minimum and maximum temperatures (°C) estimated using equations in Norton (1985).

Site	Type	Tussock Density	Alt (m)	Aspect	Slope (deg.)	Rain (mm)	Min Temp	Max Temp
ANT	2	1.19	680	42.5	1.0	2500	3.88	8.56
APS	5	1.50	880	92.5	3.7	5000	3.27	7.60
BNK	5	5.81	65	0	0	690	6.55	11.4
BRO	5	1.31	1400	110	4.2	2000	0.73	4.87
BRV	1	1.69	760	65	3.7	4000	3.64	8.19
CAH	4	1.25	870	130	7.7	1000	2.41	7.44
CAR	1	3.12	800	40	0.5	4500	3.59	7.98
CBC	1	2.19	830	0	0	1250	2.66	7.69
CFL	1	1.19	600	0	0	1250	3.71	8.09
CRV	1	0.75	640	0	0	1500	3.57	8.70
CSA	3	2.81	1340	57.5	4.0	2500	1.00	5.18
CSS	5	2.94	1240	22.5	2.5	2500	1.36	5.68
CVS	3	4.31	820	67.5	7.5	2000	2.90	7.79
DEC	1	9.25	940	55	0.7	6000	3.00	7.31
DIS	1	4.00	760	0	0	4500	3.43	8.18
GPS	3	0.44	1140	110	20	6000	2.25	6.30
GRE	1	2.81	740	0	0	3000	3.72	8.26
HLF	1	4.69	750	0	0	2250	3.27	8.20
KLO	1	0.62	635	0	0	2000	3.89	8.76
KRV	1	2.37	635	30	3	1000	3.42	8.60
LBR	1	0.31	720	0	0	2750	3.64	8.37
LHR	1	2.37	590	0	0	2500	3.90	8.99
LMR	1	3.62	720	0	0	2500	3.64	8.37
LYN	2	3.87	865	117	1.5	1000	2.47	7.46
MBV	1	10.2	880	0	0	3750	3.14	7.59
MTH	4	4.00	1120	60	4.0	1500	1.94	6.32
MTL	4	1.87	1390	10	1.2	1250	0.61	4.84
MTS	4	6.19	920	175	15.7	1250	2.55	7.31

Table 2.1: continued.

Site	Type	Tussock Density	Alt (m)	Aspect	Slope (deg.)	Rain (mm)	Min Temp	Max Temp
OTR	3	3.75	1120	140	12.5	6500	2.44	6.41
PEG	1	1.50	860	90	1.7	6000	3.35	7.71
PPS	4	1.06	1000	170	5.7	1000	2.06	6.78
RED	1	8.62	660	0	0	850	3.24	8.46
RIV	1	0.94	540	0	0	1500	4.01	9.22
SLF	2	8.56	670	129	5.7	1250	3.45	8.55
SVH	3	4.19	1240	80	12	3500	1.73	5.78
SVY	1	5.25	930	0	0	2500	2.77	7.31
TOR	4	7.31	880	157	2.5	1250	2.51	7.39
UBR	1	4.37	1000	25	8.2	6000	2.83	7.00
UHR	1	3.62	690	0	0	4000	3.62	8.52
WRV	3	2.62	1050	105	23	6000	2.71	6.74
WSH	4	8.56	1140	72.5	5.0	2500	1.88	6.25
WSS	4	0.62	1420	12.5	5.7	2500	0.87	4.85

the Canterbury Plains is constructed of glacial outwash gravel (Gage, 1969; 1977). Glaciation has been a great influence on the landscape of the study area, but post-glacial modification of landforms, taking the form of valley-floor fill by alluvium on the river floodplains, large alluvial fans and deep-cut valleys of tributary streams, has also strongly influenced the topography of the study area (Soons, 1977).

Streams and rivers in the area are typical of those throughout the Southern Alps. They are braided in character with many channels winding across extensive gravel beds. Channels differ in size and 'permanency' and the floodplains are only fully occupied by water during periods of high flood. They are turbulent and fast-flowing and prone to marked fluctuations in water levels. During heavy flooding episodes they can transport and deposit large quantities of gravel and sediment. As the current channels of most rivers and streams of this type are not greatly separated in height from vegetated portions of their fans, major changes in course occur periodically causing catastrophic damage to adjacent vegetation (Calder, 1957, 1961; Burrows, 1977d; Soons, 1977).

On the slopes are deep colluvial deposits that originate from a variety of processes, beginning with shattering of the bedrock by freeze-thaw cycles. Deposition of the shattered material occurs after falling, sliding, slow mass movement (sometimes water mobilized) or rapid mass movement in the form of landslides and debris flows. Some of these deposits are stable, capped by soils and vegetation; otherwise there are large amounts of active scree. Some screes date from a period of deforestation 500 - 800 years BP but other screes are ancient. Due to the nature of the rocks in the study area and existence of a specialised scree flora (Burrows, 1977b), screes must have always been a feature of these mountains (Soons, 1977). Freeze-thaw cycles and the formation of needle-ice in the soil at higher altitudes also facilitate the erosion and downslope transportation of material and hinder revegetation at higher altitudes or an exposed areas (Soons, 1977). Debris flows occur at times during heavy westerly rainfall.

Soils in the study area are derived almost exclusively from Torlesse rocks. The fine components (silt-sized) are mainly loessic in origin or (sand) alluvial. There is almost always a prominent stony component and this shows little sign of weathering. The most common soil types are upland and high-country yellow-brown earths on hillslopes in eastern parts of the study area with podzolised yellow-brown earths and podzols towards the Main Divide. Recent soils formed from alluvium characterize the valleys floors and riverbeds (Vucetich, 1969; Cutler, 1977).

Overall, the main mountainous portion of the study area is a highly dynamic landscape in which constant change and adjustment is a fact of life.

2.3 Climate

The climate of the study area is also characterised by changeability and variety. Due to their latitudinal location the Southern Alps are under the influence of westerlies in the

winter and high pressure zones in the summer. However in reality the climate takes the form of an almost regular procession of eastward-moving anti-cyclones with low pressure zones and often cold fronts between them (de Lisle, 1969; Greenland, 1977).

Mountainous regions always display specific climatic characteristics. There is a large variation in temperature with altitude, wind speeds are usually higher than in adjacent lowland areas and high altitude areas usually receive higher solar radiation in the absence of cloud cover. The Southern Alps strongly affect the pattern of rainfall in the central South Island (de Lisle, 1969). Air movement is dominantly east-wards and air flowing over the mountains is cooled quickly leading to orographic precipitation on the western side of the Main Divide. Dry air travelling down the leeward eastern side is warmed to form the 'nor-westers' typical of the Canterbury Plains (de Lisle, 1969; Greenland, 1977).

As a result the area is characterised by a steep rainfall gradient from high in the west to low in the east, which is much modified at the local scale by the effects of the eastern ranges. The average annual rainfall at Cass is approximately 1300 mm per year. Arthurs Pass, less than 20 km to the north-west, receives more than three times this rainfall in a year (Greenland, 1977; New Zealand Meteorological Service, 1982). Typically snow falls at low levels only on a few days each winter and seldom persists. However the mountain summits are coated with snow for several months in winter and periodically in autumn and spring.

The study area is a windy environment with average annual windspeeds at Cass of approximately 5 m per second (Greenland, 1977). North-west winds are the most frequent and usually the strongest winds of the Canterbury mountains and upper Canterbury Plains (de Lisle, 1969).

The study area is characterised by wet springs and dry summers and tends to have high summer temperatures and relatively mild winter temperatures (Fig. 2.2). This is because the air moving on to the country from the Tasman Sea to the west is relatively warm. The absolute maximum temperature recorded at Cass is 40 °C (although most summers the maxima are around 30 °C) and the minimum on record is -16 °C (Greenland, 1977).

Monthly rainfall and mean monthly minimum and maximum temperatures over the period of this study are presented in Figs. 2.2 & 2.3. The data were recorded by the Department of Geography at the Chilton Valley climate station at Cass.

2.4 Vegetation

Prior to human settlement in New Zealand the majority of the study area below timber-line would have been forested (Molloy *et al.*, 1963; Molloy 1969; Molloy, 1977). The present-day vegetation of the study area reflects changes wrought by 1000 years of human disturbance superimposed on pre-existing vegetation patterns. Scrub, dominated by *Leptospermum scoparium* and *Discaria toumatou*, tussock grassland, dominated by

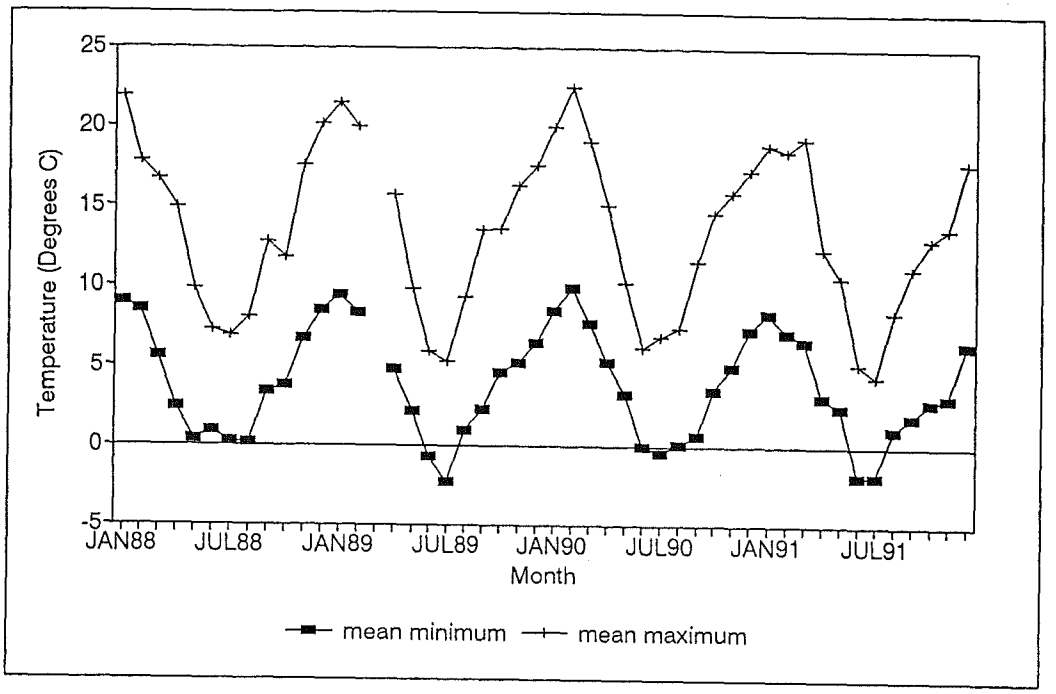


Figure 2.2: Mean monthly minimum and maximum temperatures at Chilton Valley, Cass Experimental Area (data from Department of Geography, University of Canterbury).

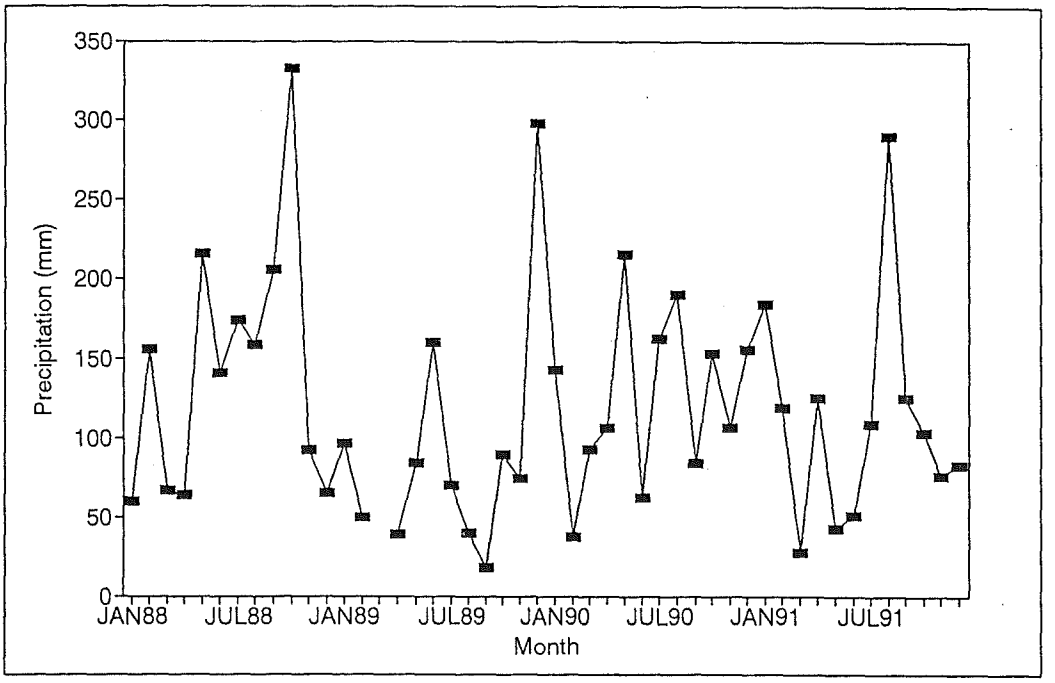


Figure 2.3: Monthly rainfall at Chilton Valley, Cass Experimental Area (data from Department of Geography, University of Canterbury).

Chionochloa species above timberline and *Festuca novae-zelandiae* at lower altitudes, and beech forest dominated by *Nothofagus* species are the main vegetation types within the study area.

Western portions of the study area, within Arthurs Pass National Park, are still relatively unmodified. East of the Main Divide, the forest is dominated by *Nothofagus* species and above timberline species of *Chionochloa* form extensive alpine meadows. In this part of the study area *F. novae-zelandiae* and other associated species of short-tussock grassland are restricted to recent or droughty river terraces and valley floor frost flats and also occur as colonists on the edges of slips and screes (Burrows, 1977a, 1986). Some other parts of the study area such as the upper Cass Valley are also relatively unmodified (sites CVS, CSS and CSA).

The Plains and the large intermontane basins within the study area have had a long history of land-clearance and grazing (Burrows, 1960; Johnson, 1969; McLeod & Burrows, 1977). Indigenous vegetation has been virtually eliminated from highly modified areas such as the Canterbury Plains and all that remain are remnants of vegetation in reserves and scattered individual plants along roadsides (Molloy, 1970; Molloy, 1971; Molloy & Ives, 1972).

In modified inland areas such as the Cass basin, induced grassland composed of both indigenous and adventive species is the dominant vegetation cover from the valley floor to 1200 m. *F. novae-zelandiae* is a characteristic plant of this grassland. Other common indigenous species include *Coprosma petriei, Cyathodes fraseri, Elymus rectisetus, Poa colensoi* and *Raoulia subsericia.* At lower altitudes adventive species such as *Agrostis capillaris, Anthoxanthum odoratum, Festuca rubra* and *Hypochoeris radicata* are common and in places a dense turf of adventive grasses dominates the inter-tussock spaces. The grassland around Cass is used for sheep grazing and hares are common in the area (Burrows, 1977c).

CHAPTER 3: REGENERATION BY SEED

3.1 Introduction

Reproduction is an essential component of plant fitness. However reproductive success is not determined by parental effort but rather by the number of progeny that survive to reproductive maturity. An assessment of a species' reproductive biology should therefore ideally include aspects of the establishment and survival of progeny.

The reproductive biology of a species is defined here as including all aspects of regeneration by seed from flower production through to seedling establishment and survival. This corresponds to the 'regeneration niche' of Grubb (1977).

Various types of reproductive strategies have been identified and described in the past, for example as part of 'r'- versus 'K'-strategies (MacArthur, 1962) or the stress-tolerator / competitor / ruderal triad of Grime (1979). However in all cases the reproductive biology of a species represents a compromise between the benefits and costs of all aspects of its life-history (Harper, 1977). Life-span, mortality with relation to age, environmental heterogeneity and availability of safe seedling sites, resource availability and patterns of predation are all factors affecting individual reproductive success and the reproductive biology of the species.

A large proportion of perennial plants possess several different forms of reproduction. Regeneration via both sexual and vegetative propagules (Grime, 1979; Harper, 1977) is common among perennial grasses. The two methods can play complementary roles; an individual can replicate vegetatively to take advantage of local conditions and reproduce sexually to ensure that at least some progeny survive in fluctuating conditions or new habitats (Tripathi & Harper, 1973; Sarukhan & Harper, 1974).

Species which replicate vegetatively are also potentially immortal and in a relatively constant habitat have little need to regenerate from seed, especially as somatic mutation can introduce additional genetic variation into a long-lived clone (Gill, 1986). However in the face of disturbance or environmental change, sexual reproduction can be more important to long-term population survival than vegetative proliferation because it provides novel genetic combinations (Williams, 1975).

Sections in this chapter provide detailed information on the reproductive output of *F. novae-zelandiae* and variation in effort and output between years and between populations in different sites. The pre-dispersal fate of seeds and seed rain and dispersal distances were investigated and quantitative estimates of seedling abundance and survival were obtained. The reproductive biology of *F. novae-zelandiae* will be compared with published information on other common perennial grasses and sedges.

3.2 Reproductive output and pre-dispersal seed fate

3.2.1 Introduction

Detailed studies involving *F. novae-zelandiae*, such as Malcolm (1925), Sewell (1947, 1952), Moore (1977) and Espie (1987) have contributed to the understanding of reproduction this species. However, no detailed quantitative study has been made of the reproductive output of individuals over time and in different environments. Neither has seed production been investigated in the same detail as for the dominant grasses of tall-tussock grassland, *Chionochloa* species (e.g. Mark, 1965b; White, 1979; Kelly *et al.*, 1992). The aim of this section is to provide detailed quantitative data on (a) variation in the reproductive output of *F. novae-zelandiae* individuals at one site between years, (b) variation in reproduction between sites and (c) variation in pre-dispersal fate of seeds between sites.

3.2.1 Methods

a) Reproductive output at Sugarloaf Fan over four years.

F. novae-zelandiae culms first emerge between October and December. Flowering occurs from November to January and fruiting in February and March (Scott, 1960; Connor, 1963). Previous years culms persist on the plant for at least a year and are easily distinguished from even older culms by the degree of blackening and damage that has occurred.

In October 1989, fourteen 1 x 1 m plots were randomly located along a 20 m transect in short-tussock grassland at Sugarloaf Fan (Plate 1) (see Fig 2.1 in Chapter 2 for location of all study sites mentioned).

All 155 *F. novae-zelandiae* tussocks within these plots were permanently tagged and examined to ascertain the proportion of individuals in the population that had flowered in the 1988/89 season and the relative contribution of individuals to the total output of culms. This was based on the presence of the previous years culms on the plants (later observations of nearby plants indicated that few culms were lost during the course of the first winter and could usually still be identified from the broken stalks). The same plants were re-examined in March 1990, March 1991 and January 1992 to assess reproductive consistency over four years.

b) Reproductive output in 1989/90 at eight sites

In March 1990, 20 x 0.5 m transects were randomly located at each of eight sites: Bankside (BNK), Cass River (CRV), Cass Saddle A (CSA), Cass Saddle B (CSS), Cass

Plate 1: Festuca novae-zelandiae grassland at Sugarloaf Fan.

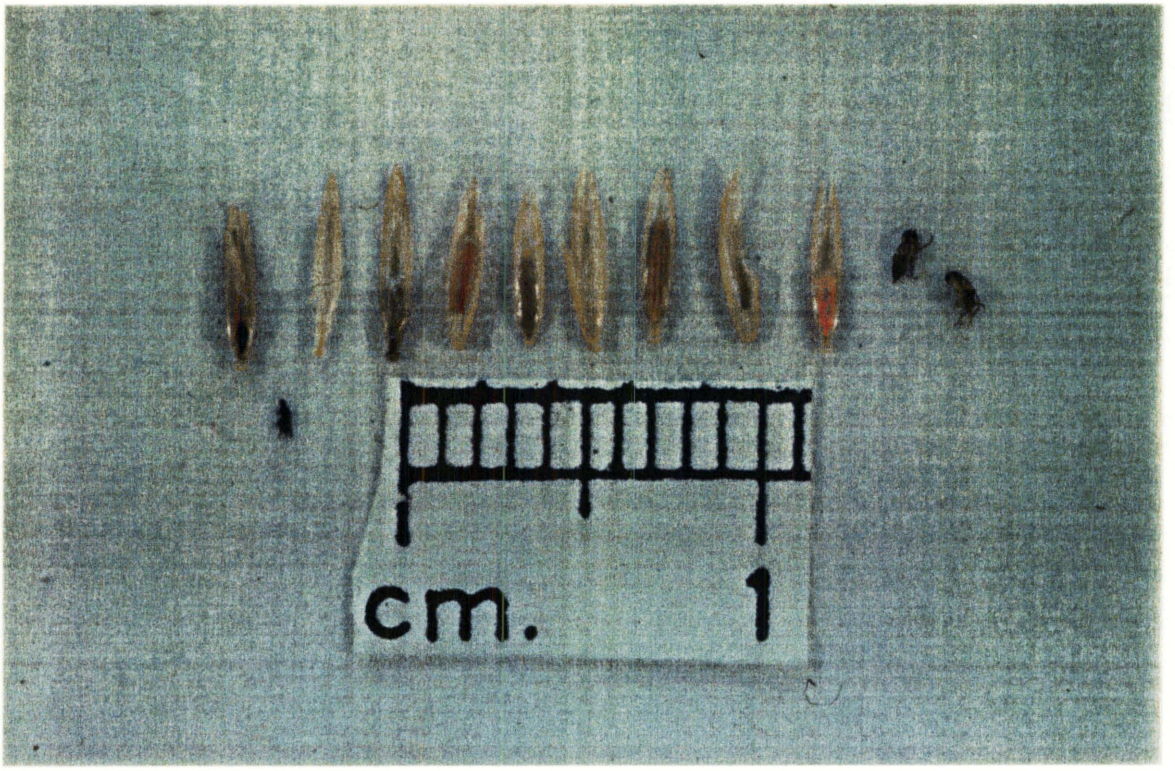


Plate 2: Seed predators and classes of seed fate from left to right: (1) Hemipterid, (2) internally predated, (3) fungus infected, (4) healthy, (5) shrivelled, (6) & (7) undeveloped, (8) externally predated, (9) Diptera larva, (10) *Diplotoxa moorei*.

Valley (CVS), Hallelujah Flat (HLF), Mount Sugarloaf (MTS) and Sugarloaf Fan (SLF). Site details are tabulated in Table 2.1 and locations shown in Figure 2.1 of Chapter 2.

At each site the first twenty reproductive plants encountered along the transect were selected, with the exception of Cass River, Mt. Sugarloaf and Sugarloaf Fan. At Cass River and Mt. Sugarloaf there were low numbers of reproductive plants generally and less than twenty reproductive plants (19 and 18 respectively) occurred within the transect. At Sugarloaf Fan, 29 reproductive individuals from nine randomly selected plots previously established to record reproductive consistency were used. This gave a total of 166 individuals over eight sites.

For each individual, four parameters were measured in the field:

1) maximum extended green leaf length excluding culm leaves,
2) mean basal diameter measured at 1 cm above ground level using a diameter tape,
3) percentage of basal area occupied by dead material estimated by eye within 5% classes, (hereafter referred to as % dead material)
4) number of current season's culms.

All culms were then collected for each individual and three parameters recorded for each culm and averaged for each individual:

1) culm height from first internode,
2) number of spikelets in each panicle,
3) number of florets in intact spikelets. Only full-sized florets were counted as the terminal floret usually had only a rudimentary palea.

Culms were collected by being plucked from the tussock, leaving the culm leaves behind. It was not discovered until January 1992 that culms plucked in this manner invariably broke cleanly at the first culm node. As a result measurements of stalk length do not represent total length as the lowermost internode was lost. However in *F. novae-zelandiae*, the lowermost internode tends to be short (2.3 cm on average, see section 5.3) so the difference between measured stalk length and actual stalk length would not be large.

c) Pre-dispersal fate of seeds

A grass 'seed' consists of the grain enclosed by two chaffy glumes - the palea and lemma - and is technically a caryopsis. However the term 'seed' will be used here for simplicity. Of the original sample of 166 individuals, 112 had produced at least 20 seeds. Randomly selected seeds from these individuals were opened and examined under a stereo microscope to assess the condition of the seed (Plate 2). All seeds produced by each individual were examined up to a maximum of 100 seeds.

Scoring categories were:

1) "healthy", meaning that the seed was full-sized, hard and pale orange to gold in colour,

2) "shrivelled", which included only partially developed but shrivelled seeds with no signs of predation, as well as full-length seeds which were brown-orange and wizened,
3) "undeveloped" where the ovary had not developed in size and the stigma and often indehiscent anthers were still present,
4) "fungus infected" where the seed was infected with either an ergot-type fungus or a mildew-type fungus,
5) and "predated" - eaten by invertebrates.

This last category was subdivided on the basis of the type of predator present within the seed. If no predator was present but the seed contained frass or a damaged ovary or seed, seeds were classified as either internally or externally predated depending on whether the palea and lemma were damaged or intact.

Analysis

a) Reproduction over four years at Sugarloaf Fan

All raw data were tested for normality used the Wilk-Shapiro rankit procedure of Statistix 3.5. If the rankit value was less than 0.95, simple transformations were performed and the transformation giving the highest rankit value above 0.95 was used for analysis. Variables which did not approach normality even after transformation were analysed using non-parametric methods.

One-way analysis of variance was performed on the number of culms per reproductive individual and per square metre at Sugarloaf Fan to test for significant differences between years.

Individual tussocks were grouped into flowering frequency classes dependent on the number of years they had flowered over the four years of the study. One-way analysis of variance was used to test for relationships between flowering frequency, mean annual culm production and morphological factors.

Linear regression was used to test for a relationship between reproductive output in a given year, previous reproductive effort and morphological factors.

b) Reproductive output and pre-dispersal seed fate in 1989/90 at eight sites

The data on reproductive output and pre-dispersal seed fate were analysed for between-population differences using one-way analysis of variance. Prior to analysis, measures of basal diameter and counts of numbers of culms were log-transformed to normalise the data. For the remaining variables the raw data approximated a normal distribution. A least significant difference pairwise comparison of means was performed for each variable.

The percentage values for pre-dispersal seed fates showed non-normal distributions.

Various transformations were tested but none sufficiently normalised the data. All variables associated with seed fate were therefore analysed using Kruskal-Wallis non-parametric tests.

Explanatory models were developed from morphological parameters and site factors for both total seed predation and culm production using linear regression.

3.2.2 Results:

a) Reproduction over four years at Sugarloaf Fan

Within the Sugarloaf Fan population the percentage of individual tussocks that flowered in a given year varied from 29% in the 1989/90 season to 50% in the 1991/92 season. In addition culm production varied between years from a minimum of 17.1 m^{-2} in the 1989/90 season to a maximum of 51.3 m^{-2} in the 1990/91 season. However the differences between years in the latter were not significant due to the large variance between individuals in any given year (Table 3.1).

There was a significant difference between years in culms produced per tussock. A test of least significance difference showed that culm production in 1990/91 was significantly higher than in the previous two seasons but not significantly different to culm production in the 1991/92 season (Table 3.1). Culm production was lowest in the 1989/90 season with not only the lowest mean number of culms per tussock but the lowest maximum and fewer individuals producing more than one culm (Fig. 3.1).

Bartlett's test for equality of variance showed that variability in culm production among individuals also differed significantly among years ($X^2 = 107.46$, $df = 3$, $P < 0.001$).

Over a third (36%) of individuals surveyed in all four years failed to flower in any year. Only 17% of individuals flowered in all four years (Table 3.2). One-way analysis of variance showed that individuals that flowered more frequently also produced more culms on average per year and were significantly taller and wider (Table 3.2). However there was no such relationship between flowering frequency and estimated percent dead volume.

Regression models for culm production indicated that culm production in any year was usually positively related to production in previous years (Table 3.3). Tussock height (maximum extended leaf length) did not contribute significantly to any of the models. However percent dead volume was negatively related and basal diameter positively related to culm production in 1990/91. In the model for culms produced in 1991/92 there was a negative relationship between reproductive effort in 1989/1990 and 1991/1992.

b) Reproductive output in 1989/90 at eight sites

Mean values for all morphological parameters measured and one-way Analysis of Variance F and P values are given in Table 3.4. Despite a large amount of overlap in the groups defined by pairwise comparison of means, the differences between sites were significant for all parameters except diameter. The greatest range was shown by number of culms (2.6-fold) and the least by culm height (1.46-fold).

Table 3.1: Flowering intensity among 155 F. novae-zelandiae tussocks at Sugarloaf Fan over four years. Results from analysis of variance are also given. Different superscripts indicate a significant difference between means according to LSD tests.

Season	1988/89	1989/90	1990/91	1991/92	F	P <
% reproductive	37.4	29.0	42.6	50.3		
mean culms m^{-2}	30.1	17.1	51.3	45.8	2.35	NS
mean culms $tussock^{-1}$	2.72 ^{ab}	1.54 ^{a}	4.64 ^{c}	4.13 ^{bc}	5.53	0.01

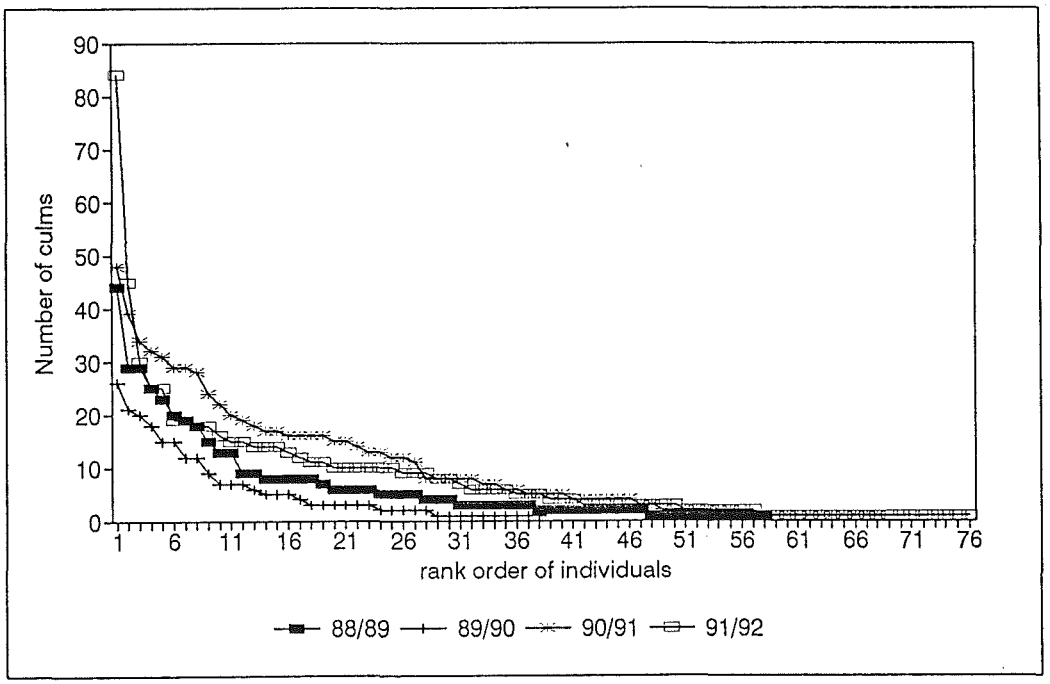


Figure 3.1: Culm production over four years at Sugarloaf Fan. Reproductive individuals were ranked by number of culms for each of the four years.

Table 3.2: Flowering frequency (years flowering out of four) among 155 F. novae-zelandiae tussocks at Sugarloaf Fan over four years. Results from analysis of variance are also given. Different superscripts indicate a significant difference between means according to LSD tests.

Flowering frequency	**0/4**	**1/4**	**2/4**	**3/4**	**4/4**	*F*	*P* <
% individuals	36.1	17.4	14.8	14.2	17.4		
mean culms yr^{-1}	0^{a}	0.35^{a}	1.90^{a}	7.13^{b}	10.73^{c}	34.97	0.001
mean height	31.9^{a}	36.5^{b}	41.2^{c}	46.4^{d}	50.7^{e}	38.99	0.001
mean diameter	1.44^{a}	2.51^{a}	4.71^{b}	7.85^{c}	10.6^{d}	56.77	0.001
mean % dead	27	28	36	32	30	1.29	NS

Table 3.3: Regression coefficients for models explaining culm production in 149 F. novae-zelandiae tussocks at Sugarloaf Fan in each of four years. Models were constructed stepwise using morphological variables and previous years reproduction. E indicates that the variable was not included in the model. '-' indicates not applicable.

				Previous culm production				
Season	**Constant**	**Diam.**	**% Dead**	**88/89**	**89/90**	**90/91**	R^2	*P* <
88/89	-1.63	0.94	E	-	-	-	0.44	0.001
P <		0.001						
89/90	0.41	E	E	0.41	-	-	0.40	0.001
P <				0.001				
90/91	1.90	0.92	-0.11	0.32	0.44	-	0.65	0.001
P <		0.001	0.001	0.01	0.01			
91/92	0.51	E	E	E	-0.42	0.93	0.62	0.01
P <					0.01	0.001		

Individual variation in height (maximum extended leaf length, in cm), log diameter (cm) and % dead material (% of basal area) jointly explained 41% of the variation in log number of culms (log culms = -0.26 + 0.01 [height] + 0.80 [log diameter] - 0.01 [% dead material], N = 165, R^2 = 0.41, P < 0.001).

The variation between sites in percent reproductive individuals was not significantly explained by variation in site attributes of altitude, aspect, tussock density, and mean, minimum and maximum temperature (the latter estimated using the regression equations of Norton (1985)). Neither did these factors significantly account for variation among sites in mean culms per individual.

c) Pre-dispersal seed fate in 1989/90 at eight sites.

Mean values for the broad classes of seed fate are given in Table 3.5a. Analysis of variance showed the sites to be significantly different for all variables.

The proportion of florets containing healthy seeds varied from 5% at Bankside to 49% on Mt. Sugarloaf. The most common fate of florets varied between populations. At Bankside, predation was by far the most common category, affecting 79% of the total number of florets examined. It was also the most common category at Hallelujah Flat, affecting 45% of florets. Healthy seeds were the most common category at Cass River, Cass Valley and Mt. Sugarloaf. Undeveloped seeds were most common in the Cass Saddle 'B' and Sugarloaf Fan populations and shrivelled seeds at Cass Saddle 'A'. However in most populations no one category dominated.

In a number of predated florets, the predator was still present and in most cases was an unidentified orange fly larva (Diptera, Chloropidae) 1 to 1.5 mm long. The only other larvae encountered were two greenish-white Lepidoptera larvae; these were included in the 'larva' category with the Chloropidae larvae. Unidentified black pupae or clear pupal cases approximately 1.5 mm long were also encountered. Mature adults of a black flightless fly, 1.5 to 2 mm long and identified (by P. M. Johns) as *Diplotoxa moorei* (Diptera, Chloropidae), were occasionally found and two were discovered within pupae very similar to those described above. Orange larvae, pupae and flies were seldom found together and even then usually only one would be abundant (Table 3.5b; CRV was an exception).

The only other seed predator commonly found inside florets was a shiny black juvenile Hemipterid less than 1 mm long. Small green grasshoppers were frequently observed on panicles in the field and may be responsible for at least a portion of the externally predated seeds found.

Kruskal-Wallis tests were performed on the components of total predation and it was found that the sites were significantly different in the percentage of seeds containing *Diplotoxa moorei*, larvae and pupa and in percent predation by unspecified external and internal predators.

Table 3.4: Means for measurements of F. novae-zelandiae tussocks in 1989/1990 season. Results from one-way ANOVA tests are given. Different superscripts indicate a significant difference between means using LSD tests. Diameter and no. culms were log-transformed before analysis but means are for untransformed data. *N* = number of plants/culms sampled. Total = 166 plants, 1264 culms.

Pop	N	Height (cm)	Diam. (cm)	%Dead mat.	No. Culms	Culm Hgt (cm)	Spikelets $culm^{-1}$	Florets $spklt^{-1}$
BNK	20/196	47.2^{e}	6.72	17^{a}	9.80^{c}	29.9^{a}	12.8^{c}	4.49^{d}
CRV	19/199	41.3^{d}	10.4	32^{bc}	10.5^{abc}	38.5^{cd}	12.1^{c}	3.10^{a}
CSA	20/83	30.6^{a}	8.80	30^{bc}	4.15^{a}	31.3^{ab}	8.61^{a}	3.81^{bc}
CSS	20/219	33.3^{ab}	8.82	25^{ab}	10.9^{bc}	43.8^{e}	12.4^{c}	3.75^{bc}
CVS	20/118	39.8^{cd}	9.22	36^{c}	5.90^{abc}	38.8^{cd}	11.6^{bc}	3.93^{c}
HLF	20/169	32.4^{ab}	5.80	35^{c}	8.45^{abc}	35.2^{bc}	11.5^{bc}	3.42^{ab}
MTS	18/87	35.4^{bc}	7.13	21^{a}	4.83^{a}	36.1^{bc}	9.67^{ab}	3.61^{abc}
SLF	29/193	46.3^{e}	8.09	31^{b}	6.65^{ab}	41.5^{de}	14.6^{d}	4.59 ^{d}
Ratio max/min		1.51	1.79	2.14	2.62	1.46	1.70	1.48
Anova *F*		17.2	0.74	4.31	2.23	8.87	7.98	12.5
P <		0.001	NS	0.001	0.05	0.001	0.001	0.001

Table 3.5: Population means for percent frequency of (a) broad classes of seed fate and (b) components of total predation of F. novae-zelandiae seeds. Values are means of results from individual plants which summed to 100%. Statistics of Kruskal-Wallis tests between populations are given. *N* = number of florets sampled.

(a)

Pop	*N*	Healthy	Shrivelled	Undeveloped	Infected	Predated
BNK	1086	5.49	7.31	7.56	0.89	78.8
CRV	287	33.8	16.7	30.5	1.54	17.5
CSA	853	16.2	28.3	30.1	5.85	19.9
CSS	1608	26.2	20.2	42.7	3.67	7.42
CVS	1416	40.4	31.4	15.5	0.43	11.1
HLF	956	9.82	20.9	21.0	2.91	45.4
MTS	523	49.1	12.7	30.5	1.87	7.75
SLF	1475	17.5	12.3	43.6	1.02	26.5
Total	8204					
K-W	*H*	62.3	41.0	72.6	22.0	86.1
	P <	0.001	0.001	0.001	0.01	0.001

(b)

POP	*N*	D. moorei adults	Larva	Pupa	Hemipterid	Internal Predation	External Predation
BNK	1086	0	0.08	0	0.34	28.6	49.8
CRV	287	4.48	3.83	0	0	9.19	0
CSA	853	0	0.08	0	0	9.54	10.3
CSS	1608	0	3.78	0	0.38	2.48	0.78
CVS	1416	0	0.44	0	0.33	6.74	3.63
HLF	956	0	0.49	4.06	0	40.7	0.14
MTS	523	0.10	1.59	0.16	0	2.33	3.57
SLF	1475	0	6.81	0.15	0.15	5.18	14.2
Total	8204						
K-W	*H*	71.5	50.6	85.8	11.4	80.8	78.6
	P <	0.001	0.001	0.001	NS	0.001	0.001

However there was no significant difference between sites for the percentage of seeds containing the Hemipterid seed predator (Table 3.5b).

Variation among individuals for log total percent seeds predated was best explained by variation in individual height (cm), log basal area (cm^2) and mean culm length (cm) (log predation = 1.91 + 0.02 [height] - 0.17 [log basal area] - 0.03 [mean culm height], $N = 84$, $R^2 = 0.49$, $P < 0.001$).

Variation among sites in log mean total percent seeds predated was best explained by variation in altitude (m) and tussock density (tussocks m^{-2}) (mean log predation = 1.43 - 0.001 [altitude] + 0.025 [density], $N = 8$, $R^2 = 0.72$, $P < 0.05$).

3.2.3 Discussion

(a) Reproductive consistency over four years at Sugarloaf Fan

Moore (1976) noted that mature plants of *F. novae-zelandiae* reproduced in most years on Molesworth Station in Marlborough, North Canterbury and it would appear that there are reproductive plants within the Sugarloaf Fan population every year. However regular reproducers are a minority within the population and most plants appear to reproduce either only occasionally or not at all.

The total reproductive output of the Sugarloaf Fan population varied significantly from year to year, not only in the proportion of individuals flowering, but also in the number of culms they produced and the evenness of contribution to total reproductive output. The same few very fecund individuals dominated the reproductive output of the population every year. The positive correlation between years in the reproductive effort of individuals distinguishes *F. novae-zelandiae* from masting species such as *Chionochloa pallens* and *C. rigida* in which there is a negative relationship between years in reproductive effort (Mark, 1965b).

Variation between years was also generally low in *F. novae-zelandiae* compared to other species. The ratio of maximum to minimum values for mean culms per tussock in *F. novae-zelandiae* from 1988 - 1991 was 3.01 whereas the ratio over the same four years for *Chionochloa pallens* in mid-Canterbury was 16.2 (Kelly *et al.*, 1992).

The standard deviation of log ([culms tussock^{-1}] + 1) in *F. novae-zelandiae* over the four years of the present study was 0.13, which is low compared with other long-lived monocotyledons. The same statistic calculated for *Phormium* species, ranged from 0.38 to 0.71 depending on site and species (Brockie, 1986) and was 0.49 for *Chionochloa pallens* in mid-Canterbury over the same four years as the present study (Kelly *et al.*, 1992).

Although reproductive output in *F. novae-zelandiae* is relatively constant, there is still significant variation among years. The availability of resources exerts a powerful influence on flowering (Harper, 1977). Factors such as variation in the availability of soil nutrients or temperature during the previous growing season may be involved in the observed variation in flowering intensity in *F. novae-zelandiae.* Fertiliser has been shown to increase flowering in *F. novae-zelandiae* (O'Connor, 1977). Temperature has been linked to variation between years in flowering of *Chionochloa* species (O'Connor & Powell, 1963; Mark, 1965b; Rowley, 1970; Payton & Mark, 1979). The relative constancy in reproductive output between years in *F. novae-zelandiae* may simply reflect the lack of marked climatic differences over the period this study was conducted (Figs. 2.2 & 2.3, Chapter 2).

(b) Variation in reproductive output between sites

The lack of relationship between both the proportion of a population reproducing and mean culm production, and tussock density, indicates that the eight populations studied did not occur at sufficiently high densities for negative density-dependent effects to come into operation. Alternatively site factors could be of sufficient importance so as to override or mask density effects (Fowler, 1988). A negative density effect on fecundity is a well-established phenomenon among populations of annuals and short-lived perennials and has been shown to contribute to the regulation of population size in both natural and experimentally manipulated populations (Harper, 1977; Watkinson & Harper, 1978; Symonides, 1979; Silvertown, 1982). However if populations of *F. novae-zelandiae* were sufficiently sparse to avoid competition between individual tussocks, culm production would relate simply to individual attributes.

Variation in culm production among the 165 individuals studied was significantly related to the size and vigour of the individuals; bigger, healthier plants produced more culms. However not all large, apparently healthy, plants at the sites studied were reproductive. This may be a result of single season, small-scale environmental variation in other aspects such as soil type and nutrient status affecting the reproductive output of individuals.

Differences between sites in percent reproductive individuals would also be due to differences in the size and vigour of the tussock populations. However the lack of a relationship between the fecundity of populations and environmental factors indicates that variation among sites in the size. vigour and reproductive output of individuals, is not so much related to large-scale environmental factors such as altitude and average temperatures, as perhaps to short-term, small-scale variation in climatic conditions and resource availability among sites.

(c) Pre-dispersal seed fate

Seed set in *F. novae-zelandiae* was highly variable between populations but overall was still relatively low. Even in the "best" sites less than half of all florets produced healthy seed. These values are similar to those obtained for various *Chionochloa* species (Kelly *et al*, 1992) but higher than values for seed set in *Chionochloa rigida* (Mark, 1965b).

Reasons for low seed set that are a result of the reproductive biology of the species include pollination failure, the action of deleterious alleles within the embryo and resource limitation on the part of the maternal parent (Lloyd, 1980b; Ayre & Whelan, 1989). Alternatively some individuals within the population may be achieving greater fitness through acting as pollen donors rather than by producing seed (Lloyd, 1979).

Other factors extrinsic to the plant can also result in low seed set. These include predation by animals and infection by fungi and other micro-organisms. The

importance of these and other factors in accounting for ovaries produced varied between the populations of *F. novae-zelandiae* studied. In some cases, for example Cass Saddle 'B' and Sugarloaf Fan, factors to do with the reproductive biology of the species were most important in reducing the production of seeds. A large proportion of the florets from both populations failed to develop seeds, possibly due to pollination failure or even an untimely frost. In other cases (e.g. Bankside and Hallelujah Flat) external factors such as predation accounted for most of the reduction in seed set.

This does not necessarily mean that pollination failure or resource limitation are not important factors at Bankside and Hallelujah Flat. These two sites represented the highest density stands of tussocks studied and while Bankside is the lowest altitude site at 65 m above sea-level (Table 2.1, Chapter 2), Hallelujah Flat, at 770 m, is close to the average altitude of the eight sites. These two sites probably suffered more seed predation because with higher tussock densities they could support larger populations of seed predators. The harsher environment of higher altitude sites with lower tussock densities may limit the abundance of seed predators so that other factors appear more important in reducing seed set.

Predation can often account for a large proportion of the seed crop in a range of species (Collins & Uno, 1985). Predation by invertebrates may be any important factor in the low seed set observed in some species of *Chionochloa* (White, 1975; Kelly *et al.*, 1992). However in long-lived perennials high losses to seed predators does not necessarily have an important impact on recruitment (Andersen, 1989). This is because recruitment is more limited by the number of 'safe' seedling sites (*sensu* Grubb, 1977) and is also buffered by the presence of a seed bank in some species.

Diplotoxa moorei appears to be an important predator of *F. novae-zelandiae* seeds and this study represents the first record of a food-plant for *Diplotoxa moorei* (P. M. Johns, *pers. com.*). While the identity of the orange larvae was not experimentally proved, the phenological separation of larvae, pupae and adult flies as well as the similarities in size strongly suggest that these all represent the same species. Another species in the genus, *D. similis*, has been found to be an important seed predator of *Chionochloa* species (White, 1975; Kelly *et al.*, 1992).

3.3 SEED DISPERSAL

3.3.1 Methods

In order to estimate seed rain density and distribution, 10 metal trays, each measuring 30 x 60 cm and greased with standard mechanical grease were placed using random number tables in dense tussock grassland on Sugarloaf Fan. These were left in position for four weeks during the peak of seed fall in February 1990 then retrieved and the number of *F. novae-zelandiae* seeds 10 cm^{-2} area of each tray recorded.

At the same time two greased trays were placed on either side of each of five tussocks along the axis of the prevailing wind in order to investigate seed rain in the immediate vicinity of fruiting tussocks. The trays were positioned so that the longest axis of each tray was parallel to the prevailing wind direction; together the trays covered an area of 30 x 120 cm each side of each plant. The plants were selected on the basis of having at least 10 flowering shoots and being relatively isolated from other reproductive tussocks. All culms were removed from any other tussocks within 5 metres of the five study plants. The trays were retrieved after four weeks and seed densities on the trays ascertained at 10 cm intervals upwind and downwind from the target tussocks.

To investigate maximum distances a seed could travel, a line of eight greased trays, 4.8 m long in total, was set up in the direction of the prevailing wind. Loose seeds were released from a height of 70 cm (representing approximate maximum culm height of tussocks at Sugarloaf Fan) at the upwind end of the trays on a windy day. The distance to the farthest seed was measured. Observations were also made of aerially borne plant material during periods of very strong winds.

A small study was also conducted to ascertain if *F. novae-zelandiae* possessed a soil seed bank. In January 1990, six 50 cm^3 soil samples were taken from the area where the trays used to assess seed rain were later laid out. A point in the inter-tussock vegetation was selected at random and the surface vegetation removed. The sample was taken from the top 10cm of the profile. The cores were spread out on trays in a glasshouse and kept moist. All seedlings were removed and identified as they emerged. The timing of sampling meant that any *F. novae-zelandiae* seeds found would have to be at least one year old.

3.3.2 Results

Spikelets of *F. novae-zelandiae* shatter easily when ripe, so seeds fall over a relatively short period of time. Only very rarely were intact spikelets found on plants in autumn and winter and usually these florets had failed to set seed. Occasional plants were found with filled seeds still present out of season and these plants were always growing in very sheltered micro-habitats, indicating the role of wind in shattering spikelets.

Seed densities on the 10 randomly located trays in short-tussock grassland varied from 0 to 17 10 cm^{-2} with a mean of 2.17 $\pm$ 0.47. This equates to 217 $\pm$ 47.5 seeds m^{-2} however the highly patchy distribution means that seeds would also occur locally at much higher densities than this. The frequency distribution of seeds 10 cm^{-2} showed a significant departure from random when tested against a Poisson distribution based on mean seed density 10 cm^{-2} (X^2 = 48.62, $P < 0.001$) (Fig. 3.2) indicating that seed rain was spatially patchy.

The distribution and total number of seeds shed by the five individually-studied tussocks varied greatly (Fig. 3.3) and was related to tussock size and number of culms (Table 3.6). However seed densities were consistently greater on the downwind side of all tussocks regardless of size. Seed rain upwind from these individuals varied from 27.8 $\pm$ 23.6 to 603 $\pm$ 269 seeds m^{-2} and downwind from 386 $\pm$ 266 to 4114 $\pm$ 914 seeds m^{-2} (Table 3.6).

Apart from plant 3, maximum seed rain occurred immediately adjacent to the parent plant. However, especially for the larger tussocks, a significant proportion of seeds appeared to be dispersing further than 120 cm from the parent plant.

The maximum distance seeds traveled was 3.69 metres. Mean distance travelled was not ascertained. The daily average wind speed in Chilton Valley, near Sugarloaf Fan, on the day maximum dispersal distances were investigated was 4.1 m sec^{-1} (data from Department of Geography, University of Canterbury). During strong north-west winds at speeds of up to 8 m sec^{-1} (*pers. obs.*), grass leaves and panicles were observed to travel more than one hundred metres at a height of 10 - 15 metres above the ground.

One *F. novae-zelandiae* seedling germinated out of the six soil samples taken to investigate the seed bank. This equates to 3330 seeds per cubic metre of soil or assuming that seeds are within the top 2 cm of the soil profile, 66 *F. novae-zelandiae* seeds m^{-2}.

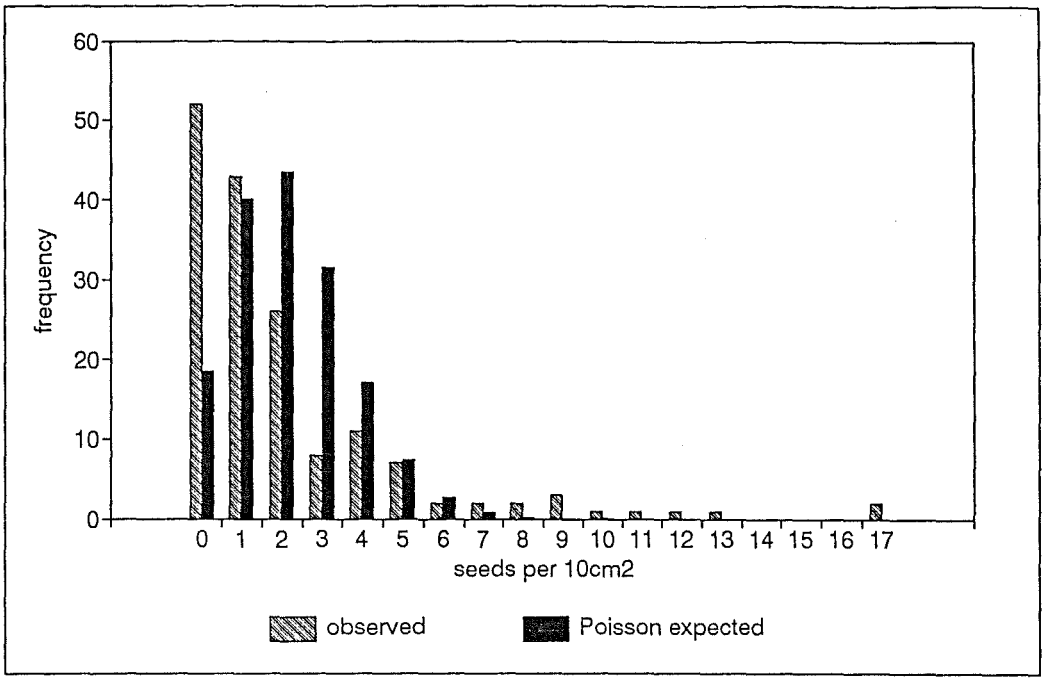


Figure 3.2: Frequency distribution of F. novae-zelandiae seeds 10 cm^{-2} compared with expected Poisson frequency distribution around a mean of 2.17.

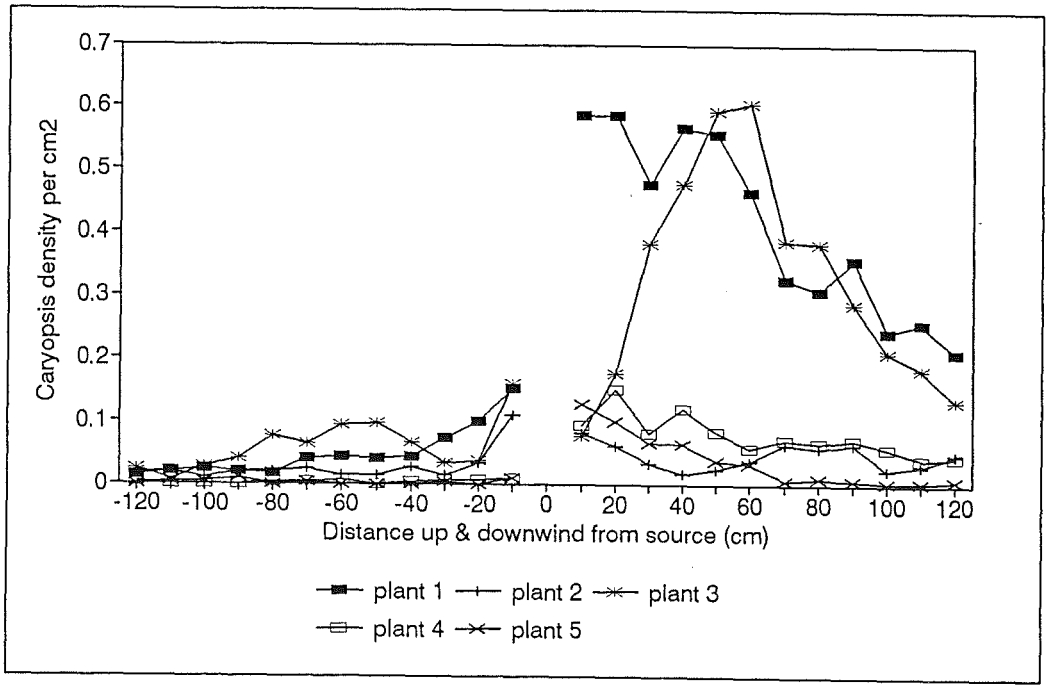


Figure 3.3: Seed rain cm^{-2} downwind of 5 reproductive tussocks.

Table 3.6: Upwind and downwind seed rain within 120 cm of source and individual characteristics of five F. novae-zelandiae tussocks at Sugarloaf Fan over a four week period during maximum seed fall.

Plant	**1**	**2**	**3**	**4**	**5**
Max leaf length (cm)	71	60	67	60	54
Max culm height (cm)	88	75	85	79	61
diameter (cm)	32	11.5	7	13	5
no. of culms	90	62	100	25	10
total seeds upwind	176	96	217	13	10
total seeds downwind	1481	160	1169	279	139
seeds m^{-2} upwind	489 ± 264	267 ± 172	603 ± 269	36.1 ± 21.1	27.8 ± 23.6
seeds m^{-2} downwind	4114 ± 914	444 ± 127	3247 ± 1117	775 ± 201	386 ± 266

3.3.3 Discussion

The dispersal phase in the life-cycle of plants is the phase of greatest mobility and strongly influences the distribution of plants. Dispersal can enable seedlings to escape competition with the maternal parent and if the parental habitat changes to become unsuitable for seedling establishment dispersal enables new generations to 'find' suitable habitats (Harper, 1977; Silvertown, 1979; Howe & Smallwood, 1982). In many cases however dispersal is not directed and closely reflects adult distribution (Howe & Smallwood, 1982).

Like many grasses, *F. novae-zelandiae* has no special adaptations to facilitate seed dispersal. However the occurrence of *F. novae-zelandiae* on previously forested sites several kilometres from the nearest 'natural' grassland indicates that the species has managed to disperse. As many of these sites have been forested for thousands of years, regeneration from a persistent seed bank is unlikely even though low numbers of seeds may survive from year to year in the soil. The colonisation of spatial isolated habitats such as young river terraces further indicates that dispersal over several kilometres does occur.

In spite of having no specific mechanisms for wind-dispersal, seeds are regularly blown several metres in moderate winds and considerably further in very strong winds. Strong winds have most likely played a important role in the dispersal of *F. novae-zelandiae* in a situation analogous to *Nothofagus* (Haase, 1989) where seeds have no special adaptations to dispersal but isolated young individuals and stands occur kilometres from the nearest seed source. The colonisation of areas made vacant by deforestation would therefore not necessarily have occurred centimetre by centimetre over consecutive generations but could have occurred relatively quickly. Dick (1956), describing a site near Cass deforested by fire 60 years previously, recorded that in some areas *F. novae-zelandiae* contributed 22% of total live vegetation cover and was the dominant species.

Janzen (1984) suggested that large herbivores may be important in the dispersal of small-seeded grassland species. During this study it was not unusual to find plants on which all or some of the culms had been removed immediately below the panicle, presumably by hares or sheep. However I have seen no *F. novae-zelandaie* seeds germinating from sheep or hare pellets. There is no way of knowing if any member of New Zealand's extinct avifauna played a role in the dispersal of grasses, however if ripe panicles are favoured by introduced mammals they might also have been browsed by native animals. Takahe (*Notornis mantelli*) have been observed to eat seed heads of *F. novae-zelandiae* (C. J. Burrows, *pers. comm.*) and seeds might also have lodged in the plumage of ground birds. However, grinding in the gizzard may have destroyed any seeds consumed by indigenous birds. Even if not, transportation in this manner would not have played nearly as important a role as periods of strong winds.

The estimate of 217 ± 46.5 *F. novae-zelandiae* seeds m^{-2} in the seed rain over four weeks is probably not far below total seed rain for this species, as the spikelets shatter easily once seeds are mature and dispersal would therefore occur over a relatively short space of time. This estimate of seed rain is comparable to annual values for other long-lived perennial grasses in perennial grasslands. Rabinowitz & Rapp (1980) obtained values of 27 - 515 seeds m^{-2} for perennial grasses in tallgrass prairie. Spence (1990) obtained similar values for perennial species such as *Chionochloa macra* (35 - 2716 seeds m^{-2}) *C. pallens* (317 - 423 seeds m^{-2}) and *Poa colensoi* (353 - 1658 seeds m^{-2}). Peart (1989) observed higher seed rain values for perennial grasses, e.g. 5100 - 63000 and 5800 - 82300 seeds m^{-2} for *Anthoxanthum odoratum* and *Holcus lanatus* respectively, but these were from a coastal annual grassland.

F. novae-zelandiae seed rain is very patchy as a result of the patchy distribution of reproductive tussocks, the large variation in reproductive effort among individuals and the concentration of seeds near parent plants. Peart (1989) observed significant spatial heterogeneity in seed rain at all spatial scales examined from centimetres to kilometres. Likewise Spence (1990) observed significant clumping of dispersing seeds but found for most species that seed rain was less patchy than vegetation cover. This would probably be due to environmental heterogeneity acting to create additional patchiness at the seedling establishment and survival stages.

Rabinowitz & Rapp (1980) found that the spatial heterogeneity of the seed rain was determined by the spatial distribution of dispersing infructescences. However even if adults were evenly distributed in space and contributed evenly to reproductive effort, seed rain could still be patchy due to the leptokurtic pattern of dispersal in relation to the maternal parent typical of all plants (Harper, 1977; Silvertown, 1979).

Limited dispersal can strongly influence subsequent seedling interactions (Rabinowitz & Rapp, 1980) and in the long-term can result in local genetic structuring within an apparently continuous population. Close neighbours are likely to be related and are also more likely to exchange pollen than distant neighbours (Levin, 1981, 1988). However this effect is much less pronounced in long-lived wind-pollinated species and the virtual self-incompatibility of *F. novae-zelandiae* would further negate any deleterious effects of limited dispersal.

3.4 SEED GERMINATION

3.4.1 Methods

Healthy seeds from collections from individual tussocks made in 1990 to investigate reproductive effort among eight populations and pre-dispersal seed fate (Chapter 3.2) were pooled by population. Seeds produced in 1990 from a population of a "high altitude" form of *F. novae-zelandiae* (see section 5.1) at Porters Pass were also included in the experiment, giving a total of nine populations.

Randomly selected seeds from each population were placed on Whatman No.1 filter paper in petri dishes and kept moist with distiled water. For all populations the germination experiments commenced within 10 days of seed collection. Treatments were three temperature/light combinations - 25 °C light/ 15 °C dark ("warm" treatment), 15 °C light/ 5 °C dark ("cool" treatment) and 25 °C dark/15 °C dark ("dark" treatment) with twelve hour alternations. Petri dishes were enclosed in black polythene photographic bags for the "dark" treatment. Each dish contained fifty seeds with four replicates per population for each of "warm" and "cool" and two replicates per population for the "dark" treatment.

Germination was defined as the emergence of either radicle or plumule. Where possible dishes were examined daily during the first flush of germination then every three to four days until the trial was terminated. Dishes in the "dark" treatment were examined every four to six days in order to minimise the risk of accidental exposure to light. Due to field work commitments, dishes in the final trial of 12 month old seeds were examined less frequently once initial germination had occurred. However, once germination had commenced no dish was left unexamined for more than nine days at any stage during the trials.

At each examination, germinating seeds were counted and removed from each dish until all seeds had germinated or the remaining seeds were soft and black, a condition taken to indicate that the seeds were no longer germinable. Seeds in the "dark" treatment were examined under a safe light in a darkened room.

Further seeds from the original collections were stored outside in a paper bag in a Stevensons screen and after six months seeds were randomly selected from each population and germination tested under all three treatments in the same manner as for fresh seeds. After twelve months storage, germination was again tested for each population under the "warm" treatment only.

Throughout all trials a record was also kept of the frequency of chlorophyll-deficient seedlings in each population.

Analysis

Within-population comparisons of germination response curves under different treatments were made using Probit and parallel line analysis on MLP (Ross, 1980). Five between-treatment comparisons were made for each population:

(1) The three temperature/light combinations were compared for fresh seed ("fresh" in Table 3.9)

(2) The three temperature/light combinations were also compared for 6 month old seed ("6 month");

(3) Germination under the "warm" treatment was compared for fresh, 6 month old and 12 month old seeds;

(4) Germination under the "dark" treatment was compared for fresh and 6 month old seeds;

(5) Germination under the "cool" treatment was compared for fresh and 6 month old seeds.

Time taken to 50% germination (50% of initial number of seeds tested) and final percent germination were separately tested for significant differences between populations and treatments using two-way analysis of variance. In three cases, 50% germination was not reached so values were extrapolated from the probit line.

The unbalanced design of the experiment did not permit separation of storage, temperature and light effects. Instead the various combinations were treated as categories of a single variable. Replicates were pooled to balance the design. Least significant difference pairwise comparisons of means were also performed.

One-way analysis of variance was used to test for significant differences in the percent frequency of chlorophyll-deficient seedlings among different aged batches of seeds.

3.4.2 Results

Seeds germinated readily in all treatments and for all populations. Germination was generally slower in the "dark" and "cool" treatments than in the "warm" treatment and in addition fewer seeds germinated in the "dark" treatment. The minimum time observed from wetting to the first germination of seed was six days and the maximum was 200 days. Longer delays before germination tended to be a feature of seeds in the "cool" and "dark" treatments rather than the "warm" treatment.

After six months storage the seeds germinated more rapidly on average in both the "warm" and the "dark" treatments. There was no further enhancement of mean germination response after 12 months storage (Fig. 3.4). The mean final percent of seeds germinating also increased in the "dark" treatment after 6 months storage but dropped off in the "warm" treatment after 12 months storage (Fig. 3.5).

The final percent of fresh seeds germinating was consistently lower for the "dark" treatment in all populations than for the other two treatments, with the exception of Porters Pass and Sugarloaf Fan collections (Figs. 3.13a & 3.14a). In these two populations germination in the dark did not differ from germination at the same temperature with 12 hour days.

Six month old seeds from Bankside and Cass River also showed a similarly lower final percent germination in the "dark" treatment compared with the other treatments (Figs. 3.6b & 3.7b). However for the remaining five populations the apparent slower response rate and lower germination of fresh seed in the dark was lost after six months storage (e.g., Fig. 3.9b).

The frequency of chlorophyll-deficient seedlings increased across all populations with increasing age of the seeds. Among fresh seeds an average of 0.13% of seeds were chlorophyll-deficient. This increased to 0.68% after 6 months storage and to 2.05% after 12 months. One-way analysis of variance showed these differences to be significant. However, pair-wise LSD comparisons of means indicated that the difference lay between 12 month old seeds and seeds that were fresh or 6 months old. The frequency of chlorophyll-deficient seeds in the latter two batches was not significantly different (Table 3.7).

No relationship was found between germination response under the "cool" treatment and the altitude of the seed source. There was also no relationship between estimated population size and percent viability as might be expected if inbreeding was affecting seed set and seed vigour.

When probit-transformed, all within-population comparisons except Cass River "cool" and Mt Sugarloaf "dark" showed highly significant differences in both slope and intercept (Table 3.8). This indicates that both the rate and the timing of germination response differed among groups of treatments within populations.

Two-way analysis of variance on mean number of days to 50% germination

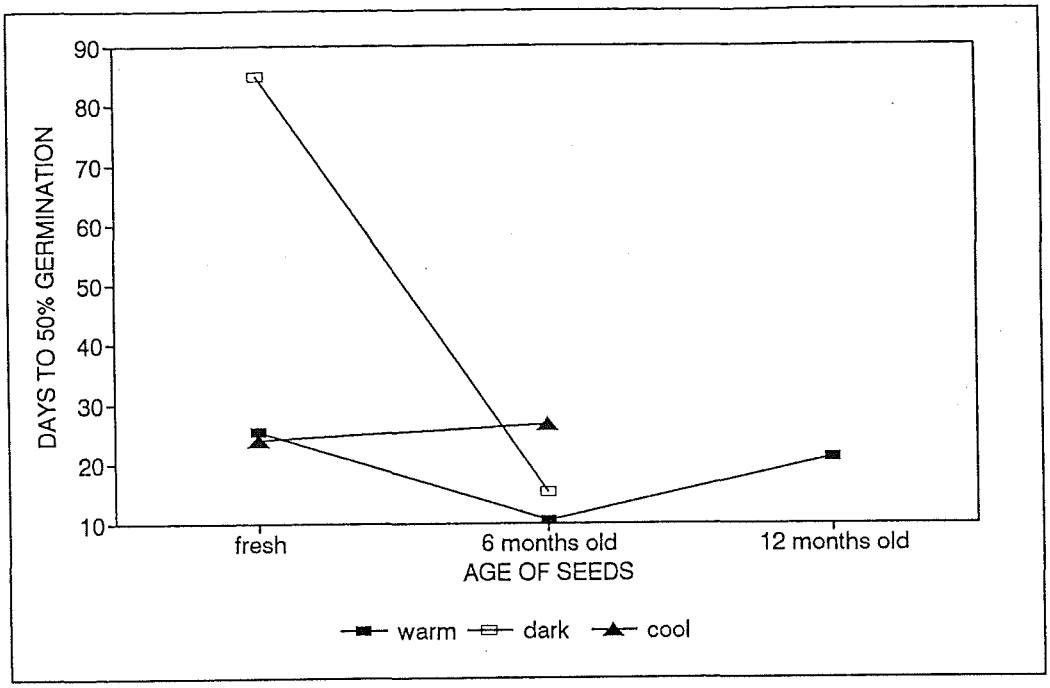


Figure 3.4: Days to 50% germination in three treatments versus seed age for all populations combined.

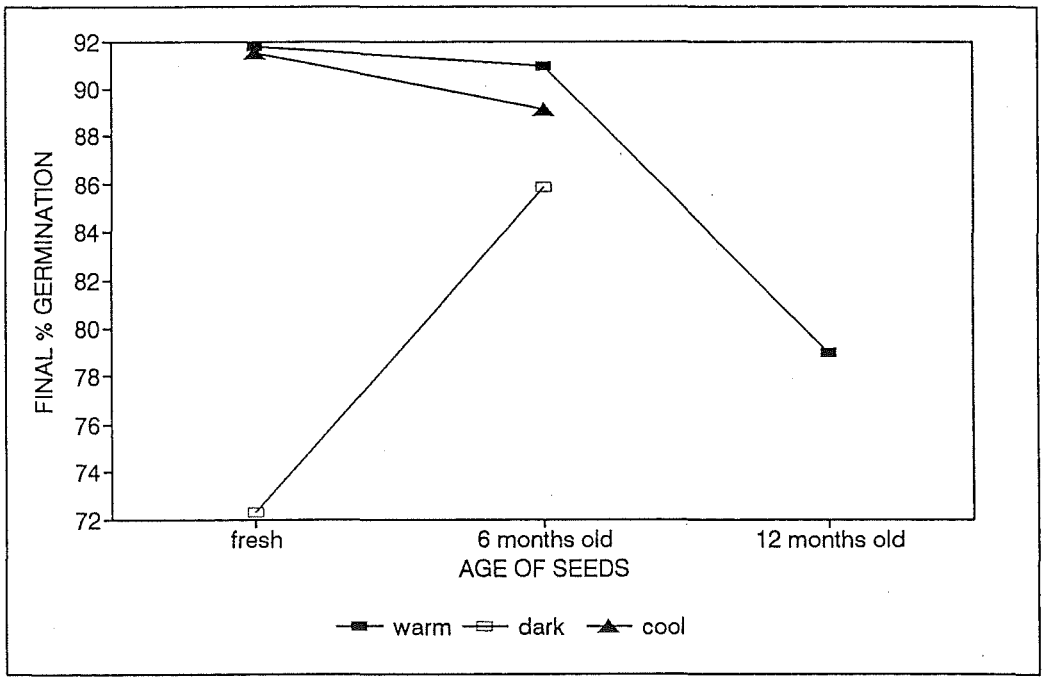
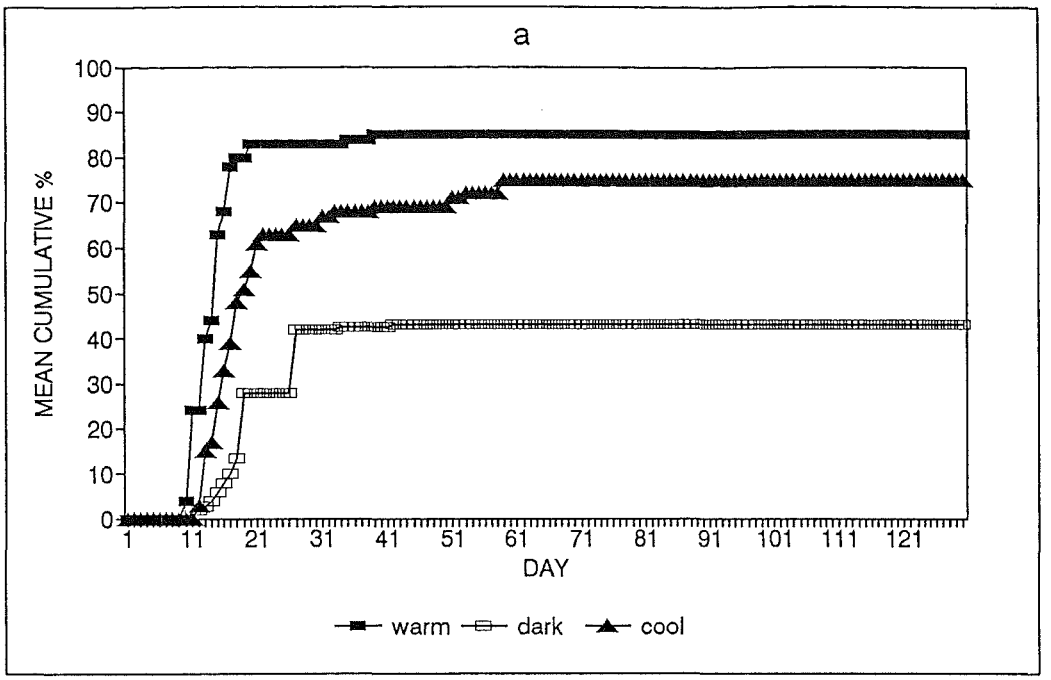


Figure 3.5: Final % germination in three treatments versus seed age for all populations combined.



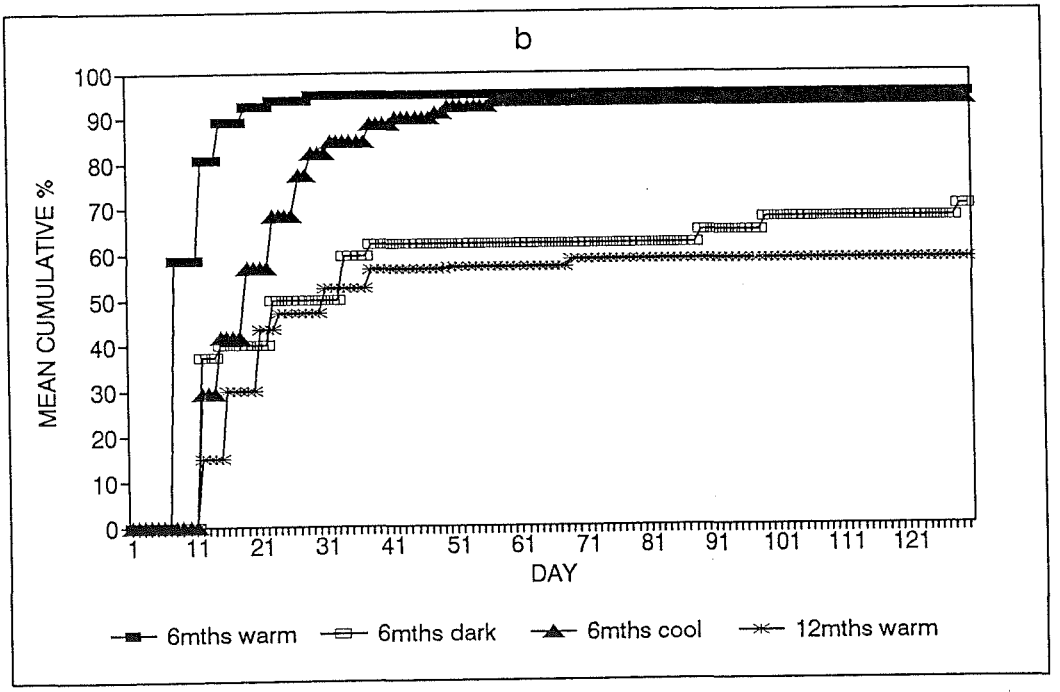
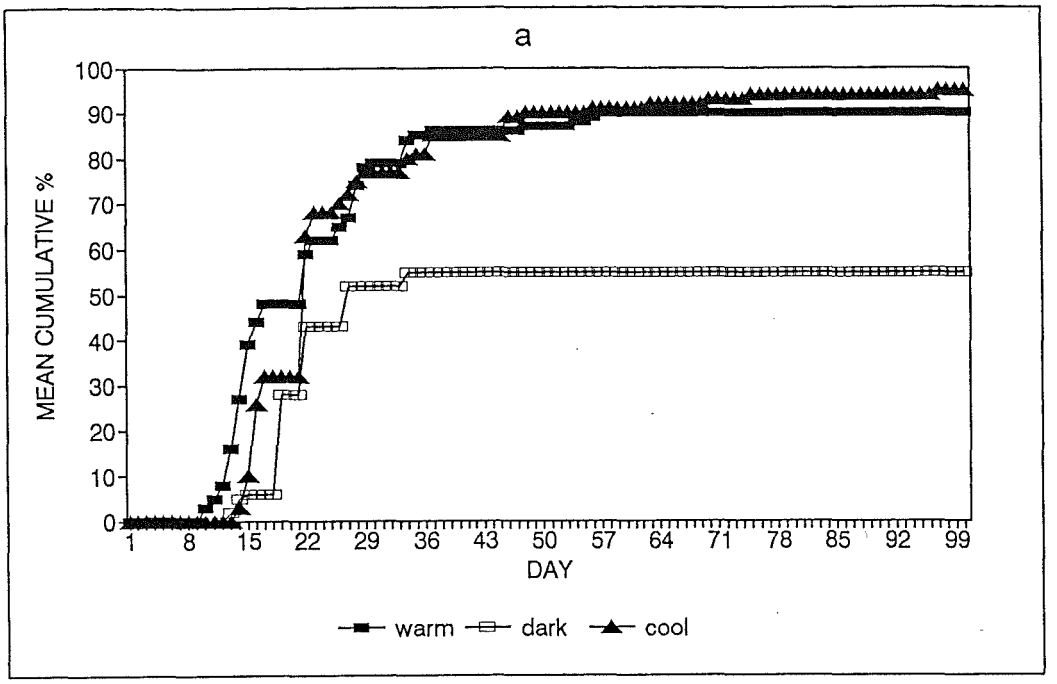


Figure 3.6: Bankside germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.



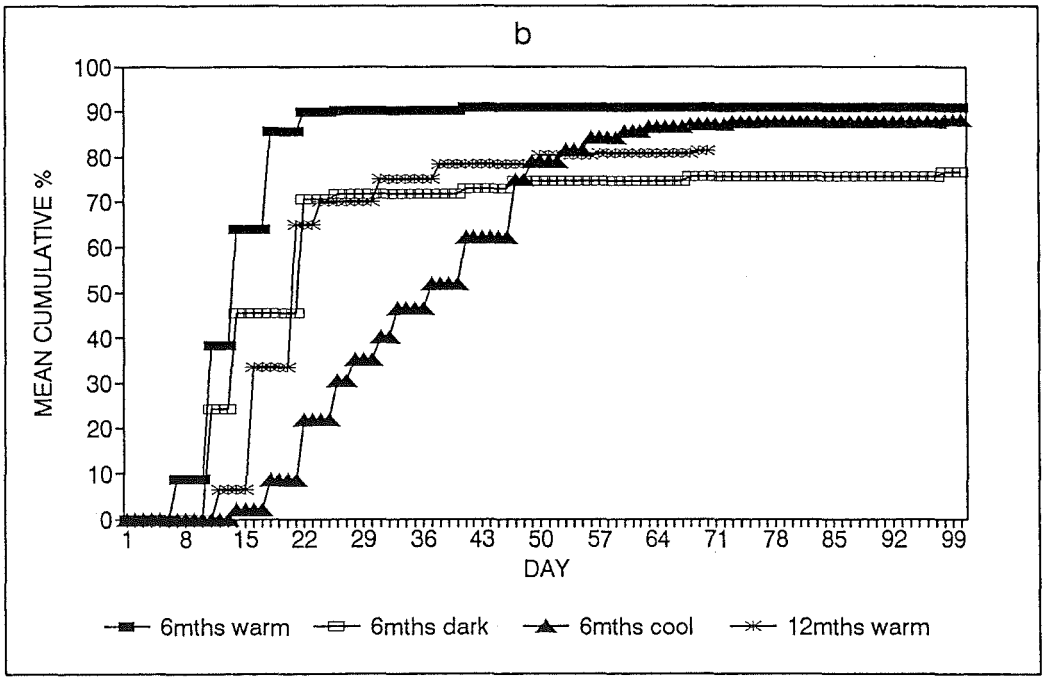
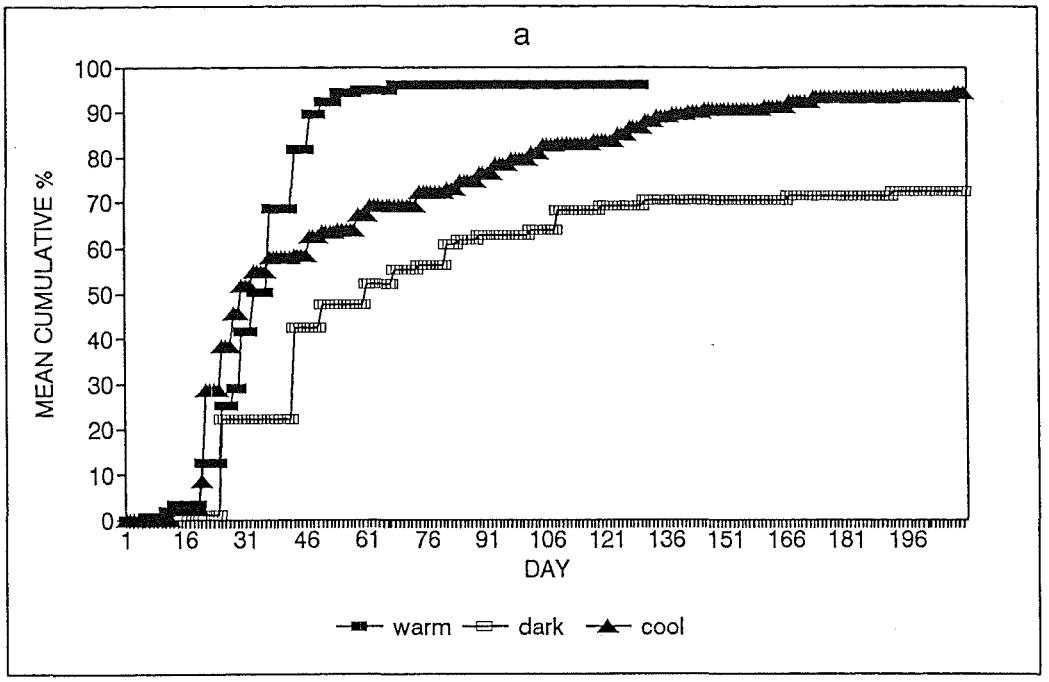


Figure 3.7: Cass River germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.



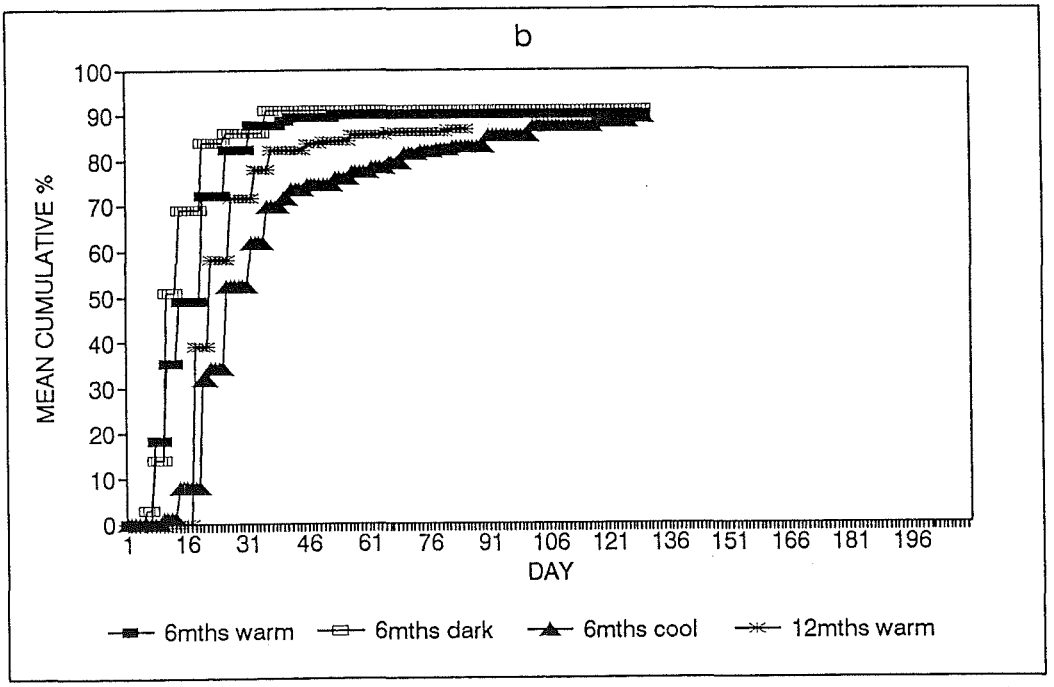
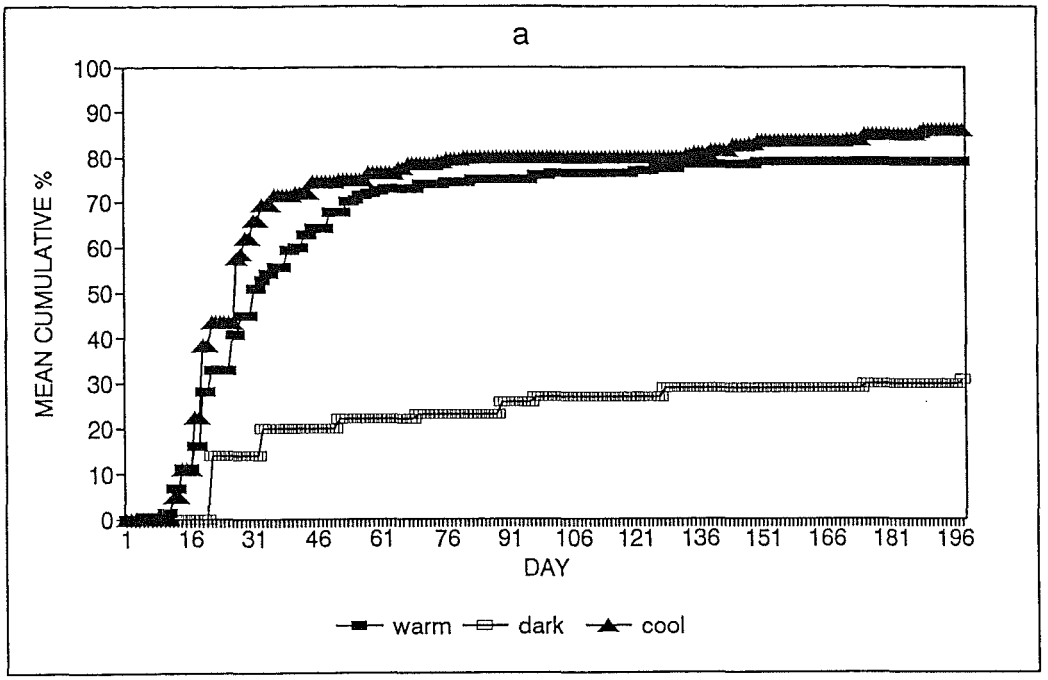


Figure 3.8: Cass Saddle 'A' germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.



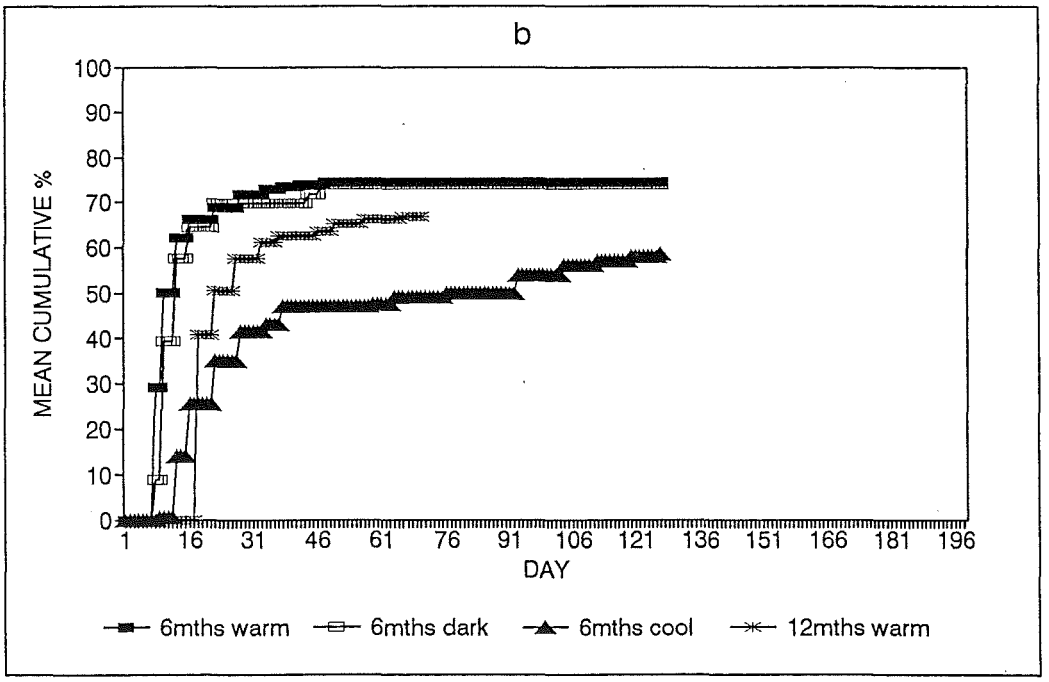
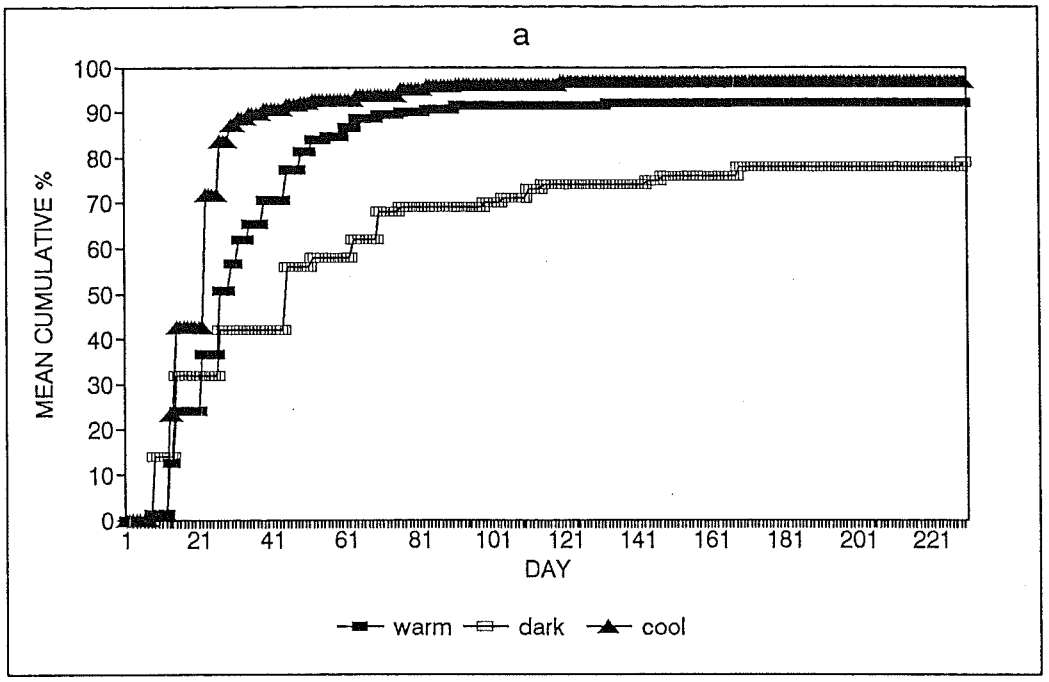


Figure 3.9: Cass Saddle 'B' germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.



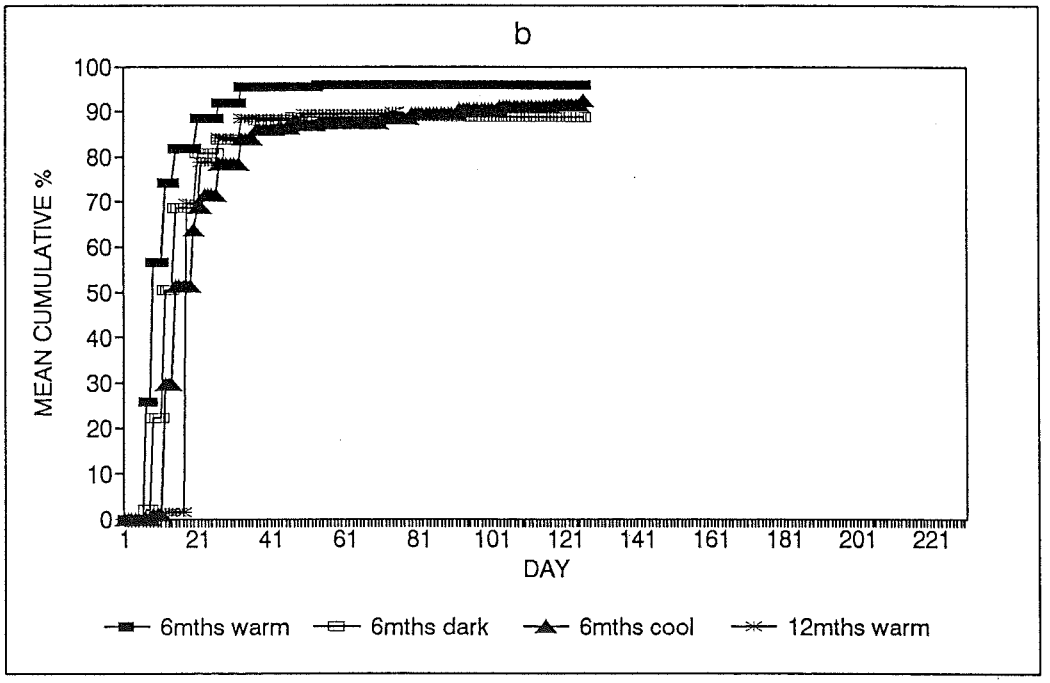
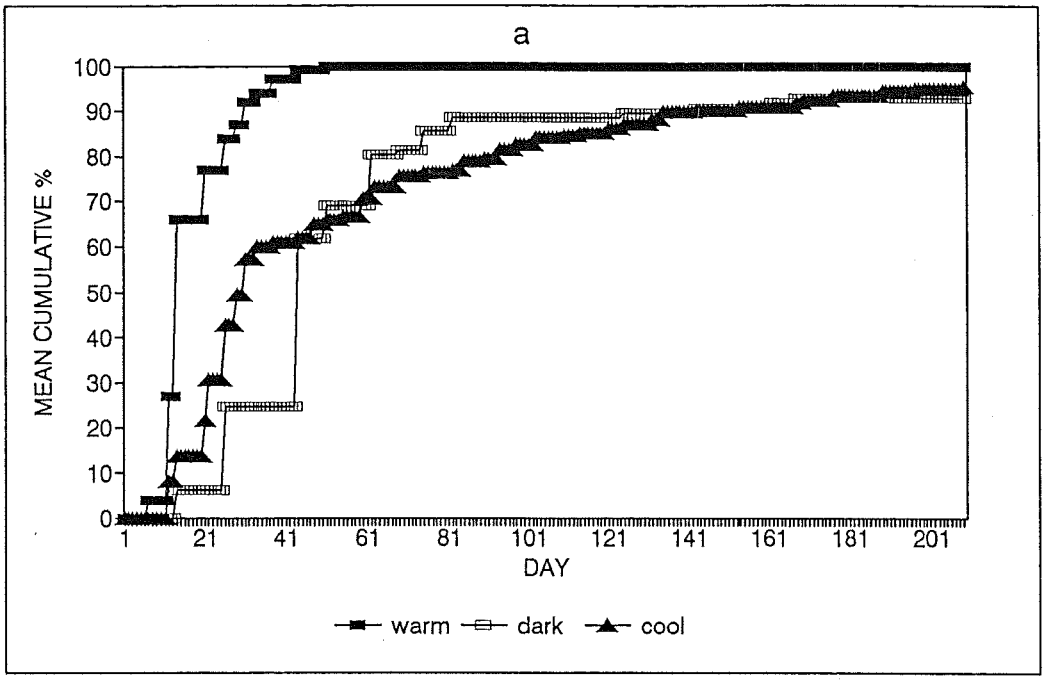


Figure 3.10: Cass Valley germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.



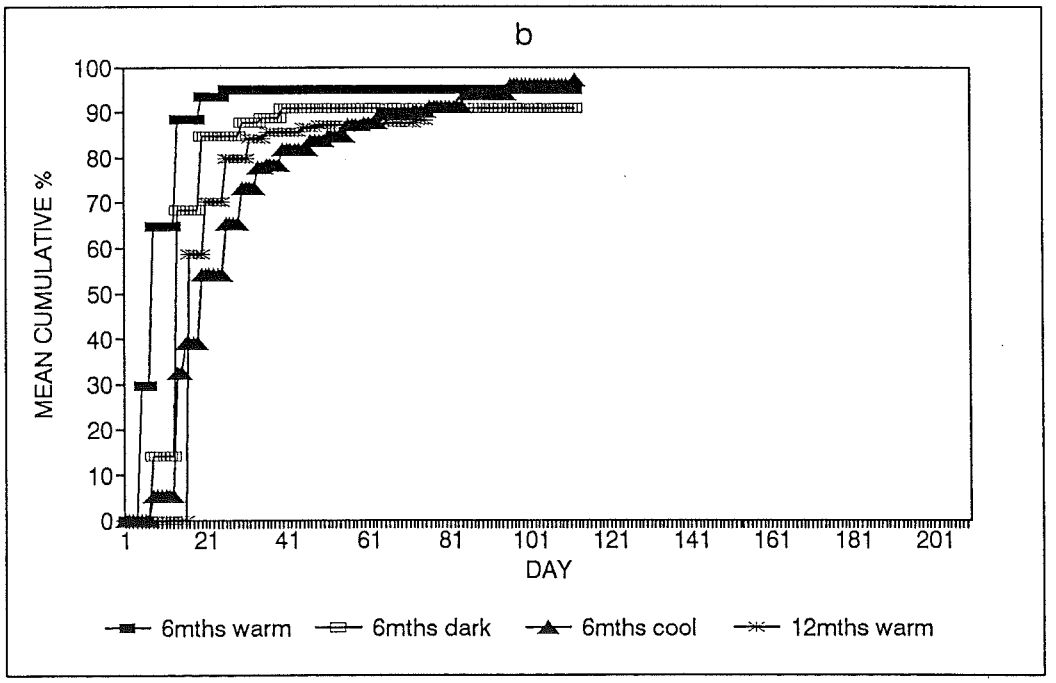
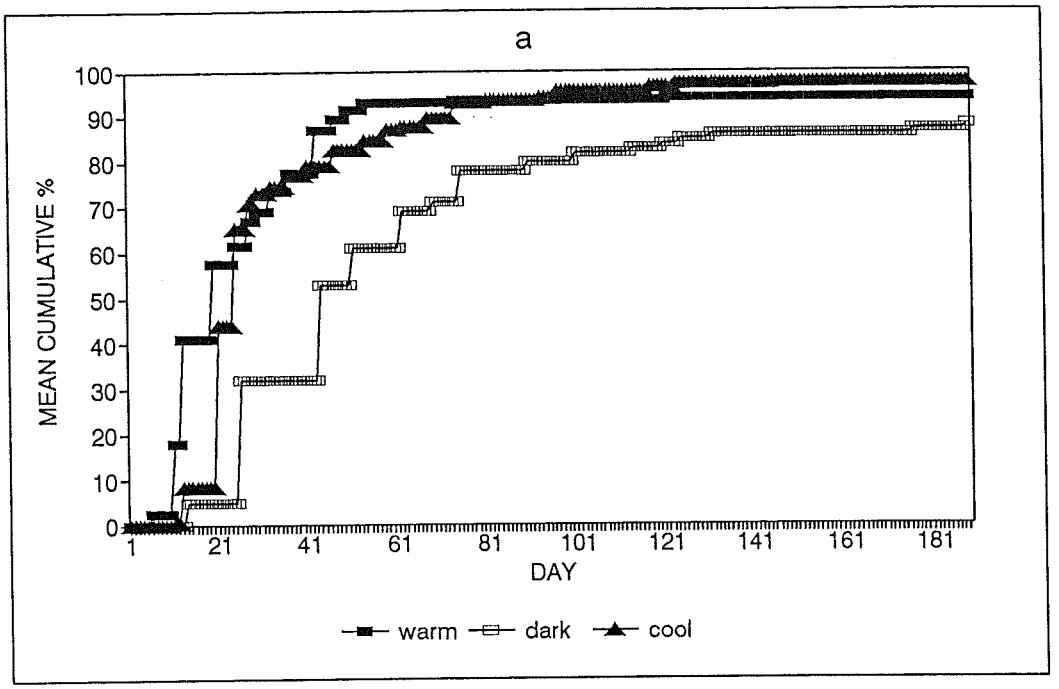


Figure 3.11: Hallelujah Flat germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.



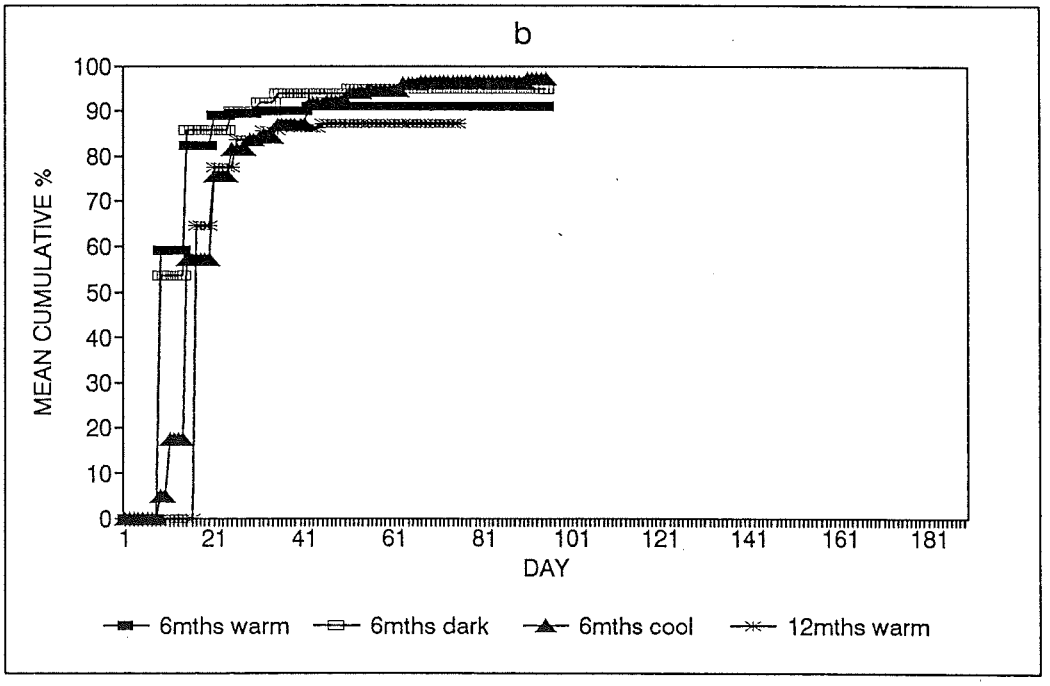
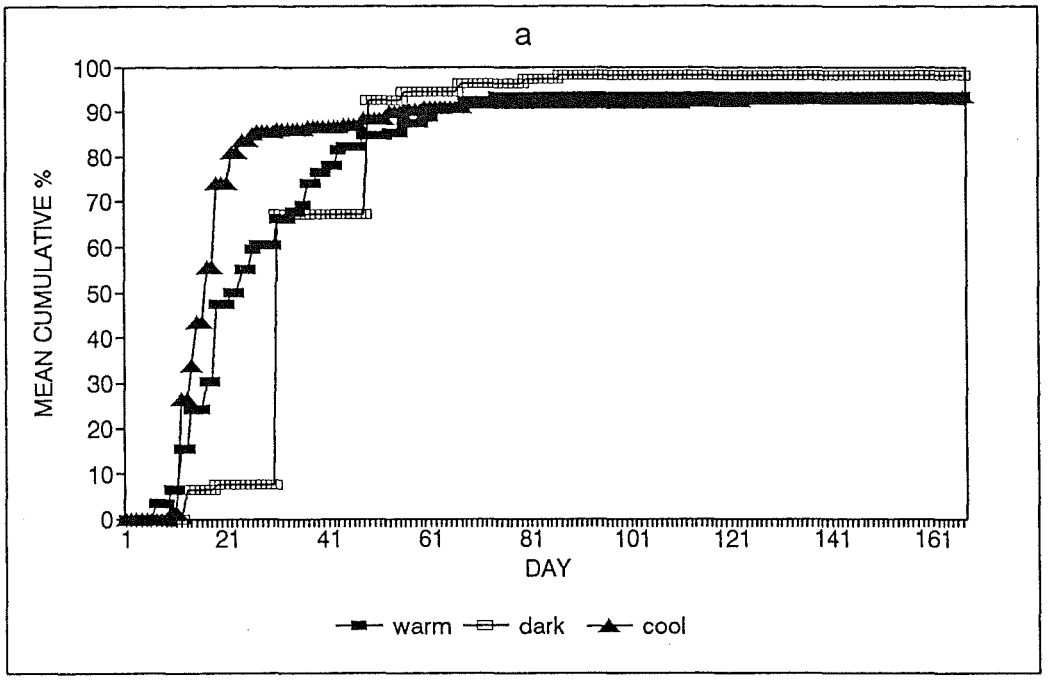


Figure 3.12: Mt Sugarloaf germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.



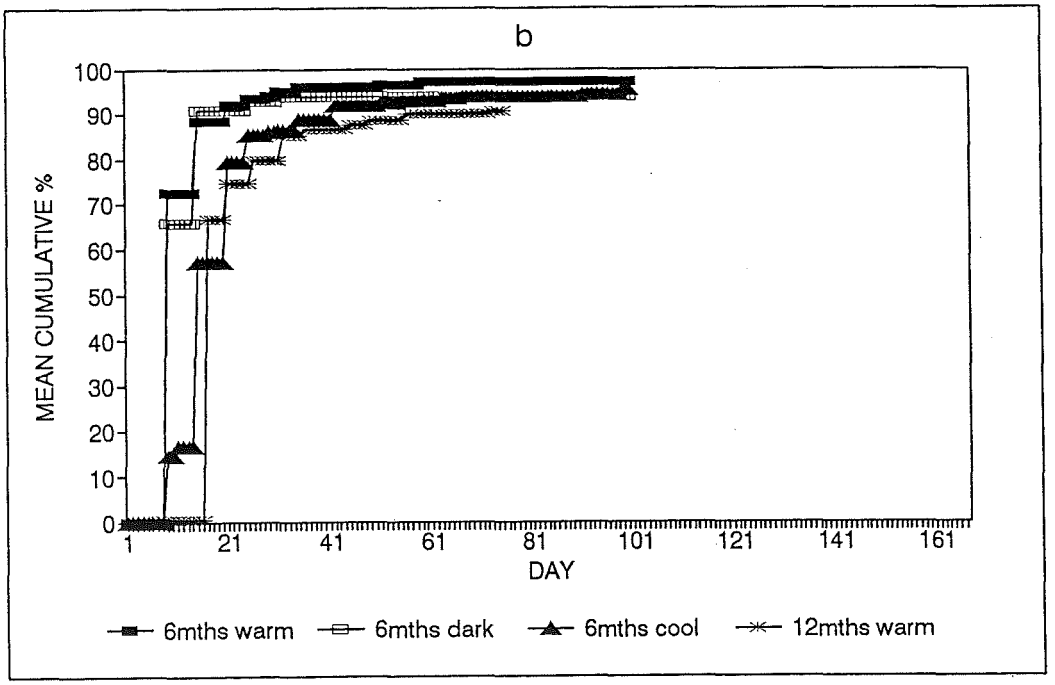
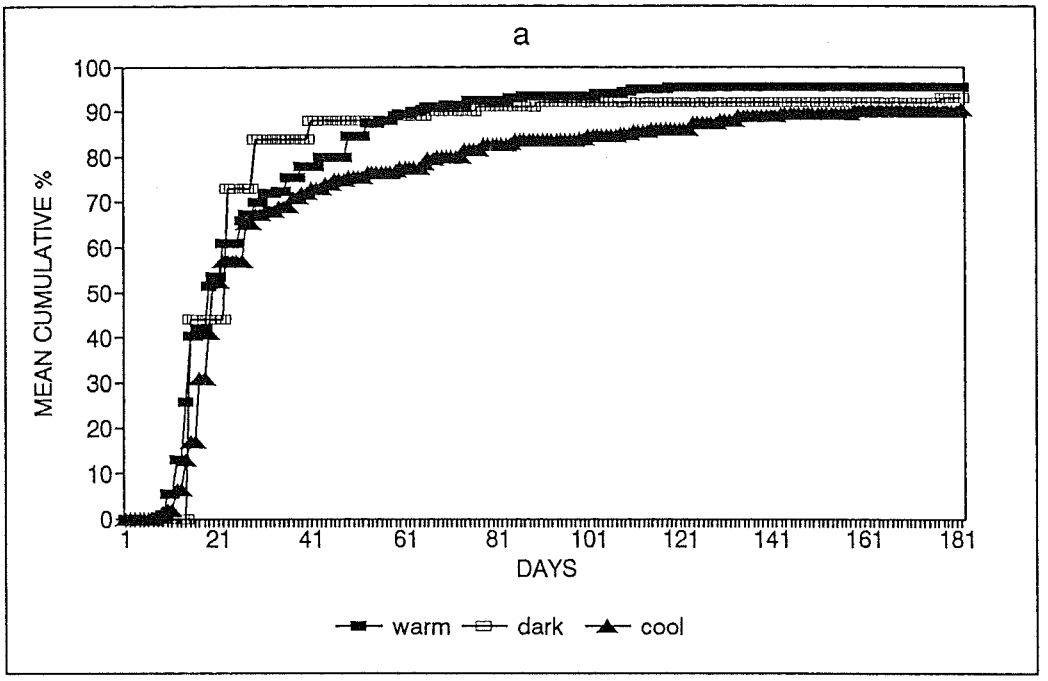


Figure 3.13: Porters Pass germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.



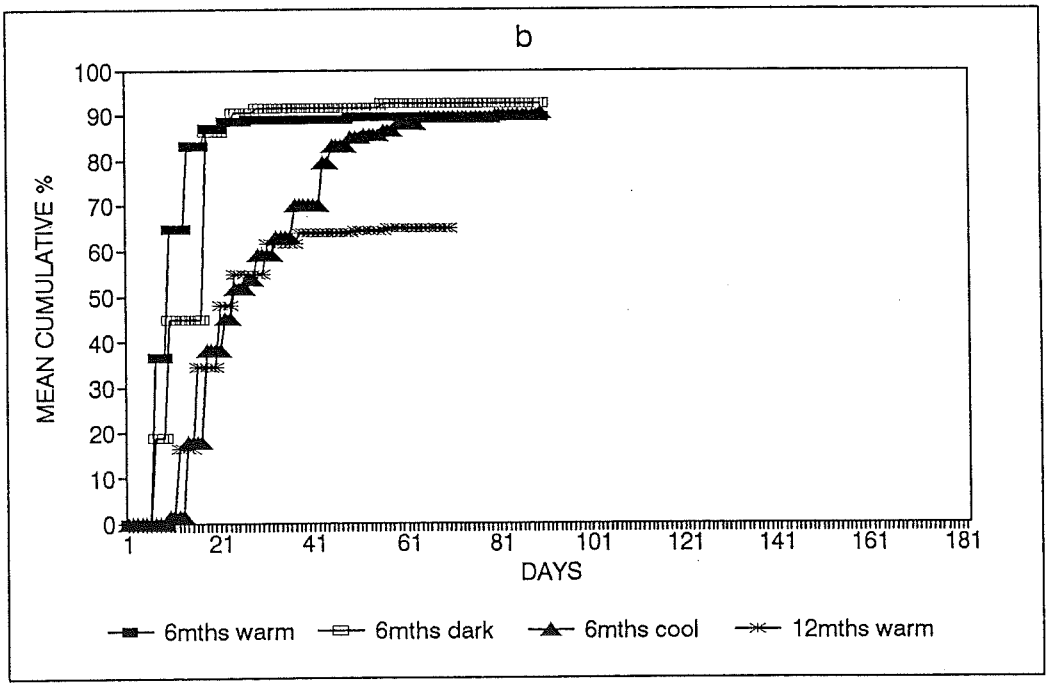


Figure 3.14: Sugarloaf Fan germination response curves for (a) fresh seeds and (b) 6 month old and 12 month old seeds.

Table 3.7: Percent frequency of chlorophyll-deficient seedlings of F. novae-zelandiae in nine populations during germination trials. Result of a one-way analysis of variance test is given. Different superscripts indicate means differed significantly in an LSD test.

Population	**Fresh seeds**	**6 months old**	**12 months old**		
Bankside	0	1.50	2.00		
Cass River	0	1.20	3.00		
Cass Saddle 'A'	0.20	0.40	0.50		
Cass Saddle 'B'	0.20	0.80	1.50		
Cass Valley	0.40	0.60	1.00		
Hallelujah Flat	0	0.60	1.50		
Mt Sugarloaf	0	0.40	0.50		
Porters Pass	0.20	0.40	2.50		
Sugarloaf Fan	0.20	0.20	6.00		
ANOVA:				F	$P <$
Mean % frequency:	0.13^{a}	0.68^{a}	2.05^{b}	8.54	0.01

Table 3.8: Chi-squared values for tests on intercept and slope of probit lines fitted to germination response curves. Intercept represents response timing and slope the response rate. * indicates $P < 0.05$, ** $P < 0.001$, *** $P < 0.001$ and NS not significant. See text for explanation of comparisons.

Comparison:	fresh	6 month	warm	cool	dark
Bankside					
intercept	676.58***	216.45***	523.97***	76.65***	30.80***
slope	24.73***	66.49***	68.76***	7.23**	77.07***
Cass River					
intercept	98.20***	872.03***	381.27***	327.57***	75.12***
slope	7.64*	207.11***	59.81***	3.35ns	72.18***
Cass Saddle 'A'					
intercept	364.36***	532.38***	415.19***	108.09***	313.24***
slope	365.57***	35.95***	221.61***	9.56**	63.04***
Cass Saddle 'B'					
intercept	965.95***	590.86***	420.16***	391.14***	227.52***
slope	112.14***	7.44*	67.62***	14.269***	24.55***
Cass Valley					
intercept	763.99***	296.47***	740.77***	29.42***	157.49***
slope	243.07***	42.66***	0.35ns	88.11***	83.44***
Hallelujah Flat					
intercept	565.97***	529.37***	235.72***	435.24***	229.56***
slope	119.51***	10.09**	119.76***	25.06***	2.55ns
Mt Sugarloaf					
intercept	456.04***	210.99***	336.73***	211.06***	344.01***
slope	23.52***	58.00***	28.21***	5.49*	0.14ns
Porters Pass					
intercept	166.44***	340.62***	966.87***	11.09***	335.38***
slope	129.52***	30.59***	55.66***	11.45***	33.86***
Sugarloaf Fan					
intercept	279.19***	719.63***	774.61***	69.69***	32.13***
slope	107.38***	29.93***	58.23***	80.66***	29.73***

indicated significant differences between populations and between treatments across populations as well as a significant interaction between the two (Table 3.9). Differences in days to 50% germination due to treatment differences made the largest contribution to overall variation (38.6%).

Pairwise comparison among population means for days to 50% germination resulted in four groups in which means did not differ significantly (Table 3.9a). The largest group contained six populations all with mean times to 50% germination of around 20 days. Cass Saddle 'B' had the highest mean time to 50% germination at 56.1 days and was the only population that differed significantly from all others.

Pairwise comparisons of mean time to 50% germination among treatments resulted in three groups in which means did not differ significantly from each other (Table 3.9b). The group of treatments with the fastest germination response consisted of "6 months old warm", "6 months old dark" and "12 months old warm". The "fresh dark" treatment was the only treatment to differ significantly from all others.

Analysis of variance on final percent germination likewise indicated significant population and treatment effects and a significant interaction (Table 3.9). Differences due to population contributed 23.3% to overall variation with between treatment differences accounting for 17.8%.

The Porters Pass population had the highest mean percent germination at 94.6% and Cass Saddle 'B' was the lowest at 66.7%. Pairwise comparison among population means indicated substantial differentiation with five out of the nine populations differing significantly from all others (Table 3.9a).

Pairwise comparisons among treatment means resulted in four groups in which means did not differ significantly (Table 3.9b). Final percent germination was lowest for the "fresh dark" treatment and highest in the group containing "fresh warm", "fresh cool", "6 months old warm" and "6 months old cool".

Table 3.9: (a) Population and (b) treatment means for days to 50% germination and final % germination for F. novae-zelandiae seeds. Treatment categories are combinations of storage and temperature/light treatments. Results of two-way analysis of variance tests are also given. Different superscipts indicate a significant difference between means using LSD tests.

(a)

Population	**Days to 50%**	**Final %**
Bankside	45.6 cd	74.1 b
Cass River	35.7 bc	82.4 c
Cass Saddle 'A'	27.6 ab	88.6 de
Cass Saddle 'B'	56.1 d	66.7 a
Cass Valley	23.9 ab	90.8 def
Hallelujah Flat	21.0 a	94.2 ef
Mt Sugarloaf	21.4 a	92.8 def
Porters Pass	17.2 a	94.6 f
Sugarloaf Fan	18.6 a	88.1 d

(b)

Treatment	**Days to 50%**	**Final %**
Fresh Warm	25.4 b	91.8 d
Fresh Cool	23.9 b	91.5 d
Fresh Dark	84.9 c	72.3 a
6 months old Warm	10.6 a	91.0 d
6 months old Cool	26.6 b	89.1 cd
6 months old Dark	15.2 ab	85.9 c
12 months old Warm	21.1 ab	79.0 b

ANOVA: source	F	P <	F	P <
Population	8.67	0.001	23.3	0.001
Treatment	38.6	0.001	17.8	0.001
Pop x Treatment	4.72	0.001	2.81	0.001

3.4.3 Discussion

Most *F. novae-zelandiae* seeds germinate readily however some seeds exhibited delayed germination. Delayed germination was more a feature of seeds in the "cool" and "dark" treatments indicating that *F. novae-zelandiae* was polymorphic for germination response in less than ideal conditions.

An overall slower germination response of fresh seed at lower temperatures was observed in four populations: Bankside, Cass Saddle 'A', Hallelujah Flat and Sugarloaf Fan (Figs. 3.6a, 3.8a, 3.11a and 3.14a). This would be a direct result of the effect of temperature on metabolic rates. However the remaining populations showed little reduction in the germination rate of fresh seeds with lower temperature.

The slightly faster germination response observed in six month old seed could be due to fresh seeds not being fully mature when they were collected, as seeds for this experiment were collected while they were still on the panicle. A similarly enhanced germination rate with storage has also been observed for *Deschampsia caespitosa* (Davy, 1980).

Darkness appeared to have an inhibitory effect on the germination of fresh seeds. In *Deschampsia caespitosa* germination was also depressed by darkness and complete inhibition was produced by a combinations of darkness and constant temperature (Thompson *et al.*, 1977; Davy, 1980). Temporary dark inhibition could be advantageous if the reduction in parental fitness of seeds germinating in an unsuitable site (e.g. under dense vegetation) was with time outweighed by cost of seeds not germinating at all. Alternatively dark inhibition which lessened with increasing temperature fluctuations could provide a mechanism by which seeds in the soil could respond to the creation of a vegetation gap (Thompson *et al.*, 1977) although for this mechanism to operate seeds need to be able to remain viable in the soil.

The high values for percent viability found in this study conform with Dunbar's (1970) report of 95% germination during laboratory trials. However Dunbar gave no indication of the conditions under which the germination trial was conducted. Scott (*pers. comm.*) found that 17% and 57% of healthy *F. novae-zelandiae* seeds germinated after 14 and 40 days respectively under an 18/25 °C temperature regime. This is lower than the result from this study which found an average across the 9 populations of 27.4 $\pm$ 8.93% germination after 14 days and 73.7 $\pm$ 8.94% after 40 days at 15/25 °C.

After 12 months storage in a Stevensons screen, seeds still showed high percent germination. They can probably then maintain viability for longer periods under artificial conditions, despite a gradual accumulation of mutations as evidenced by the increase in chlorophyll-deficient seeds. However this result cannot be taken to indicate that seeds survive for long periods in the field.

The significant interaction between populations and treatments in the analysis of variance tests indicates that the populations tested responded differently to germination

conditions. However there seem to be no clear trends in response patterns with reference to site factors such as temperature, altitude or rainfall. It would appear then that clearly differentiated adaptation to different environments by means of germination response has not occurred among the populations tested.

However the apparent polymorphism in populations for germination response under less favourable conditions may represent a bet-hedging strategy. It could be that a cool autumn triggers dormancy in some seeds which then germinate in spring. In chapter 3.5 a few seedlings were observed to emerge in spring. The majority of seeds which germinate immediately would presumably have the advantage of a wet season in which to become established but also risk being damaged or dislodged by early frost and needle ice.

3.5 SEEDLING EMERGENCE AND SURVIVAL

3.5.1 Methods

Two sites on Sugarloaf Fan, differing in altitude and vegetation cover, were selected for a seedling monitoring experiment. The lower site, 650 m in altitude, was an area of sparse open vegetation with abundant mats of *Coprosma petriei* and *Raoulia subsericia.* The upper site, 850 m in altitude, was more densely vegetated with abundant *Poa colensoi.* Twenty 50 cm x 50 cm plots were located at random intervals along a transect laid out at each site. Mean tussock density at each site was obtained by averaging tussock density in 20 contiguous 1 m x 1 m quadrats laid out along either side of the transect on which the seedling plots were located.

Each plot was searched thoroughly in May 1989 and all seedlings of *F. novae-zelandiae* were mapped and tagged with coloured plastic-coated paper-clips, and the number of leaves on each seedling recorded. Although these first seedlings will subsequently be referred to as the 1989 cohort they most likely represent several cohorts and only a minimum age can be assigned to them.

Seedlings were identified by leaf, sheath and ligule characters and confirmed by caryopsis characters for seedlings where the caryopsis was still attached and visible. The seedlings were censused for both growth and survival every three months from May 1989 to November 1991. Census months - February, May, August and November - were selected to coincide with transitions between seasons. At each census the plots were again searched and new seedlings tagged and mapped as they were encountered.

The substrate of each seedling was recorded when the seedlings were first tagged. The frequency of substrates within the vegetation was measured by systematic point-sampling along the transect on which the seedling plots were located. A needle was lowered into the vegetation at 25 cm and 50 cm distances from the transect on each side at 1 m intervals and the type of substrate encountered was recorded (see Table 3.10 for substrate types).

The frequency of seedling establishment on substrates was compared with the abundance of those substrates at the two sites using a Chi-squared test. One-way analysis of variance was used to test for significant differences in tussock density, seedling density, growth and survival between sites and differences in survival between substrate types.

3.5.2 Results

Mean tussock density was 1.80 ± 0.92 m^{-2} at the lower site and 8.10 ± 1.16 at the upper site. This difference between the two sites in tussock density was significant when tested with one-way analysis of variance (F = 79.0, P < 0.001).

In total of 226 seedlings were located and monitored over the study period. Seedling density per 50 x 50 cm plot was 4.10 ± 1.84 at the lower site and 7.25 ± 2.72 per plot at the upper site. Seedling density did not differ significantly between the two sites when tested with one-way analysis of variance. Average seedling density over both sites was 22.7 ± 6.58 m^{-2}.

Most new seedlings were located at the May census of each year meaning that seedling emergence was predominantly an autumn phenomenon (Fig 3.15). For the 1990 and 1991 cohorts 75.8% and 92.8% of recruits were located at the May census. Further recruits were tagged at the August and November censuses; however their contribution to overall recruitment was minor.

The majority of seedlings found occurred on mats of *Coprosma petriei*, around flatweeds such as *Senecio bellidioides* and *Hypochoeris radicata* or at the base of tussocks. A chi-squared test revealed that seedling establishment was non-random with reference to substrate type (Table 3.10). The frequency of establishment on different substrates also differed significantly between sites (X^2 = 31.9, df = 10, P < 0.001). At the lower site, more seedlings than expected established around flatweeds and tussocks and fewer than expected established in areas of moss (usually *Racomitrium lanuginosum*). At the upper site seedlings established preferentially on *Coprosma* mats and were far less frequent than expected in areas of dense grass. No significant difference was found in seedling survival among the different substrate types when tested with one-way analysis of variance.

Seedlings were commonly very slow growing with an average net increase of 0.61 ± 0.07 leaves per year. Only three seedlings grew to the two-tiller stage and the largest of these had 10 leaves and was 7 cm high after at least 33 months growth.

Mortality was high and continued to occur even in the oldest cohort throughout the study period (Fig. 3.16). Seedlings were most at risk during the first few months of life; 47.8% of all seedlings died within nine months of first being located (Fig. 3.17). At the lower site seedlings survived on average 12.3 ± 1.77 months and at the upper site mean survival was 11.6 ± 1.28 months. There was no significant difference between survival at the two sites. The half-life of the group of seedlings tagged 1989, averaged across both sites, was 11 months, however these seedlings probably represented cohorts from more than one year. The cohort that germinated in 1990 had a half-life of 12 months.

Burrowing or feeding activity by ground invertebrates was the most common identifiable cause of death, accounting for 11% of total mortality. Other identified

Table 3.10: Observed seedling substrate frequencies (%) and expected frequencies based on point-sampling. Values from Chi-squared tests for goodness-of-fit are also given.

Substrate	Freq. at lower site		Freq. at upper site	
	Observed	Expected	Observed	Expected
Coprosma	23.0	24.4	48.5	8.88
Coprosma/grass	23.0	17.7	16.1	17.7
Coprosma/moss	3.84	17.7	8.82	0
Coprosma/Raoulia	1.92	4.44	0	2.22
Raoulia	0.96	0	2.94	2.22
Raoulia/grass	0.96	0	0	0
Raoulia/moss	0	6.66	1.47	0
moss	3.84	0	0	0
grass	4.80	4.44	7.35	33.3
moss/grass	2.88	8.88	2.94	6.66
flatweeds	21.1	6.66	7.35	4.44
tussock base	13.4	0	4.41	24.4
shrub base	0	6.66	0	0
rock base	0	2.22	0	0
X^2	54.5		73.6	
$P <$	0.001		0.001	

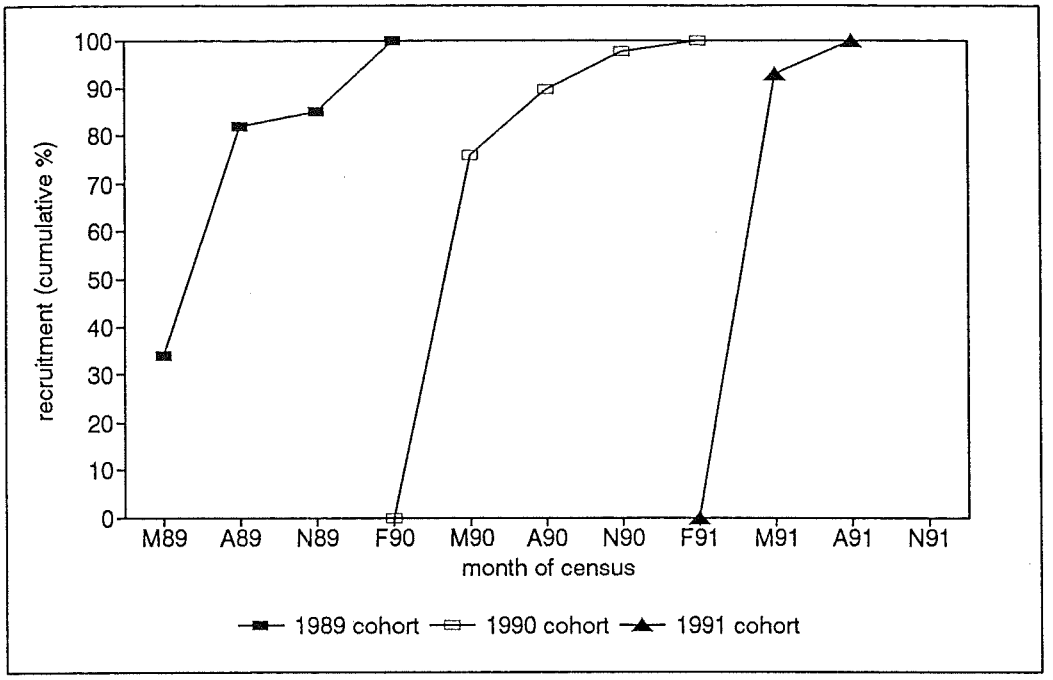


Figure 3.15: Cumulative seedling recruitment at Sugarloaf Fan over 30 months.

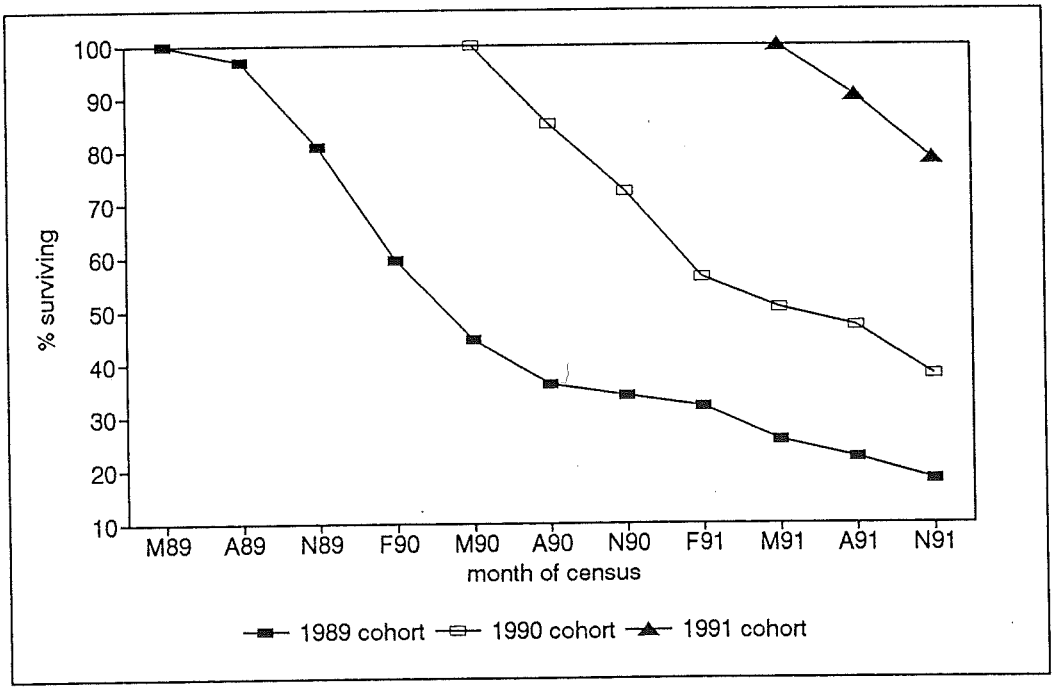


Figure 3.16: Survival of seedling cohorts at Sugarloaf Fan over 30 months.

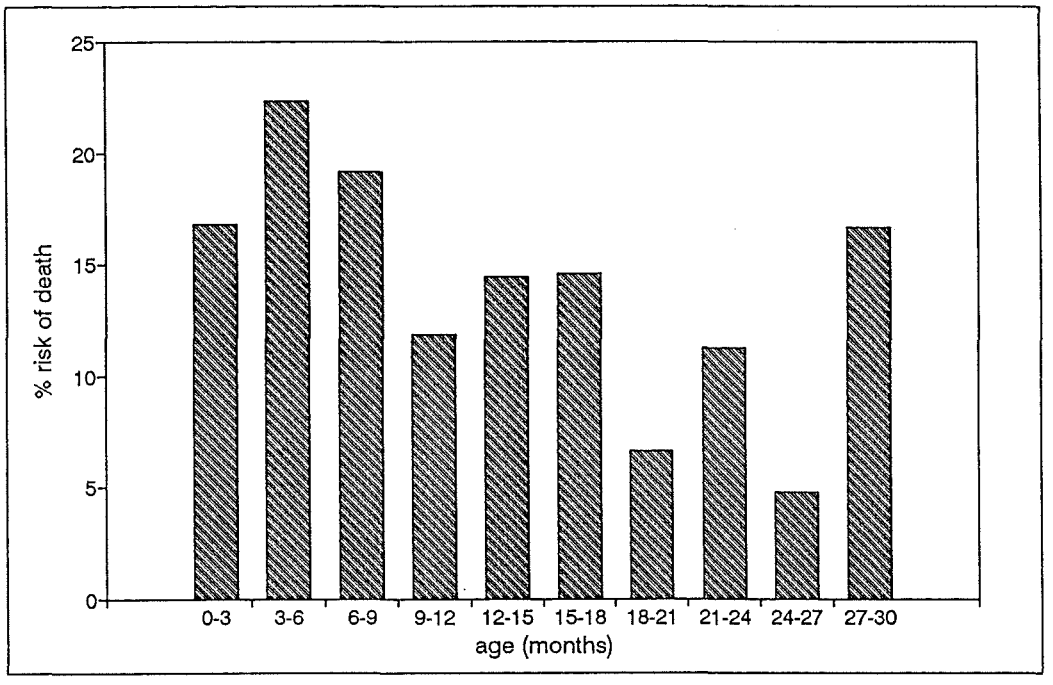


Figure 3.17: Risk of death compared with seedling age for F. novae-zelandiae seedlings at Sugarloaf Fan.

causes of death were browsing (probably by grasshoppers) (3.2%), failure to root due to the seed germinating while suspended in moist vegetation (1.1%) and frost heave (0.9%). However for the vast majority (84%) of deaths, cause of death was not identified.

Mortality due to unknown causes showed no significant seasonal pattern when all seedling cohorts were considered ($X^2 = 3.83$, $df = 3$, $P > 0.05$). However the rate of cumulative percent increase in deaths was higher over the period August 1990 to February 1991 among seedlings that emerged in 1990 than among seedlings from the 1989 cohort (Fig. 3.16).

3.5.3 Discussion

The seedling densities recorded in this study are in keeping with results from other long-lived grasses and sedges in relatively unmodified grassland. *Eriophorum vaginatum*, a caespitose sedge of tundra vegetation was found to have 55.1 $\pm$ 6.4 (S.E.) seedlings m^{-2} in 'closed' vegetation (McGraw & Shaver, 1982). Rose & Platt (1990) found that seedling densities of *Chionochloa pallens* ranged from 0.6 to 96 m^{-2} depending on the availability of suitable microsites. In a study of Californian coastal grassland, Peart (1989) found that seedling densities for three perennial bunchgrasses, *Anthoxanthum odoratum, Deschampsia holciformis* and *Holcus lanatus*, ranged from 1.8 $\pm$ 1.8 (S.E.) to 40.9 $\pm$ 19.9 (S.E.) depending on species and patch type.

Williams (1970) found considerably lower seedling densities of 0.19 seedlings m^{-2} for *Chloris acicularis*, a tussock grass in semi-arid Australian grassland. However the community under study was severely degraded as a result of heavy grazing. However, a short-lived opportunist grass in the same community, *Danthonia caespitosa*, had seedling densities of 2.66 - 205 m^{-2}.

Autumn seedling emergence is a common feature of grasses in areas where rainfall occurs mainly during the cool season (Grime, 1979) as is the case in this study area. Lack of innate dormancy allows for germination at the beginning of the moistest part of the year. As a result, seedlings have a greater chance of becoming established before the onset of water limitations the following summer.

Sewell (1947, 1952) recorded that *F. novae-zelandiae* seedlings only established in litter around tussock bases and Scott & Archie (1976) found that seedlings germinating close to a tussock suffered relatively lower mortality during dry summer months. The present study has shown that *F. novae-zelandiae* seedlings also commonly establish on mats of *Coprosma petrei* and around flatweeds. Rose & Platt (1990) found similar trends in seedling establishment for *Chionochloa rigida*. In their study seedlings were three times more frequent on litter or mat vegetation than in rocky areas or taller vegetation.

The differences between the two sites in seedling substrate affinity can be related to

factors affecting seedling establishment at each site. At the lower site the vegetation was quite open and lack of moisture could be a major factor in germination failure and early seedling mortality. The apparent affinity of seedlings at the lower site for tussock bases and flatweeds could be because seeds falling on these substrates had a more sheltered, slightly moister microclimate and were therefore successful in germinating.

At the upper site seedlings were noticeably more common on mats of *Coprosma petriei* than expected and much less common in areas of dense grass. The upper site was more densely vegetated than the lower site and casual observation suggested that soil moisture tended to be higher. The observed pattern of substrate affinity at the upper site could indicate that, rather than moisture stress, other factors such as light availability were affecting the establishment of seedlings. The close dependence of seedling establishment and survival on substrate and vegetation type means that previously published statements about *F. novae-zelandiae* seedling establishment must be referred back to the local environment in which the studies were conducted.

Site attributes probably affect recruitment in different ways at different stages from germination to maturation. Dunbar (1970) found that the emergence and density of *F. novae-zelandiae* seedlings was inversely related to vegetation density but the survival of established seedlings was positively related. In the present study the different mortality rates of the 1989 and 1990 cohorts during spring and early summer 1990, indicated by the differing slopes of the two survival curves over that time period (Fig. 3.16) would certainly suggest this.

Seedlings of *F. novae-zelandiae* have previously been reported as uncommon or entirely absent in short-tussock grassland (Boyce, 1939; Sewell, 1947; Moore, 1976; Espie, 1987). However as *F. novae-zelandiae* seedlings seldom survive beyond the one-tiller stage they are readily overlooked. The results of this study indicate that *F. novae-zelandiae* seedlings can be relatively abundant on certain substrate types.

Although the two sites studied differed significantly in tussock density and therefore probably also in seed rain, there was no difference between them in seedling density. This would indicate that seedling densities are limited not by lack of seeds but by lack of suitable substrate. This appears to be a feature of stable populations of long-lived perennials, where in most years recruitment is limited by the number of safe sites rather than by seed production or losses to seed predators (Andersen, 1989).

Spatial heterogeneity and the availability of suitable microsites has been shown repeatedly to be a major factor in seedling survival (Harper *et al.*, 1965; Harper, 1977). For example, McGraw & Shaver (1982) found that seedling densities of species in Alaskan tundra varied greatly depending on substrate availability and Reader (1991) found that emergence of seedlings in an abandoned pasture was greatly influenced by microtopography and its effect on ground cover.

The low growth rates measured for seedlings in the present study confirm observations made by Moore (1976) on a South Island high country station. She found

that seedlings could remain only a few centimetres tall with one or two tillers for at least seven years. However she also observed that seedlings in sheltered, moist microsites could reach half the height of mature plants in three years and form thick tussocks in five years.

Due to the limited time available for this study, the data are inadequate to ascertain the proportion of seedlings that survive to become juvenile tussocks on Sugarloaf Fan (see chapter 4.4 for definition of a juvenile). Survival to maturity rather than seedling establishment would appear to be the crucial stage for the maintenance of *F. novae-zelandiae* populations by regeneration from seed.

Recruitment rates are only valid when viewed in the context of the adult life-span (McGraw & Shaver, 1982). In a long-lived plant, even high levels of mortality among seedlings do not necessarily signify regeneration failure (Mark, 1965b). In fact high seedling mortality is common among long-lived iteroparous herbs (Harper, 1977; Davy, 1980; Symonides, 1985). Even very low levels of seedling recruitment to the adult population can adequately maintain population density of a very long-lived species (Mark, 1965b).

The rates of *F. novae-zelandiae* seedling mortality observed in the present study are higher than those observed for *Chionochloa rigida* by Mark (1965b). In the present study 18% of the seedlings initially tagged in 1989 were still alive after 30 months, whereas in Mark (1965b) seedling numbers were reduced by approximately half after 36 months. Mortality due to seedlings being dislodged by frost heave was not as important in this study as in Mark (1965b), presumably due to the lower altitude and higher vegetation cover at the present study site. Mark's seedling study was conducted at 1220 m in grassland that had been burnt eight months previously.

With low recruitment and replacement, many adult populations particularly on disturbed sites could well be dominated by one or two pioneering cohorts. The substrates apparently favoured by *F. novae-zelandiae* seedlings in closed grassland, such as mats of vegetation, are a feature of the early colonisation of river terraces or slips in the montane and alpine zones (Calder, 1958, 1961). In a situation analogous to *Eriophorum vaginatum* (McGraw & Shaver, 1982) seedling recruitment in *F. novae-zelandiae* may assume special importance in relation to the invasion of new habitats and the peripheral spread of populations after disturbance rather than being important in population turnover in "closed" grassland.

3.6 SUMMARY AND DISCUSSION OF CHAPTER 3.

F. novae-zelandiae is not a mast-seeder in the sense of Silvertown (1980) which distinguishes it from the physiognomic dominants of tall-tussock grassland, *Chionochloa* species (Mark, 1965b; Kelly *et al.*, 1992). However individuals that flowered every year were in the minority (17.4%) in the population studied from 1988 to 1992 at Cass. The most fecund individuals were generally large tussocks. Over one third (36.1%) of plants monitored over that time period produced no culms at all and the remainder reproduced intermittently. Nonreproductive individuals were usually small.

Reproductive output in a given year was usually positively related to output in the previous two years. Plants were showing short-term consistency in their contribution to total reproduction which reflected their overall size and vigour. The Sugarloaf Fan population showed a typical L-shaped distribution of fecundity (Levin & Wilson, 1978) (Fig. 3.1) that results in a few individuals dominating the reproductive output of a population. Due to the correlation in reproduction between years, these same individuals would be contributing a proportionally large number of seeds to the seed rain over several years.

This uneven contribution to the next generation has important genetic implications. If the few very fecund individuals are successful due to the possession of favoured heritable traits then the response of the population to selection will be accelerated relative to a situation where reproductive contribution was more evenly spread among individuals (Levin & Wilson, 1978). However if uneven reproduction output among individuals was largely due to spatial environmental heterogeneity than the genetic effects with regard to the population's genepool would be less significant.

When reproduction in several populations of *F. novae-zelandiae* was compared, a significant amount of between-population variation in reproductive effort at all levels from the number of culms per tussock to florets per spikelet and total seed set was found. However, overall the reproductive output of *F. novae-zelandiae* is characterised by relatively constancy perhaps due to conservative responses to yearly changes in resource availability. The lack of a density effect on culm production does not rule out the importance of density-dependant processes. However it does perhaps indicate that tussocks usually occur at densities low enough to avoid inter-plant interference and that sites factors may commonly be more important to reproduction.

Pre-dispersal fates of seeds varied between populations with invertebrate predation affecting nearly 80% of florets at the lowest altitude site but only 7.4% at one of the higher altitude sites. In other populations, factors such as failure of seeds to develop or embryo abortion accounted for the majority of lost ovaries. The most common identifiable predator was a flightless Chloropid fly *Diplotoxa moorei*.

Although *F. novae-zelandiae* has no specialised mechanisms for seed dispersal, seeds were found to be dispersed over several metres in normal strong winds and

considerably further in gale-force winds. However seed rain was significantly patchy with most seeds falling adjacent to the parent plant. The estimate of 217 $\pm$ 46.5 seeds per m^2 for *F. novae-zelandiae* is comparable to other long-lived perennial grasses.

The majority of *F. novae-zelandiae* seeds germinated regardless of temperature and light conditions however some seeds in the "cool" and "dark" treatments exhibited a delay in germination of up to 200 days. A slight inhibitory effect on the overall germination rate of seeds at the cooler temperature treatment were observed for most populations. Also a overall lower germination rate and final percent germination was observed for some populations when seeds were germinated in the dark. Seeds showed an enhanced germination response in all treatments after six months storage. There seemed to be no clear trends in the pattern of germination with respect to treatment and the environment of the sites from which the seeds originated.

Mean seedling density at Cass was found to be 22.7 $\pm$ 6.6 per m^2 which is comparable with values from other long-lived grasses and sedges. When compared with the values recorded for seed-rain this represents an 83% to 94% mortality among seeds in the soil.

Seedling emergence was concentrated in autumn and seedling densities were non-randomly associated with vegetation types; around flatweeds, the bases of large tussocks and mats of *Coprosma petriei* being 'preferred' substrates. The observed differences between the two areas studied in seedling substrate affinity were possibly due to differences between the areas in microclimate. Seedlings grew by an average of 0.61 $\pm$ 0.07 leaves per year and the half-life of the longest studied single-year cohort was 12 months.

The reproductive strategy of *F. novae-zelandiae* conforms with that of many of the commonest perennial grasses of temperate grassland, e.g. *Bromus erectus, Dactylis glomerata, Festuca pratensis* and *F. rubra*, in regions where rainfall is restricted mainly to the cool season (Grime, 1979). Species of this type are characterised by relatively large seeds with no innate dormancy and the absence of a sizeable seed bank (Grime, 1979; Thompson & Grime, 1979). Germination and seedling emergence is concentrated in the autumn when the surrounding vegetation is at its sparsest after the typically dry summer. In contrast, autumn germination was rare in a moist tall grassland that lacked the same seasonal fluctuations in moisture availability (Masuda & Washitani, 1990).

CHAPTER 4: STRUCTURE AND DYNAMICS WITHIN INDIVIDUALS AND POPULATIONS

4.1 INTRODUCTION

Tussock-forming grasses are very simple in construction, essentially being composed of many functionally equivalent tiller modules. Each plant can be regarded as a population of modules derived, originally from one parent plant (White, 1979), which interact within the clone in both a positive and a negative manner. Because of this architecture, the population structure and dynamics of tussocks must be studied at both the within-clone and within-population levels.

A study of within-clone population dynamics is the key to understanding individual growth and regeneration. This is because in a tillering grass the tiller is the fundamental ecological unit (White, 1979). For the genet as a whole to grow, the individual tillers must reproduce vegetatively and for the genet to die, the whole population of tillers must die.

In the study of structure and dynamics at the level of the population, herbaceous perennials with a modular architecture present the researcher with two important problems. One is the definition of an individual; does the genet or the functionally independent ramet constitute the individual to be studied? The other is the difficulty involved in aging individuals.

In species of modular construction where the modules are equivalent, potentially independent units it is largely impossible to count the number of genetic individuals in a population (Harper, 1978). In *F. novae-zelandiae*, individual tussocks may be only portions of a larger fragmented genetic individual (genet) or may be composed of more than one genet. A more precise approach to the population biology of such plants is to study modules rather than genets (Harper, 1978; White, 1979). However it is difficult to extrapolate from this type of data to the dynamics of genets and populations and ultimately the explanation of evolutionary phenomena must lie in studies at the level of genets (Harper, 1978).

The approach taken in the definition of individuals throughout the present study is much less rigid than that taken by Espie (1987). Espie defined elongated groups of tillers as representing two genetic individuals unless an external factor such as the proximity of a rock or shrub could have influenced the growth pattern. He regarded quasi-circular groups of small tillers as individual small tussocks unless connections of dead material between them indicated that they represented the remnants of a senescent tussock.

In the present study structurally continuous tussocks, regardless of shape, were treated as individuals. However groups of small tussocks were treated in a manner similar to that described above. The margin of error between this method of defining

individuals and the true number of genetic individuals present depends on the frequency of clonal fragmentation in populations of *F. novae-zelandiae*. This is investigated in Chapter 4.5.

The other difficulty involved in demographic studies of long-lived clonal herbs is that of the age of individual plants. Assessing population structure directly by aging individuals is impossible for clonal plants that are composed of continually replaced modules as, except in very young plants, the age of the oldest module is unlikely to at all resemble the age of the genet (Harper, 1977). Many long-lived species display considerable demographic and morphological plasticity and as a result size, fecundity and mortality are not necessarily associated with strict chronological age. The inability to age these types of plants is therefore not necessarily a problem as age would not be particularly useful in the examination of population structure. An approach based on the functional stage of individuals, defined by morphological, physiological or demographic characters would provide more meaningful information on population structure (Rabotnov, 1965; Harper, 1977; Gatsuk *et al.*, 1980).

The aim of this section is to examine the structure and dynamics of both populations of tillers within clones and populations of tussocks. Tussock population structure will be examined using a stage-based approach and at the same time the validity of this type of approach will be assessed. The effect of competition from invasive adventive species on within-clone growth and overall population structure will also be examined and the question of the genetic distinctiveness of spatially separate tussocks will be addressed.

4.2 TILLER DYNAMICS

4.2.1 Methods

Seventy-five tillers on 26 tussocks of varying sizes on Sugarloaf Fan (see Fig. 2.1, Chapter 2 for location) were tagged in November 1989. The tillers were selected at 2 cm intervals along a transect through the middle of each tussock in order to test for the effect of position on growth and tillering. Ten tillers in a further five tussocks were tagged in May 1990 in order to increase representation among tillers from small tussocks.

The tillers were censused in February, May, August and November of 1990 and 1991 and all new tillers arising from tagged tillers were also marked and monitored. The condition of each tiller (vegetative, flowering, dead) and the number of leaves per tiller were recorded at each census.

One-way analysis of variance was used to investigate the effect of tiller position and tussock size on growth and tillering rates of individual tillers.

4.2.2 Results

F. novae-zelandiae tillers are produced intra-vaginally and emerge between the sheath of the parent tiller and the prophyll of the new tiller. The prophyll is a modified leaf that precedes the emergence of the first true leaf. New tillers are first externally visible when they have elongated beyond the sheath of the parent tiller. At this stage they usually consist of one or two green leaves. Flowering is determinate so once flowering and fruiting has finished the tiller dies.

By the end of the study period, a total of 225 tillers had been tagged and monitored. Of these, 128 were still alive at the end of the study and 24 of these tillers were members of the original sample. This represented an increase of 150.6% in two years. During this time 134 new tillers were produced, 85 tillers died without flowering and 6 flowered and died.

Tillering showed very marked seasonal trends with a spring flush of new tillers becoming visible between November and February of each year (Fig. 4.1). This seasonal production of tillers is also reflected in the rate of tillering among established tillers. Parent tillers produced one daughter tiller every 15.2 $\pm$ 1.63 months on average; 0.07 $\pm$ 0.01 tillers month^{-1}. However tillers were most commonly produced at approximately yearly or two-yearly intervals (Fig. 4.2).

Mortality also showed seasonal trends, being concentrated mainly in late winter and spring (Fig. 4.1). Mortality was substantially higher between August and November 1991 than in the previous two years possibly due to the relatively cold winter (Fig. 2.2, Chapter 2). The life-span of single tillers averaged 15.2 $\pm$ 1.05 months, however life-

spans of three months, one year or two years were most common (Fig. 4.3).

Daughter tillers were produced by 36.2% of all tillers tagged. Of these, over half produced only one daughter tiller. However one tiller produced five daughter tillers during its lifetime (Fig. 4.4). The number of daughter tillers produced per tiller and the rate at which they were produced did not differ significantly between tillers occupying different positions in a tussock or between individual tussocks or diameter size classes. The location of a tiller in relation to the tussock edge had no significant effect on tiller longevity when tested with one-way analysis of variance ($F_{4,219} = 0.53$, NS). There was also no significant difference among individual tussocks or diameter size classes in tiller longevity ($F_{30,193} = 0.76$, NS).

Tillers produced an average of 0.16 ± 0.01 leaves per month, which is approximately one leaf every 6 months. There was no significant difference in growth rate between tillers occupying different positions within a tussock ($F_{4,219} = 0.26$, NS). However there was a significant difference in tiller growth rates between individual tussocks ($F_{30,193} = 1.54$, $P < 0.05$). This difference was not, however, related to differences in tussock diameter.

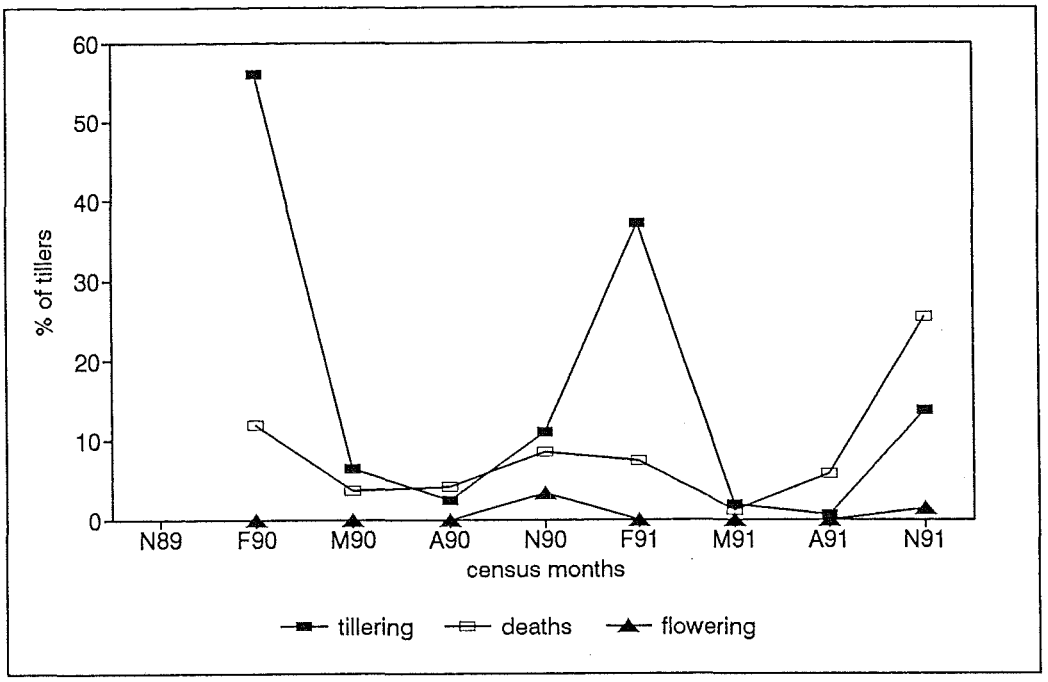


Figure 4.1: Tiller recruitment and mortality of 225 tillers in 25 F. novae-zelandiae tussocks on Sugarloaf Fan monitored over 30 months.

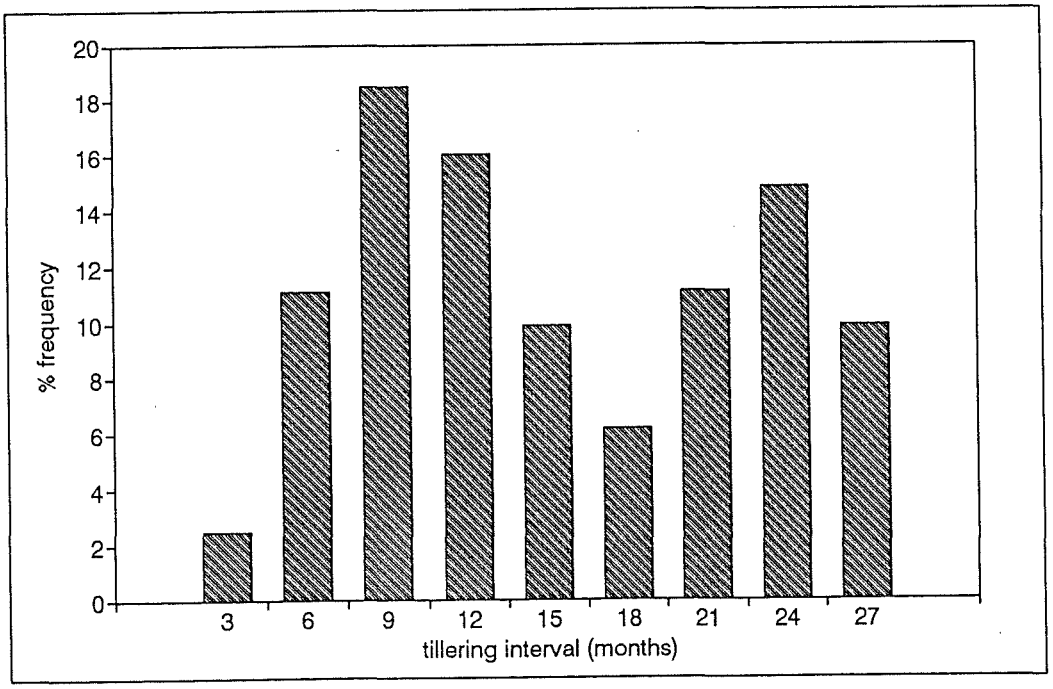


Figure 4.2: Frequency of tillering interval for 225 tillers in 25 F. novae-zelandiae tussocks on Sugarloaf Fan monitored over 30 months.

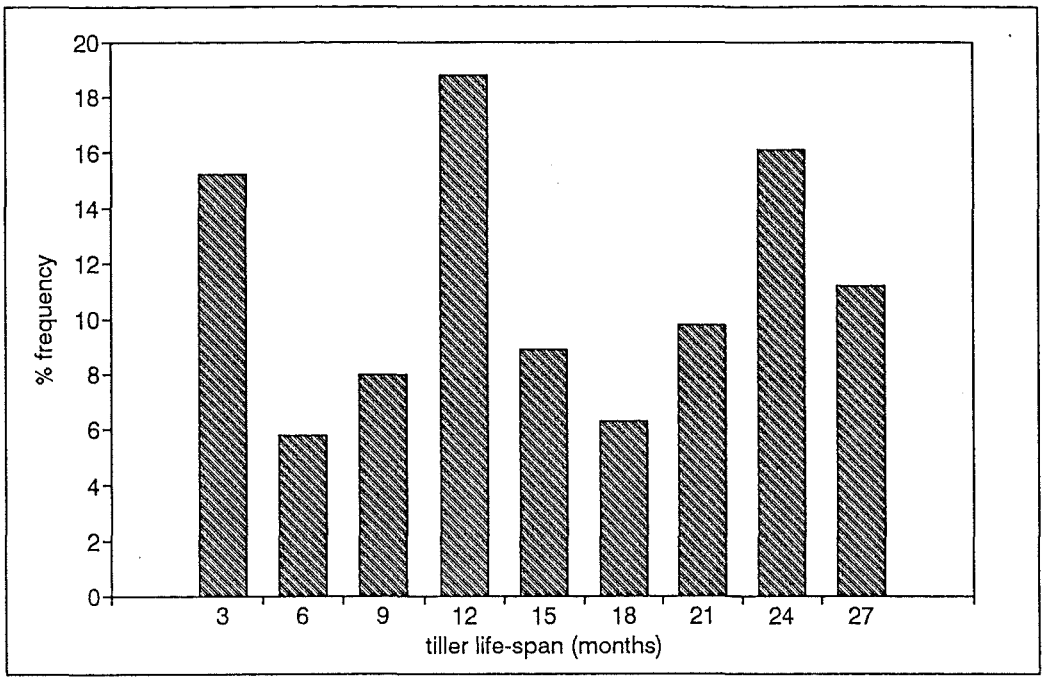


Figure 4.3: Life-span of 97 F. novae-zelandiae tillers dying during the 30 month study period at Sugarloaf Fan.

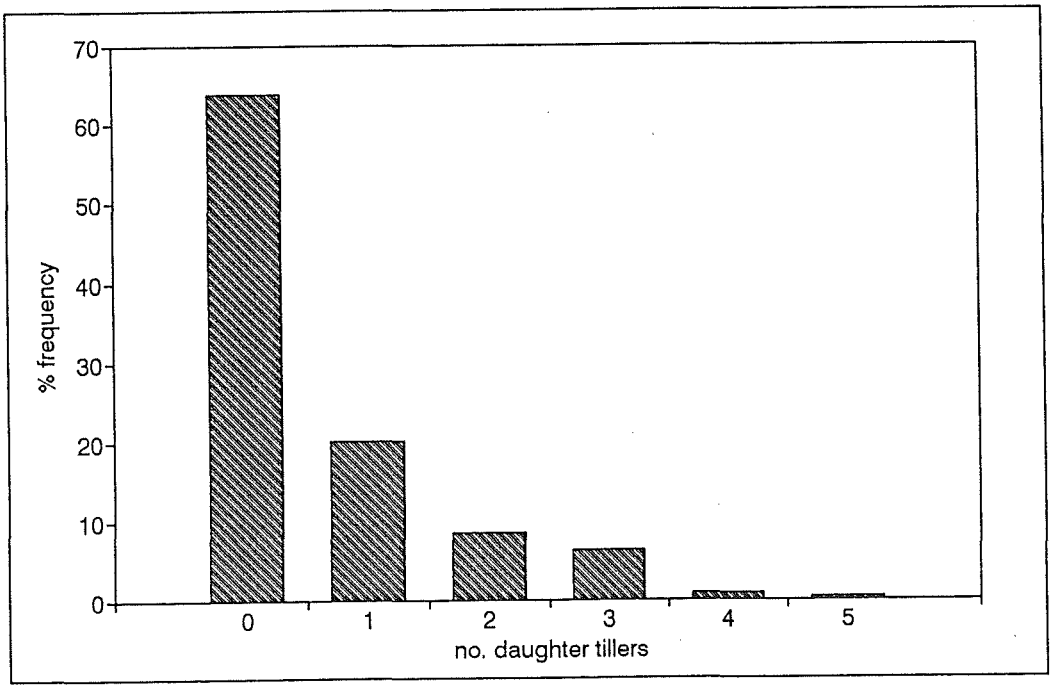


Figure 4.4: Daughter tiller production among 225 tillers in 25 F. novae-zelandiae tussocks on Sugarloaf Fan monitored over 30 months.

4.2.3 Discussion

As tillers were not recorded until they were externally visible, tillering would have been initiated some time before new tillers were observed. New *F. novae-zelandiae* tillers recorded as early as November were already about 15 cm in height, so tiller induction most probably occurred in autumn with some growth taking place before winter. Tiller elongation is most probably triggered by increased temperatures in spring. *F. novae-zelandiae* tillers appear to be able to survive for more than two years. However most tillers in this study were replaced within two years.

Connections between tillers appear to remain intact for at least two years. However observations of tussock structure made while transplanting and dividing tussocks indicate that connections between tiller clumps eventually break down so that the tussock comes to be comprised of one to many independent families of tillers.

Fetcher & Shaver (1982) found that the ratio of daughter tillers to adult tillers decreased with increasing tussock diameter in the long-lived caespitose sedge *Eriophorum vaginatum*. In *Bellis perennis*, a dicotyledonous herb with a tightly-packed, 'phalanx' clonal structure, Schmid & Harper (1985) found that module density within clones was under precise control due mainly to the regulation of the birth rate of modules. A similar regulation of tiller density has been found in *Carex bigelowii*, a rhizomatous sedge (Carlsson & Callaghan, 1990). In *Schizachyrium scoparium*, a perennial bunchgrass, both intra- and inter-clonal density-dependent interference controlled ramet densities (Briske & Butler, 1989).

However other studies among phalanx clonal species have indicated that density-dependent ramet mortality is uncommon when inter-ramet connections are maintained for a season or more (Hutchings, 1979; Hutchings & Slade, 1988). An efficiently foraging phalanx species, that is making maximum use of available area and resources, should be maintaining ramet size and density at just below the level where density-dependent mortality occurs (Hutchings & Slade, 1988).

No reduction in tillering rate with increasing clone size was found in *F. novae-zelandiae* indicating that crowding within a large tussock was not reaching sufficient levels to bring density-dependent effects into operation. Tillering rate in *F. novae-zelandiae* was probably more a product of the genotype and immediate environment of each plant.

Brisk & Butler (1989) found much higher rates of tiller recruitment on the periphery of tussocks of *Schizachyrium scoparium* as opposed to the interior of the tussocks. Surprisingly no effect of position on tillering vigour or survival was found within *F. novae-zelandiae* tussock. Numerous authors (e.g., Zotov, 1938; Moore, 1976; Gatsuk *et al*, 1980; Espie, 1987) have commented on the tendency of *F. novae-zelandiae* and other tussock-forming grasses to decay in the centre and fragment into a peripheral ring of tillers. This does not appear to be due to innate differences in tiller

vigour with position and may be more a result of fungal or insect attack encouraged by the damp, sheltered environment in the tussock interior (Kelsey, 1957).

4.3 THE EFFECT OF COMPETITION

4.3.1 Introduction

Over the last century short-tussock grassland has been undergoing a process of radical change from a community dominated by indigenous grasses, forbs and shrubs to one dominated by adventive species. Early accounts of short tussock grassland (e.g. Wall, 1922; Cockayne, 1928; Zotov, 1938) list species that are now rare or absent in many areas and much of the present-day short tussock grassland has been fragmented into patches of indigenous species in an alien matrix (Lord & Norton, 1990).

Some of the common adventive species in short tussock grassland such as *Agrostis capillaris* L., *Anthoxanthum odoratum* L. and *Festuca rubra* L. were deliberately introduced in order to improve the value of the vegetation for grazing (O'Connor, 1982, 1986). However many others such as *Hypochoeris radicata* L., *Hieracium* species, *Linum catharticum* and *Rumex acetosella* have spread by accidental introductions.

In the Cass area, where the present study was conducted, the main influx of adventive presumably occurred in the early 1860's with the advent of pastoral farming (Dobson, 1977). In 1915 a number of species including *Anthoxanthum odoratum, Holcus lanatus, Rumex acetosella* and *Trifolium repens*, which are common in the area today, were already present (Cockayne & Foweraker, 1916). Interestingly *Agrostis capillaris*, which is one of the most dominant inter-tussock species on Sugarloaf Fan today, was not recorded from Cass even as late as the 1920's (Malcolm, 1925). However by 1944 it was common on the valley flats (Cumberland, 1944) and possibly was deliberately sown (Dobson, 1977).

It is difficult to empirically determine the impact of biological invasion on the resident community as effects are often subtle and slow to be manifest. However recent long-term studies have linked the decline in indigenous species diversity in New Zealand grassland to the increasing dominance of adventive species (Scott *et al.,* 1988; Lord, 1990; White, 1991; Treskonova, 1991). Invasive species often affect the resident community directly by interference competition. The simplest way to test for a competitive effect is, as Tansley (1914) stated 'by clearing a patch of ground of some or all of the species present and seeing what happens.' It was the aim of this experiment to investigate the influence of adventive species on the growth and reproduction of *F. novae-zelandiae* by removing adventive species from areas containing *F. novae-zelandiae*.

4.3.2 Methods

A 20 m transect was randomly located in short tussock grassland at Sugarloaf Fan and 14 pairs of 1 m x 1 m plots randomly located along the transect. All adventive species were removed by hand from one randomly selected plot in each pair in January 1990. Rhizomes of *Agrostis capillaris* and *Hieracium* species were carefully dug out with a knife. All tussocks in the control plots were tagged and all plants in the weeded plots were mapped.

Every tussock was measured for maximum extended leaf length and mean basal diameter (using a diameter tape). In addition the percentage of tussock basal area occupied by dead material (% dead) was estimated and the number of culms counted for each plant. The plots were weeded again in May and November 1990 and finally in February 1991. In January 1992 the same plants were reassessed for maximum extended leaf length, mean basal diameter, % dead and number of culms.

The initial measurements made in 1990 for each variable were subject to one-way analysis of variance to test that plants in weeded and control plots were statistically comparable samples; i.e., that there was no initial bias between the treatments that could effect the final analysis.

As the data consisted of identical measurements on the same individuals over a period a time, a repeated measures analysis of variance model was used for analysis. Each of the four variables measured was tested for differences between plants in different treatments, differences within plants between years and for an interaction between the two terms. Relative reproductive effort, calculated as the number of culms cm^{-2} of live basal area, was also tested for significant differences due to treatment and time.

4.3.2 Results

A total of 255 tussocks were measured in January 1990 and 246 of these were still alive in January 1992. All nine deaths occurred in weeded plots.

One-way analysis of variance found no significant difference between control versus weeded plots for initial values of any of the four measured variables indicating that the tussocks within the two different kinds of plots were initially comparable prior to experimental manipulation.

Repeated measures analysis of variance using initial and final measurements showed that in all treatments, plants decreased significantly in height through time (Table 4.1). There was also a significant interaction between treatment and time indicating that the change in height over time was affected by whether they occurred in weeded or control plots. However between-plant differences in height corresponding to the effect of weeding alone were not significant.

Plants in all treatments also increased significantly in diameter over the two years. Between-plant differences in diameter due to treatment alone were significant, as was the interaction between time and treatment (Table 4.1).

There was no treatment effect on the percentage of tussock area occupied by dead material. However % dead decreased significantly in all plants over the two years of the study. The magnitude of change within individual plants over time did not vary significantly between weeded and control plots (Table 4.1).

The number of culms per tussock increased significantly over all tussocks between 1990 and 1992 and the effort put into culm production in relationship to tussock size also increased significantly (Table 4.1). Weeding alone had a significant positive effect on culm production, however there was no similarly positive effect on relative reproductive effort. The significant increase in culm production among plants in weeded plots is therefore undoubtedly due to the overall larger diameter of these plants. Neither of these variables showed a significant interaction between treatment and time.

The most common adventive species removed from the weeded plots were *Agrostis capillaris* and *Anthoxanthum odoratum*. Both of these grasses formed dense to open patches that interdigitated with other patch-forming species such as *Poa colensoi, Coprosma petriei* and *Cyathodes fraseri*. The act of removing the adventives unavoidably disturbed these and other patch-forming species and therefore no results could be obtained on the effect of the experiment on species other than *F. novae-zelandiae*. However shrubs of *Cassinia leptophylla sensu lato* growing within the weeded plots responded to the removal of adventive species by sprouting vigorously from the base. Also two seedlings of *Aciphylla subflabellata* were observed to establish in weeded plots. None were observed in control plots.

Table 4.1: Mean values for 1990 and 1992 measurements of F. novae-zelandiae tussocks in weeded and control plots at Cass. Height and Diameter are in cm. 'Rel. eff.' is relative effort calculated as culms m^{-2} of live basal area. Results from repeated measures analysis of variance tests are also given. NS = not significant. Dead plants were excluded from the analysis.

		Height	Diam.	% Dead	No. culms	Rel. eff.
1990:	Control	39.4	4.64	29.6	1.54	5.33
	Weeded	41.2	5.60	32.9	2.60	5.36
1992:	Control	38.2	5.44	16.6	4.13	11.0
	Weeded	36.0	8.09	15.5	7.05	8.68
Source of Variation						
Treatment:	*F*	0.11	10.3	0.01	5.87	0.47
	P<	NS	0.01	NS	0.05	NS
Time:	*F*	72.0	103	50.8	34.9	10.05
	P<	0.001	0.001	0.001	0.001	0.01
Trmt x Time:	*F*	32.3	19.5	1.57	1.95	0.66
	P<	0.001	0.001	NS	NS	NS

4.3.3 Discussion

The increased growth among plants in weeded plots indicates that adventive species are affecting *F. novae-zelandiae* tussocks. The lack of difference between weeded and control groups in percent dead tillers indicates that the greater increase in the size of plants in weeded plots was a result of an increase in tiller births rather than a decrease in the death and decay of tillers. The difference in culm production between plants in weeded and control plots was simply a function of the higher tillering rate among plants in weeded plots; reproduction relative to size was not significantly different between the treatments.

The removal of adventive species also had a negative effect. Whole plant mortality, particularly among smaller plants, increased in weeded plots presumably due to the increased exposure of plants and risk of wind damage and desiccation. Also unavoidable disturbance of the soil and root zone of tussocks during weeding may have increased the likelihood of death.

In a species removal experiment in a mown field in North Carolina, Fowler (1981) found that species generally increased in abundance on the removal of other species but that competitive interactions were diffuse rather than specific. It is possible that the findings of my study relate to competition generally rather than the specific effect of adventive species. *F. novae-zelandiae* might have shown a similarly positive response had I removed all other indigenous species instead of the adventives. However no other indigenous species was as abundant in the grassland I studied as the most abundant adventive species. The adventive species therefore represent the primary source of competition with *F. novae-zelandiae* tussocks at the study site.

The tillering response shown by plants in the weeded plots could have been due to higher light levels or temperatures at the tussock base. Kays & Harper (1974) found that mutual shading among populations of *Lolium perenne* affected tillering rates. Gold & Caldwell (1989) found that removing dead foliage from the base of *Agropyron desertorum* tussocks stimulated greater regrowth than removing upper portions. The effect of adventive grasses on adult *F. novae-zelandiae* tussocks may be to depress tillering rates and hence flowering by competing for light.

The trend among all plants regardless of treatment of increasing diameter and culm production and decreasing height and percent dead tillers could be a response to the climatic fluctuations of the last five years. The drought of 1987 - 1988 was observed to affect *F. novae-zelandiae* tussocks (C. J. Burrows *pers. com.*) as well as adventive grasses. Rainfall has been higher in recent years and the observed growth of tussocks could represent an ongoing recovery from the effects of the drought. If this were the case then the effect of competition from adventives is to slow the rate of population recovery rather than reverse it.

The sward of adventive grasses on Sugarloaf Fan may not be dense enough to have

the direct negative impact on tussock growth and survival observed in more fertile grassland (Lord, 1990). However adventive grasses such as *Agrostis capillaris* are still increasing in the area (White, 1991) and have formed a dense sward on some areas of Sugarloaf Fan.

If the abundance of adventive species remained at present-day levels, they would probably have little direct impact on the adult *F. novae-zelandiae* population. However observations during the course of this study indicate that the spread of adventive grasses may be negatively affecting species such as *Coprosma petriei* that are important substrates for the regeneration of *F. novae-zelandiae* by seed (see chapter 3.5). Even in the absence of a negative effect on adult plants this would ultimately reduce the abundance of *F. novae-zelandiae* at the site.

4.4 STAGE-CLASS ANALYSIS OF POPULATION STRUCTURE

4.4.1 Introduction

The demographic literature contains two broad types of stage-based population studies. One follows the Russian "age-state" style of analysis which aims to describe the life-history of species of different growth forms by the construction of a detailed classification of recognisable biological stages. Each stage is defined by the appearance of new characteristics or structures and the absence of others (Gatsuk *et al.*, 1980). Stage-classes are taken to represent successive stages in the ontogeny of genetic individuals and are usually presented as a linear developmental sequence from seedling to senescent individual (e.g. Gatsuk *et al.*, 1980; Kurchenko, 1985; Vorontzova & Zaugolnova, 1985; Zhukova & Ermakova, 1985). Population structure is represented by the complement of stage-classes present within the population (Rabotnov, 1969). However the strength of this approach is in its summation of the life-history of the species.

Two major problems arise with the use of this age-state approach. One is how to construct a classification that reflects real groupings within the data. The other is that as soon as a sequence of classes has been constructed the implicit or explicit assumption is made that normal individuals will progress in a linear manner through the classes. Because of their modular structure through tillering, individuals of perennial grass species are capable of both expansion and contraction and therefore do not necessarily progress in a linear sequence through ontogenic stages.

The other commonly published type of stage-based study involves the use of stage- or size-classes as a data-base with which to construct a model of population dynamics (e.g. Werner & Caswell, 1977; Bierzychudek, 1982; Moloney, 1988; Babcock, 1991). These models are usually matrix-orientated and based on the methods of Leslie (1945), Leftovitch (1965), Vandermeer (1975) and Caswell (1986) (see Manly (1989) for a discussion of theory and application). Transition probabilities between stages are used to accurately describe and predict population dynamics.

These two approaches to stage-based population studies differ both in emphasis and in information content of classes. The Russian approach aims to produce classes of sufficient information content so that by simply examining the stages an uninformed reader will gain insight into the biology and ecology of the species being studied.

The information content of classes in the matrix approach is essentially irrelevant as the approach is concerned with movement between classes. The emphasis in this approach is on population dynamics rather than individual ontogeny or population structure.

The aim of this section is to firstly evaluate the naturalness of stage-classes and the linearity of stage-class transitions using data from *F. novae-zelandiae* and secondly to

examine population structure in nine different populations of *F. novae-zelandiae* as defined by stage-class frequency distributions.

4.4.2 Methods

(a) The naturalness of stage-classes

Four 2 m x 2 m plots were randomly located at each of the nine populations used in Section 3.4. All adult tussocks in the plots were measured for maximum extended leaf length, basal diameter (measured for two perpendicular axes so as to give a mean value and a measure of shape) and the percentage of dead tillers within the tussock was estimated. In addition the numbers of 1989 and 1990 culms were counted. Seedlings, consisting of a primary shoot only and retaining their connection with the caryopsis, were excluded from the data-base.

Individual tussocks were subjectively allocated to six stage-classes based on the methods and classification used in Russian studies of long-lived caespitose grasses (Gatsuk *et al*, 1980). The six classes were defined as follows:

(1) **Juvenile**: non-reproductive plants < 1 cm diameter, with no or few dead tillers (usually 0 - 5%). In these plants the connection with the caryopsis had been lost, tillering had begun, adventitious roots were few and the plants were still shorter than adult tussocks.

All reproductive plants were assigned to one of the following three classes depending on size and vigour.

(2) **Young Reproductive**: a few culms had been produced, tillering and adventitious rooting was well underway but dead tillers were still few (usually 0 - 15%) and scattered throughout the tussock. Plants were usually 1 < x < 5 cm diameter with a firm round tussock habit and produced one or a few culms in intermittent years.

(3) **Mature Reproductive**: plants produced several to many culms in most years, were large and had moderate numbers of dead tillers (10 - 30%) scattered throughout the tussock with some small areas consisting only of dead tillers.

(4) **Old Reproductive**: culm production low and often irregular and plants had moderate to high numbers of dead tillers (> 30%) with areas within the tussock consisting entirely of dead tillers. Tussocks tended to be irregular in shape and some were becoming fragmented into two or more parts.

The final two classes consisted of non-reproductive plants in various states of decay.

(5) **Senescent**: tussock diameter and the amount of dead material within the tussock reached a maximum and the genet had became fragmented.

(6) **Remnant**: the clone had become reduced to a remnant similar in size to juvenile tussocks but containing or adjacent to old dead material and growing on a mound built up by the original genet.

Non-reproductive plants that were too big to qualify as "juvenile" or "remnant" but insufficiently decrepit to qualify as "senescent" were allocated to one of the three reproductive classes according to size and vigour. This was justified in light of the results of section 3.2 which indicated that not all plants reproduced every year. The "immature" or "virginal" stage of Gatsuk *et al.* (1980) was not used as the sometimes irregular flowering of individuals meant that mature virginal plants could not be distinguished from plants that had reproduced in previous years but were not reproductive in the year of the study.

The data from all nine populations was combined and subject to canonical discriminant analysis, as implemented by SAS, using stage-class as the classification variable. The aim of the analysis was to test whether the six stage-classes could be distinguished in multivariate space using the data obtained from measurements of size, vigour and reproductive effort of the individual tussocks. In addition, differences among the stage-classes for single characters were tested using one-way analysis of variance.

(b) Linearity of stage-class transitions

Data from 255 individuals used in the competition experiment of section 4.3 was classified into stage-classes using the discriminant function developed in (a) above. As initial measurements and final measurements were separated by a space of two years (January 1990 - January 1992) in this dataset, estimates could be made of the change in the stage-class of an individual over time. The probability of individual plants moving between classes was calculated for both weeded and unweeded plants in the form of a transition matrix (Leftovich, 1965). The probability of death for individuals in each class was also calculated.

(c) Stage-class comparisons among nine populations

For each of the nine populations used in (a), the frequency of stage-classes as assigned by the discriminant function was tabulated. Pairwise Chi-squared tests of independence were used to test for significant heterogeneity among the populations for stage-class frequency distribution.

4.4.3 Results

(a) The naturalness of stage-classes

A total of 392 live tussocks was measured and allocated to the six stage-classes. The "young reproductive" and "mature reproductive" classes contained the most individuals; 108 and 114 respectively. A total of 78 individuals across the nine populations were allocated to the "juvenile" class and 58 to the "old reproductive" class. The "senescent" and "remnant" classes emerged as the smallest with 17 and 23 individuals respectively.

The first four axes of the canonical discriminant analysis showed significant discrimination ($P < 0.001$) between the six stage-classes, using measurements of maximum extended leaf length, mean basal diameter, percent dead tillers, degree of fragmentation, mean number of culms over two years and flowering consistency over two years. When classification to stage-class was re-evaluated using the discriminant function developed, 66.3% of individuals were found to have been classified to the same stage-class in the original subjective allocation.

The number of individuals reclassified by the discriminant function varied considerably between stage-classes. The subjective "juvenile" class was the most consistent with 79.2% of individuals being objectively classified as "juvenile" and the remainder assigned to the "young reproductive" or "remnant" classes by the discriminant function (Table 4.2). The "mature reproductive", "senescent" and "remnant" classes were also well-defined with over 70% of individuals classified identically in the original subjective classification. The "young reproductive" and "old reproductive" stage-classes were the least consistent with 52.8% and 58.6% of individuals being classified as such by the objective classification.

Of the 132 reclassifications made by the discriminant function, 106 involved a move out of one of the three reproductive classes into either a non-reproductive class or another reproductive class. Only 26 reclassifications involved a move out of a non-reproductive class. However the three reproductive classes jointly contained over twice as many individuals as the non-reproductive class (278 as compared with 114). When the frequency of the four types of reclassification (R - N (reproductive to non-reproductive), R - R, N - R, N - N) was tested for heterogeneity with a chi-squared test there was no significant departure from expected frequency ($X^2 = 4.84$, $df = 3$, $P > 0.05$).

However there was significant heterogeneity among stage-classes in the percentage of individuals originally within the class being reclassified to other classes by the discriminant function ($X^2 = 17.4$, $df = 5$, $P < 0.01$). There were more misclassified individuals in the "young reproductive" class than expected and less in the "juvenile" class.

These two classes were involved in the single most common type of reclassification,

Table 4.2: Stage-class classification summary of 392 F. novae-zelandiae individuals based on measured morphological variables. Values represent percent reclassified by a linear discriminant function into each stage-class from each stage-class.

	Percent reclassified by discriminant function into objective class							
	Juvenile	Young	Mature	Old	Senescent	Remnant	Plants in subjective class	
From subjective class							No.	%
Juvenile	79.2	16.7	0	0	0	4.17	72	18.9
Young	32.4	**52.8**	13.9	0	0	0.93	108	27.0
Mature	0	19.3	**72.8**	7.89	0	0	114	29.1
Old	0	8.62	6.90	**58.6**	12.1	13.8	58	14.8
Senescent	0	0	0	5.88	**70.6**	23.5	17	4.34
Remnant	8.70	13.0	0	0	4.35	**73.9**	23	5.87
Plants in objective class:							**Total**	**Total**
No.	94	99	102	44	20	33	392	
%	24.0	25.3	26.0	11.2	5.10	8.42		100%

Table 4.3: Objective stage-class means for measured morphological variables. Results from one-way ANOVA tests among classes are given. Different superscripts indicate a significant difference between means using LSD tests. For number of culms, standard errors and critical values of differences varied due to unequal sample sizes so LSD test could not be applied.

Stage-Class	N	Height (cm)	Diam. (cm)	% Dead	No. culms
Juvenile	94	20.4^{a}	1.38^{a}	7.23^{a}	0.01
Young	99	29.4^{c}	2.85^{b}	13.1^{b}	0.23
Mature	102	36.8e	6.83^{c}	16.1^{c}	3.40
Old	44	34.1^{d}	8.42^{d}	35.1^{d}	1.81
Senescent	20	33.3^{d}	10.5^{e}	49.0^{e}	0.07
Remnant	33	24.6^{a}	1.97^{ab}	48.3^{e}	0.07
ANOVA:	*F*	83.6	105	259	37.7
	P <	0.001	0.001	0.001	0.001

from "young reproductive" to "juvenile" which involved 31.5% of individuals originally classified as "young reproductive" and accounted for 25.7% of total reclassifications. All except two of the individuals reclassified in this manner were non-reproductive individuals greater than 1 cm in diameter that had been originally allocated to the "young reproductive" class on the basis of size in spite of their lack of culms. The other two individuals reclassified from "young reproductive" to "juvenile" were juvenile in size but had both produced a single culm in the two years encompassed by the study.

The most common reclassification types after "young" to "juvenile" were "senescent" to "remnant" involving 23.5% of "senescent" individuals and "mature" to "young" involving 19.3% of "mature" individuals.

There was also significant heterogeneity among the nine populations in the number of individuals reclassified ($X^2 = 21.59$, $df = 8$, $P < 0.01$). The Cass Saddle 'B' population had the most individuals reclassified (44.1%) while only 17.6% of individuals in the Porters Pass population were reclassified.

In case this heterogeneity was due to differences in mean tussock size between populations the discriminant analysis was repeated on data standardised by population. This resulted in the proportion of observations reclassified by the discriminant function increasing from 33.7% to 34.9% and heterogeneity among populations also increased rather than decreased ($X^2 = 51.84$, $df = 8$, $P < 0.001$).

In addition to being distinct in multi-variate space, the six objectively defined stage-classes also differed significantly in their univariate distributions for each of the variables measured (Table 4.3). Each variable also showed a distinct trend of a low mean value in the "juvenile" class increasing to a peak in the "mature reproductive" to "senescent" classes then decreasing again to the "remnant" class. Mean height and culm production reach their maximum in the "mature reproductive" class. Mean diameter and percent dead tillers reach a maximum among "senescent" individuals.

(b) Linearity of stage-class transitions

If the developmental sequence of stages in a species was linear, such that movement between stages consisted of growth into the next stage-class, a matrix of transition probabilities would be comprised of a non-zero leading diagonal representing static individuals and a non-zero sub-diagonal representing movement into the next stage-class. This was not the case for the two transition matrices compiled for the 155 control and 100 weeded individuals used in the competition experiment at Sugarloaf Fan (Table 4.4).

Among these plants there was considerable movement between stage-classes within the space of two years. However little of this movement represented a shift into the next largest or "older" stage-class. Transitions occurred in 27 of the possible 36 combinations and transitions to "younger" classes above the diagonal were more

Table 4.4: Stage-class transition probability matrices for (a) unweeded and (b) weeded groups of F. novae-zelandiae at Sugarloaf Fan. Individuals were allocated to stage-classes using a discriminant function developed using 392 classified F. novae-zelandiae individuals from nine populations.

(a) Unweeded Plots N = 155

	Objective stage-class in Jan 1990					
	Juvenile	Young	Mature	Old	Senescent	Remnant
Jan 1992						
Juvenile	**0.50**	0.09	0	0	0	0.33
Young	0.50	**0.71**	0.07	0.27	0.33	0.55
Mature	0	0.11	**0.78**	0.38	0.33	0.05
Old	0	0.02	0.15	**0.27**	0	0
Senescent	0	0	0	0.04	**0**	0
Remnant	0	0.07	0	0.04	0.33	**0.05**
Dead	0	0	0	0	0	0

(b) Weeded Plots N = 100

	Objective stage-class in Jan 1990					
	Juvenile	Young	Mature	Old	Senescent	Remnant
Jan 1992						
Juvenile	**1.00**	0.20	0	0	0	0.08
Young	0	**0.56**	0.13	0.09	0	0.25
Mature	0	0.12	**0.76**	0.68	0	0
Old	0	0	0.08	**0.14**	0.50	0
Senescent	0	0	0	0	**0**	0
Remnant	0	0	0.03	0.04	0	**0.33**
Dead	0	0.12	0	0.04	0.50	0.33

common (29.8% of individuals) than transitions to "older" classes below the diagonal (16.5%). However the majority of plants (53.7%) remained in the same stage-class over the two year period. Transitions between adjacent classes were more common, involving 30.2% of individuals, than transitions between non-adjacent classes (16.1%). When a chi-squared test was applied, no significant difference was found between weeded and unweeded plants in the frequency of no change and transitions above and below the diagonal (X^2 = 0.515, df = 2, NS).

(c) Among-population comparisons of stage-class frequency

Pair-wise chi-squared tests for 392 plants in nine populations using the objective classes from (a) above found significant differences between pairs of populations for 32 of the 36 comparisons of stage-class frequency distributions (Table 4.5). Four populations, Bankside, Cass River, Mt Sugarloaf and Porters Pass differed significantly from all other populations in their stage-class frequency distribution.

Bankside was characterised by a predominance of plants in the "older" classes and a lack of small healthy reproductive individuals (Fig. 4.5). The stage-class frequency distribution of Cass River was dominated by "mature reproductive" plants with fewer small plants and no "senescent" or "remnant" plants (Fig. 4.6). At Porters Pass the population was dominated by small plants with few large reproductive or senescent individuals (Fig. 4.7). The stage-class profile of Mt Sugarloaf was similar to that of Cass River except individuals of the "young reproductive" class dominated (Fig. 4.8).

Sugarloaf Fan, Hallelujah Flat and Cass Saddle 'B' formed a group in which stage-class frequency distribution did not differ significantly. Their stage-class frequency distributions were characterised by higher frequencies of reproductive plants (Fig. 4.9). Cass Saddle 'A' and Cass Valley also did not differ significantly in stage-class frequency distribution. These populations were both characterised by high numbers of "juveniles" but few small reproductive plants (Fig. 4.10).

Table 4.5: Pair-wise X^2 tests of stage-class frequency distribution among nine populations using objective classes defined by a discriminant function. * indicates $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ and NS indicates not significant.

	BNK	CRV	CSA	CSS	CVS	HLF	MTS	PPS
CRV	92.9 ***	-	-	-	-	-	-	-
CSA	83.8 ***	31.4 ***	-	-	-	-	-	-
CSS	68.6 ***	11.3 *	23.8 ***	-	-	-	-	-
CVS	58.1 ***	27.8 ***	8.13 NS	16.9 **	-	-	-	-
HLF	42.3 ***	23.1 ***	36.9 ***	9.91 NS	16.6 **	-	-	-
MTS	93.2 ***	34.1 ***	36.7 ***	20.6 **	32.5 ***	27.2 ***	-	-
PPS	83.2 ***	43.0 ***	21.0 ***	20.9 ***	23.1 ***	34.0 ***	16.9 **	-
SLF	49.7 ***	17.3 ***	29.2 ***	5.23 NS	13.4 *	1.96 NS	22.8 ***	24.8 ***

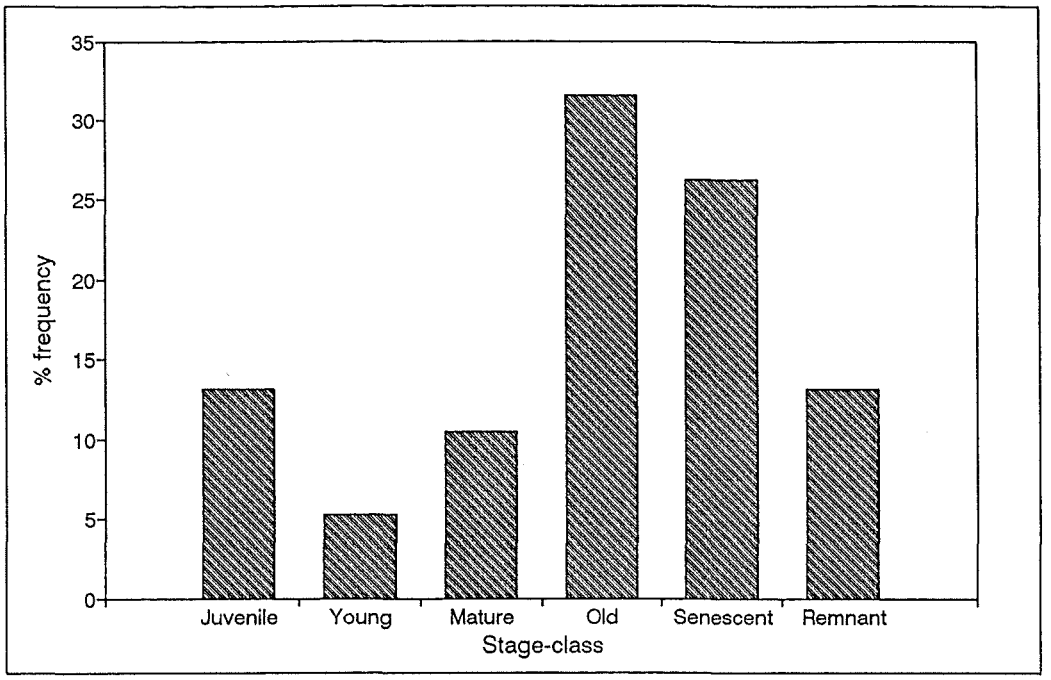


Figure 4.5: Stage-class frequency distribution of F.novae-zelandiae tussocks at Bankside.

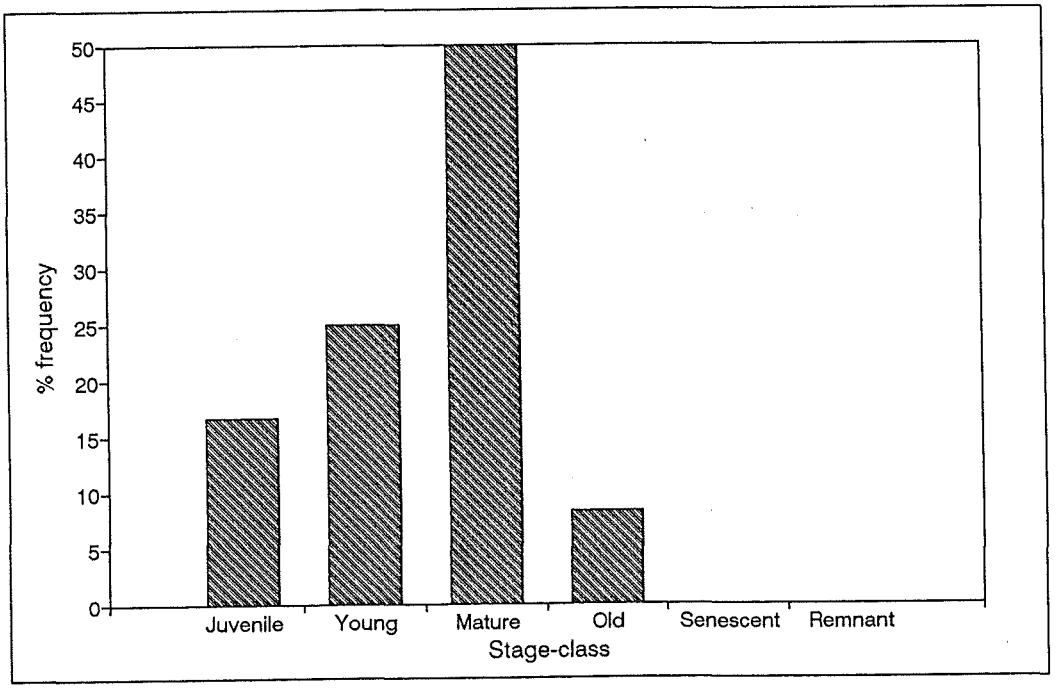


Figure 4.6: Stage-class frequency distribution of F.novae-zelandiae tussocks at Cass River.

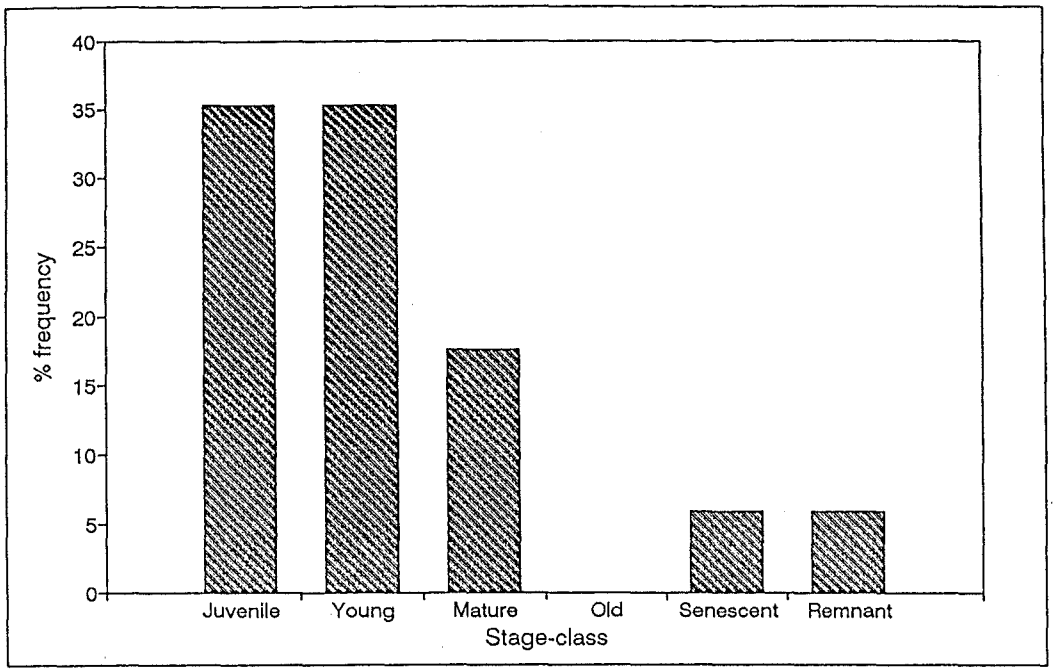


Figure 4.7: Stage-class frequency distribution of F.novae-zelandiae tussocks at Porters Pass.

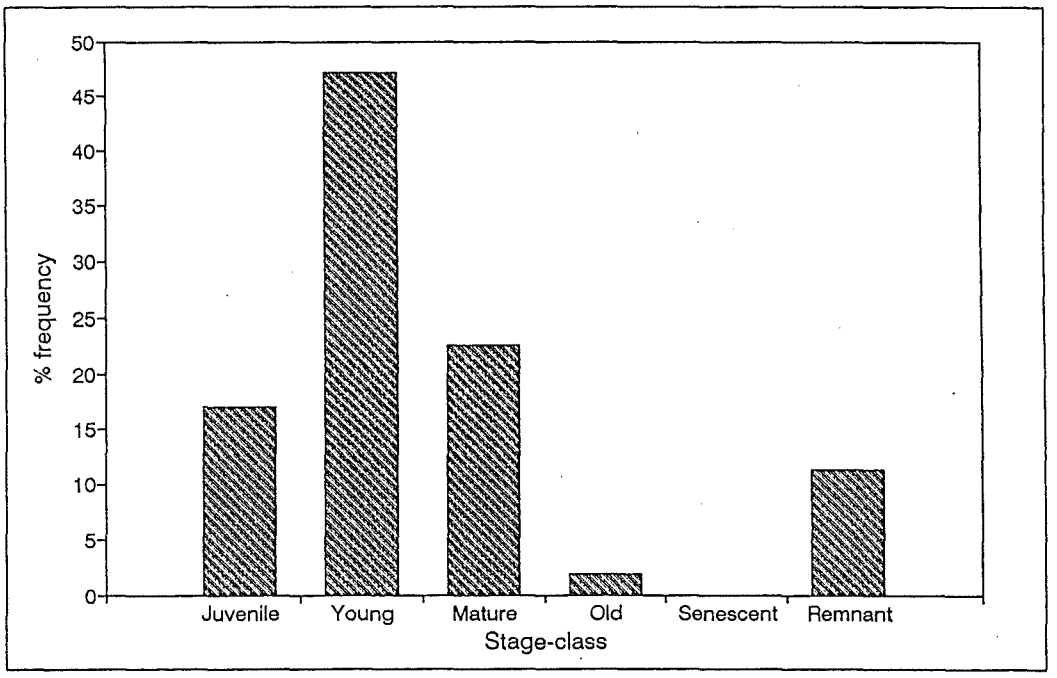


Figure 4.8: Stage-class frequency distribution of F.novae-zelandiae tussocks at Mt Sugarloaf.

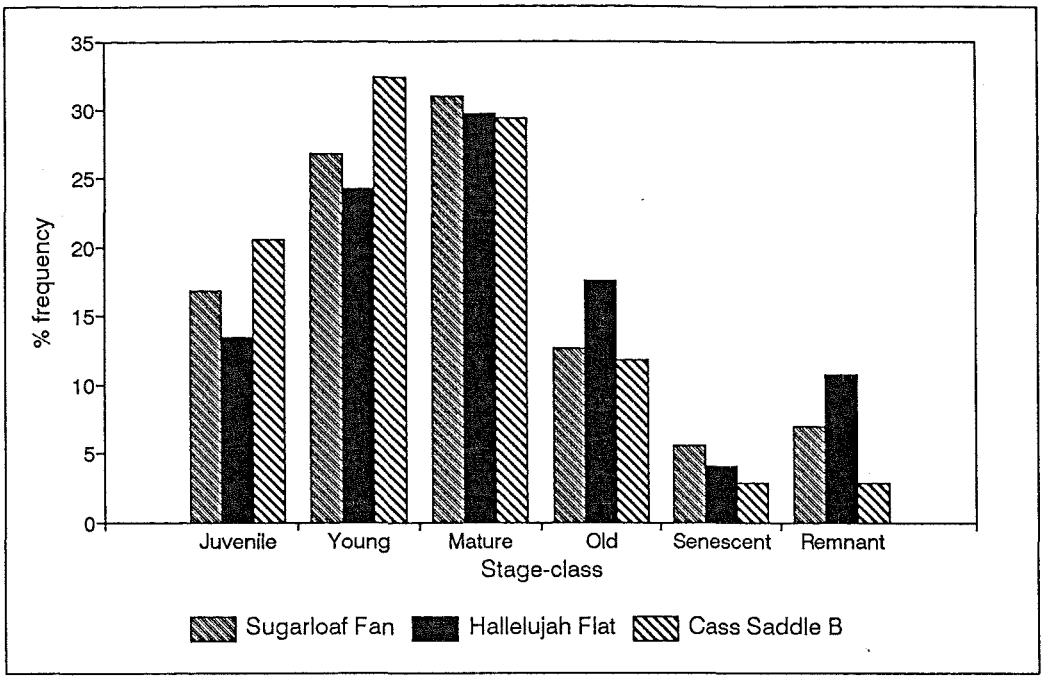


Figure 4.9: Stage-class frequency distribution of F. novae-zelandiae tussocks at Sugarloaf Fan, Hallelujah Flat and Cass Saddle 'B'.

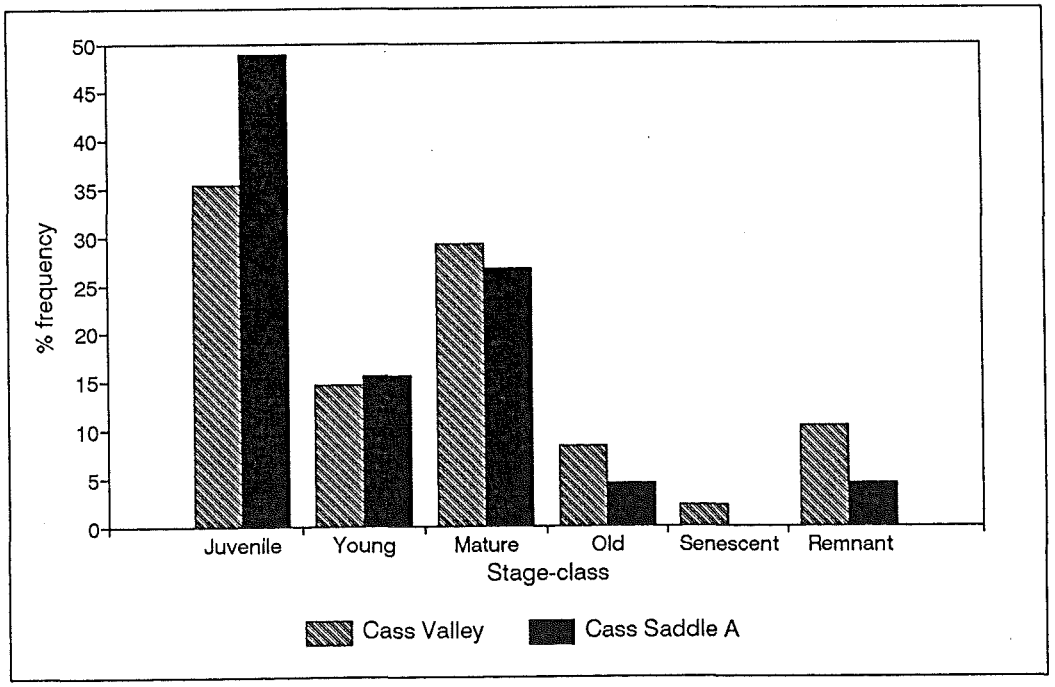


Figure 4.10: Stage-class frequency distribution of F. novae-zelandiae tussocks at Cass Valley and Cass Saddle 'A'.

4.4.4 Discussion

(a) The validity of a stage-class approach

The discriminant analysis and analysis of variance tests indicate that the stage-class classification reflects real groupings within the data. An examination of the reclassifications made by the discriminant function provides much information on the manner in which the subjective classification was performed and on the life-history of *F. novae-zelandiae* individuals.

The main factor influencing reclassifications appeared to be the differential weighting of characters in the subjective definition of classes. For example, all reproductive individuals were allocated to one of the three reproductive classes regardless of size, in effect weighting culm production ahead of other variables. Basal diameter was much more important in distinguishing "senescent" from "remnant" individuals than other characters whereas percent dead tillers was important in distinguishing "remnant" from "juvenile" individuals. Differing importances among characters in defining different groups is implicit in Russian-type stage-based studies (e.g. Gatsuk *et al.*, 1980) but is never commented on by the respective authors.

The varying importance of different characters in the definition of different groups cannot be replicated by a multivariate technique such as discriminant analysis in which any character weightings must be applied consistently across all groups. Therefore subjective and multivariate classifications would automatically differ regardless of any other complicating factors.

It was initially thought that the emphasis placed on reproduction would prove to be a complicating factor in classification. However, in spite of the differential treatment of reproductive versus nonreproductive individuals the allocation of individuals to reproductive versus nonreproductive classes was not a source of misclassification any more than would have been expected. This was probably due to the "young", "mature" and "old reproductive" classes also containing nonreproductive individuals. It is generally recognised in the age-state literature, although not always specifically stated, that individuals in the "reproductive" phase can be generative or vegetative during that period of their ontogeny (Rabotnov, 1969, 1978, 1985; Vorontzova & Zaugolnova, 1985). This was also found for *F. novae-zelandiae* at Sugarloaf Fan in the present study (section 3.2).

If classes were defined strictly according to reproductive status intermittent reproduction would create problems for stage-class frequency comparisons either between populations or between years.

One approach would be to ignore reproductive status and classify individuals on the basis of size and vigour alone as was done for *Chionochloa pallens* by Rose & Platt (1990). However this approach results, essentially, in size classes rather than ontogenic

stages and the classes themselves have very low information content.

However by assigning currently nonreproductive individuals that appear large enough and healthy enough to be reproductive to reproductive classes, the problem of intermittent reproduction is circumvented. The method of allocating these nonreproductive individuals is therefore more a multi-variate approach based on overall similarity.

Variation among individuals in size at first reproduction and intermittent reproduction among small individuals would result in a lack of close correlation between reproduction and size in the "juvenile" and "young reproductive" classes. This would explain why so many reclassifications involved individuals from the "young reproductive" class and why this class was generally poorly defined. Intermittent reproduction also tends to be a feature of "old reproductive" individuals (Rabotnov, 1985) and this class was also poorly defined with a large proportion of "old reproductive" individuals being reclassified.

The low incidence of misclassification among juveniles was to be expected as this is the only class that can be associated at all accurately with age. However little can be said either about the age at which juveniles become reproductive or the age of plants in other classes. As is the case with most long-lived species, suppressed individuals can persist as small non-reproductive members of the population for considerable lengths of time as observed in North Canterbury short tussock grassland by Moore (1977) and in the present study (section 3.5). These plants can function as a store of recruits for when conditions become favourable (Silvertown, 1982; Chesson, 1984).

Death of adult tussocks was infrequent in the *F. novae-zelandiae* population studied; however the deaths that were observed were concentrated in the 'older' stage-classes. Canfield (1957) monitored individuals of perennial grass species in Arizona over 17 years. Four of the species he studied showed survivorship patterns of low death risk in middle age followed by a high risk of death as plants aged. This pattern of increasing mortality with age was also found in *Corynephros canescens*, a tussock-forming perennial grass of northern European sand-dunes (Symonides, 1979). In this species tillers often failed to form roots in old plants. Harper suggested that this lack of rooting was a result of the tussock habit (Harper, 1977, p591). Increasing tiller density and litter accumulation within an old large tussock may hinder the rooting of new tillers and significantly increase the death risk of the whole plant.

The sequence of stage-classes from "juvenile" through "mature" to "remnant" can be interpreted as representing a series of ontogenic stages in the development of an individual tussock from a seedling through reproductive maturity to senescence. During this development tussock height increases rapidly from the juvenile stage to the mature stage and reaches its maximum among individuals in the mature stage-class (Fig. 4.5). Diameter increases more slowly and is parallelled by the accumulation of dead tillers within the circumference of the tussock.

However the presentation of a sequence of stage-classes as an ontogenic series belies the diversity of developmental pathways that individual plants can follow. The series of stage-classes represents an idealised life-history that is probably followed in full by few individuals. Under unfavourable conditions individual plants may stay in the "juvenile" class for long periods of time without increasing appreciably in size or reproducing. These individuals may appear to pass directly into the "remnant" class due to the gradual accumulation of dead tillers. Similarly plants that begin reproducing and enter the "young reproductive" class may never reach the size or fecundity levels that characterise "mature reproductive" individuals and instead pass directly into the "old reproductive" or "senescent" classes. Studies of *Deschampsia caespitosa*, a long-lived perennial tussock, have shown that remnants of larger clones can regenerate and take on the characteristics of a juvenile (Gatsuk *et al.*, 1980). Given favourable conditions this no doubt occurs within populations of *F. novae-zelandiae*.

Transitions of this type as well as many others occurred within two years in the Sugarloaf Fan population. It is quite clear from the transition matrices constructed that developmental pathways among *F. novae-zelandiae* individuals are not only non-linear but also change dramatically over relatively short spaces of time. This contrast with previous descriptions of *F. novae-zelandiae* as slow-growing (Sewell, 1947, 1952).

As *F. novae-zelandiae* is modular in structure it is able to respond rapidly to changes in environmental conditions. Given the differences in transition probabilities between weeded and unweeded groups of plants it is obvious that year-to-year variation in environmental factors such as rainfall and biotic factors such as competition can have a dramatic impact on the size, vigour and reproductive status of individual plants.

(b) Among-population comparisons of stage-class frequency

In light of the above conclusions concerning the complexity of stage-class structure, between-population differences can only be discussed with reference to short-term conditions that may have influenced stage-class frequencies. The stage-class profile of a population cannot be assumed to bear any relationship to the older establishment and disturbance history of that population except with reference to the numbers of individuals present. Furthermore, differences between sites in factors such as soil fertility would result in differences in the mean size of plants and in plant vigour so that the age and establishment history of the population would be of even less importance.

Sugarloaf Fan, Hallelujah Flat and Cass Saddle 'B' all have stage-class frequency distributions typical of a normal population in which all stages are present and frequencies are distributed evenly around the mature stage (Rabotnov, 1969). These three populations also all occur within relatively dense montane to subalpine shrubland

/ grassland under moderate to high rainfall. The distribution of frequencies around the mature stage may therefore not be a product of the age of the population but rather of resource availability. The "young" and "mature" stages are the most expensive in terms of resources because in addition to relatively vigorous tillering, energy is also being allocated to culm production. The distribution of stages in these three populations may therefore reflect recent favourable conditions combined with recruitment to the juvenile stage.

The pattern of stage-class distribution in the Cass Valley and Cass Saddle 'A' populations can also be interpreted as reflecting environmental conditions and resource allocation strategies. Both sites are open, stony, exposed with poorly developed soils. Although rainfall is relatively high, a moisture deficiency probably occurs during summer. The predominance of "juveniles" may be due to an accumulation of plants with insufficient resources to enter larger classes by growing or producing culms. Large healthy "mature" plants are the most common among the three reproductive classes indicating that smaller or less vigorous plants lack sufficient resources to produce culms.

Similar factors may have shaped the stage-class distribution of the Porters Pass population where rainfall is lower (1000 mm yr^{-1} versus 2500 mm yr^{-1} on Cass Saddle (Greenland, 1977)). Here "juveniles" and smaller vigorous plants with few culms are more common than large plants with many culms. The difference in reproductive classes between Porters Pass and Cass Saddle 'A' may be due to differences in relative allocation to tillering versus culm production. Plants at Cass Saddle 'A' and Cass Valley may put more effort into culm production when they do reproduce whereas Porters Pass may only allocate a small portion of reserves to reproduction in any one year thereby being able to reproduce while still relatively small. Such a difference in allocation of resources to culm production between these two populations is also indicated in Section 5.6.

The stage-class frequency distributions of Bankside and Mt Sugarloaf are also interpretable in terms of environmental conditions combined with the presence or absence of recruitment. The Bankside site is the driest of the nine sites (average annual rainfall of 690 mm) and has the most decrepit population. The Mt Sugarloaf population occurs on an exposed face in subalpine grassland / shrubland and appears to be lacking in recruits and large plants.

The Cass River population, on a sparsely vegetated low river terrace, may be the only population more affected by its establishment history than by its immediate environment. The stage-class profile of this population resembles a wave of establishment and growth with a subsequent reduction in recruitment with changing conditions. This scenario is perfectly reasonable in the context of riverbed successional dynamics and past studies have indicated that riverbed populations of *F. novae-zelandiae* may each represent only a single establishment episode (Calder, 1958, 1961).

In summary, natural stage-based divisions do exist within populations of *F. novae-zelandiae* tussocks. However life-histories are complex and individuals can change rapidly either "backwards" or "forwards" between classes in response to annual changes in biotic and climatic conditions. As a result the stage-class structure of a population is a product of its history and environment and recent environmental conditions in particular.

4.5 CLONAL FRAGMENTATION

4.5.1 Introduction

In the literature concerning *F. novae-zelandiae* references have been made to the possible role of clonal spread and fragmentation in maintaining individual tussock numbers. The hypothesis is that as tussocks age and increase in diameter, central portions die and the vigorous growth around the circumference gradually breaks up into independent plants (Zotov, 1938; Moore, 1976; Espie, 1987). Fragmentation of this nature can also be facilitated by factors such as burning and grazing (Sewell, 1947) or insect attack (Kelsey, 1957).

This process has already been recognised as an integral part of the life history of some Northern Hemisphere caespitose grasses (Chadwick, 1960; Davy, 1980; Gatsuk *et al*, 1980; Kurchenko, 1985; Vorontzova & Zaugolnova, 1985; Zhukova & Ermakova, 1985) and the age of some fragmented clones has been estimated as more than 1000 years (Harberd, 1961, 1962, 1967).

The aim of this experiment was to determine if clonal fragmentation was a factor in maintaining population density in *F. novae-zelandiae.*

4.5.2. Methods

A 3 m x 3 m plot was located in dense *Festuca* tussock grassland on the upper portion of Sugarloaf Fan and the position of all *F. novae-zelandiae* tussocks was mapped.

Tiller clumps were collected from every individual and grown on under uniform condition in the University glasshouse. Isozyme electrophoresis was used to obtain a genetic profile of each individual based on allele presence and absence at seven reliable loci: PGI 1 and 2, APH 1 and 2, 6PG, MR and PGM. A full description of isozyme methodology and enzyme names is contained in Chapter 5.5. Isozyme analysis has previously been used to determine genotype identity in sward-forming grasses (McNeilly & Roose, 1984) and bunchgrasses (Belsky, 1986).

The frequency of phenotypes at each locus was used to calculate the probability of two unrelated plants having identical isozyme profiles, because plants possessing all of the most common phenotypes would be more likely to appear identical even if they were unrelated. $P < 0.01$ was used as the criterion for accepting pairs or groups.

4.5.3. Results

The 3 m x 3 m plot contained 121 individual tussocks of *F. novae-zelandiae* possessing a total of 69 allelic combinations. Of these 69 combinations, 21 were possessed by two or more individuals and 14 such groups satisfied the $P < 0.01$ criterion.

Four groups represented close pairs of plants ('g', 'j', 'k', 'n', Fig. 4.11). All four groups consisted of one large tussock and one smaller tussock and all occurred in the lower right-hand corner of the plot where tussock density was higher and litter more prevalent. In one case ('g') the plants were connected by an area of accumulated tussock litter. However, groups of tussocks connected by litter generally had different isozyme profiles and there were no rings or close groups of identical plants as would be expected if a clone had spread at the periphery and fragmented into separate tussocks. Some identical pairs and groups were relatively distant; the maximum distance observed between apparently identical plants was 2.9 metres.

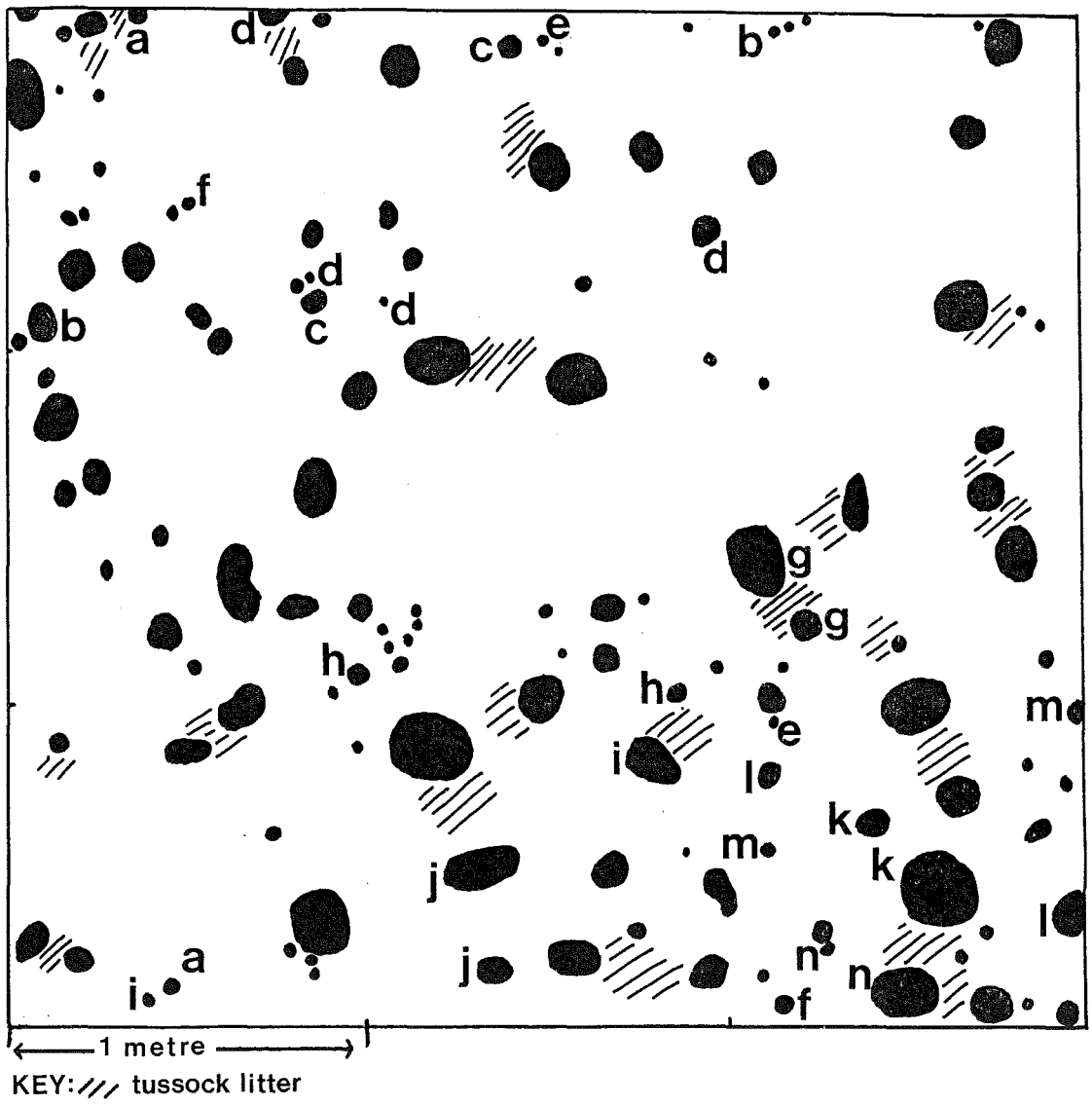


Figure 4.11: Genetic identity, assessed using isozyme electrophoresis, of 121 mapped F. novae-zelandiae tussocks in a 3 x 3 m plot on Sugarloaf Fan. Letters indicate pairs or groups of tussocks possessing identical isozyme phenotypes with a probability $P < 0.01$ that the similarity is due to the chance sharing of common alleles.

4.5.4 Discussion

Given that forest has been absent from this site for 500 years (Molloy, 1977) and assuming that *Festuca* has been present on the site ever since, an annual spread of 6 mm consistently in a single direction is required to account for the observed maximum separation of apparently identical plants. Over two years at Sugarloaf Fan tussocks in control plots used for a competition experiment (section 4.3) increased, on average, 8 mm in diameter. This is clearly not a sufficient rate of expansion. However plants in the weeded plots increased, on average, 34.9 mm in diameter in two years, which equates to an average annual radial spread of 8.7 mm. This rate of expansion may be much more typical of the behaviour of *F. novae-zelandiae* when it first invaded the area subsequent to the removal of forest. However it is unlikely that sufficient rates of expansion have been maintained since the establishment of *F. novae-zelandiae* on the site to account for the more distant pairs of apparently identical plants.

Chadwick (1960) investigated clonal spread in *Nardus stricta* subsequent to changes in pasture management and found that an annual spread of 2 cm was consistent with the growth rate of the species and could account for the observed sizes of patches. However he was dealing with spread over just 40 years and the original genets were still intact. Given the longer time frame under consideration for the spread of *F. novae-zelandiae* at Sugarloaf Fan, a much faster rate of spread than 6 mm per year would have to be envisaged due to the probability that, once the original genet had fragmented, the individual ramets would spread and themselves fragment in random directions.

It is more likely that most groups of apparently identical plants represent family groups resulting from crosses between similar parents and the isozyme information used was not sufficiently detailed to distinguish between the individuals.

Some of the closer pairs of plants, particularly the pair connected by tussock litter ('g'), probably represent recently separated parts of a single clone, so clonal fragmentation may still be occurring. However overall it would appear that clonal fragmentation does not contribute significantly to the maintenance of tussock density. While tussocks do appear to die in the centre and possibly fragment, the inequality of size observed among close pair of isozymically identical tussocks suggests that there are large differences in the vigour of fragments. On most occasions probably only one part of the original plant persists in the long term.

Belsky (1986) suggested that the clonal spread of *Andropogon greenwayi*, a non-stoloniferous, non-rhizomatous grass was facilitated by grazing and trampling by large herbivores. During the course of the present study spreading, fragmented patches of *F. novae-zelandiae* and *Poa cita* were observed in areas subject to grazing and trampling. While mammalian grazing and trampling would not have occurred in pre-human New Zealand, extinct indigenous ground birds may have pulled tussock tillers in a manner

similar to takahe (*Notornis mantelli*) (Mills *et al.*, 1989) which can do major damage to tussocks (C. J. Burrows, *pers. comm.*). This may have facilitated the fragmentation of tussocks in pre-human grassland. However proliferation by clonal fragmentation is unlikely to have been important in the maintenance of populations of *F. novae-zelandiae*.

4.6 SUMMARY AND DISCUSSION OF CHAPTER 4.

Most of the tillers within an individual tussock of *F. novae-zelandiae* are replaced within two years, with a distinct spring / summer flush in tiller births and a spring peak in deaths. Births exceeded deaths among the tillers being monitored and total tillers tagged had increased 150.6% over the two years of the study. While the majority (63.8%) of tillers failed to produce daughter tillers some tillers produced as many as five daughter tillers within two years.

As a result of vegetative regeneration, a single genet can be virtually immortal and yet consist of modules each only a few years old. The phalanx clonal structure of species such as *F. novae-zelandiae* allows for an optimal use of resources in the immediate environment while keeping the risk of being supplanted by another species very low (Hutchings, 1979).

However the competitive ability of *F. novae-zelandiae*, like that of *Deschampsia caespitosa,* is restricted by its growth form (Davy, 1980). The compact habit of both species restricts their area of interference and the density of established tussocks results in self-shading and litter accumulation that could affect tiller growth and survival. The competitive ability of long-lived tussock grasses is more a product of their ability to persist at a site and resist invasion.

Although aggressive stoloniferous species such as *Hieracium pilosella* appear able to establish within mature tussocks, the structure of *F. novae-zelandiae* tussocks makes them moderately resistant to invasion by most adventive species. However adventive species such as *Agrostis capillaris* still appear to have a negative effect on tussock growth. Tussocks in areas where adventive species had been removed showed increased tillering resulting in larger size and more culms relative to plants in control plots. This is possibly due to increased light levels at the tussock base. If tillering is a response to light then the dense growth of adventive grasses around the plants being monitored could have acted to lessen the differences in light levels reaching tillers in small tussocks and large tussocks. However, no effect of self-shading in large tussocks on tillering rate was found in the tiller monitoring experiment.

There was a general increase in diameter and culm production and decrease in height and percent dead tillers in all plants monitored from 1990 to 1992 regardless of treatment, indicating that the size and vigour of populations changes continually in response to the climatic and biotic environment. The ability of *F. novae-zelandiae* to change in size, vigour and reproductive status from year to year has important implications for the use of a stage-based approach to analysing population structure. While natural stage-classes differing in morphological attributes and reproductive status can be defined within a population of tussocks, transitions among classes are non-linear and can occur over relatively short periods of time in response to changes in growing conditions.

Recruitment to the smaller stage-classes by means of clonal fragmentation and the subsequent survival of several parts of the original clone appears to occur within populations of *F. novae-zelandiae*. However, in the grassland studied, this form of vegetative reproduction does not appear to be sufficiently common to constitute an important alternative to seedling recruitment as a mechanism of population growth.

The modular, high-turnover architecture of tussocks is an ideal vehicle for the expression of phenotypic plasticity. This is particularly the case with dense intra-vaginally tillering grasses such as *F. novae-zelandiae* which expand vegetatively in a tightly-packed phalanx form. Studies with dicotyledonous herbs (Schmid, 1985) have shown that phalanx species where the genet remains in a fixed position rely much more on phenotypic plasticity than do guerrilla species. In the later, genetic specialization is not disadvantageous because the genet can 'travel' by clonal growth to find favourable patches.

Plastic responses, although most important at the level of the genet in terms of population processes, are a product of the individual responses of the independent modules (tillers or groups of tillers) that comprise the clone. At the level of the individual plant, genets would appear to be varying the number of vegetative and floral tillers in response to their environment, however this is a product of between-tiller variation in the initiation of vegetative and floral apices. A population of tussocks is essentially a meta-population of clonal populations (White, 1979) and while genetic variation is stored among clones, the short-term response to environment fluctuations occurs at the level of independent modules within clones.

The modules that comprise a tussock clone are of course not completely independent even if connections between them have broken down. For example, tillers can negatively affect each other through intra-clonal competition (Briske & Butler, 1989) and the death of large groups of tillers can affect the remaining live tillers by smothering them or encouraging fungal growth. However, there are also positive effects associated with a closely packed arrangement and one of the most important is site occupancy. A firm, large tussock is unlikely to be invaded by other species. By assuming a tight phalanx habit the plant preempts biological space and is resistant to invasion unless damage or module death creates an opening within the clone.

In a healthy population of tussocks in a spatially heterogeneous environment, not all plants will have the resources in a given year to contribute to total reproduction and many will exist as small suppressed individuals. The modular architecture and high plasticity in growth of *F. novae-zelandiae* means that such individuals could still contribute to the reproductive output of the population at a later date, under more favourable conditions. In the meantime, these individuals act as a store of genetic variation and source of adult recruits that can be accessed more readily than a store of seeds (Chesson, 1984).

The modular architecture of perennial tussocks such as *F. novae-zelandiae* and the short life-span of modules means that these plants theoretically live in a state of perpetual somatic youth (Harper, 1977). As a result of this the overall size, condition and reproductive output of a

plant is more a product of its environment over the previous few years than a result of its age or establishment history. Examining the stage-class profile of populations of modular plants such as *F. novae-zelandiae* is useful for predicting the future of the population and giving some insight into recent environmental conditions but is of limited use in tracing the past. One still needs to know the real age of plants before any study of selection, genetic change or micro-evolution can be conducted (Harper, 1977).

CHAPTER 5: PATTERNS OF VARIATION

5.1 INTRODUCTION

5.1.1 Recent evolution in *F. novae-zelandiae*

Although the history of New Zealand vegetation over geological time has been characterised by sometimes quite rapid change, the changes that have occurred in the New Zealand landscape probably rival or surpass any previous event in terms of both magnitude and speed. There is ample evidence for the reduction and elimination of palatable species from certain areas during the explosive phase of pastoral development in the South Island (O'Connor, 1986). Even where species were not severely reduced, a shift in genetic constitution and range of morphologies could have occurred in any species of reasonable abundance in the most actively settled areas due to selection pressures operating on populations.

It has been suggested by O'Connor (1986) that the tussock form of *F. novae-zelandiae* is a recent phenomenon resulting from the intense selection pressure of mammalian herbivory and frequent fire. His arguments are based on the early taxonomy of *Festuca* species, including the usage of the term 'tussock' in species description and on pre-1880 assessments of indigenous grass palatability. He hypothesized that in the space of 50 to 60 years of European settlement the lowland and montane species of *Festuca* had gone from being a fine, highly palatable subdominant species with a slender, densely tufted habit to the coarse, unpalatable dominant tussock known today as *Festuca novae-zelandiae*. Tussocks are clearly visible in photographs of montane Canterbury dating from 1868 and 1880 (by D. L. Mundy and Burton Bros respectively, reproduced in Burrows, 1977a) and are also visible in photographs of Christchurch taken by A. C. Barker in 1860 and 1864 (held in the Canterbury Museum).

O'Connor's hypothesis has important implications for this study as any discussion of patterns of variation within a taxon, with reference to its perceived history, would be invalid if that taxon in its present form was of very recent origin.

As described in Appendix 1, early *Festuca* taxonomy was confused and characterised by 'lumping' of taxa. Therefore early assessments of grass palatability cannot be taken as necessarily referring to particular present-day species. Arguments that recent evolution has occurred within *Festuca* based on taxonomy and palatability alone are therefore invalid.

However as pointed out by O'Connor, the term 'tussock' was never applied to New Zealand species of *Festuca* initially grouped under *F. duriuscula*. This does not mean that there were no tussock *Festuca* species in New Zealand prior to 1880. It simply may not have been used in formal taxonomic description. The European *F.*

duriuscula on which the New Zealand taxon was based would never have been described as a 'tussock' as this was a term peculiar to New Zealand. Secondly as New Zealand *F. duriuscula* contained a range of entities (see Appendix 1) the tussock growth-form would not have been a diagnostic character of the whole group.

Poa cita (known then as *Poa caespitosa* or *Poa australis* var *laevis*) was the grass most often referred to as 'tussock' (e.g. Buchanan, 1868; J. F. & J. B. Armstrong, 1872; J. B. Armstrong 1880; Buchanan, 1880), however *Festuca* species occurred with *Poa cita* on the Canterbury Plains and Banks Peninsula (J. F. Armstrong, 1870; J. B. Armstrong, 1880). That the two species were of similar abundance is indicated by J. B. Armstrong's (1880) description of the vegetation of the Canterbury Plains and foothills to 2000 feet: "Grasses form here the principal part of the vegetation . . . The most abundant grasses are the tussockgrass, *Poa caespitosa* etc., an undescribed species of fescue usually referred to *Festuca duriuscula* Linn., by most New Zealand collectors . . . The vegetation of the downs does not differ materially from that of the plain."

In the species list appended to his report, Armstrong lists both *P. caespitosa* and *F.* sp (*F. duriuscula* Hook. f. non Linn.) as abundant in the lowland and montane zones. A later report by Laing in 1918 identifies the abundant species of *Festuca* on Banks Peninsula, referred to *F. duriuscula* by the Armstrongs, as *F. novae-zelandiae*.

Despite the lack of specific reference to a tussock *Festuca* in the early botanical literature, there is no reason why *F. novae-zelandiae* as it is today was not already present in the flora prior to European settlement. Petrie noted in 1895 that the common *Festuca*, then still referred to *F. duriuscula*, was being confounded by some botanical workers and most settlers with *Poa cita*. This would suggest that the common *Festuca* was also a tussock. In a situation analogous to manuka and kanuka, *Festuca novae-zelandiae* appears to have been regularly lumped with *P. cita* during the early decades of New Zealand botany.

5.1.2 Variation in present-day New Zealand tussock Festuca.

Over half of New Zealand's grass genera, including *Festuca*, are cosmopolitan or tropical, however the majority of species are endemic. This pattern of generic relationship to world floras and specific endemism is apparent in many other New Zealand genera (e.g. *Epilobium* and *Ranunculus*) and is usually taken to indicate recent, rapid evolution (Raven, 1973).

Some New Zealand grass genera also show a high degree of interspecific fertility and there are uniform chromosome numbers in some large genera such as *Chionochloa* (Connor, 1991) and *Poa* (Edgar, 1986). This may indicate not only recent radiation but also the potential importance of interspecific recombination of genetic material (Raven, 1973).

The frequent changes in habitat conditions and consequent vegetation migration that has characterised the recent geological history of New Zealand may have been a factor in the evolution of only partly genetically isolated ecologically-differentiated biotypes within certain genera. Limited gene-flow between such entities may have been important in the adjustment to glacial cycles, as recombinants might be able to respond to altered conditions more rapidly than genetically isolated taxa (Anderson & Stebbins, 1954). Ogden (1989) has suggested that limited gene-flow between ecologically distinct taxa contributed to the survival of certain tree species during Pleistocene oscillations. Such groups of taxa where the number and characteristics of differentiated entities have varied through time are often best regarded as 'coenospecies' *sensu* Clausen *et al.*, (1939, 1940) and Fisher (1965).

Festuca is a large genus; world-wide it contains about 500 species. However the genus is represented in New Zealand by relatively few species; Cheeseman (1925) described seven and Druce (1989) listed five formally described species and four informal taxa. Despite being a cosmopolitan genus, *Festuca* holds to the pattern described above, of endemism at the species level. All of the New Zealand species of *Festuca*, except *F. contracta* which has a southern circumpolar distribution, are endemic to the New Zealand Botanical Region.

In northern hemisphere *Festuca,* specific delineation is often indistinct and considerable subspecific variation has been described in some taxa (Stace, 1989; Wilkinson & Stace, 1991). Likewise New Zealand *Festuca* appears to contain variable species with indistinct boundaries. *F. novae-zelandiae* is the most widespread indigenous *Festuca* and exhibits both of these features.

F. novae-zelandiae is closely related to and often difficult to distinguish from *Festuca matthewsii* Chees.; as detailed in Appendix 1 these two species were initially both described as varieties of *F. ovina*. *F. novae-zelandiae* and *F. matthewsii* undoubtedly arose from a common genetic stock during the climatic fluctuations of the

Pleistocene. Due to ecological specialisation it is likely that they evolved allopatrically (Connor, 1968).

In present-day New Zealand *F. matthewsii* is a tussock of higher rainfall areas of South Island, occurring in the subalpine to alpine zone east of the Southern Alps (Plate 3) (Connor, 1961, 1964, 1965).

Both *F. novae-zelandiae* and *F. matthewsii* are hexaploid (2n = 6x = 42) and represent the lowest ploidy level found so far in the New Zealand species of *Festuca* (Beuzenberg & Hair, 1983). The two species can be easily crossed to produce fertile hybrids (Connor, 1968) and are morphologically very similar in habit and leaf anatomy (Connor, 1960). Both species are out-crossing and *F. novae-zelandiae* has been shown to be virtually self-incompatible (Connor & Cook, 1955; Connor, 1960). The distributional boundary between *F. novae-zelandiae* and *F. matthewsii* is often indistinct, particularly in the mountains of central South Island.

It has often been suggested that the ecological amplitude of widespread species is, at least in part, due to their variability and ability to form races adapted to local conditions (Van Valen, 1965; McMillan, 1967). *F. novae-zelandiae* is widespread today and Cockayne and Allan (1934) made the comment that the name *F. novae-zelandiae* was applied to a "very complex group of jordanons (variants) and hybrids that had not been satisfactorily analyzed".

The contraction and expansion in range of *F. novae-zelandiae* over the last 100,000 years - i.e. a glacial-interglacial cycle - is not dissimilar to range changes that must have occurred with the climatic fluctuations that have characterised the last 2 million years. This type of process, occurring with repeated climatic changes and over thousands of years, is fertile ground for rapid evolutionary change and speciation (Grant, 1971). Similarly the range expansion and invasion of newly-formed sites by previously small populations, as has happened with *F. novae-zelandiae* in the last 1000 years, is also an evolutionary opportunity.

There is evidence that differentiation within *F. novae-zelandiae* has occurred both in pre-human and recent time-frames. A distinct high altitude form of *F. novae-zelandiae* has been recognised that is most probably of pre-human origin and occurs above timberline on the drier eastern mountains (Plate 4). It is fully compatible with lowland *F. novae-zelandiae* but differs morphologically (Connor, 1960, 1968; Connor & Edgar, 1986) and physiologically (Scott, 1970).

Espie (1987) found differences in nutrient uptake among populations of *F. novae-zelandiae* in a controlled fertilizer experiment. The populations originated from induced grasslands in the Cass area on soils of different ages. The differences that Espie found could represent adaptation to local nutrient availability that has evolved within the 500 years those sites have been without forest.

Plate 3: *Festuca matthewsii* tussocks scattered in subalpine vegetation at the Arthurs Pass study site (APS) on the Main Divide.

Plate 4: "High altitude" *Festuca novae-zelandiae* at 1400 m altitude at the Broken River study site (BRO).

The aim of this section is to investigate the degree of differentiation that has occurred within *F. novae-zelandiae* with reference to its pre-human and recent distribution and examine the relationship between *F. novae-zelandiae* and *F. matthewsii* to see what it reveals about the evolutionary history of this group.

In the following section I will be comparing the vegetation association, morphology, biochemistry and phenology of three taxa, treating "high altitude" *F. novae-zelandiae* as a separate taxon alongside *F. novae-zelandiae s.s.* and *F. matthewsii*. This does not imply that I consider it to be a distinct species or subspecies but rather that it represents variation on a lower taxonomic scale than that between *F. novae-zelandiae* and *F. matthewsii*.

5.2 VEGETATION COMPOSITION AT SITES CONTAINING TUSSOCK FESTUCA.

5.2.1 Methods

Forty-two sites containing tussock *Festuca* were selected in mid-Canterbury to cover a range of environments from the Main Divide of the Southern Alps to the Canterbury Plains (see Fig. 2.1, Chapter 2 for site locations). All sites were at least two kilometres apart.

Slope (measured with an Abney level), aspect (compass reading), altitude (read from a topographic map) and tussock density were recorded at each site. At each site four 2 m x 2 m plots were randomly located. Within each plot the abundance of all vascular species present was recorded in the following cover classes: 1 = < 1% total cover within a plot; 2 = 1 - 5% cover; 3 = 6 - 10% cover; 4 = 11 - 25% cover; 5 = 26 - 50% cover; 6 = 51 - 75% cover and 7 = 76 - 100% cover. For analysis, species were assigned the median value of the cover class (i.e. 1 = 0.5%, 2 = 3%, 3 = 8%, 4 = 18%, 5 = 38%, 6 = 63%, and 7 = 88%) and values from the four plots averaged for each site. The total percent cover of vascular vegetation, cryptogams, litter and rocks or stones was estimated to the nearest 5%.

The mean annual rainfall of each site was obtained either from a nearby climate station (New Zealand Meteorological Service, 1982) or estimated from a rainfall isohyet map of the area (Greenland, 1977). Mean annual minimum, maximum and mean temperatures were estimated for each site using the regression equations of Norton (1985).

One-way analysis of variance was used to test for significant differences between sites containing *F. novae-zelandiae s.s.*, "high altitude" *F. novae-zelandiae* and *F. matthewsii* in environmental factors and attributes of the vegetation.

Detrended Correspondance Analysis as implemented by CANOCO (Ter Braak, 1990) was used to investigate trends in the vegetation of the 42 sites. Measured environmental factors were correlated with the first two axes from the ordination of sites by species.

Simultaneous classification of the 42 sites was performed using TWINSPAN (two-way indicator species analysis), a polythetic divisive technique (Hill, 1979) that classifies sites into broadly similar vegetation types based on the presence and abundance of species. Default options were used in both analyses.

5.2.2 Results

Relatively unmodified sites containing tussock *Festuca* were typically stream and river terraces, fans, open exposed areas and stabilised margins of debris slopes regardless of rainfall, altitude or taxon. Tussock *Festuca,* usually *F. novae-zelandiae s.s.* also occurred on hill slopes and older surfaces where the forest cover had been removed.

The 42 selected sites ranged in altitude from 65 m asl to 1420 m and in rainfall from 690 mm to 6000 mm per annum. Sixteen sites contained populations of *F. matthewsii,* six contained plants referable to "high altitude" *F. novae-zelandiae* and the remaining 20 sites contained *F. novae-zelandiae s.s.* Seven populations (DIS, GRE, HLF, LMR, SVY, UHR and WSH), while being assigned to either *F. novae-zelandiae s.s.* or *F. matthewsii,* possessed morphological attributes of both species.

Sites at which the three taxa occurred differed significantly in altitude, annual rainfall and temperature (Table 5.1). Sites containing *F. novae-zelandiae s.s.* had the lowest mean altitude and rainfall. Sites containing "high altitude" *F. novae-zelandiae* had the highest mean altitude but were also dry and sites containing *F. matthewsii* were intermediate in altitude but had the highest mean rainfall.

Mean vegetation cover per site ranged from 42% to 96.5% and was significantly lower at sites containing *F. matthewsii* and the "high altitude" form of *F. novae-zelandiae* than for sites containing *F. novae-zelandiae s.s.* (Table 5.1).

Total cover abundance of adventive species per site ranged from 0 to 112% (values in excess of 100% are due to multiple layers within the vegetation) and differed significantly between taxonomic groups with *F. novae-zelandiae* sites having the highest mean adventive cover abundance and sites containing the "high altitude" form of *F. novae-zelandiae* the lowest.

Mean tussock density varied from 0.31 to 10.2 m^{-2} and did not differ significantly between the three taxonomic groups. There was also no significant difference between the three taxa in the site attributes of slope, aspect, and percent of ground covered by cryptogams or litter.

A total of 214 species was recorded from the 42 sites; however, 66 of these represented single plot occurrences or were of very low cover value (typically <1% in two or three plots) at single sites. Ordination was performed on the remaining 148 species with the exclusion of *F. matthewsii* and *F. novae-zelandiae s.l.* so as not to force differentiation between sites.

There was a wide range of vegetation types between the 42 sites and as a result the first two axes of the DCA ordination accounted for only 16% of the variation in the species data. However, the spread of sites against axes 1 and 2 (Fig. 5.1) corresponded reasonably well to taxonomic groups. The first axis separated sites containing populations of "high altitude" *F. novae-zelandiae* were separated from sites containing *F. novae-zelandiae s.s.* The second axis separated *F. novae-zelandiae*

Table 5.1: Attribute means of 42 sites containing populations of F. novae-zelandiae *s.s.*, "high altitude" F. novae-zelandiae and F. matthewsii and results from one-way analyses of variances. Different superscripts indicate a significant difference between means in a row. NS = not significant.

Attribute	F.novae-zel.	high alt.	F. matthewsii	F	P <
No. of sites sampled	20	6	16		
% Adventive cover	38.7^{b}	1.23^{a}	15.9^{a}	6.26	0.01
Altitude (m)	738^{a}	1278^{c}	907^{b}	16.1	0.001
Annual Rainfall (mm)	1630^{a}	1790^{a}	4750^{b}	42.0	0.001
Aspect (degs. from N)	47.2	70.0	50.2	0.38	NS
% Bare Ground	1.6^{ab}	3.5^{b}	0.2^{a}	4.08	0.05
% Cryptogamic cover	9.3	4.6	9.2	0.66	NS
% Litter ground cover	3.0	3.2	3.8	0.22	NS
Mean maximum temp.	13.1^{c}	9.71^{a}	11.8^{b}	18.5	0.001
Mean temperature	8.18^{c}	5.47^{a}	7.45^{b}	16.5	0.001
Mean minimum temp.	3.26^{b}	1.20^{a}	3.07^{b}	13.9	0.001
Slope (degrees)	2.61	4.17	5.39	1.13	NS
% Stony/rocky ground	4.9^{a}	24^{b}	21^{b}	7.77	0.01
Vegetation cover (%)	81^{b}	65^{a}	66^{a}	6.99	0.01
Tussock density (m^{-2})	3.87	1.95	3.67	1.27	NS

Table 5.2: Pearson coefficients for correlations between site attributes and the first two ordination axes from a Detrended Correspondance Analysis of 42 sites containing tussock Festuca using the cover abundances of 146 species.

Variable	AXIS 1	*P* <	AXIS 2	*P* <
% Adventive cover	-0.80	0.001	0.22	NS
Altitude	0.79	0.001	-0.06	NS
Annual rainfall	0.24	NS	-0.71	0.001
Aspect	0.30	NS	0.10	NS
Mean max. temperature	-0.80	0.001	0.11	NS
Mean min. temperature	-0.72	0.001	-0.12	NS
Mean temperature	-0.79	0.001	0.02	NS
Slope	0.43	0.01	-0.13	NS
Total vegetation cover	-0.44	0.01	0.37	0.05

s.l. sites from *F. matthewsii* sites. Populations of tussocks referred to one of the two species but possessing some morphological characters of the other, occurred in the area of overlap in vegetation type between the two species.

The spread of sites along the first ordination axis was most highly correlated with variation in mean maximum temperature and the cover abundance of adventive species at each site (Table 5.2, Fig. 5.1). Variation in the altitude of sites was also highly correlated with this axis as were mean and minimum temperatures. The second ordination axis was most highly correlated with variation in annual rainfall.

TWINSPAN was performed using all 210 species in the dataset. After inspection of the results the first three levels of divisions were accepted giving a total of eight groups (Fig. 5.2). The first division appeared to be primarily related to the abundance of adventive species; *Trifolium repens* and high values for *Anthoxanthum odoratum* characterised one side of the division and two indigenous species (*Celmisia spectabilis* and *Lycopodium fastigatum*) characterised the other.

All of the 6 sites containing "high altitude" *F. novae-zelandiae* occurred on the side of the primary division associated with indigenous species (Fig. 5.2). Sixteen of the 20 *F. novae-zelandiae s.s.* sites occurred on the side of the primary division associated with adventive species. The 16 *F. matthewsii* sites were distributed on either side of the primary division.

Groups 1 and 2 were distinguished from groups 3 and 4 by the presence of *Muehlenbechia axillaris*, a common species of drier, stony sites such as river terraces and floodplains. High values of *Agrostis capillaris*, an abundant adventive grass, were associated with groups 3 and 4.

The seven sites in group 1 (Fig. 5.2) were all *F. novae-zelandiae* sites on river terraces, fans and hill slopes and five of the seven were sites that had probably supported forest prior to the arrival of humans in New Zealand. Group 2 sites occurred mainly on fans and river terraces. All of the sites in group 1 and group 2 were characterised by abundant adventive grasses and included the lowest rainfall sites in the dataset. The *F. novae-zelandiae* sites in these groups represented typical short tussock grassland in montane mid-Canterbury.

Sites classified into group 3 were typically stony river terraces in mainly higher rainfall environments which contained relatively high amounts of adventive species. Group 4 consisted entirely of *F. matthewsii* sites at medium altitudes that possessed some adventive species.

Groups 5 and 6 were distinguished from groups 7 and 8 by the presence of *Deyeuxia avenoides,* an indigenous grass of eastern, montane, short-tussock grassland and stony sites, and the absence of *Chionochloa pallens*, an indigenous alpine grass more common in higher rainfall portions of the study area.

Groups 5 and 6 contained the four remaining *F. novae-zelandiae* sites and all of the "high altitude" *F. novae-zelandiae* sites. The *F. novae-zelandiae* sites on this side

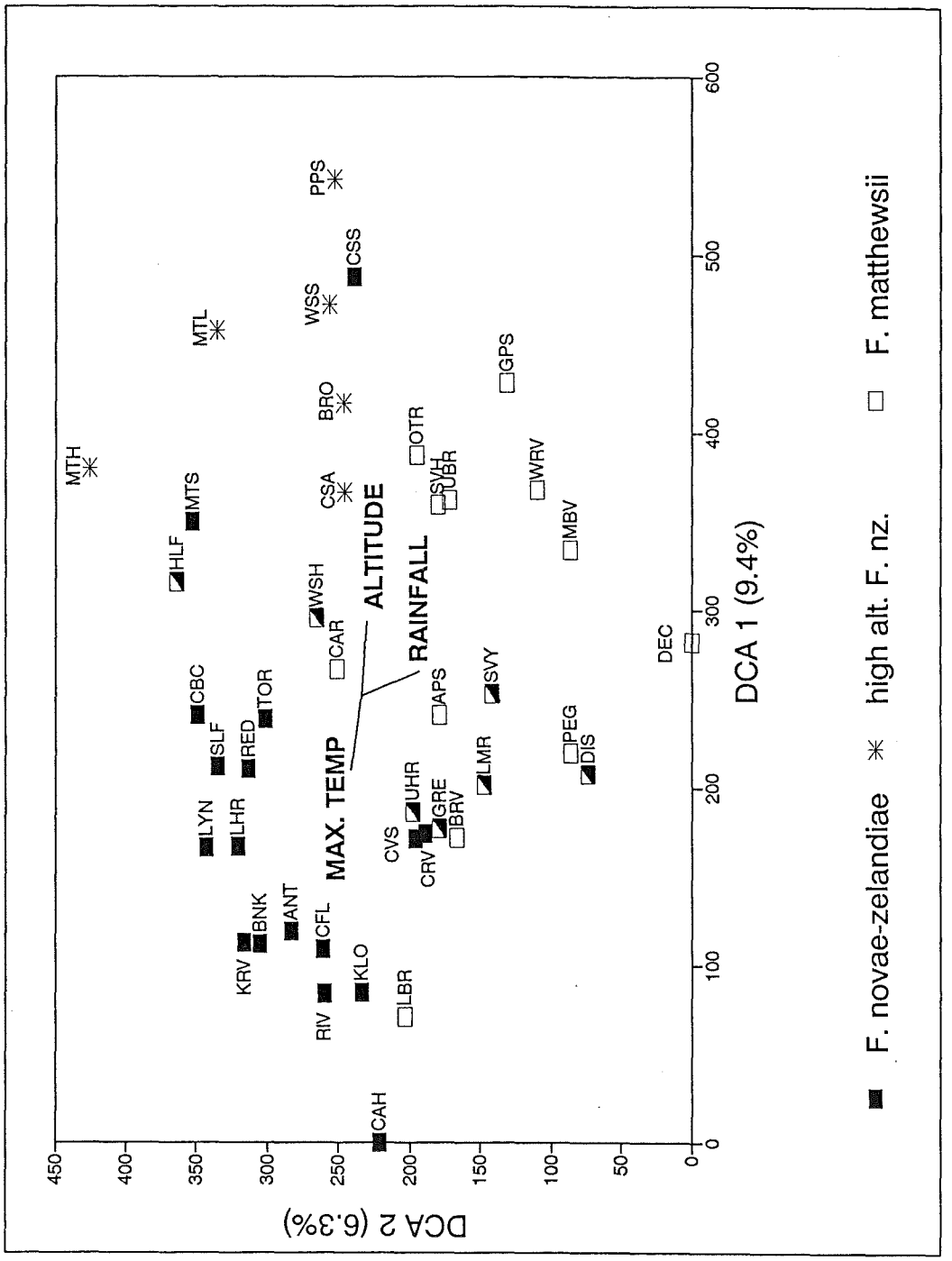
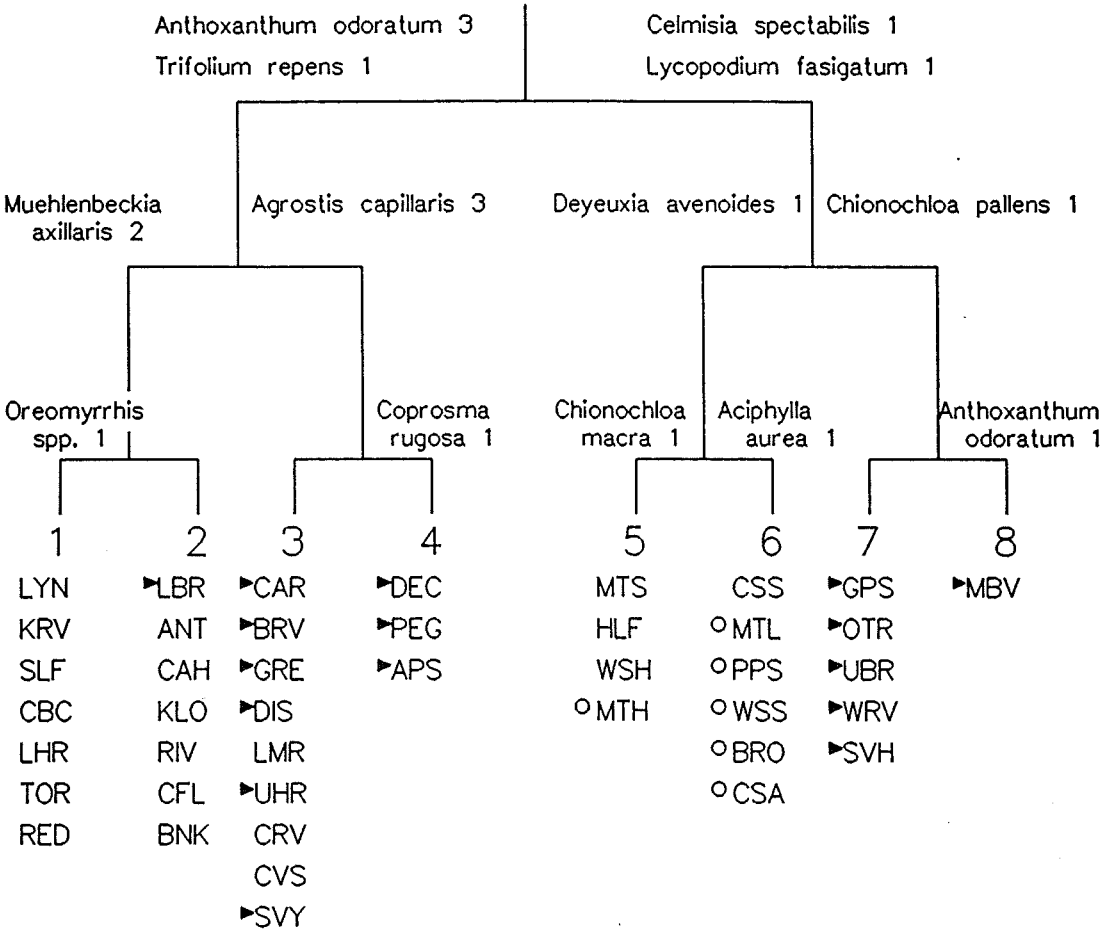


Figure 5.1: Axes 1 and 2 from an ordination of 42 sites containing tussock *Festuca* using cover abundance values for 146 species.



► F. matthewsii , ○ "high altitude" F. n-z., rest F.novae-zelandiae s.s.

Figure 5.2 : TWINSPAN classification of sites containing tussock Festuca. Numbers after indicator species are abundance: 1=<2%, 2=2-<5%, 3=5-<10%.

of the primary division represent the highest altitude *F. novae-zelandiae* sites in the dataset. Group 6 contained the highest altitude sites of all sites surveyed.

Groups 7 and 8 consisted of the remainder of the *F. matthewsii* sites. These sites represent open alpine grassland / shrubland communities on stony slopes in a high rainfall environment on or close to the Main Divide.

5.2.3 Discussion

Trends in the vegetation composition of the sites sampled reflected environmental gradients in altitude, rainfall and temperature associated with the large-scale topography of the study area. However the effect of human-induced modification and the invasion of adventive species was also important in determining the vegetation of sites.

The recent changes that have occurred in grassland communities, particularly at lower altitudes, limit the amount of information that can be extracted from an analysis of the vegetation. The invasion of adventive species has decreased vegetation diversity among sites at lower altitudes and in settled parts of the study area. The longevity of genetic individuals of *F. novae-zelandiae* and their ability to adjust plastically to environmental change through time (section 4.4) means that the present vegetation composition of a site does not necessarily indicate the conditions that favoured *F. novae-zelandiae* establishment. When the plants at a site established, the vegetation of that site may have been different and their subsequent survival may be due to plasticity in growth responses rather than adaptation to that particular vegetation type.

However despite the strong influence of adventive species on the separation of sites by ordination, the observed ecological separation of *F. matthewsii* and *F. novae-zelandiae* is supported by differences in the environment and the vegetation in which they occur. The association between apparently intermediate populations and shared vegetation types strongly suggests that the boundary between *F. matthewsii* and *F. novae-zelandiae* is not clear cut but is affected by environmental factors.

Populations referred to "high altitude" *F. novae-zelandiae* were also relatively distinct in terms of vegetation from the remaining *F. novae-zelandiae* populations sampled. There appears to be more overlap in vegetation composition between *F. matthewsii* and *F. novae-zelandiae* sites than there is between sites containing "high altitude" *F. novae-zelandiae* and *F. novae-zelandiae s.s.* This would support the hypothesis that this "high altitude" form represents an ecologically distinct entity within *F. novae-zelandiae*.

5.3 MORPHOLOGICAL VARIATION

5.3.1 Methods

(a) Variation among 42 populations in 40 characters.

In the summer of 1990/91 tussock populations at each of the 42 sites in section 5.2 were sampled. At each site, ten reproductive tussocks were randomly selected and a clump of at least five tillers with at least one culm was collected from each individual. The sites covered all three of the taxonomic groups discussed in section 5.1. Sixteen contained populations of *F. matthewsii,* six contained plants resembling the "high altitude" form of *F. novae-zelandiae* and the remaining 20 sites were *F. novae-zelandiae sensu stricto.* Seven populations (DIS, GRE, HLF, LMR, SVY, UHR and WSH), while being assigned to either *F. novae-zelandiae s.s.* or *F. matthewsii,* possessed morphological attributes of both species. Representative material of all populations was deposited in the University of Canterbury herbarium. Accession numbers are tabulated in Appendix 2.

The material from each of the 420 individuals was examined for 40 quantitative morphological characters covering both vegetative and floral characters (Table 5.3). Individual values for each character were then averaged to give a mean value for the population. The material was initially examined fresh, then pressed and dried for detailed morphological examination.

Characters of the sheath and lamina were measured on the oldest intact green leaf on a randomly selected tiller. Lamina adaxial hair length was measured immediately above the ligule. The structures referred to as 'hairs' ranged from stiffly strigose hairs and acute 'prickle teeth' to rounded 'dewy' structures. Lamina width and abaxial hair length and density were measured at the mid-point between ligule and lamina apex.

All remaining characters were measured on the longest culm present. Width, hair length and hair density on the upper (3rd) culm internode were measured 1 cm below the first inflorescence node. Hair length and density on the inflorescence rachis, branch and pedicel were measured on the faces as opposed to the edges (these structure are variously biplanar, plano-convex or trigonous). Characters of the pedicel and spikelet were measured on the penultimate spikelet of the second inflorescence branch, the first branch being the basal branch. All floret characters were measured on the second floret on this spikelet.

All measures of hair density were 0.06 mm^{-2}. Hair length and density were measured under 40x magnification using a gradicule. Lamina, culm and rachis width and the length of glumes, palea, lemma and awn were measured under 10x magnification using a gradicule.

One-way analysis of variance was used to test each character for significant differences between the three taxa. Principal Components Analysis as implemented by CANOCO and using default options, was used to investigate the relationships between populations and between morphology and environmental gradients. In addition, the 40 morphological characters were used as pseudo-environmental variables in order to discern which characters were most strongly correlated with the ordination axes. Likewise the first two ordination axes of a Detrended Correspondance Analysis of the same 42 sites by vegetation composition (section 5.2) were included in the principal

Table 5.3: Character means for F. novae-zelandiae *s.s.*, "high altitude" F. novae-zelandiae and F. matthewsii with results from one-way ANOVA tests. Superscripts indicate significant differences using LSD tests. NS = not significant.

CHARACTER	F. novae-zel.	"high altitude"	F. matthewsii	*F*	*P* <
Pops./plants sampled	20/200	6/60	16/160		
Sheath length (cm)	8.95	7.90	7.90	2.67	NS
Lamina :					
length (cm)	21.8^{b}	17.9^{a}	19.4^{a}	5.79	0.01
width (mm)	0.54^{a}	0.58^{ab}	0.62^{b}	12.6	0.001
adaxial hair length (mm)	0.09	0.09	0.09	0.14	NS
abaxial hair length (mm)	0.04^{b}	0.04^{b}	0.00^{a}	81.5	0.001
" hair density (0.06mm^{-2})	2.27^{b}	1.37^{b}	0.14^{a}	29.4	0.001
Auricle length (mm)	0.57	0.65	0.67	2.29	NS
Ligule length (mm)	0.39^{a}	0.50^{b}	0.54^{b}	10.3	0.001
Culm :					
lower sheath length (cm)	9.22^{b}	8.09^{a}	8.24^{a}	4.75	0.05
upper sheath length (cm)	12.1^{c}	9.54^{a}	11.3^{b}	7.31	0.01
1st internode length (cm)	2.18^{a}	1.79^{a}	3.30^{b}	11.7	0.001
2nd internode length (cm)	5.11^{a}	4.25^{a}	6.71^{b}	6.32	0.01
3rd internode length (cm)	30.5^{b}	21.5^{a}	27.2^{ab}	4.92	0.05
3rd internode width (mm)	0.69	0.65	0.68	0.28	NS
3rd int. hair length (mm)	0.04^{b}	0.04^{b}	0.00^{a}	63.8	0.001
" hair density (0.06mm^{-2})	5.67^{b}	4.58^{b}	0.53^{a}	46.2	0.001
Inflorescence :					
length (cm)	12.8^{b}	8.98^{a}	12.6^{b}	12.7	0.001
number of nodes	7.36^{b}	6.48^{a}	6.89^{a}	6.47	0.01
number of spikelets	14.3^{b}	10.1^{a}	13.1^{b}	6.25	0.01
1st internode length (cm)	4.37^{b}	2.98^{a}	4.04^{b}	14.8	0.001
Rachis :					
width (mm)	0.58	0.58	0.62	1.33	NS
hair length (mm)	0.04^{b}	0.05^{b}	0.01^{a}	38.4	0.001
hair density	6.58^{b}	5.33^{b}	1.09^{a}	42.4	0.001
1st inflorescence branch :					
length (cm)	5.46^{b}	3.60^{a}	6.52^{c}	22.0	0.001
angle (degrees)	15.5^{a}	10.3^{a}	50.6^{b}	21.2	0.001
hair length (mm)	0.05^{b}	0.05^{b}	0.02^{a}	34.2	0.001
hair density (0.06mm^{-2})	5.70^{b}	4.94^{b}	1.79^{a}	28.1	0.001
number of spikelets	3.93^{b}	2.71^{a}	4.10^{b}	8.82	0.001
dist. 1st spikelet (cm)	2.09^{b}	1.35^{a}	3.07^{c}	29.4	0.001

Table 5.3: continued.

CHARACTER	F. novae-zel.	"high altitude"	F. matthewsii	*F*	*P* <
Pedicel :					
length (mm)	2.10[a]	2.14[a]	3.37[b]	22.6	0.001
hair length (mm)	0.04[b]	0.04[b]	0.02[a]	18.3	0.001
hair density (0.06mm^{-2})	4.42[b]	3.97[b]	1.16[a]	13.3	0.001
Spikelet :					
length (mm)	10.1[a]	10.7[ab]	11.1[b]	8.58	0.001
number of florets	4.77	4.62	4.71	0.19	NS
1st glume length (mm)	5.06[a]	5.14[a]	5.40[b]	11.1	0.001
2nd glume length (mm)	3.65[a]	3.79[a]	4.06[b]	13.3	0.001
Floret :					
awn length (mm)	0.85[a]	0.96[ab]	1.23[b]	5.04	0.05
palea length (mm)	5.54[a]	5.88[b]	6.12[b]	15.4	0.001
lemma length (mm)	5.55[a]	5.75[a]	6.12[b]	18.3	0.001
lodicule length (mm)	0.84[a]	0.95[b]	0.95[b]	7.71	0.01

Table 5.4: Attributes of eight sites in the upper Waimakariri River. Map references are for NZMS 260 series. Rain = annual rainfall estimated from isohyets.

Site	Dist up valley.	Location (m)	Alt. (mm)	Rain	Other important species
Riversdale	0 km	K34 076100	540	1500	Discaria toumatou, Coprosma petriei, adventive grasses
Klondike	2 km	K34 947985	635	2000	Discaria toumatou, Hieracium pilosella, adventive grasses
Anticrow	4 km	K34 900991	680	2500	adventive grasses, Trifolium spp Muehlenbeckia axillaris
Greenlaw	5 km	K33 852007	740	3750	Raoulia spp, Pernettya macrostigma, adventive grasses
Waimakariri	6 km	K33 841028	770	4000	adventive grasses, Poa colensoi, Muehlenbeckia axillaris
Carrington	7 km	K33 835042	800	4500	Raoulia spp, Pernettya macrostigma, Coriaria plumosa
Kilmarnock	8 km	K33 818042	880	5000	Raoulia spp, adventive grasses, Muehlenbeckia axillaris
White River	9 km	K33 810030	1050	5500	Poa colensoi, Blechnum penna-marina, Muehlenbeckia axillaris

components analysis as pseudo-environmental variables in order to test the degree of concurrence between the two ordinations.

The role of environmental gradients in altitude, rainfall and temperature in the observed patterns for particular characters was examined using stepwise linear regression. The methods used to obtain rainfall and temperature data are detailed in section 5.2.

(b) Variation at the boundary between *F. novae-zelandiae* and *F. matthewsii*.

The nature of the boundary between *F. matthewsii* and *F. novae-zelandiae* in the upper Waimakariri catchment was examined. The Waimakariri River is a braided river system and changes in the course of channels leave isolated river terraces which are colonised by a range of species including *Festuca* species. At lower altitudes, roughly below 700 m, plants clearly belong to *F. novae-zelandiae s.s.*. In the head waters of the Waimakariri above about 900 m, and in a tributary, White River, plants were clearly referable to *F. matthewsii*. However populations at intermediate altitudes in the river valley display varying degrees of affinity to each of the two species.

Six populations from the sample of 42 populations used in (a) occurred in a sequence from 540 m to 1050 m altitude in the Waimakariri and White Rivers. The morphological data described in (a) was used to investigate the nature of the boundary between *F. novae-zelandiae* and *F. matthewsii* along this sequence. Two additional populations in the Waimakariri and White River valleys, Waimakariri at 770 m and Kilmarnock at 880 m were sampled in the same manner in order to increase the representation of populations in the transition zone. Distances between populations decreased with increasing altitude, however all populations were at least 1 kilometre apart.

The sequence examined therefore consisted of eight populations in sites ranging in altitude from 540 m to 1050 m in comparable habitats but under increasing annual rainfalls at higher altitudes (Table 5.4). Representative material of all populations was deposited in the University of Canterbury herbarium. Accession numbers are tabulated in Appendix 2.

Mean values for lamina length, lamina abaxial hair density, culm height and upper culm internode hair density were calculated for each site. In addition the proportion of individuals at each site with glabrous leaves and culms was determined.

(c) Attributes of 18 populations in cultivation.

Plants from 18 of the 42 populations were grown on under uniform conditions in the University shadehouse for a year. The plants were in pots filled with standard potting mix. They were watered regularly and were exposed to full sunlight.

Twelve of these populations had already been selected for cultivation to provide material for isozyme analysis (section 5.5) and material consisted of at least 10 individuals per population. Logistical constraints prevented the cultivation of a similar amount of material from all 42 populations so a subsample of six additional populations was selected and at least two plants brought into cultivation from each population. The additional material consisted of two populations of "high altitude" *F. novae-zelandiae*, two *F. matthewsii* populations and two populations situated along the

sequence of sites in the upper Waimakariri. After a year in cultivation 128 healthy individuals were remeasured for a subset of vegetative characters. No floral characters were remeasured as not all of the material flowered in cultivation.

Paired T-tests were used to compare initial measurements with measurements taken after a year in cultivation.

5.3.2 Results

(a) Variation among 42 populations for 40 characters.

The 40 characters measured differed in the amount of variation present. Some characters such as lamina adaxial hair length remained virtually static for all populations while others showed substantial among-population variation. One-way analysis of variance found significant differences between the three taxa for 34 of the 40 characters (Table 5.3).

F. matthewsii and *F. novae-zelandiae s.s.* differed significantly in 28 characters. *F. matthewsii* and "high altitude" *F. novae-zelandiae* differed significantly in 24 characters. "High altitude" *F. novae-zelandiae* differed significantly from *F. novae-zelandiae s.s.* in 15 characters, most of which were associated with the size or numbers of vegetative or reproductive parts.

Principal components analysis using the 40 morphological characters produced a good separation of the 42 sites. The first ordination axis accounted for 87% of the total variation present within the data and was strongly associated with inflorescence branching angle and overall scabridity (hair densities) (Fig. 5.3, Table 5.5). *F. novae-zelandiae s.l.* and *F. matthewsii* were most distinct with reference to this axis. One population of *F. novae-zelandiae s.s.* (HLF) occurred on the far right of the ordination with the *F. matthewsii* populations. This was due to the very wide branching angles among individuals in this population. The mean branching angle for the population was 95.7 $\pm$ 37.0° which was the highest mean value recorded.

The second principal components axis accounted for a further 8% of the variation in the data and was related to factors of overall size which included length of leaf blade and height of culm. *F. novae-zelandiae s.s.* and "high altitude" *F. novae-zelandiae* were separated mainly with reference to this second axis (Fig. 5.3, Table 5.5).

Altitude, temperature and rainfall were strongly correlated with overall morphological trends (Fig. 5.4, Table 5.5). Rainfall was associated most strongly with the first axis and therefore with the separation of *F. novae-zelandiae* and *F. matthewsii*. Altitude and maximum annual temperature were most strongly associated with the second axis and therefore with the separation of *F. novae-zelandiae s.s.* and "high altitude" *F. novae-zelandiae*.

The first two axes from an ordination of the 42 sites by vegetation composition (section 5.2) were significantly related to the ordination of the same sites by morphology (Fig. 5.4). The first morphological axis was significantly correlated with the second vegetation axis and the second morphological axis was significantly correlated with the first vegetation axis (Table 5.5).

Stepwise regression was used to develop explanatory models for 5 characters; lamina length, lamina abaxial hair density (used as a measure of lamina scabridity), branch angle, 3rd culm internode length and 3rd culm internode hair density (used as a measure of culm scabridity). These characters were selected to represent the general trends in size and scabridity identified by principal components analysis.

Variation among the sites in maximum annual temperature explained 42% and 35% respectively of the variation in lamina length and 3rd culm internode length among all 42 populations (Table 5.6a). When populations of *F. matthewsii* were omitted from the analysis the amount of

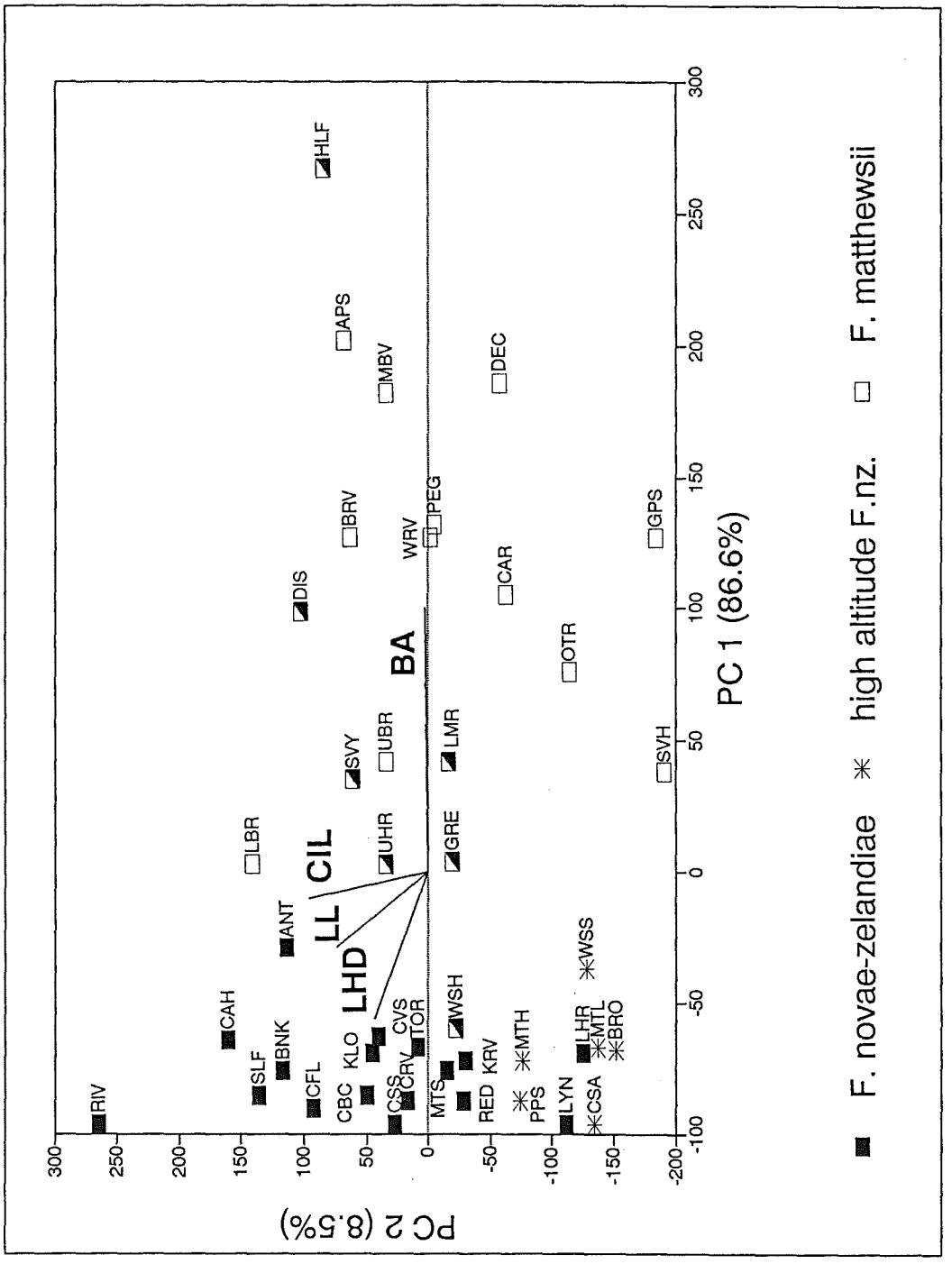


Figure 5.3: Axes 1 and 2 from a Principal Components Ordination of 42 populations of tussock *Festuca* by 40 morphological characters. The direction and magnitude of trends in selected characters are superimposed. LHD = lamina abaxial hair density, LL = lamina length, CIL = 3rd culm internode length, BA = 1st inflorescence branch angle.

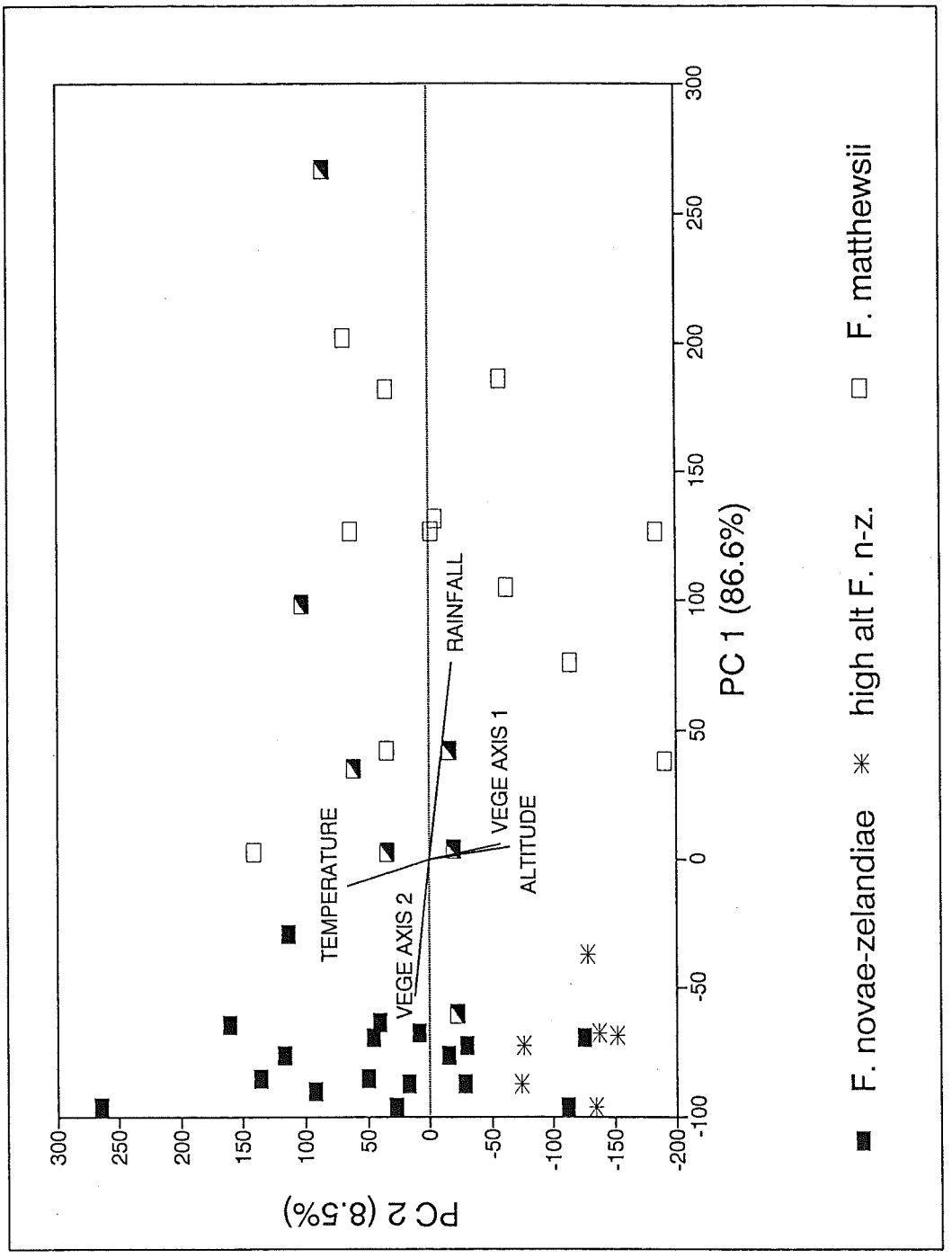


Figure 5.4: Axes 1 and 2 from a Principal Components Ordination of 42 populations of tussock *Festuca* by 40 morphological characters. The direction and magnitude of trends in environmental variables and axes 1 and 2 from an ordination of the 42 sites by vegetation composition are superimposed.

Table 5.5: Pearsons coefficients from correlations of Axes 1 and 2 of a PCA ordination of 42 tussock Festuca populations by morphology with (a) morphological characters, (b) environmental variables and (c) Axes 1 and 2 from a DCA ordination of the 42 sites by species composition.

VARIABLE	AXIS 1	*P* <	AXIS 2	*P* <
(a)				
Lamina length	-0.29	NS	0.73	0.001
Lamina abaxial hair density	-0.56	0.001	0.43	0.01
3rd culm internode length	-0.10	NS	0.95	0.001
3rd culm int. hair density	-0.75	0.001	0.26	NS
upper culm sheath length	-0.68	0.001	0.76	0.001
Spikelets per inflorescence	0.30	NS	0.76	0.001
1st inflor. branch angle	1.00	0.001	0.02	NS
(b)				
Altitude	0.05	NS	-0.64	0.001
Annual rainfall	0.76	0.001	-0.19	NS
Mean max. temperature	-0.10	NS	0.66	0.001
(c)				
Vegetation DCA Axis 1	0.06	NS	-0.58	0.001
Vegetation DCA Axis 2	-0.53	0.001	0.11	NS

Table 5.6: Coefficients from step-wise regression of morphological characters on environmental variables for (a) 42 populations of F. novae-zelandiae *s.s.*, "high altitude" F. novae-zelandiae and F. matthewsii and (b) as for (a) but excluding the 16 populations of F. matthewsii.

Dependant Variable	Constant	MaxTmp	PPT	R^2	*P* <
(a)					
Lamina length	5.61	1.22		0.42	0.001
Lamina abax. hair density	2.76		-5x10-4	0.53	0.001
1st inflor. branch angle	-0.58		0.01	0.56	0.001
3rd culm internode length	-1.83	2.46		0.35	0.001
hair density	7.09		-1x10-3	0.62	0.001
(b)					
Lamina length	7.14	1.12		0.56	0.001
Lamina abax. hair density	3.51		-9x10-4	0.25	0.01
1st inflor. branch angle					NS
3rd culm internode length	3.69	2.01		0.29	0.01
hair density					NS

variance explained increased to 56% for lamina length and decreased to 29% for culm length (Table 5.6b).

Variation in annual rainfall among sites constituted the best correlative for variation in inflorescence branching angle, lamina and culm scabridity among all 42 populations (Table 5.6a). Variation in annual rainfall was also an important factor in variation in lamina scabridity when only populations of *F. novae-zelandiae* were considered. However no environmental variable was significantly related to branch angle or culm scabridity (Table 5.6b).

The branching angle of the lowest inflorescence branch appeared to be associated with the growth of a brown callus between the branch base and the rachis. Smaller calluses were also observed at the base of upper inflorescence branches. *F. matthewsii* typically possessed at least a callus at the lowest inflorescence branch, as did some *F. novae-zelandiae* individuals with wide branching angles, for example from the Hallelujah Flat (HLF) population. Cheeseman (1925) mentioned this "curious brown pulvinate callus" at the junction of the lamina and sheath and the inflorescence branches and the rachis as a feature of *F. matthewsii* but it appears to be associated with branching angle regardless of taxon.

(b) Variation at the boundary between *F. novae-zelandiae* and *F. matthewsii*.

Plants within the eight populations studied displayed a range of combinations of characters from *F. matthewsii* and *F. novae-zelandiae*. For example plants with long glabrous leaves and short scabrid culms would occur adjacent to plants with short scabrid leaves and long glabrous culms.

The eight populations formed a cline in lamina and culm scabridity, with increasing numbers of glabrous individuals in higher altitude populations. This result was not due to these populations being composed of individuals of both species as culm and leaf scabridity varied independently (Fig. 5.5). Similarly mean values for both lamina and culm internode hair density declined sharply with increasing altitude (Figs. 5.6 & 5.7).

Mean values for lamina length and culm height formed a more complex pattern. The lower altitude *F. novae-zelandiae* populations had the highest values for mean lamina length (Fig. 5.8). Plants become progressive shorter on average with increasing altitude up to 800 m after which lamina length appeared to increase slightly.

Lower altitude populations also had the longest culms on average and culm height decreased with increasing altitude up to 800 m (Fig. 5.9). However the two highest altitude *F. matthewsii* populations, Kilmarnock and White River, had culms comparable in length to the lower *F. novae-zelandiae* populations.

(c) Attributes of 18 populations in cultivation

After one year in cultivation five characters (lamina length, lamina width, lamina abaxial hair length, lamina abaxial hair density and sheath length) were remeasured for each of 128 plants from 18 populations. These characters were selected on the basis that they were associated with the morphological trends identified in the ordination of all 42 sites and were also easy to remeasure on

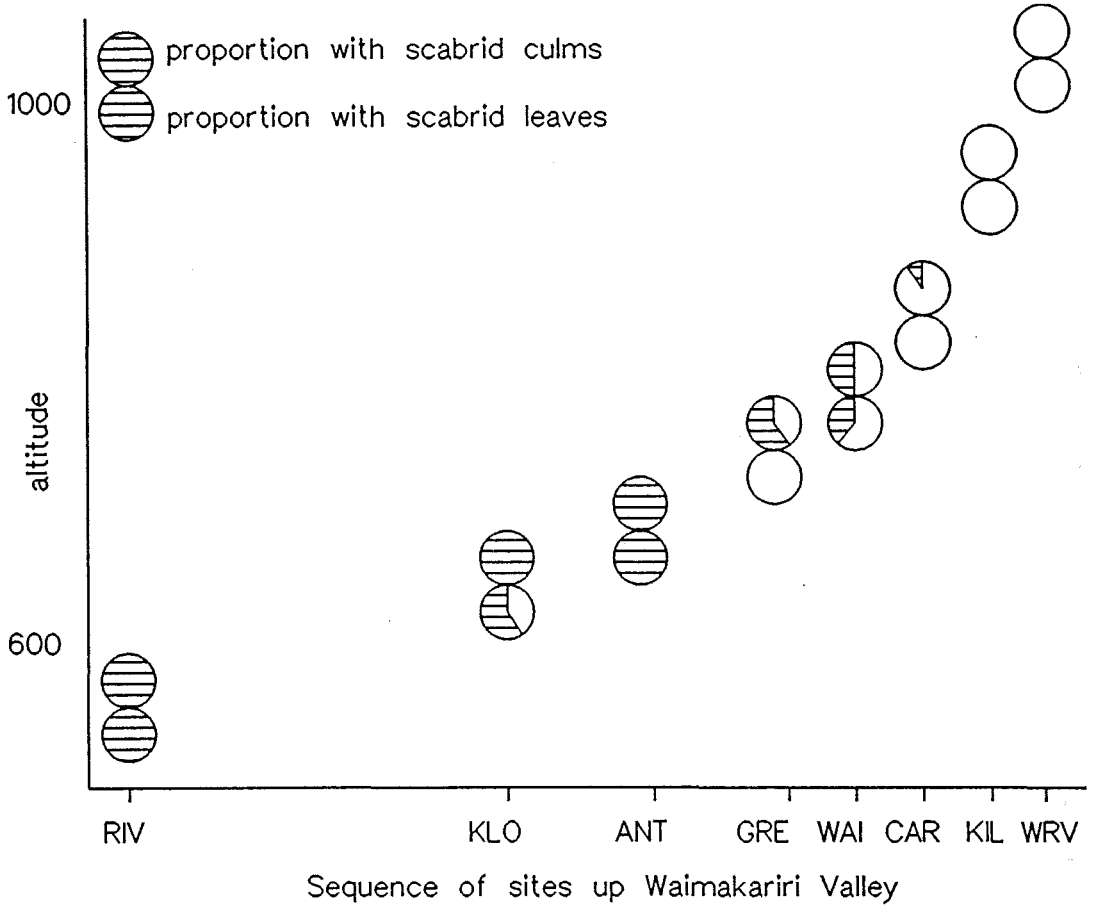


Figure 5.5 : Frequency of scabrid plants in populations at the distributional boundary of F. novae-zelandiae (left) and F. matthewsii

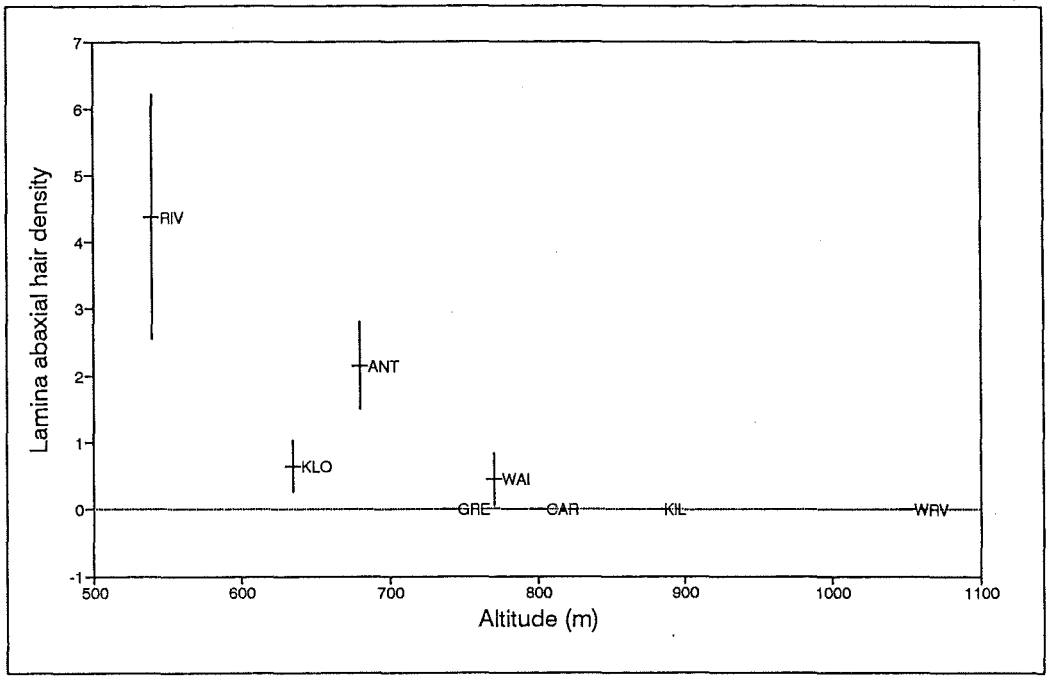


Figure 5.6: Mean lamina scabridity (abaxial hair density) in populations at the distributional boundary of *F. novae-zelandiae* and *F. matthewsii*. Hair density is 0.06 mm^{-2}.

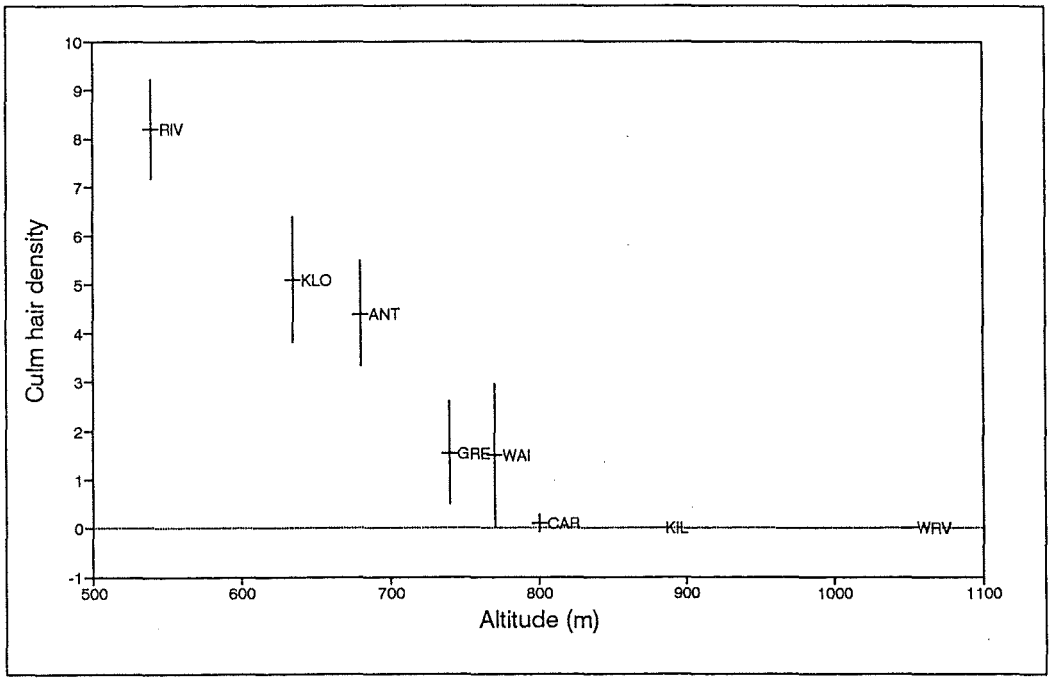


Figure 5.7: Mean culm scabridity (3rd internode hair density) in populations at the distributional boundary of *F. novae-zelandiae* and *F. matthewsii*. Hair density is 0.06 mm^{-2}.

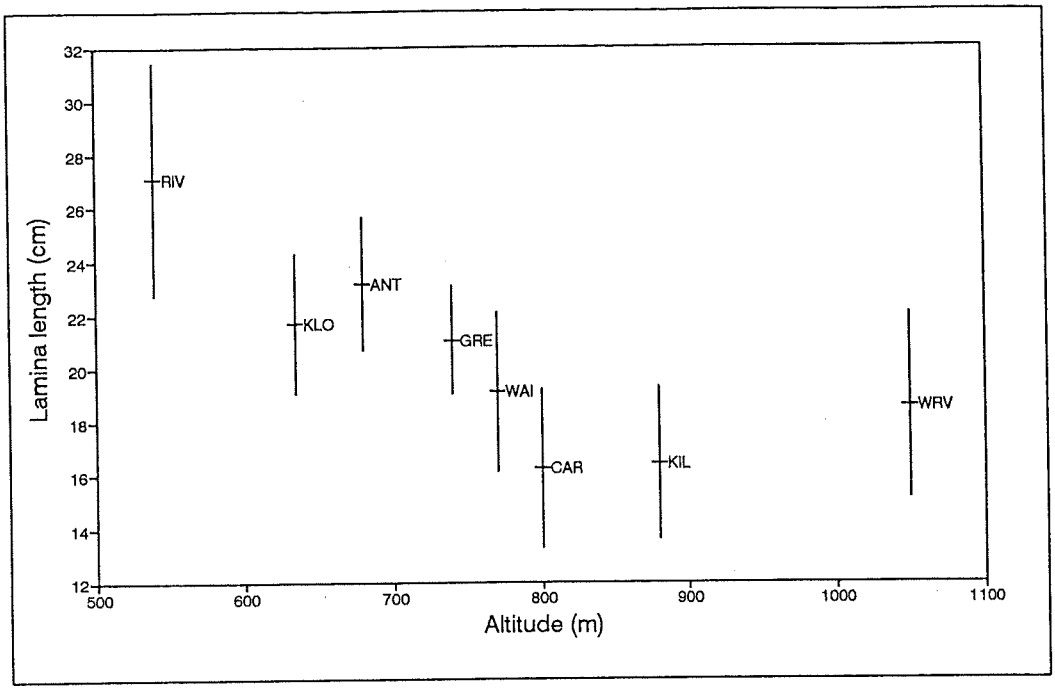


Figure 5.8: Mean lamina length in populations at the distributional boundary of *F. novae-zelandiae* and *F. matthewsii*.

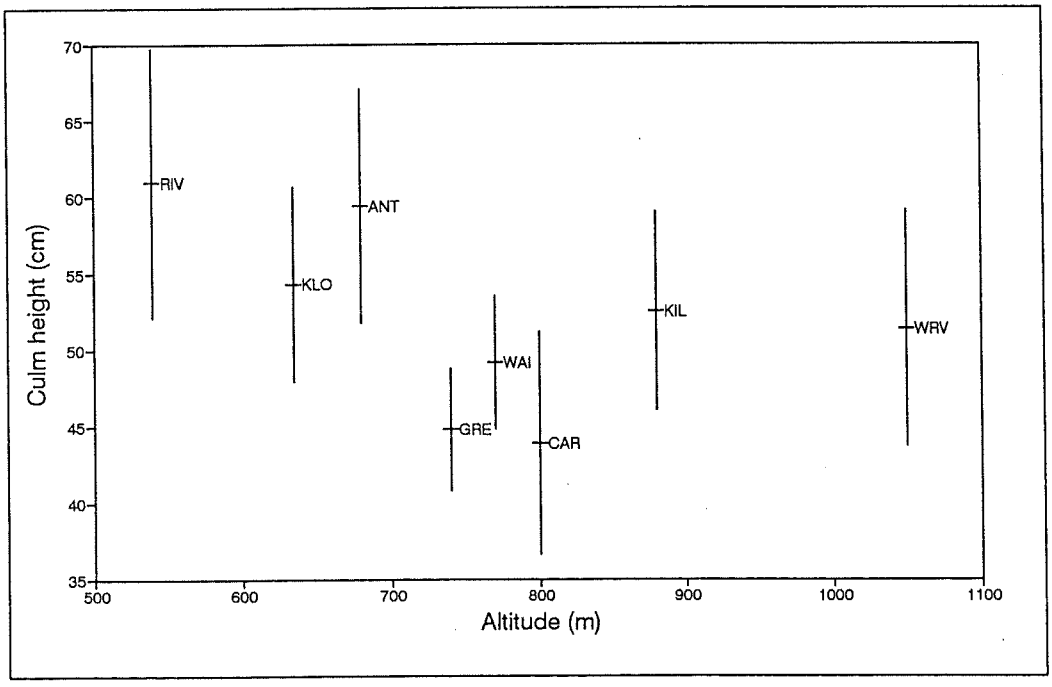


Figure 5.9: Mean culm height in populations at the distributional boundary of *F. novae-zelandiae* and *F. matthewsii*.

non-reproductive material.

When field and glasshouse measurements for all populations were compared using a paired T-test, lamina length was found to have increased significantly under cultivation ($T = 2.27, P < 0.05$). In five populations mean lamina length in cultivation was shorter than in the field however the differences were slight (Fig. 5.10).

Overall lamina abaxial hair density also decreased significantly in cultivation ($T = -2.68, P < 0.05$). Three populations showed an increase in lamina abaxial hair density in cultivation but once again the differences were slight (Fig. 5.11). No significant overall change was found in sheath length, lamina width or lamina abaxial hair length under cultivation.

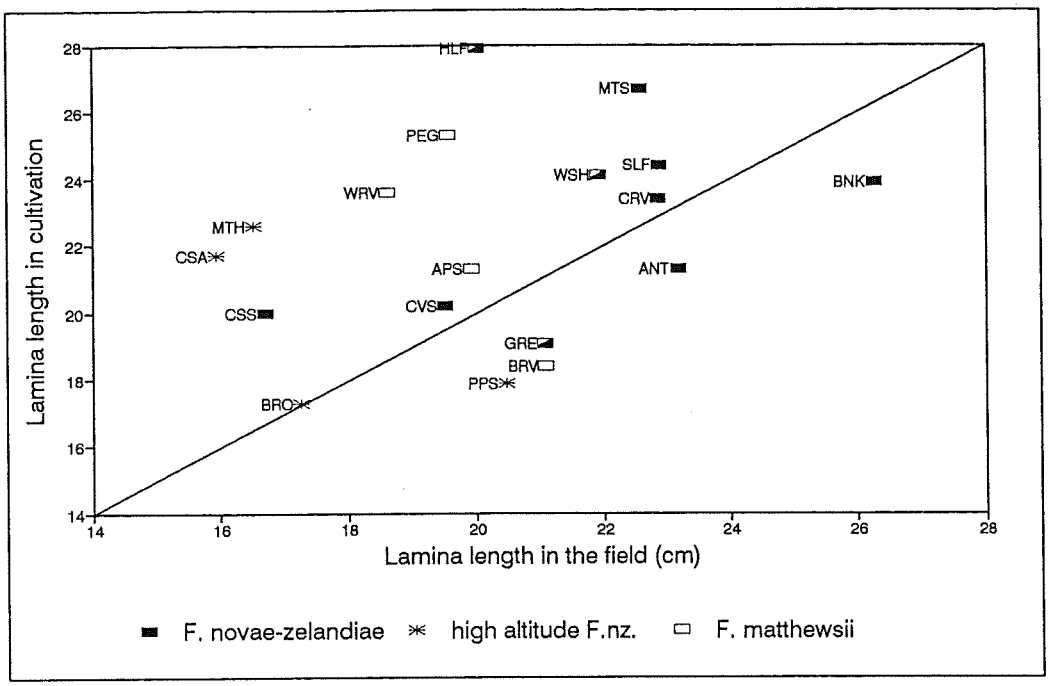


Figure 5.10: Mean lamina length of 18 populations of tussock *Festuca* in cultivation compared with lamina length in the field.

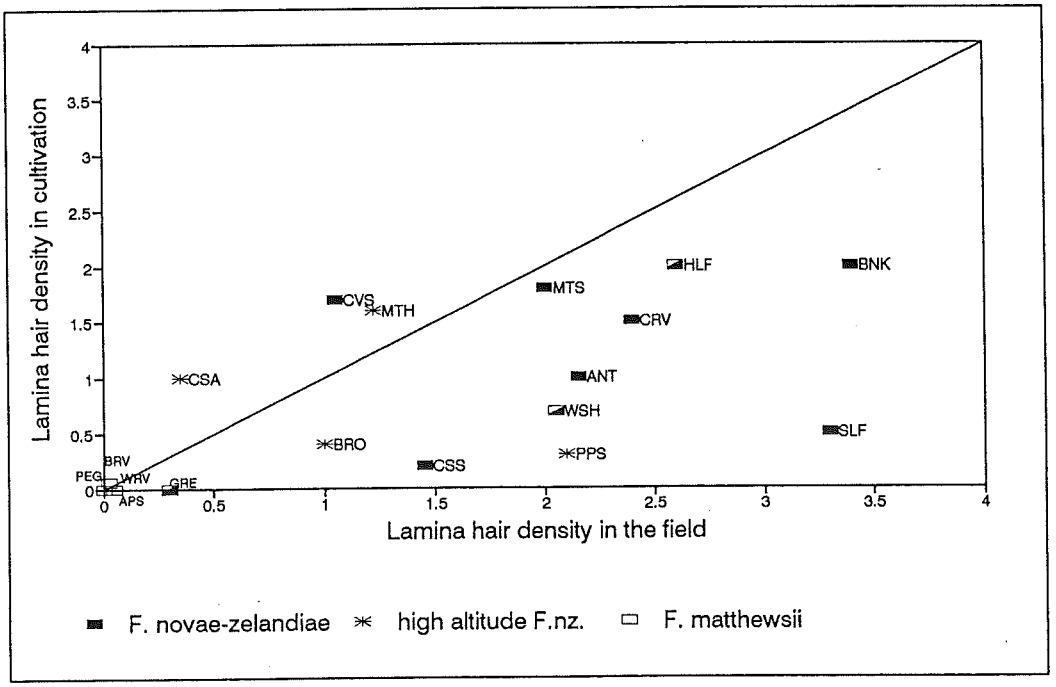


Figure 5.11: Mean lamina scabridity (abaxial hair density) of 18 populations of tussock *Festuca* in cultivation compared with lamina scabridity in the field. Hair density is 0.06 mm^{-2}.

5.3.3. Discussion

(a) Variation among 42 populations belonging to three taxa

The strong environmental gradients that affect central South Island appear to be of major importance to patterns of morphological variation among tussock-forming *Festuca*. The combination of a prevailing westerly air flow and the Southern Alps produces a pronounced west-east rainfall gradient superimposed on gradients of altitude and temperature.

The differences between *F. novae-zelandiae s.s.* and *F. matthewsii* are mainly quantitative rather than qualitative, however studies of plants in cultivation both here and by Connor (1968) have shown that distinguishing characters of glabrousness and inflorescence structure are genetically fixed in *F. matthewsii*.

Degree of scabridity also varies within *F. novae-zelandiae s.s.* apparently in relation to rainfall. Some higher altitude / rainfall populations contain glabrous individuals. Therefore the pattern of genetically determined differences between *F. novae-zelandiae s.s.* and *F. matthewsii* is echoed by smaller genetic and phenotypic differences among populations within *F. novae-zelandiae s.s.* which experience similar conditions.

"High altitude" *F. novae-zelandiae* was generally less scabrid than *F. novae-zelandiae s.s.* and mean values for other characters of "high altitude" *F. novae-zelandiae* were intermediate between *F. novae-zelandiae s.s.* and *F. matthewsii*. However it is unlikely that hybridization with *F. matthewsii* was a factor in the evolution of the "high altitude" form of *F. novae-zelandiae* (H. E. Connor *pers. comm.*) despite the tendency for "high altitude" populations to display features more usually associated with *F. matthewsii*, as "high altitude" *F. novae-zelandiae* has a predominantly eastern distribution. Instead the genetically-fixed shared character-states are most likely due to the selective influence of similar environmental conditions.

The similarity between the ordinations of these 42 sites by morphology and by vegetation composition could be a result of the importance of the same environmental gradients to both patterns of variation. The relationship between the two sets of axes was not sufficiently strong to indicate that differences in the vegetation *per se* were driving patterns of morphological variation.

(b) The nature of the boundary between *F. novae-zelandiae s.s.* and *F. matthewsii*.

Clinal variation at the boundary between *F. novae-zelandiae s.s.* and *F. matthewsii* could be due to any one or a combination of three factors. The intermediate populations could be a result of hybridization, as the two species are in contact and freely interfertile (Connor, 1968). Alternatively environment influences could have brought about the parallel evolution of *F. matthewsii*-type characters in populations of *F. novae-zelandiae s.s.* in higher altitude and rainfall areas, as may have happened with "high altitude" *Festuca novae-zelandiae*. Alternatively populations of *F. novae-zelandiae s.s.* at higher altitudes and rainfalls may mimic aspects of *F. matthewsii* via phenotypic plasticity.

Examination of the plants in cultivation has shown that differences between populations are at least partly genetic. Therefore the clinal variation observed at the boundary of *F. novae-zelandiae s.s.* and *F. matthewsii* is not entirely due to the plasticity of either species in response to an environmental gradient. Connor (1968) expressed doubts about the natural occurrence of hybrids between *F. novae-zelandiae s.s.* and *F. matthewsii* due to their being ecologically separated. He considered that the two species evolved allopatrically with little opportunity in pre-human New Zealand to hybridize. However large river valleys such as the one studied would have been natural contact zones between the two species thereby facilitating limited gene-flow via hybridization.

The pattern of clinal variation observed among tussock-forming *Festuca* in the upper Waimakariri River could be a result of the genetic specialisation of each population to its position along an environmental gradient, augmented by phenotypic plasticity. However it is more parsimonious to hypothesize that the cline represents a zone of limited hybridization. Hybrid offspring may be adaptive within a limited portion of the prevailing environmental gradient but, as the zone of intermediacy appears to be limited, hybrids may not competitive enough in the habitats of either parent to facilitate complete merging of the two species.

Selective forces generated by the differential adaptiveness of two hybridizing taxa are thought to be sufficient to maintain a stable, narrow hybrid zone (Moran, 1981) and the more intense the selection the narrower the zone (Levin, 1988; Freeman *et al.*, 1991). The zone of intermediacy between *F. matthewsii* and *F. novae-zelandiae s.s.* in the upper Waimakariri is approximately six kilometres long up the river valley and spans approximately 100 vertical metres. This zone is relatively narrow considering the ranges of the parent species. This would suggest that *F. matthewsii* and *F. novae-zelandiae s.s.* are differentially adapted to their positions along the dominant environmental gradients of the South Island mountains and differential selective forces maintain their separation.

Experimental crosses between *F. matthewsii* and *F. novae-zelandiae s.s.* conducted by Connor (1968) indicated that *F. matthewsii* characters were dominant among F1 progeny. However the F2 generation involved a range of recombinations of *F. novae-zelandiae s.s.* and *F. matthewsii* characters and an overall reduction in panicle size.

Plants in the populations suggested here as representing a hybrid zone also showed a range of recombinations of *F. matthewsii* and *F. novae-zelandiae s.s.* characters. There also appeared to be a reduction in culm length and lamina length in these intermediate populations compared with values for the parent species. These patterns further reinforce the hypothesis that a naturally occurring zone of hybridization does exist between *F. matthewsii* and *F. novae-zelandiae s.s.*.

(c) Attributes of 18 populations under cultivation.

Although the 18 populations studied varied in the magnitude of morphological changes observed under cultivation no direct between-population comparisons in levels of plasticity can be made using these data. This is because the change in environment from site of origin to the University shadehouse is not of equal magnitude for all 18 populations.

However if the differences observed among populations in the field were solely a result of phenotypic plasticity, all plants should become more similar when grown in the same environment.

Convergence was not observed in any character measured and the range of values among populations in cultivation is comparable to that among the populations in the field. This would suggest that differences observed in the field are in part due to genetically determined traits.

Changes in lamina length in cultivation differed among the four *F. matthewsii* populations and as a result the range of lamina length among these populations actually increased under cultivation. The conditions experienced by these populations in the field would therefore appear to be acting in a stabilizing manner. Phenotypic plasticity enables them to appear more similar in the field than under uniformly favourable conditions (Bradshaw, 1965).

The four "high altitude" *F. novae-zelandiae* populations also appeared to respond differently to conditions in cultivation. Porters Pass (PPS) and Broken River (BRO) showed little change in lamina length whereas the lamina length of plants from Mt. Horrible (MTH) and Cass Saddle 'A'(CSA) increased markedly. This would suggest that the first two populations are genetically fixed for small size and therefore correspond closely to the "high altitude" form of *F. novae-zelandiae* described by Connor & Edgar (1986) and Connor (*pers. comm.*). However the other two populations may well be *F. novae-zelandiae s.s.* but resemble "high altitude" *F. novae-zelandiae* phenotypically due to a plastic response to local site conditions.

5.4 PHENOLOGICAL VARIATION IN CULTIVATION

5.4.1 Methods

Of the 18 populations in cultivation that were used in section 5.3(c), 44 plants from 11 different populations flowered in the season of 1991/92. The number of plants flowering per population varied from 1 to 9. Six of the 11 populations were of *F. novae-zelandiae s.s.* originating from a variety of sites ranging in altitude from 65 m to 1240 m. Four of the populations were of *F. matthewsii* and one populations was of "high altitude" *F. novae-zelandiae* from Porters Pass. A record was made of the date culms were first observed on each plant and the timing of anthesis.

Linear regression was used to investigate the importance of altitudinal variation among the sites from which the populations originated in explaining the observed variation in flowering phenology.

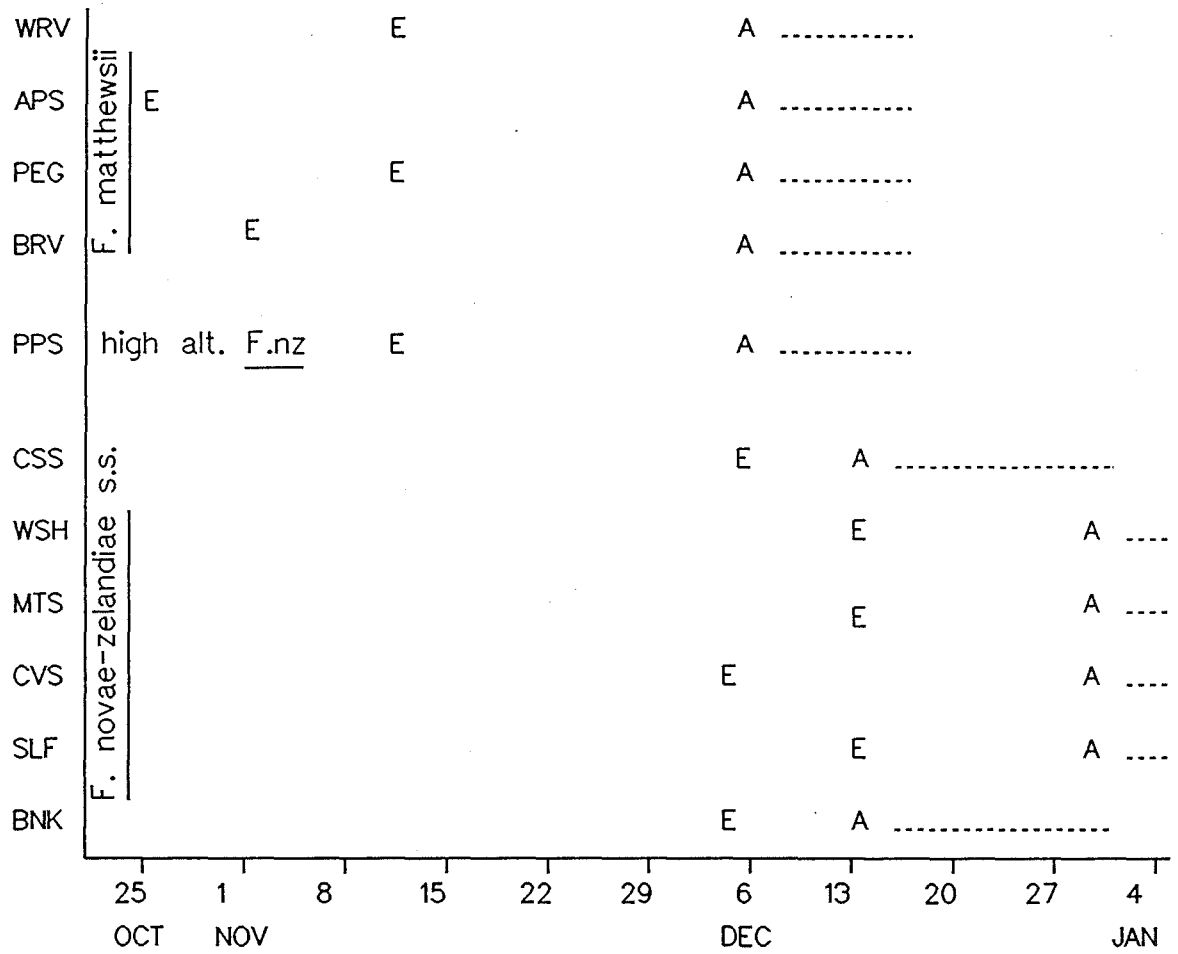
5.4.2 Results

Plants of *F. matthewsii* were the first to produce culms in cultivation in late October (Fig. 5.13). Plants of *F. novae-zelandiae s.s.* first produced culms in early December. All four *F. matthewsii* populations produced culms earlier than any of the six *F. novae-zelandiae s.s.* There was limited overlap between *F. matthewsii* plants and *F. novae-zelandiae s.s.* plants in the timing of anthesis.

Three plants from the "high altitude" *F. novae-zelandiae* population at Porters Pass flowered. However timing of initial culm emergence and anthesis was in synchrony with *F. matthewsii* plants rather than *F. novae-zelandiae s.s.*

Altitudinal variation among the sites from which the 11 populations originated was not significant in explaining variation in date of culm emergence (R^2 = 0.01, *df* = 9, NS). Even when regressions were performed within each species rather than between species, variation in altitude did not significantly explain variation in flowering phenology (*F. matthewsii* : R^2 = 0.28, *df* = 3, NS; *F. novae-zelandiae s.s* : R^2 = 0.01, *df* = 5, NS). However, when tested with One-way Analysis of Variance, the date of culm emergence was found to differ significantly between the three taxa ($F_{2,8}$ = 42.2, $P < 0.001$).

Figure 5.12 : Flowering phenology in cultivation of 11 populations of tussock Festuca in 1991/92. E=culm emergence. A=anthesis.



5.4.3 Discussion

Differences in flowering phenology can serve as an effective barrier to hybridization between species and can lead to the evolution of genetic reproductive isolation (Stam, 1983). *F. matthewsii* and *F. novae-zelandiae s.s.* are phenologically distinct in cultivation with regard to timing of culm emergence, with *F. matthewsii* producing culms six to ten weeks earlier than *F. novae-zelandiae s.s.*. The earlier timing of emergence of *F. matthewsii* is probably a result of its adaptation to cooler spring temperatures; culm elongation being able to commence at lower temperatures than in *zelandiae s.s.*. Alternatively culm elongation in spring may be cued by different daylengths in the two species.

However because plants appear to overlap in the timing of anthesis, the flowering phenology of these species presents only a minor barrier to hybridization where the species co-occur. Differences in culm emergence but an overlap in anthesis have previously been observed between these two species in cultivation (Connor, 1964). Reported timing of flowering of the two species in the field (Scott, 1960; Connor, 1968) indicates that they also could overlap at anthesis where they co-occur (Connor, 1968). Observations made during the course of this study on the flowering stage of populations encountered over the summer indicate that populations of *F. matthewsii* at the heads of river valleys overlap in timing of anthesis with populations of *F. novae-zelandiae s.s.* further down the valley. As stated in section 5.3, the boundary between *F. matthewsii* and *F. novae-zelandiae s.s.* appears to be characterised by a zone of intermediacy. The flowering phenology of populations within, and either side of, this zone would not provide a significant barrier to gene-flow and hybridization.

The early flowering and anthesis of the Porters Pass plants indicates that this taxon, in a similar manner to *F. matthewsii*, has adapted to cooler spring conditions and culm elongation commences at lower temperatures than in *F. novae-zelandiae s.s.*

Although adaptation to cooler temperatures is suggested by the differences in flowering phenology of *F. matthewsii* and "high altitude" *F. novae-zelandiae*, when compared with *F. novae-zelandiae s.s.*, no similar genetically fixed differences appear to occur within either *F. matthewsii* or *F. novae-zelandiae s.s.* with relation to altitude. This result could be due to small sample sizes and insufficiently frequent monitoring obscuring subtle differences between populations. However a lack of finer scale specialisation would be in keeping with what has already been discovered about the biology of *F. novae-zelandiae s.s.*. Due to long generation times, low population turnover and infrequent episodes of disturbance and recolonisation, populations of both species may not have the opportunity to become specialised to a particular environment. Instead populations within each species appear to share a fixed flowering phenology that reflects the mean environment encountered by the species as a whole.

5.5 BIOCHEMICAL VARIATION

5.5.1 Introduction

Allozyme electrophoresis was used to investigate the amount of genetic variation and the degree of population differentiation present within *F. novae-zelandiae* and the manner in which this species was related genetically to *F. matthewsii*.

Allozyme electrophoresis is ideal for investigating genetic variation at the species and population level as large numbers of individuals can be screened quickly and cheaply. The technique relies on the existence of electrophoretically distinguishable forms of enzymes (= allozymes). In any one individual these can be coded for by genes from more than one locus and any one locus can be multi-allelic with allele frequencies behaving according to the laws of Mendelian segregation.

5.5.2 Methods

(a) Electrophoretic Procedure

Nine *F. novae-zelandiae* populations used for previous experiments (sections 3.4 & 4.3), an additional *F. novae-zelandiae* population with characteristics intermediate between *F. novae-zelandiae* and *F. matthewsii* and two *F. matthewsii* populations were selected for analysis (Table 5.7). Tillers were collected from at least 20 randomly selected plants at each site and grown in a heated glasshouse for a minimum of eight weeks to allow for the production of new tillers under standard conditions.

For the analysis a young vigorous tiller was selected from each plant and 15 mm of unpigmented tissue from the tiller base was homogenised in 2 drops of extraction buffer using a mechanical grinder. The extraction buffer consisted of 50 mls 0.1 M tris(hydroxymethyl)aminomethane, 6 mM ascorbic acid, 6 mM cysteine, 0.5 M sucrose, 1 mM dithiothreitol, 0.05 mM EDTA, 4% w/v polyvinyl pyrolidione and 3 drops B-mercaptoethanol brought to pH 7.5 with HCl.

The homogenate was absorbed onto 3 mm wide wicks made of Whatman No. 1 filter paper. The samples were prepared directly from growing material the same day the gels were to be run, as either freezing or refrigeration resulted in loss of enzyme activity.

The prepared wicks were inserted in a chilled 12.5% (w/v) starch gel 70 mm wide, 230 mm long and 10 mm thick. Two buffer systems were used:
(1) Electrode buffer: 0.06 M lithium hydroxide / 0.3 M boric acid pH 8.1. Gel buffer: 1/100 dilution of electrode buffer
(2) Electrode buffer: 0.125 M Tris adjusted to pH 7.0 with citric acid. Gel buffer: 0.014 M L-histidine 0.002 M EDTA adjusted to pH 7.0 with Tris.

The gels were run under a constant current of 50 mA per gel for 4 hours, during which time they were kept cool by trays of ice.

The gels were then sliced horizontally and separate slices stained for specific enzyme systems. Banding patterns were interpreted in terms of putative allelic and hybrid bands and the frequency of different allelic phenotypes recorded for each population. The procedure was repeated for all populations using material from the same plants in order to confirm results.

Table 5.7: Populations of tussock Festuca used for allozyme electrophoresis. Map references are NZMS 260 series except HLF which is NZMS 1. ALT = altitude (m), PPT = annual rainfall (mm).

Species	Population	Abbr.	Map Ref.	Alt	PPT
F. novae-zel.	Bankside	BNK	M36 423193	65	690
F. novae-zel.	Cass River	CRV	K34 071942	640	1500
F. novae-zel.	Cass Saddle 'B'	CSS	K34 031888	1240	2500
F. novae-zel.	Cass Valley	CVS	K34 053915	820	2000
F. novae-zel.	Hallelujah Flat	HLF	S59 286284	620	2250
F. novae-zel.	Mt. Sugarloaf	MTS	K34	1060	1250
F. novae-zel.	Sugarloaf Fan	SLF	K34 098959	670	1250
F. novae-zel.	Woolshed Hill	WSH	K33 093028	1140	2500
high alt. F. n-z.	Cass Saddle 'A'	CSA	K34 027883	1340	2500
high alt. F. n-z.	Porters Pass	PPS	K35 080673	1000	1000
F. matthewsii	Arthurs Pass	APS	K33 923095	880	6000
F. matthewsii	Bealey River	BRV	K33 925075	760	5000

Table 5.8: Enzyme system standard abbreviations and codes, buffer systems used, number of loci consistently scorable and total number of alleles observed per locus.

Enzyme	Standard Code	Buffer used	No. of Loci	No. of Alleles
6PG	EC 1.1.1.44	2	1	4
ACP	EC 3.1.3.2	2	2	2,2
G6P	EC 1.1.1.49	2	2	5,4
IDH	EC 1.1.1.42	2	1	3
LAP	EC 3.4.11/13	1	1	1
MDH	EC 1.1.1.37	2	1	5
MR	EC 1.1.1.40	2	1	5
PGI	EC 5.3.1.9	1	2	2,5
PGM	EC 2.7.5.1	2	1	3
SOD	EC 1.15.1.1	1	2	2,1

(b) Analysis

Polyploidy creates difficulties in the interpretation of allozyme banding patterns and the species being investigated in this experiment are hexaploid. The analysis of progeny arrays or haploid tissue can reveal the parent's genome or comparisons can be made with related diploid taxa (e.g. Brown *et al*, 1974; Werth, 1978; Barrett & Shore, 1989).

If observed banding patterns are simple, the relative intensity of bands can be interpreted as 'gene dosage' and thus provide allele frequency data (Kephart, 1990; A. H. D. Brown *pers. comm.*). However these techniques cannot be easily applied to high-polyploid out-crossing species such as *F. novae-zelandiae* and *F. matthewsii* which lack close diploid relatives. Instead I have utilised two alternative methods involving allele frequency estimates and phenotype frequencies.

i) Estimated allele frequency

For a diploid species, allele frequencies can be calculated directly from genotype frequencies,

p = freq. homozygote 'aa' + 1/2 freq. heterozygote 'ab'

where p is the frequency of allele a.

In this study only banding phenotype frequencies were known and each phenotype could represent more than one genotype. However by using an extended version of the equation above, an estimate of allele frequency can be obtained from phenotype frequencies i.e.

p = freq. homozygote + 1/2 freq. of biallelic heterozygote + 1/3 freq. of triallelic heterozygote + . . .
+ 1/n freq. of n-allelic heterozygote.

Of course this equation does not represent expected genotype frequencies under Hardy-Wienberg equilibrium as the influences of genomic structure and modes of segregation are totally ignored, but it does at least provide an index of allele frequency. However this method does have the drawback that a population exhibiting uniform fixed heterozygosity at a locus will be recorded as being polymorphic at that locus with frequency estimates identical for all alleles. It would therefore be indistinguishable from a population in which the alleles actually occurred at equal frequencies, but segregating into homozygotes and heterozygotes according to Hardy-Wienberg expectations. This would result in an over-estimate of the proportion of loci exhibiting polymorphisms, an over-estimate of within-population variation and possibly an under-estimate of between-population variation.

I tested the accuracy of the method by comparing calculated allele frequencies with known frequencies from an artificial population that corresponded to a diploidised autoploid with identical allele frequencies across parental loci: a highly unlikely situation but an easy model to deal with.

Vickery (1990) dealt with polyploid allozyme data by using the percent presence of each allele at each locus as the gene frequency. However his method lacked the degree of resolution possible in the method described above and resulted in ambiguity when frequencies were compared between ploidy levels.

ii) Phenotype frequency:

Allozyme phenotypes have previously been used to obtain basic qualitative information on population variation in the absence of a formal genetic interpretation (e.g., Grant *et al*, 1984). However phenotype frequencies are also amenable to statistical analysis in a similar manner to allele frequencies.

For example the measure of genetic identity, 'I', put forward by Nei (1972) can in its simplest form be applied to phenotype frequencies without any change to the equation itself. This is because the equation concerns probabilities of identity. In a similar manner Nei's (1973) genetic diversity statistics can also be applied to phenotype frequencies as measures of phenotypic diversity. This method makes no assumptions about the underlying genetic structure and mode of inheritance in the species studied and is therefore relatively robust. The only assumption required is that allozyme phenotypes reflect underlying genetic structure.

(iii) Further analyses

One-way analysis of variance was used to test for significant differences between the two species for each of percent loci polymorphic, mean alleles per locus, mean percent heterozygosity and the frequency of higher level multi-allelic phenotypes.

Pearson correlation was used to investigate the relationship between the geographical distance between pairs of populations and their phenotypic and genetic similarity as measured by Nei's genetic identity, *I* (Nei, 1972). Correlations were calculated for all pairs of populations including both species and for pairs of *F. novae-zelandiae* populations only.

The partitioning of genetic diversity within populations, between populations and between species was calculated for all populations from allele frequency estimates using Nei's (1973) diversity statistics. Allele frequency estimates were also used to calculate the partitioning of genetic diversity within populations and between populations for *F. novae-zelandiae* populations only.

Total phenotypic diversity and the partitioning of phenotypic diversity were likewise calculated from phenotype frequencies using Nei's diversity statistics for all populations of both species and for *F. novae-zelandiae* populations only.

The above measures of variability, similarity and partitioning of diversity were calculated using BIOSYS-1 (Swofford & Selander, 1981), a program designed specifically for electrophoretic data.

Principal Components Analysis of both allele frequency estimates and phenotype frequencies, as implemented by CANOCO using default options, was used to summarise the relationships between the populations and examine the importance of altitude, annual rainfall and temperature in the observed patterns of variation. Annual rainfall was based on recorded values from nearby stations (New Zealand Meteorological Service, 1982) and a rainfall isohyet map of the Waimakariri catchment (Greenland, 1977). Mean annual temperature was estimated using the regression equations of Norton (1985).

Principal Components Analysis was also performed on the 12 populations using morphological data collected earlier (section 5.3) and Detrended Correspondence Analysis was performed using vegetation data from section 5.2 for the same 12 populations. The axes from the ordination of phenotype frequencies were included in the above analyses as pseudo-environmental variables in order to investigate the concurrence between patterns of genetic, morphological and ecological variation.

5.5.3 Results

Of 17 enzyme systems examined for activity, 10 were consistently interpretable in all populations. These gave a total of 14 reliable loci exhibiting 43 alleles (Table 5.8). Two loci, LAP and SOD-2, were monomorphic for the same allele in all populations. The number of alleles observed at the remaining loci ranged from two to five (Table 5.8). The number of alleles per locus averaged across all loci for each population ranged from 2.2 to 2.9 (Table 5.9). *F. matthewsii* had significantly more alleles per locus on average than *F. novae-zelandiae* ($F = 6.32, P < 0.05$) although individual *F. novae-zelandiae* populations had values approaching those of *F. matthewsii*.

The number of allelic bands for any one individual ranged from one to four with multi-allelic phenotypes the rule. The two *F. matthewsii* populations had significantly more individuals with 3-allele and 4-allele phenotypes than the *F. novae-zelandiae* populations ($F = 32.85, P < 0.001$ and $F = 26.18, P < 0.001$ respectively).

The percentage of loci that displayed allelic polymorphism and percent heterozygous individuals per locus ranged from 71.4 to 85.7 and 45.5 to 72.2 respectively (Table 5.9) but neither showed a significant difference between species. Percent phenotypically polymorphic loci was lower, ranging from 57.1 to 85.7. The mean difference due to apparently 'fixed' heterozygosity was 7.2% (Table 5.9).

Three populations, Bealey River, Arthurs Pass (both *F. matthewsii*) and Sugarloaf Fan possessed unique alleles. Pooling the populations by species resulted in *F. novae-zelandiae* having four and *F. matthewsii* having three species-specific alleles. In all cases these alleles were rare.

When allele frequency estimates calculated by method 1 for an artificial population were compared with true values, in the simplest case of two alleles at a locus they were found to deviate in a systematic manner (Fig 5.13). The estimate coincided with the true value when the alleles were equal in frequency (i.e. $p = 0.5 = q$) or when one allele was fixed (e.g. $p = 1$ and $q = 0$). However the method over-estimated p when it was less than 0.5 and under-estimated it when it was greater than 0.5. This method would therefore tend to minimise frequency differences between alleles at a locus and between populations that differed only in which allele was most common.

Nei's genetic identity coefficients (Nei, 1972) based on allele frequency estimates resulted in the two *F. matthewsii* populations being on average as similar to *F. novae-zelandiae* (0.94 ± 0.08) as *F. novae-zelandiae* was within itself (0.94 ± 0.08). However the same comparison using phenotype frequencies produced smaller values. The phenotypic identity of *F. matthewsii* and *F. novae-zelandiae* populations was 0.75 ± 0.03 while within *F. novae-zelandiae* phenotypic identity was 0.83 ± 0.02.

The similarity between pairs of populations based on allele frequency estimates was significantly correlated with similarity based on phenotype frequencies when tested with Pearson correlations ($R^2 = 0.841, P < 0.001$).

Table 5.9: Allozyme variation within 12 populations of tussock Festuca. S = mean sample size per locus; P_a = % loci with > 1 allele; P_p = % loci with > 1 phenotype; A = mean alleles per locus; H_o = mean % heterozygosity (includes fixed).

Population	S	P_a	P_p	A	H_o
Bankside	24	78.6	78.6	2.5	53.87
Cass River	15	71.4	71.4	2.2	64.13
Cass Saddle 'A'	16	78.6	64.3	2.2	69.58
Cass Saddle 'B'	17.6	78.6	78.6	2.6	67.16
Cass Valley	17.8	78.6	71.4	2.7	68.20
Hallelujah Flat	12.6	78.6	71.4	2.5	64.73
Mt Sugarloaf	16.3	78.6	78.6	2.5	56.04
Sugarloaf Fan	66.9	85.7	71.4	2.6	45.47
Woolshed Hill	16	85.7	78.6	2.8	71.84
Porters Pass	30	85.7	78.6	2.7	62.14
Arthurs Pass	18	85.7	78.6	2.9	72.17
Bealey River	18	85.7	85.7	2.9	71.71

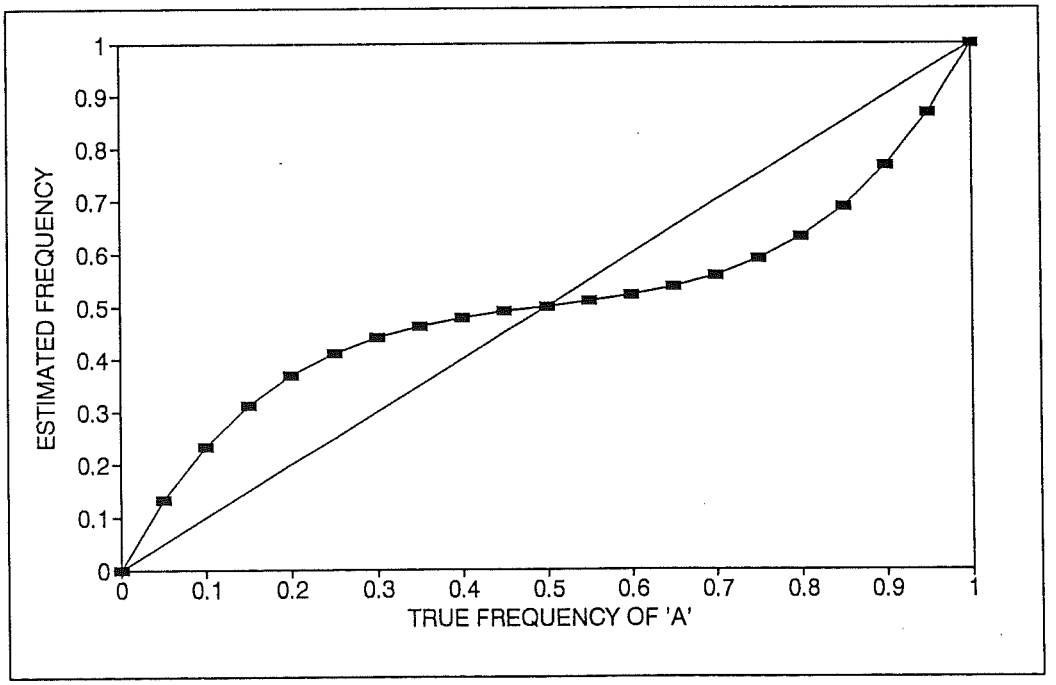


Figure 5.13: Relationship between true allele frequency and frequencies estimated using a Hardy-Wienberg analogue.

The geographical distance between pairs of populations was not significantly correlated with between-population similarity based on either allele frequency estimates or phenotype frequencies when tested with Pearson correlations (R^2 = -0.018, P > 0.05 and R^2 = -0.052, NS). When the correlations were repeated for pairwise comparisons within *F. novae-zelandiae* only, there was still no significant relationship between similarity based on either allele frequency estimates or phenotype frequencies and geographical separation between populations (R^2 = 0.132, NS and R^2 = 0.164, NS respectively).

Nei's diversity statistics using allele frequency estimates resulted in a mean total genetic diversity for polymorphic loci of 0.52 $\pm$ 0.08 for all populations (Table 5.10a). SOD-1 exhibited the lowest diversity (0.33) and G6P-2 the highest (0.67). On average the vast majority of this diversity (95.3 $\pm$ 3.04%) was due to within-population diversity, as opposed to between-population diversity which contributed 4.18 $\pm$ 3.08%. Between-species diversity contributed only 0.50 $\pm$ 0.43% on average to total genetic diversity as estimated by allele frequency calculations.

When the analysis was repeated with *F. novae-zelandiae* populations only, mean total genetic diversity decreased slightly to 0.51 $\pm$ 0.08. Between-population diversity accounted for on average 5.69 $\pm$ 4.27% of total diversity, however at two loci (SOD-1 and PGI-1) over 20% of the observed diversity was due to between-population differences (Table 5.10b).

The same statistics calculated using phenotype frequencies resulted in similar values for total phenotypic diversity for all populations (0.50 $\pm$ 0.09) but higher values for mean between-population and between-species diversity (22.0 $\pm$ 10.3% and 3.98 $\pm$ 3.63 respectively) (Table 5.11a). When the apportionment of phenotypic diversity was calculated for *F. novae-zelandiae* alone, 24.2 $\pm$ 11.5% of total phenotypic diversity was due to between-population differences (Table 5.11b). At the SOD-1 and PGI-1 loci the proportion of total phenotypic diversity due to between-population differences exceeded 60%.

PCA ordinations of the 12 populations using allele frequency estimates and phenotype frequencies were very similar. In the ordination of allele frequency estimates, the first two principal components axes jointly summarised 57% of the variation among populations (Fig. 5.14). In the ordination using phenotype frequencies, the first two axes jointly summarised 62% of the variation among populations (Fig. 5.15). Altitude, annual rainfall and maximum, mean and minimum annual temperatures were all significantly correlated with the observed trends in both ordinations (Table 5.12).

Both ordinations showed a similar pattern of relationships among the 12 populations. The two *F. matthewsii* populations occurred in close proximity to each other and the closest *F. novae-zelandiae* population to them in both cases was Woolshed Hill (WSH). The three *F. novae-zelandiae* populations from the upper Cass Valley, Cass Saddle 'A' (CSA), Cass Saddle 'B' (CSS) and Cass Valley (CVS) occurred together in both ordinations. The lower altitude *F. novae-zelandiae* populations Sugarloaf Fan (SLF), Hallelujah Flat (HLF) and Bankside (BNK) also occurred together in both ordinations. Mt. Sugarloaf (MTS) although geographically closest to Sugarloaf Fan shows as much similarity with the other high altitude populations.

Table 5.10: Total diversity (Nei, 1972) calculated from allele frequency estimates and percentage due to variation within and between populations and species, (a) for all 12 populations of both F. matthewsii and F. novae-zelandiae, and (b) for 10 populations of F. novae-zelandiae only.

(a)	**Total Diversity**	**% Within Populations**	**% Between Populations**	**% Between Species**
6PG	0.58	96.6	2.91	0.51
APH-1	0.18	94.5	2.75	2.75
APH-2	0.47	97.9	2.13	0
G6P-1	0.61	96.7	2.63	0.66
G6P-2	0.67	99.8	0	0.15
IDH	0.51	100	0	0
MDH	0.65	97.4	2.62	0
MR	0.63	94.7	4.31	0.96
PGI-1	0.47	86.9	13.0	0
PGI-2	0.63	99.0	0.95	0
PGM	0.54	98.7	0.37	0.93
SOD-1	0.33	81.4	18.5	0
mean	0.52	95.3	4.18	0.50
95% C.I.	± 0.08	± 3.04	± 3.08	± 0.43
(b)				
6PG	0.56	96.9	3.04	
APH-1	0.16	93.6	6.37	
APH-2	0.46	97.8	2.17	
G6P-1	0.58	97.2	2.76	
G6P-2	0.67	100	0	
IDH	0.51	99.4	0.59	
MDH	0.65	96.9	3.06	
MR	0.60	95.3	4.70	
PGI-1	0.46	86.2	21.6	
PGI-2	0.63	99.0	0.96	
PGM	0.54	99.4	0.56	
SOD-1	0.33	77.4	22.6	
mean	0.51	94.9	5.70	
95% C.I.	± 0.08	± 3.61	± 4.27	

Table 5.11: Total phenotypic diversity and percentage due to variation within and between populations and species calculated using Nei's diversity formulae (Nei, 1972), for (a) all 12 populations of both F. matthewsii and F. novae-zelandiae, and (b) 10 populations of F. novae-zelandiae only.

(a)

	Total Diversity	**% Within Populations**	**% Between Populations**	**% Between Species**
6PG	0.65	73.1	11.2	15.5
APH-1	0.32	86.1	12.6	0.95
APH-2	0.43	74.2	25.6	0.23
G6P-1	0.53	61.4	19.1	19.5
G6P-2	0.24	89.5	3.78	6.30
IDH	0.36	84.8	15.1	0
MDH	0.70	73.1	26.8	0
MR	0.75	76.7	18.1	5.03
PGI-1	0.41	37.3	62.6	0
PGI-2	0.56	91.5	8.49	0
PGM	0.61	95.4	4.26	0.33
SOD-1	0.48	43.9	56.1	0
mean	0.50	73.9	22.0	3.98
95% C.I.	± 0.09	± 9.92	± 10.3	± 3.63

(b)

6PG	0.57	87.2	12.8	
APH-1	0.27	85.8	14.2	
APH-2	0.47	77.0	23.0	
G6P-1	0.40	74.4	25.6	
G6P-2	0.16	94.4	5.55	
IDH	0.40	84.6	15.4	
MDH	0.71	72.0	28.0	
MR	0.71	80.8	19.1	
PGI-1	0.43	33.3	66.7	
PGI-2	0.53	91.7	8.29	
PGM	0.59	95.6	4.37	
SOD-1	0.49	32.8	67.1	
mean	0.48	75.8	24.2	
95% C.I.	± 0.09	± 11.5	± 11.5	

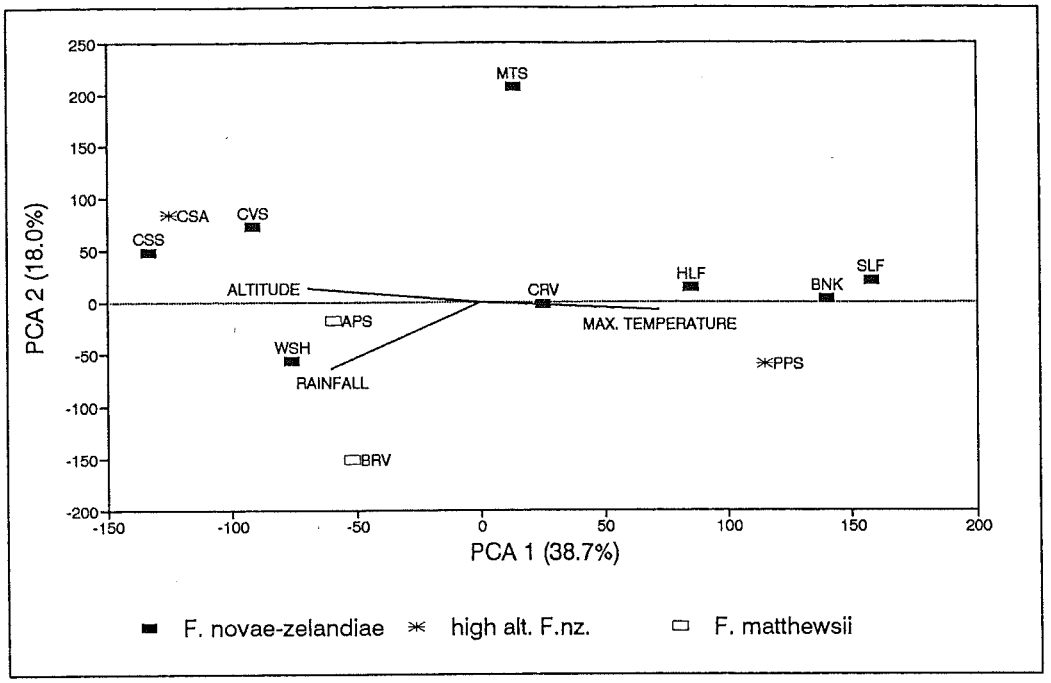


Figure 5.14: Axes 1 and 2 from an ordination of 12 populations of tussock Festuca using allozyme allele frequency estimates.

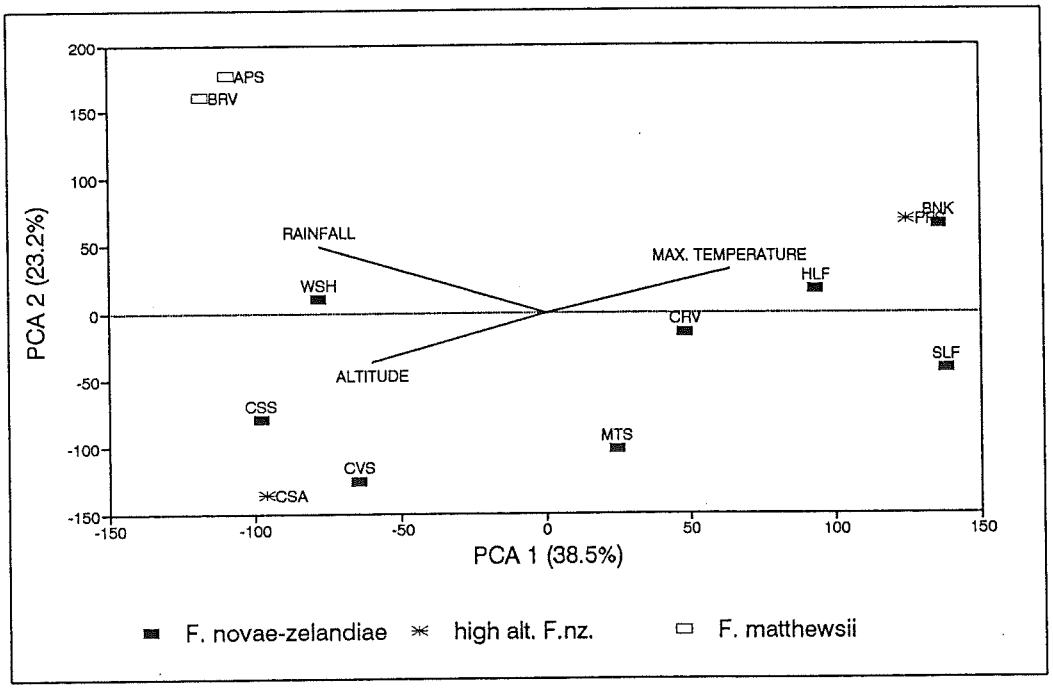


Figure 5.15: Axes 1 and 2 from an ordination of 12 populations of tussock *Festuca* using allozyme phenotype frequencies.

Table 5.12: Pearson coefficients and levels of significance for correlations between environmental variables and the first two principal components axes from ordinations of 12 tussock Festuca populations using, (a) allozyme allele frequency estimates, and (b) allozyme phenotype frequencies.

VARIABLE	AXIS 1	*P* <	AXIS 2	*P* <
(a)				
Altitude	-0.692	0.05	0.126	NS
Annual rainfall	-0.602	0.05	-0.633	0.05
Maximum temperature	0.724	0.01	-0.087	NS
Mean temperature	0.682	0.05	-0.144	NS
Minimum temperature	0.610	0.05	-0.213	NS
(b)				
Altitude	-0.60	0.05	-0.36	NS
Annual rainfall	-0.78	0.01	0.49	NS
Maximum temperature	0.64	0.05	0.32	NS
Mean temperature	0.58	0.05	0.38	NS
Minimum temperature	0.49	NS	0.45	NS
Morphology Axis 1	0.83	0.001	-0.23	NS
Morphology Axis 2	0.06	NS	-0.73	0.01
Vegetation Axis 1	0.12	NS	-0.36	NS
Vegetation Axis 2	-0.62	0.05	-0.13	NS

While the western "high altitude" *F. novae-zelandiae* population Cass Saddle 'A' (CSA), was placed with other *F. novae-zelandiae* populations that occurred at higher altitudes, the other, Porters Pass (PPS), was not. Surprisingly the eastern "high altitude" *F. novae-zelandiae* population at Porters Pass was placed in both ordinations with the lower altitude populations and particularly with Bankside (BNK), the most eastern population of the twelve.

Some differences existed between the two ordinations; the two *F. matthewsii* populations emerged as more distinct when phenotype frequencies were used (Fig. 5.15) than when the ordination was performed using allele frequency estimates (Fig. 5.14). In addition Mt. Sugarloaf (MTS) becomes less distinct from the other populations generally and Sugarloaf Fan (SLF) more so when phenotype frequencies rather than allele frequency estimates were used.

When the 12 populations were ordinated by 40 quantitative morphological characters (Fig. 5.16), the spread of sites was similar to both ordinations using allozyme data. The two *F. matthewsii* populations were most similar to each other and WSH was the closest *F. novae-zelandiae* populations to them. The lower altitude *F. novae-zelandiae* populations, (BNK, CRV, HLF and SLF) occurred together as did the higher altitude *F. novae-zelandiae* populations (CSS, CVS, MTS and WSH). The two populations referred to 'high altitude' *F. novae-zelandiae*, CSA and PPS were much more similar morphologically than biochemically. The first axis of the ordination of populations by morphology was significantly correlated with the first ordination axis of populations by phenotype frequency and the second axes from both ordinations were also significantly correlated (Table 5.12).

The first two axes from an ordination of the vegetation composition of 12 sites from which the populations originated summarised only 23.1% of the variation in the data, indicating that the vegetation among these 12 sites was very diverse. The spread of sites on the ordination diagram (Fig. 5.17) differed from that of the ordinations by allozyme data and morphology and appeared to be more influenced by landform. For example, the two sites on young river terraces, BRV and CRV emerged as most similar to each other despite the fact that they contain different species of *Festuca*. The first axis of the ordination by vegetation composition was not significantly correlated with each of the two ordination axes using allozyme data (Table 5.12). The second vegetation axis was significantly correlated with the first allozyme axis; however this second vegetation axis summarised very little of the variation among sites.

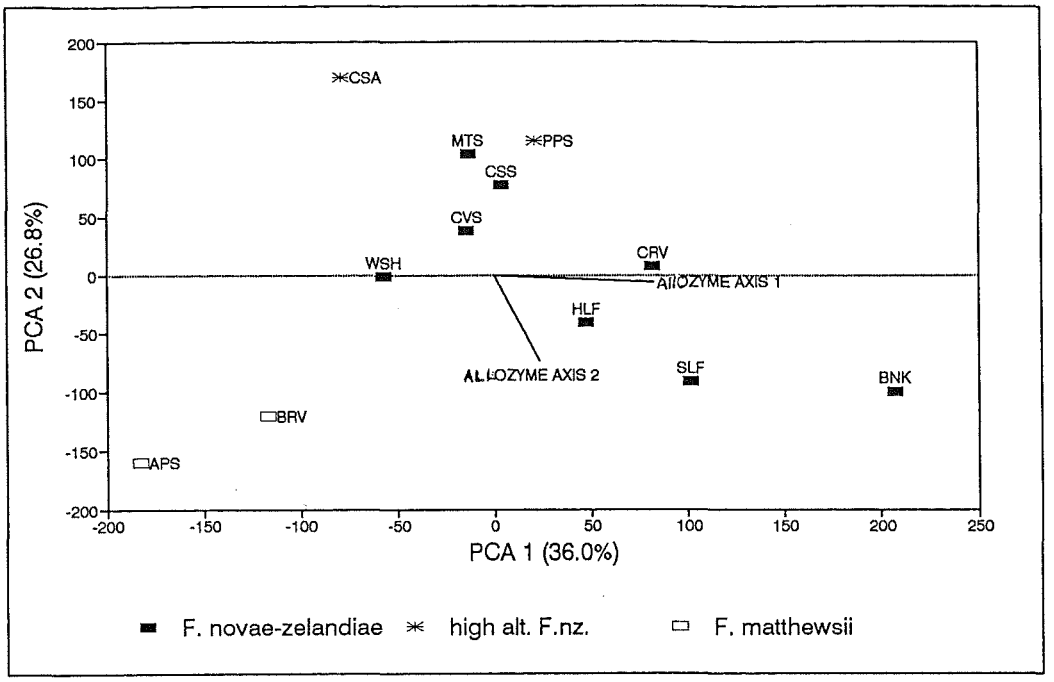


Figure 5.16: Axes 1 and 2 of an ordination of 12 populations containing tussock Festuca using 40 morphological characters. Axes 1 and 2 from an ordination of the same populations by allozyme phenotype frequencies are superimposed.

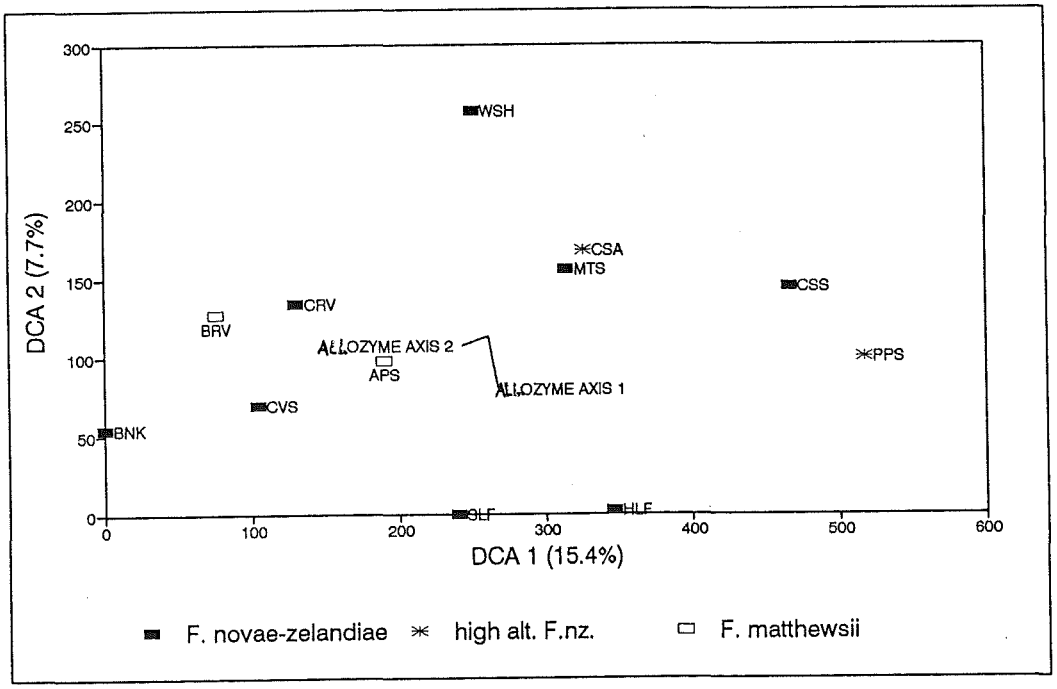


Figure 5.17: Axes 1 and 2 of an ordination of 12 populations containing tussock Festuca using vegetation composition of sites of origin. Axes 1 and 2 from an ordination of the same populations by allozyme phenotype frequencies are superimposed.

5.5.4 Discussion

The frequency of polymorphic loci and heterozygous individuals in *F. novae-zelandiae* and *F. matthewsii* are high compared with values reported for other grass species (Hamrick, 1983) and mean values for monocotyledones and widespread herbaceous taxa generally (Karron, 1987; Hamrick & Godt, 1989) but they are not outside reported ranges. Relatively high amounts of variation could be expected, given the out-crossing, wind-pollinated life history of these species and their potentially long-lived perennial habit (Hamrick, 1989). The difference between allelic and phenotypic polymorphism highlights the impact of the 'fixed' heterozygosity of polyploids on observed genetic variation; mean values in the literature are derived largely from studies of diploid taxa.

The number of alleles per locus observed was also higher than mean values for similar organisms, but presumably the high level of ploidy in *F. novae-zelandiae* and *F. matthewsii* was directly involved in this difference. The predominance of multi-allelic phenotypes indicates that both species are allopolyploid, but more interestingly, the complete absence of five- and six-allele phenotypes could suggest that one of the three parental genomes may be a duplicate.

The low amount of diversity due to differences between species is hardly surprising considering that only two *F. matthewsii* populations were sampled but the results are ambiguous concerning the amount of between-population differentiation in *F. novae-zelandiae*. Low values for between-population diversity are a feature of out-crossing and wind-pollinated species (Hamrick, 1989) and in this case these factors could have been further depressed by the effect of polyploidy and the local nature of the study. However, it also seems that the method used to estimate allele frequencies tended to minimise differences between populations. Population differentiation was much higher when phenotype frequencies were considered.

Assigning a single frequency to an allele at a particular locus as was done in method 1, is technically incorrect for an allopolyploid such as *F. novae-zelandiae*, as there are, in fact, as many duplicate loci as there are parental genomes and allele frequencies and allelic compliments will almost certainly differ between these duplicate loci (Werth, 1978; Gottlieb, 1981). The measure of between-population differentiation based on phenotypic variation may in fact be more representative of true genetic divergence than that based on allele frequency estimates.

The lack of correlation between the genetic similarity of populations and their proximity does not rule out gene-flow as an influencing factor. However the distances between populations may be generally too great for much gene-flow to occur. While gene-flow can counteract the tendency of small populations to randomly diverge, its influence will be over-ridden if selection disadvantages plants possessing 'foreign' genes (Levin, 1981). Strong selective forces have been shown to maintain genetic differences within a number of grass species over distances of a few metres (Gregory & Bradshaw, 1965; Antonovics & Bradshaw, 1970; Snaydon & Davies, 1982; McCain & Davies, 1983; Wilson & Bell, 1985).

The four populations in the Cass Valley were all connected by a sequence of small, scattered *F. novae-zelandiae* populations. The similarity of the three uppermost populations may be a function of gene-flow; Cass Saddle 'A' and Cass Saddle 'B' are particularly close. However the selective influence of the different type of environment experienced by the lowermost population, Cass River, may have over-ridden any effects of gene-flow from higher altitude populations.

The correlation between allozyme profile and environmental factors in the principal components analyses does not prove the 'adaptiveness' of allozyme substitutions. However it is apparent that populations within *F. novae-zelandiae* in broadly similar environments have similar allozyme profiles. Lower altitude populations experiencing lower annual rainfalls and warmer temperatures appear to be similar genetically as do higher altitude populations experiencing higher annual rainfalls and cooler temperatures.

The concurrence between ordinations by allozyme data and by morphology suggest that both are responding to the same broad environmental gradients and that morphological variation has a genetic basis. The lack of concurrence between ordination by vegetation and by allozyme data is somewhat surprising considering that the environmental variables that were most important to variation in vegetation composition generally (chapter 5.2) were also most important for allozyme variation. The lack of concurrence between variation in vegetation composition and in allozyme profile appears to be due, in part, to the diversity of vegetation types among the 12 sites sampled and also to the overriding influence of human disturbance. Sites such as BRV and CRV, with totally different climates, are relatively similar in vegetation because they both contain a large adventive element. Because of this, patterns of similarity among these populations based on allozyme data and morphology would be a more accurate representation of true between-population relationships.

The major disjunction between the western and eastern "high altitude" populations in allozyme profile could be due to the importance of the east-west gradient in rainfall that affects the study area. However it could be that this apparently distinct form has had multiple origins and represents the typical response of *F. novae-zelandiae* when it encounters a certain type of environment. Also it could be that the populations classified in this study as "high altitude" in fact consist of both true "high altitude" *F. novae-zelandiae* with an eastern distribution and other populations that morphologically resemble "high altitude" *F. novae-zelandiae* due to shared environmental conditions.

In summary, both *F. novae-zelandiae* and *F. matthewsii* appear to be allopolyploid with perhaps a genomic constitution of ABB. *F. novae-zelandiae* contains a large amount of genetic variation, augmented by 'fixed' heterozygosity and population differentiation has taken place at different rates for different loci. Phenotypic differentiation, which is probably more representative of the true genetic situation, indicates overall between-population diversity to be in the order of 20% of total phenotypic diversity.

There appears to have been only limited genetic divergence between *F. novae-zelandiae* and *F. matthewsii*. However it is quite likely that if the electrophoretic profiles of a wider range of *F. matthewsii* populations were investigated then more between-species differences would emerge.

Divergence among populations of *F. novae-zelandiae* is low but significant. The selective influence of the environment in which the plants occur appears to be a major factor in between-population differences.

5.6. RECIPROCAL TRANSPLANT EXPERIMENT

5.6.1. Introduction

The overall adaptiveness of observed patterns of variation among populations can be assessed by comparing the general performance of plants of different origins in their own versus other environments in a reciprocal transplant experiment. This type of experiment has been the classic method to test for adaptive variation and was a major part of the work of Jens Clausen, David Keck and William Hiesey in experimental taxonomy (Clausen *et. al.*, 1939, 1940).

Reciprocal transplants are most adept at detecting discontinuous variation that relates to edaphic and climatic factors. If variation is, in fact, continuous, a reciprocal transplant will still only allow the recognition of distinct types. The distinctiveness of types recognised using a reciprocal transplant is therefore very much affected by the scale at which patterns of variation are sampled.

McMillan (1959, 1969) cited the ability of perennial grasses to form ecotypes in response to habitat gradients as a major factor in the dominance of grassland over very large areas. He found ample evidence for ecotypic differentiation among five grass taxa that related to latitude and photoperiod (McMillan, 1956, 1957).

Ecotypic differentation in the ability of plants to extract nutrients from the soil has already been demostrated for *F. novae-zelandiae* by Espie (1987). Espie conducted nutrient trials using populations from different soil types and found differences in uptake that appeared to reflect nutrient availability at the site of origin.

The aim of this experiment is to test for the existence of adaptively differentiated forms among populations of *F. novae-zelandiae* in terms of demographic factors such as survival, growth and reproduction.

5.6.2. Methods

Four populations, Cass Saddle 'A', Sugarloaf Fan, Porters Pass and Waimakiriri Gorge were selected to cover the range of environments occupied by *F. novae-zelandiae* within the study area (See Fig. 2.1 for locations). Plants from Porters Pass represented a distinct high altitude form of *F. novae-zelandiae*. The Cass Saddle 'A', Sugarloaf Fan and Porters Pass populations all occurred in short tussock grassland / shrubland with a high indigenous component. The Waimakiriri Gorge material was collected from roadside remnants in the Waddington - Oxford area of the upper Canterbury Plains. This material was used in preference to material from Bankside, the lowland population used in previous experiments, because it was the closest in origin and altitude to the preselected low altitude planting site in an experimental plot in a garden at Waddington.

In April 1990 three tussocks from each population were randomly selected, divided into four and grown on in sterilised potting-mix in a glasshouse for 4 months. These 48 plants were then divided again into four parts of approximately 1 to 2 cm in diameter each. These 192 plants were grown on for a further 6 weeks in sterilised potting-mix. The experimental material therefore consisted of 16 cloned plants of each of three genotypes from each of four populations.

Prior to planting all plants were measured for height and basal diameter. The number of live tillers (showing green leaves) were also counted and all dead tillers removed. It was decided not to use biomass as a measure of performance because of the difficulties in controlling for root-weight and soil water content.

In October 1990 the plants were planted back into each of the sites of the three populations from predominantly indigenous vegetation and also into the fourth site at Waddington. Each population was represented at each site by four replicates of each of the three original plants collected from that population, giving a total of 48 plants per site. The Sugarloaf Fan plot was situated in short tussock grassland with a dense growth of adventive species; The Cass Saddle plot was located on a slope just below the top of the Saddle and the Porters Pass plot was situated in a small south-west facing gully. The Waddington experimental plot was in an area of cleared ground surrounded by lawn. It was not watered during the study period but was weeded in autumn and spring of 1991.

The plants were planted into a 2 m x 2 m plot at each site. Random number tables were used to assign plants to positions on the intersection points of a 20 cm grid laid across the plot. Each plant was identified with a coded metal tag and X,Y co-ordinates were also recorded. All sites were planted within a 7 day period.

The plants were all watered with approximately 500 mls of water per plant at the time of planting. Heavy rainfall in the study area during the fortnight after planting negated the need for further watering. Minimum-maximum thermometers were placed at each site, face-down at ground level under adjacent vegetation, in November 1990 and read and reset every month.

In January 1992, 14 months after planting, all plants were removed intact. Plants from the three areas of predominantly indigenous vegetation were removed before anthesis so as to avoid genetic contamination of adjacent natural populations of *F. novae-zelandiae*. Each plant was measured for height and basal diameter and the number of live tillers, dead tillers and culms were

counted. No plants had flowered in the 1990/1991 season so all culms present had been produced in the 1991/1992 season.

A mixed-model analysis of variance was performed on five measures of performance. These were:

(1) increase in height as a percentage of initial height,

(2) increase in basal diameter as a percentage of initial basal diameter,

(3) final number of live and dead tillers as a percentage of initial tillers,

(4) dead tillers as a percentage of the final number of tillers,

(5) number of culms per final number of live tillers.

Least significant difference (LSD) pairwise comparisons of means were performed on population grand means across all sites and site grand means across all populations for each of the five measures of performance.

5.6.2 Results

Climate differed between the four sites (Fig. 5.18, a & b). Thermometer readings were not taken for June at Porters Pass or from July to October at Cass Saddle due to heavy snow falls burying the sites. The Waddington site was the most moderate with higher minimum temperatures and intermediate maximum temperatures. The Cass Saddle site was the most extreme, recording the lowest minimum temperature and the highest maximum temperature of the four sites. The other high altitude site, Porters Pass was less extreme possibly due to greater vegetation cover and topography; the plot at Porters Pass was situated in a gully, whereas the Cass Saddle plot was situated on the exposed slope of the saddle.

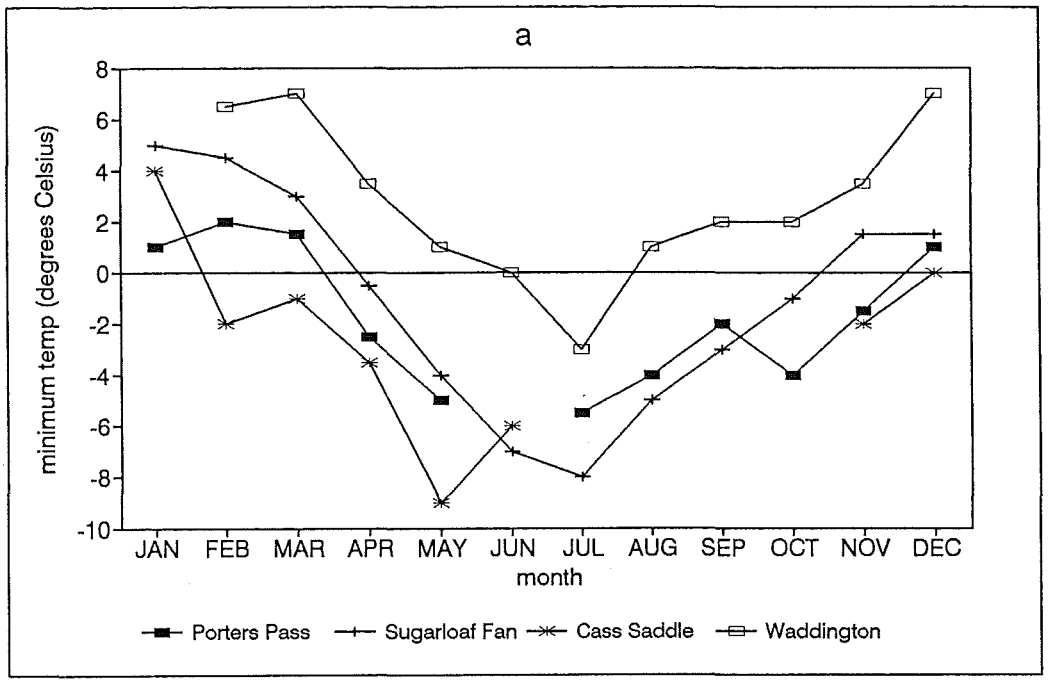
Deaths occurred only at the Waddington site where 11 plants out of 48 died. At the remaining three sites all plants had at least some green leaves at the conclusion of the experiment. Plants had initiated culms at every site but differences in timing of flowering meant that plants from different sites were not at the same stage of culm development when the experiment was terminated. As a result no comparison was made of culm height between sites. The timing of culm elongation was also not recorded at each site because it was not anticipated that the plants would flower after just one season *in situ*.

Dead plants at Waddington disintegrated rapidly so that at the end of the experiment the plants were not sufficiently intact for tillers to be counted. In order to retain a balanced design for analysis, dead plants were assigned values of -100% for increase in height and diameter, 100% for dead tillers and zero values for tillers per initial tiller and culms per tiller.

Most plants at most sites decreased in height from the initial height measured in the glasshouse. However plants that survived at Waddington increased enormously in diameter and tiller number. The deaths at this site could well have been exacerbated by competition between adjacent tussocks. The largest observed increase in tillers was by a plant from Porters Pass growing at Waddington that had 9 tillers when planted and 130 dead and 958 live tillers after 14 months at the site, an increase of 12088%.

Results from a mixed-model analysis of variance indicated significant differences between sites for all measures of performance (Table 5.13). The Waddington site was the most productive with virtually all populations performing better there for all variables than at any other site. When site grand means across all populations were compared using LSD tests, for all measures of performance except culm production the difference between sites was due to the difference in performance between Waddington and the others (Table 5.14).

There were also significant differences between the populations in mean performance across all sites. The Porters Pass population out-performed other populations in all variables except culm production, for which it was the least productive. Sugarloaf Fan was consistently third or fourth in performance at all sites and for all variables except culm production (Table 5.14). The difference among populations for percent dead tillers was due entirely to the difference between Sugarloaf Fan and the other



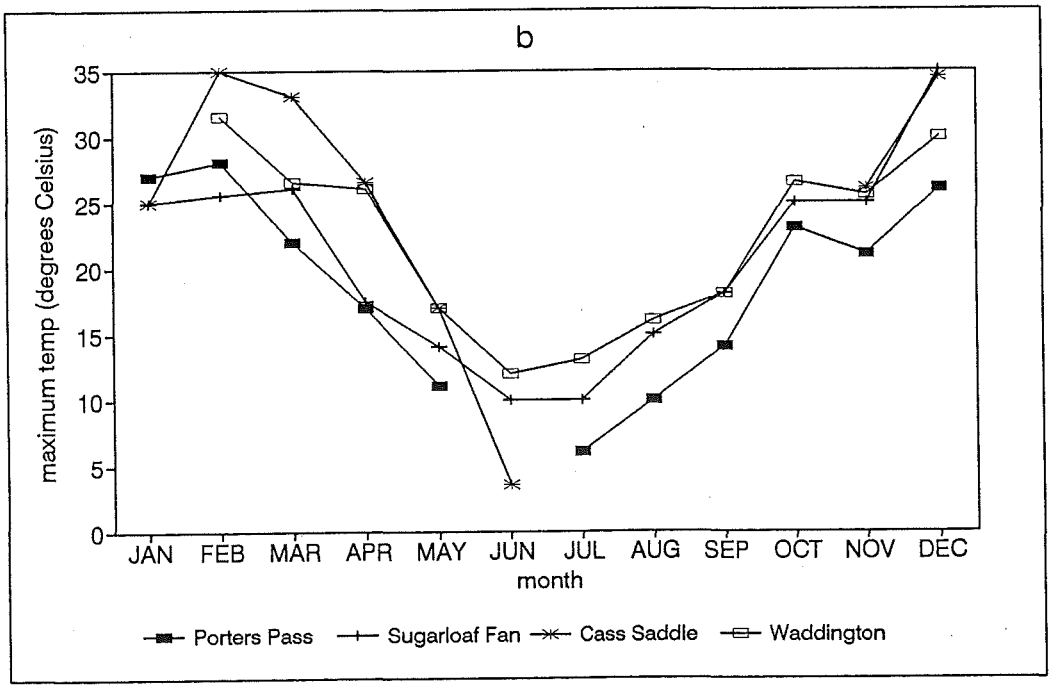


Figure 5.18: Monthly (a) minimum and (b) maximum temperatures (^{o}C) read at ground level over 12 months at each of four reciprocal transplant sites.

Table 5.13: Results of a mixed model analysis of variance for five variables associated with performance of cloned F. novae-zelandiae tussocks in a reciprocal transplant experiment. NS indicates value is not significant.

Source of Variation		**% Diameter Increase**	**% Height Increase**	**Tillering Rate**	**% Dead Tillers**	**Flowering Intensity**
Site	*F*	16.8	39.6	29.6	19.9	31.5
	P <	0.001	0.001	0.001	0.001	0.001
Population	*F*	5.97	3.40	12.5	3.19	2.85
	P <	0.01	0.05	0.001	0.05	0.05
Site x Pop	*F*	1.25	3.28	2.06	1.68	1.26
	P <	NS	0.01	0.05	NS	NS
Site x Clone	*F*	3.31	3.73	1.73	4.50	3.49
within Pop	*P* <	0.001	0.001	0.05	0.001	0.001

Table 5.14: Population means for (a) percent increase in diameter (b) percent increase in height (c) percent increase in tiller number (d) percent dead tillers (e) culms per tiller of cloned F. novae-zelandiae tussocks at each of four sites in a reciprocal transplant. Different superscripts indicate a significant difference between population and site grand means using LSD tests.

Site: **Altitude (m):**	**CSA** **1340**	**PPS** **1000**	**SLF** **670**	**Waddington** **350**	**Population** **Grand Mean**
(a) Diameter					
Cass Saddle	205.8	166.5	141.9	457.6	243.0 ^{c}
Porters Pass	205.8	147.8	105.0	326.8	196.4 ^{bc}
Sugarloaf Fan	75.0	62.6	75.5	138.3	87.8 ^{a}
Waimak Gorge	35.6	55.1	51.8	307.9	112.6 ^{ab}
Site Grand Mean	130.6 ^{a}	108.0 ^{a}	93.6 ^{a}	307.7 ^{b}	
(b) Height					
Cass Saddle	-43.0	-40.6	-35.2	-12.4	-32.8 ^{ab}
Porters Pass	-47.5	-38.2	-30.3	23.6	-23.1 ^{b}
Sugarloaf fan	-54.4	-47.4	-38.4	-33.5	-43.4 ^{a}
Waimak Gorge	-62.5	-51.3	-46.2	4.82	-38.8 ^{a}
Site Grand Mean	-51.9 ^{a}	-44.4 ^{a}	-37.5 ^{a}	-4.35 ^{b}	
(c) tiller number					
Cass Saddle	481.7	353.6	329.7	1660	706.2 ^{ab}
Porters Pass	928.5	565.3	342.2	2543	1095 ^{b}
Sugarloaf Fan	240.0	185.4	193.6	676.1	323.8 ^{a}
Waimak Gorge	234.4	287.4	272.6	2300	773.7 ^{ab}
Site Grand Mean	471.1 ^{a}	347.9 ^{a}	284.5 ^{a}	1795 ^{a}	
(d) % dead tillers					
Cass Saddle	15.0	10.1	21.9	48.7	23.9 ^{a}
Porters Pass	6.39	9.40	16.5	41.1	18.3 ^{a}
Sugarloaf Fan	47.7	35.5	39.7	72.8	48.9 ^{b}
Waimak Gorge	18.6	24.8	36.7	33.9	28.5 ^{a}
Site Grand Mean	21.9 ^{a}	20.0 ^{a}	28.7 ^{a}	49.1 ^{b}	
(e) culms tiller^{-1}					
Cass Saddle	0.03	0.22	0.11	0.12	0.12 ^{b}
Porters Pass	0.002	0.10	0.02	0.05	0.04 ^{a}
Sugarloaf Fan	0.02	0.13	0.10	0.07	0.08 ^{ab}
Waimak Gorge	0.01	0.19	0.08	0.10	0.10 ^{b}
Site Grand Mean	0.02 ^{a}	0.16 ^{c}	0.08 ^{b}	0.09 ^{b}	

populations. The two high altitude sites differed significantly from each other in culm production only. The two lower altitude sites differed significantly only in percent dead tillers.

Despite significant site and population effects only two variables, percent height increase and percent increase in tiller numbers, showed a significant site x population interaction (Table 5.13). For the remaining three measures of performance, populations showed no significant tendency to grow best at their site of origin. However there was a significant difference among genotypes within populations in performance at different sites (Table 5.13).

5.6.3. Discussion

The large differences in overall performance between the four sites emphasises the ability of this species to respond plastically to changes in environmental conditions. Plants from all populations responded with an impressive burst of tillering activity in the favourable growing conditions at the lowest altitude site. Genetically identical plants showed very conservative rates of growth under the harsher conditions of the highest altitude site.

The consistent differences between populations across all sites indicates that some populations are innately more vigorous than others or have a better ability to respond plastically to different environments. The ecological amplitude or adaptability of a population has often been associated with its levels of genetic variation (Van Valen, 1965; Babbel & Selander, 1974; Allard *et. al.*, 1978; Nevo *et. al.*, 1984; Antonovics *et. al.*, 1988). The Sugarloaf Fan population which did so poorly at all sites in the reciprocal transplant also contained fewer heterozygotes than Cass Saddle 'A' or Porters Pass when analysed using isozyme electrophoresis (section 5.5). However this may simply be a coincidence and as genetic variation was not examined in the Waimakiriri Gorge population the relationship between ecological amplitude and heterozygosity cannot be tested here.

Lambrechtsen (1968) in a study of the perennial grass *Anthoxanthum odoratum* found that high altitude plants were more 'adaptable' when exposed to different experimental regimes than lowland plants. In this study the two populations from high altitudes tended to perform best at all sites. Plants in alpine environments have to cope with extremes in temperature, exposure and physiological drought and yet maximise growth during the shorter growing season. Species that are restricted to an alpine environment are often genetically specialised to cope with the conditions and often don't thrive when transplanted to a lowland environment (e.g. Dahl, 1951).

However both *A. odoratum* and *F. novae-zelandiae* are widespread species. In alpine populations of a widespread species the degree of genetic specialisation possible may be restricted by the pre-existing genetic composition of the species. An alpine environment could instead selectively advantage genotypes with well developed phenotypic plasticity (Bradshaw, 1965; Schlichting, 1986) resulting in higher levels of adaptability among high altitude populations of widespread species. The nature of a plastic response is under genetic control like any other character (Bradshaw, 1965; Schlichting, 1986) and the plasticity of a character can evolve independently of the character it controls (Scheiner & Lyman, 1991). This could be a possible explanation of the superior performance of the two high altitude populations of *F. novae-zelandiae* in this study.

There also appears to be a difference between the two high altitude populations in allocation of resources to vegetative growth versus reproduction. Both populations responded equally in terms of increase in size and tiller number but while plants from Cass Saddle produced the most culms on average, plants from Porters Pass produced the least. A difference in resource allocation between these two populations has already been suggested as a partial explanation of differences in stage-class distribution (Section 4.4).

The Porters Pass population represents a high altitude form of *F. novae-zelandiae* that is not genetically distinct (Section 5.5). Nor does it appear to be specifically adapted to an alpine environment versus a lowland one. None-the-less, it would appear that this population differs in the

nature and timing of resource allocation to reproduction compared with the other high altitude population examined.

Espie (1987) found evidence for ecotypic differentiation between populations of *F. novae-zelandiae* in terms of their response to added nutrients during a glasshouse pot trial. However when he conducted a reciprocal transplant he found that differences between the populations in growth and flowering were not due to local genetic specialisation but were more a function of site conditions. The present study, using four different populations from a wider range of sites than those of Espie (1987). However the lack of a significant interaction between populations and sites for most variables measured indicates that only limited ecotypic differentiation has occurred among these populations in terms of the demographic attributes of growth and survival. This finding is in agreement with the results from the isozyme analysis (Section 5.5) which indicated that between-population genetic differentiation was not high.

The significant interaction between sites and genotypes indicates that considerable differences exist within populations in terms of ability to respond to different environments. This result exactly parallels the findings of Rapson & Wilson (1988; 1992a) who tested between-population differentiation in *Agrostis capillaris*. They found little evidence of adaptation to different environments among populations in terms of growth, floral phenology and tiller population dynamics. The majority of variation they observed was due to differences between genotypes rather than populations and the effect of phenotypic plasticity. However they did find differentiation among populations in response to site differences in soil-water availability and soil nitrogen and phosphorus levels (Rapson & Wilson, 1992b).

Lack of ecotypic differentiation, with respect to growth and reproduction, has been reported on several occasions among populations of widespread perennial grasses. Mark (1965c) conducted reciprocal transplant experiments with *Chionochloa rigida*, a long-lived New Zealand tussock grass, using characters of morphology, phenology and growth as measures of performance. He recognised one distinctive high-altitude ecotype but found little difference between the remaining lower altitude populations. His distinctive ecotype was later described as a separate species (*C. macra*) and therefore his experiments showed that there was little ecotypic differentiation between populations of *C. rigida sensu stricto*.

Similarly Platenkamp (1990) found little evidence of ecotypic differentiation for survival and reproductive output in a reciprocal transplant experiment with *Anthoxanthum odoratum*. In his study, phenotypic plasticity accounted for almost all of the observed variation in mortality and reproductive output. However Lambrechtsen (1968) found marked differences between populations of *Anthoxanthum odoratum* in their ability to extract soil nutrients that related to nutrient availability at the sites. Also Lee *et al.* (1983) found evidence for ecotypic differentiation with respect to ultramafic tolerance in both *Anthoxanthum odoratum* and *Agrostis tenuis* (= *capillaris*).

Roy (1985) compared demographic and phenological attributes of populations in contrasting environments for two grass species, *Bromus erectus* and *Dactylis glomerata*. As in this study and that of Rapson & Wilson (1988, 1992a) she found high within-population variation but little evidence for ecotypic differentiation in overall performance. She suggested that this lack of differentiation is due to the buffering capacity of polyploidy and the long life-span of these species.

The above findings, and the results of the present study when considered in light of Espie (1987), would indicate that ecotypic differentiation with reference to the physiology of nutrient uptake evolves more readily, or is more readily detected, than differentiation in the demographic characters of growth and reproduction. Studies involving only a limited set of attributes, that claim to have found or not have found ecotypic differentiation should therefore be careful to state that their findings are relevant to those attributes only and don't necessarily represent the overall evolutionary condition of the species.

5.6 SUMMARY AND DISCUSSION OF CHAPTER 5.

The pattern of variation among tussock *Festuca* in mid-Canterbury is dominated by the patterns of variation in rainfall, altitude and temperature in the study area. These environmental factors influence not only the vegetation in which populations of tussock *Festuca* occur but also patterns of morphological and biochemical variation among them.

The ecological differentiation of *F. matthewsii* and *F. novae-zelandiae s.s.* is paralleled by morphological and phenological differences; however biochemical differences are less marked. For most characteristics investigated the differences between the two species were quantitative (for example, significantly different species means for continuously distributed variables), rather than clear-cut dichotomous distinctions. A similar lack of clear-cut distinctions in the leaf anatomy of *F. novae-zelandiae* and *F. matthewsii* was found by Connor (1960). The plants he examined showed considerable variation in anatomical characters but none of it related to taxonomic, ecological or geographic groupings.

The results of the present study indicate that *F. novae-zelandiae s.s.* and *F. matthewsii* intergrade ecologically and morphologically. Populations possessing intermediate characteristics occur in higher rainfall areas just east of the Main Divide. This intergradation may be due to hybridization between the two species, although Connor (1968) was doubtful as to the occurrence of hybrids in the field. If the observed zone of intermediacy is a hybrid zone, the differential adaptiveness of the parent species probably acts as an genetic isolation mechanism and restricts hybridization to a relatively small contact area. A similar situation has been found for hybridizing subspecies of sagebrush; the hybrid offspring are not competitive in the habitats of either parent and are restricted in a narrow zone of intermediate conditions (Freeman *et al.*, 1991). Whether due to hybridization or selection, both the morphological and isozyme data indicate that *F. novae-zelandiae s.s.* in higher altitude environments becomes more similar to *F. matthewsii*. The observed morphological similarities between *F. novae-zelandiae s.s.* from higher rainfall sites and *F. matthewsii* appear to be both phenotypic and genetic.

The results of the present study indicate that "high altitude" *F. novae-zelandiae* possesses genetically-fixed morphological and phenological differences that distinguish it from *F. novae-zelandiae s.s.* Scott (1970) also found genetically determined differences between two taxa in relative growth rates at low temperatures; "high altitude" *F. novae-zelandiae* grew optimally at 12 ^{o}C whereas *F. novae-zelandiae s.s.* grew optimally at 18 ^{o}C. The ordination analysis of vegetation composition at sites containing these taxa indicated that "high altitude" *F. novae-zelandiae* and *F. novae-zelandiae s.s.* are ecologically distinct; the vegetation at sites containing "high altitude" *F. novae-zelandiae* appeared to differ more from sites containing *F. novae-zelandiae s.s.* than the latter did from sites containing *F. matthewsii*.

However, some of the morphological differences found between these two taxa in the field appeared to be the result of phenotypic plasticity. Moreover, the populations regarded as "high altitude" *F. novae-zelandiae* based on morphology and ecology showed no isozymic differentiation from *F. novae-zelandiae s.s.* but, rather, most resembled adjacent *F. novae-zelandiae s.s.* populations in similar environments. This could suggest that these two taxa are not sufficiently differentially adapted to their different environments to prevent gene-flow from maintaining relative levels of

similarity between their gene-pools. Also selection or random drift may not have had much impact on the respective gene-pools. Alternatively these two taxa could have diverged only recently.

Unfortunately the genetic data are insufficient to determine whether "high altitude" *F. novae-zelandiae* originated only once or has had multiple origins. However it is apparent that "high altitude" *F. novae-zelandiae* is a distinct ecotype within *F. novae-zelandiae*.

CHAPTER 6: SYNTHESIS AND CONCLUSIONS.

Among the grasses of New Zealand, large tussock grasses in the endemic genus *Chionochloa* have received the most attention from researchers. This attention has been justified considering the dominant role of members of this genus in New Zealand montane and alpine grasslands. *F. novae-zelandiae* is an ecologically important, widespread indigenous grass of lowland and montane grassland and is therefore also worthy of intensive study. The present study contributes to the understanding of the biology of *Festuca novae-zelandiae.* Few other indigenous herbs have been studied in as much detail and from such a broad range of aspects.

In this final chapter I will summarise the principal findings of the present study and examine how these findings challenge previously published hypotheses concerning *F. novae-zelandiae*. I will also comment on the likely future of *F. novae-zelandiae* in the face of land degradation and biological invasion. Finally I will examine how the findings of my studies apply to evolutionary and ecological theories concerning 'life-history strategies' and 'adaptation' in long-lived, perennial grasses.

6.1 The Biology of *Festuca novae-zelandiae*

The reproductive biology of *F. novae-zelandiae* is characterised by many, annual reproductive episodes, the intensity of which varies in response to annual fluctuations in climatic conditions and resource availability. While reproduction between years varies significantly, the differences from year to year are smaller than differences displayed by 'masting' species (Silvertown, 1980) such as *Chionochloa* species (Kelly *et al.,* 1992).

There are significant differences in reproductive expenditure among individuals. Many of the individuals studied did not flower at all in four years, and the majority of individuals did not flower every year. Plants that did flower every year also produced the most culms and set the most seed. Since *F. novae-zelandiae* flowers are hermaphroditic, pollen production and therefore the total contribution of individuals to seeds will follow this pattern of seed production. As a result, the total reproductive output of a population would tend to be dominated in successive years by just a few individuals.

Seeds of *F. novae-zelandiae* tend to fall adjacent to the parent plant and seed rain patchiness is a consequence of the patchy distribution of reproductive tussocks. However dispersal over longer distances occurs in strong winds and has undoubtedly been important in the colonisation of new habitats by *F. novae-zelandiae.*

Seed viability was found to be high and in artificial storage, seeds remained viable for at least a year. The majority of seeds germinated readily, confirming the findings of Dunbar (1970). Seedling emergence in the field occurred mainly in the autumn, so under natural conditions seeds probably germinate within a few weeks of falling.

The present study found that seedlings of *F. novae-zelandiae* were relatively common in natural stands, particularly on mat-vegetation and had a half-life of 12 months. While none of the seedlings monitored grew to more than the two-tiller stage, the presence of "juvenile" tussocks (< 1 cm diameter, 5 - 10 tillers) in the population indicated that some seedlings are becoming established.

This contrasts with previously published observations that seedlings were uncommon in short-tussock grassland and establishment rare (Boyce, 1939; Sewell, 1947; Moore, 1976; Espie, 1987). It also contrasts with statements that seedlings established exclusively in litter at the base of large tussocks (Sewell, 1947, 1952). The difference in findings between those studies and the present study could reflect differences between the various study areas in microclimatic factors effecting seedling survival but may also reflect differences in the intensity of search. In the present study, seedling substrate preference differed between two study plots, presumably due to differences in factors causing mortality.

Seedling density was more affected by the availability of 'safe-sites' than by variation in seed rain. This appears to be a feature of stable populations of long-lived perennials (Andersen, 1989). Seedling mortality was higher than has been recorded for *Chionochloa rigida* (Mark, 1965b) and seedlings grew slowly. Those seedlings that did survive more than a year did not increase appreciably in size, as had been observed elsewhere for *F. novae-zelandiae* seedlings by Moore (1976). Seedling survival to the juvenile stage appears to be the critical phase in the regeneration of *F. novae-zelandiae* by seed.

The inequality of reproductive output between *F. novae-zelandiae* individuals results in an L-shaped fecundity distribution (Fig. 3.1) typical of many plant populations (Harper, 1977; Levin & Wilson, 1978). Such a fecundity distribution can accelerate the response of a population to selection, irrespective of generation time, if the most fecund individuals possess favourable genotypes (Levin & Wilson, 1978). For long-lived species, the environment encountered by successive cohorts of offspring may change during the course of the parents reproductive life (Levin, 1978). The attributes possessed by the parent that have enabled it to be reproductively successful may not necessarily confer seedling success. In addition, the attributes possessed by the parent that enabled it to survive as a seedling may no longer be adaptive if environmental conditions have changed. This means that the fitness of individuals, in terms of the number of offspring that reach reproductive maturity, is not necessarily correlated with fecundity. The result obtained by the model of Levin & Wilson (1978), that an L-shaped fecundity distribution can increase the response rate to selection, therefore does not apply to species where the generation time is equal to or greater than the periodicity of environmental fluctuations.

In a closed grassland such as that at Cass, the chances of a seed landing in a suitable site and surviving to germinate and become established are low. Recruitment of young plants to the adult population therefore probably occurs only at low levels in closed grassland. However, it may be more common on more open sites such as young river terraces colonised by mat-vegetation (Calder, 1958, 1961). Due to the longevity of individuals and the changes that have occurred in montane grassland in the last 50 years (Rose, 1983; Scott *et al.*, 1988; Treskonova, 1991; White, 1991), the observations made in the present study on seedling emergence and survival may be atypical of the conditions under which the adults in the Sugarloaf Fan population became established.

The reproductive strategy of a species is intimately associated with its life-span and the nature of the environment in which it occurs (Giesel, 1976; Harper, 1977, Lloyd, 1980a). *Festuca novae-zelandiae* is a long-lived species and an individual can reproduce many times during its life-span. Flowering, seedling establishment or recruitment failure in one year, or even many successive

years, does not necessarily have the same consequences for a long-lived species as it would for a short-lived species (Mark, 1965b; Harper, 1977).

Longevity and iteroparity are often, but not always, found together in plant species. When the probability of reproductive success varies through time, long-lived individuals which reproduce in many, approximately equal episodes during their life-time may have a higher fitness than shorter-lived individuals reproducing in fewer, larger episodes (Giesel, 1976). This can also be the case when mortality is high among offspring but low among adults (Giesel, 1976). By spreading reproductive expenditure among many years, there is more chance of seed being available in those years which are more favourable for seedling establishment and survival.

The reproductive expenditure of *F. novae-zelandiae* from culm production to seedling recruitment is conservative but sustained. As a result this species is relatively unaffected by short-term fluctuations in the favourability of conditions for regeneration from seed. Longevity and iteroparity mean that, should conditions change to favour seedling survival, seed will always be available. The reproductive strategy of *F. novae-zelandiae* could be seen as a response to an unpredictable, temporally heterogeneous environment that affects seedling more than adult survival.

A number of authors (e.g. Zotov, 1938; Sewell. 1952; Moore, 1977; Espie, 1987) have suggested that fragmentation of *F. novae-zelandiae* tussocks into several independent plants provides a mechanism for the maintenance of tussock numbers in what they perceived to be the absence of seedling recruitment. The present study found, with the aid of isozyme electrophoresis, that clonal fragmentation involving short distances had possibly occurred. However, the levels of fragmentation found discount this process as an important mechanism for the maintenance of population density in the grassland studied.

The population dynamics of *F. novae-zelandiae,* at both the level of tillers within tussocks and tussocks within populations, are characterised by flexibility in the face of environmental heterogeneity. The dynamic nature of the tiller population that comprises an individual tussock of *F. novae-zelandiae* provides a means by which risk can be spread among many functionally equal units and expenditure can be adjusted seasonally to accommodate environmental change (White, 1979). The findings of this study with regard to the dynamic nature of the tiller population within a tussock discount previously published statements by Sewell (1947, 1952) about slow growth and lack of change in *F. novae-zelandiae* individuals.

The modular structure of tussock grasses means that genets are potentially immortal, but are composed of modules each of which is only a few years old. The continual replacement of modules allows the genet as a whole to increase or decrease in size in response to environmental fluctuations (Harper, 1977; White, 1979). As a result, chronological age and tussock size and vigour are quite unrelated and adult mortality is low. For plants like *F. novae-zelandiae* where genets are potentially immortal and adult mortality low, genetic differentiation through random drift or selection will be low, because of low levels of turnover in established populations, i.e. long generation times (Levin & Wilson, 1978).

The present study examined in detail the use of a stage-based approach (reviewed in Gatsuk *et al.,* 1980) to the investigation of population structure and dynamics in *F. novae-zelandiae.* It was found that 'natural' stage-classes could be defined relatively objectively using discriminant analysis,

and that the resulting classes were useful in terms of elucidating developmental pathways in the species studied. It was also found that individuals did not proceed in a linear sequence from small, healthy plants, through large, reproductive classes, to become decrepit and then die. This linear progression through classes is often implied by descriptive stage-class studies (e.g. Gatsuk *et al.,* 1980; Vorontzova & Zaugolnova, 1985; Zhukova & Ermakova, 1985). The present study found that the size and 'vigour' of particular *F. novae-zelandiae* individuals changed dramatically (both increasing and decreasing) within the space of only two years, in response to short-term environmental fluctuations. This has important implications for stage-based studies of population structure in similar species. The study conducted by Rose & Platt (1990), for example, used stage-classes to reconstruct the establishment history of *Chionochloa pallens* populations. If this species is as plastic in its growth response to environmental fluctuations as *F. novae-zelandiae*, then Rose & Platt's results relate more to differences in environmental conditions between sites, than the chronological age of individuals and populations.

6.2 Evolution within New Zealand Tussock *Festuca.*

Species can respond to new or changed environmental circumstances in two ways; individuals can adjust phenotypically and populations can shift in genetic constitution (Lewontin, 1957). Of course these two types of responses are not mutually exclusive and species can and do respond in both ways. Tussock *Festuca* in New Zealand displays both types of patterns in response to recent and earlier environmental changes.

The amount of differentiation that has occurred within *F. novae-zelandiae s.s.* varies, depending on the attribute being considered. Morphologically there are apparently genetically-fixed differences between populations that reflect different environmental conditions. There also appears to be biochemical differentiation among populations and Espie (1987) found differentiation among populations with respect to nutrient uptake.

Phenologically there is no discernible differentiation among populations of *F. novae-zelandiae s.s.*, even though the populations came from quite different environments. Neither was any 'home-site advantage' evident, in terms of survival, growth and flowering, in a reciprocal transplant experiment involving four populations from markedly different habitats.

Variation within *F. novae-zelandiae s.s.* is therefore a complex problem. It would appear that different attributes have evolved at different rates and that selection has not equally affected all aspects of the biology of the species.

The three entities studied, *F. novae-zelandiae s.s.*, 'high altitude' *F. novae-zelandiae* and *F. matthewsii,* appeared to be characterised by ecological and genetic differentiation at the level of taxonomic units within a coenospecies, and plasticity or generalisation with limited differentiation, at the level of populations.

The findings of this study support the conclusions of Connor (1960, 1968) that *F. novae-zelandiae s.l.* and *F. matthewsii* are a closely related pair of ecologically and morphologically differentiated, but somewhat intergrading, species. Despite being differentiated in some aspects they can be easily crossed to produce fully fertile hybrids (Connor, 1968) and the present study found little biochemical differentiation between them. Lack of reproductive isolation between otherwise differentiated species is often associated with generalist species occupying a range of habitats (Grant, 1971; Stebbins, 1989). As well as being a feature of generalists, morphological and ecological rather than genetic differentiation appears to be a feature of recently evolved species complexes (Grant, 1971; Fisher, 1973; Coates & Hnatiuk, 1990; Vickery, 1990). However, measures of differentiation obtained from isozyme frequencies and analysis of morphological traits are not necessarily comparable. Lewontin (1984) established that it was much harder to detect significant differences in gene frequencies than in morphological traits when the loci influencing the traits were equally differentiated.

Connor (1968) expressed scepticism concerning hybridization between *F. novae-zelandiae* and *F. matthewsii* in the field. The present study's finding of clinal variation in morphological characters in populations at the distributional boundary between the two species, while not providing conclusive evidence of a natural hybrid zone, strongly suggest that one could well exist.

The findings of this study concerning 'high altitude' *F. novae-zelandiae* support the suggestions of Connor (1960, 1968) and Connor & Edgar (1986) that this represents a partially differentiated, but none-the-less distinctive, entity within *F. novae-zelandiae*. It probably arose from populations isolated above timberline during a mild, forested period in the history of South Island, but has evolved features more usually associated with *F. matthewsii*, possibly due to the selective pressure of a similar environment.

6.3 The Future of *F. novae-zelandiae*

O'Connor (1991) used a life-history approach to postulate the occurrence of an 'extinction-prone perennial grass' as an element in many perennial grasslands. He suggests that such a grass would typically be palatable, obligate seed reproducer with a poorly developed seed-bank, producing low numbers of large seeds that are poorly dispersed. Such a grass could easily become locally extinct under the combined influences of drought and heavy grazing.

O'Connor's model, while developed for C_4 grasses in semi-arid grassland, also may account, in part, for the replacement of *Chionochloa* species by *F. novae-zelandiae* following the advent of pastoral farming in montane Canterbury (Connor & MacRae, 1969). Compared with *Chionochloa* species, *F. novae-zelandiae* is less palatable, more tolerant of burning (O'Connor, 1982, 1986) and, as the present study reveals, it flowers and produces seed every year.

In present-day montane short-tussock grassland, *F. novae-zelandiae* has, to some extent, assumed the role of the 'extinction-prone perennial'. In comparison with invasive adventive grasses such as *Agrostis capillaris, Anthoxanthum odoratum, Dactylis glomerata* and *Festuca rubra*, *F. novae-zelandiae* is slow-growing and somewhat uncompetitive (e.g. Scott, 1970). However, a major factor that limits the 'extinction-proneness' of *F. novae-zelandiae* is its unpalatability and low feed value (Dryden & Archie, 1980). Grazing by sheep may become an important tool in some localities for the maintenance of tussock populations in modified grassland (Meurk *et al.*, 1989; Lord, 1990). However, in other situations (e.g. in dry climates with light soils such as in the MacKenzie Basin and Central Otago) *F. novae-zelandiae* is succumbing under combined pressure from periodic drought, rabbit grazing, declining soil fertility and competition from invasive plants such as *Hieracium pilosella*.

The environmental conditions that provided the window of opportunity for *F. novae-zelandiae* to expand its range, no longer exist. Competition from adventive species, land degradation and pastoralisation are bringing about range contraction in *F. novae-zelandiae*, particularly in the lowland and montane zones (Scott, 1979; O'Connor, 1982; Scott *et al.*, 1988). The invasion of montane grassland by adventive species, such as *Agrostis capillaris, Anthoxanthum odoratum, Festuca rubra* and *Hieracium* species (Rose, 1983; Scott *et al.*, 1988; White, 1991; Treskonova, 1991), means that in many areas the majority of adult tussocks in existence today will not be replaced. This is not unusual for the species. In pre-human New Zealand analogous situations would have occurred where *F. novae-zelandiae* occupied sites for only one or two generations before being competitively excluded by other species, particularly woody species such as *Discaria toumatou* (Calder, 1957, 1961).

The long-term result of such a selective elimination of lowland populations and the survival of higher-altitude populations may be to force the means of some character traits in *F. novae-zelandiae* towards those of *F. matthewsii*. Range contraction could therefore potentially have more of an influence on evolution within *F. novae-zelandiae* than range expansion has.

6.4 Generalist and Specialist 'Strategies' in Long-lived, Perennial, Polyploid Grasses.

The ability of an organism to adapt to its environment is determined by genetic constraints and the temporal and spatial scale of environmental heterogeneity with reference to the organism's life-history.

The life-history and genetic background of *F. novae-zelandiae* limits the degree to which this species can genetically track environmental changes. Adults are long-lived and seedling establishment rates are low. Populations are most probably dominated by pioneer cohorts and the reproductive output of a population is dominated by a few individuals. All these factors contribute to genetic inertia in the face of selective forces and resistance to differentiation among populations in different environments by random processes.

Polyploidy further increases the resistance of *F. novae-zelandiae* to genetic change. As polyploidy acts as a store of variation, populations would be buffered against founder effects and random drift. Mutation in any one gene would have less effect on the genotype as a whole than would be the case in a diploid species (Lewis, 1980).

However the modular structure and perpetual somatic renewal of the tussock habit is a perfect vehicle for tracking short-term environmental changes through phenotypic plasticity (White, 1979). Individuals are able to endure periods of unfavourable conditions and then respond rapidly to an improvement in the environment. As a result the structure of populations of tussock species such as *F. novae-zelandiae* is more a product of its recent past than of its age structure or establishment history.

All these features of *F. novae-zelandiae* argue for the greater importance of phenotypic plasticity rather than genetic differentiation as a means of coping with environmental change. However it is the scale of environmental heterogeneity that is important. *F. novae-zelandiae* would appear to utilise phenotypic plasticity and an all-purpose genotype to track short-term environmental change. Nevertheless, the present study indicates that genetic differentiation has occurred within *F. novae-zelandiae* in response to selection pressures that have been operating over long time-scales (i.e. thousands of years).

Patterns of variation in morphological and biochemical characters between populations indicate that *F. novae-zelandiae* appears to be genetically attuned to long-term environmental trends and large-scale environmental gradients. This conforms with the findings of McMillan (1956, 1957, 1959) that genetically-fixed differences in the phenology of long-lived North American grasses reflect large-scale climatic differences and day length variation among their sites of origin. Of necessity and as a function of the species' biology, *F. novae-zelandiae* adopts a generalist strategy in the face of short-term or small-scale heterogeneity.

The expansion of *F. novae-zelandiae* into the new habitats created by human deforestation and disturbance was undoubtedly facilitated by pre-existing genetic adaptation to broad climatic regimes. Opportunistic generalist behaviour in combination with a capacity for plastic response were probably more important in bringing about such a dramatic range expansion.

The genetic, phenotypic and life-history attributes displayed by *F. novae-zelandiae* typify a hitherto poorly recognised common suite of attributes characteristic of long-lived, polyploid, out-

crossing grasses. These species are characterised by high within-population genetic variation, low between-population genetic differentiation and generally high phenotypic plasticity. Typically there is little differentiation among populations in morphology, or the demographic characters of growth and reproduction when tested with reciprocal transplant experiments. However physiological differences between populations are more common. Some or all of these attributes have been found in *Agrostis capillaris, Anthoxanthum odoratum, Bromus erectus, Calamagrostis canadensis, Chionochloa rigida, Dactylis glomerata* and *Holcus lanatus.*

Agrostis capillaris exhibits the same pattern of high within-population and low between-population variation in isozymes as *F. novae-zelandiae* (G. Rapson, *pers. comm.*). Reciprocal transplant experiments found little differentiation among populations in attributes of growth, phenology and reproduction (Rapson & Wilson, 1988, 1992a). However standard garden and pot trials have revealed differences in response to fertiliser and soil water as well as ecotypic differentiation in heavy metal tolerance in this species (Gregory & Bradshaw, 1965; Snaydon & Davies, 1982; Lee *et al.,* 1983; Rapson & Wilson, 1992b).

Platenkamp (1990) tested for adaptive differentiation among populations of *Anthoxanthum odoratum* using a reciprocal transplant experiment and found no evidence of significant divergence in characters of survival, reproductive output and growth. Yet *Anthoxanthum odoratum*, like *Agrostis capillaris*, has been shown to form specialised races under strong selective pressures involving mineral nutrition, such as ultramafic and heavy metal contaminated soils or in manipulated experimental plots (Lambrechtsen, 1968; Antonovics & Bradshaw, 1970; Lee *et al.*, 1983; McCain & Davies, 1983).

Roy (1985) found high within-population variation in above-ground biomass in hexaploid and octaploid *Bromus erectus* and tetraploid and hexaploid *Dactylis glomerata* but no significant difference between populations. She also found no significant differences between populations for germination, root and shoot growth, phenology or seed weights despite the populations coming from quite different environments. Lumerat (1984) investigated the isozyme profile of *D. glomerata* and also found high within-population diversity.

MacDonald *et al.* (1991) found that populations of tetraploid *Calamagrostis canadensis* had failed to differentiate isozymically to any great extent despite occurring in different vegetation types. The findings of Mark (1965c) indicated little ecotypic differentiation in *Chionochloa rigida* in terms of morphology, growth and reproduction, yet this species contains distinct triterpene methyl ether-synthesising and -nonsynthesising chemodemes within the vicinity of Mark's study area (Connor & Purdie, 1976).

Billington *et al.* (1990) transplanted *Holcus lanatus* individuals between habitats and found that the amount of morphological variation due to genetically-fixed population attributes was low compared to the influence of phenotypic plasticity. Other studies of long-lived herbaceous species, e.g. *Ranunculus repens* (Lovett Doust, 1981) and *Plantago lanceolata* (Antonovics and Primack, 1982), have revealed a similar predominance of environmental effects and phenotypic plasticity over genetic population differentiation.

Several suggestions have been made concerning the lack of differentiation in certain attributes among long-lived, polyploid grasses. The populations in some studies may have had insufficient time in new environments for selection to produce differences between populations in the

attributes investigated, e.g. introductions to New Zealand like *Agrostis capillaris* (Rapson & Wilson, 1988) or pasture species such as *Anthoxanthum odoratum* on recently abandoned farmland (Platenkamp, 1990). Also the selection differential between the sites studied may not have been large enough to produce adaptive variation in demographic attributes and the lack of strong directional selection may have precluded the development of specialised races (Platenkamp, 1990).

The attributes listed above, of high levels of variation but low levels of differentiation, are particularly a feature of polyploid species. Polyploids are thought to be generally more tolerant of stress and extreme conditions (Levin, 1983). They can function as generalists and occupy a wider ecological niche than comparatively 'specialist' diploid relatives (Roose & Gottlieb, 1975; Lumerat, 1985). This would appear to be due to their higher stores of fixed and / or segregating genetic variation promoting biochemical diversity at the level of individuals (Adams & Allard, 1977; Gottlieb, 1981

The apparently contradictory findings outlined above indicate that adaptation to environment does not necessarily take the form of morphological or demographic differentiation. Perhaps the physiology of perennial, long-lived polyploid species is more amenable to evolution *via* natural selection than its overall morphology or behaviour. Grime (1979) lists physiological adaptation without morphogenetic change as a feature of stress-tolerant species. However, the species listed above do not all resemble Grime's concept of a stress-tolerator. Rather they display attributes associated with each of his three primary strategies - competitive stress-tolerant and ruderal; their ability to compete or tolerate is more dependent on the specific edaphic and biotic circumstances of the habitat.

In the above studies, those in which differences were found between populations from different environments largely involved pot or garden trials, experimental manipulation or very strong environmental gradients. Those studies that have failed to find evidence for ecotypic differentiation in long-lived perennial grasses have typically involved reciprocal transplants in 'natural' habitats. 'Natural' habitats are usually characterised by small scale spatial patchiness and temporal variation. Fitness differences between populations in characters of growth and reproduction may only become apparent when compared over a sufficient number of 'normal' and 'extreme' years (Thoday, 1953). As a result, laboratory experiments on adaptation can be misleading. Harper (1977, p769) explained it thus - "Organisms in nature live in environments that contain rhythms and unpredictabilities, patterns and noise. The environment varies both in space and time and although it is apparently rather easy for many out-breeding organisms to adapt to a stable or reliably rhythmic environment, nature sets an infinitely more difficult problem of adaptation to environments that are unstable."

Different attributes evolve at different rates (Stebbins, 1983) and selection for differentiation in response to environmental differences will not necessarily act equally on all aspects of the biology of a species. This does not mean that I advocate the trait-by-trait approach to adaptation criticised by Gould & Lewontin (1979). Nonetheless, the degree of differentiation between populations is bound to differ between different types of traits because when variation in a single trait confers fitness, selection will act on that trait alone. Even when selection acts jointly on a range of traits expressed in the phenotype, the effect of selection will differ between traits because of differences in heritability,

selective advantage and developmental correlation (Gould & Lewontin, 1979; Stebbins, 1983; Bradshaw, 1984).

In long-lived perennial species of modular construction such as *F. novae-zelandiae,* the challenges posed by environmental variation and novel habitats can often be met by phenotypic plasticity (White, 1979). In the case of environmental variation at a scale less than the generation time of the organism, its response to environmental heterogeneity can only be plastic (Bradshaw, 1965; Lloyd, 1984; Schlichting, 1986). However this does not necessarily represent a limitation. If a species possesses an all-purpose genotype (e.g. Baker, 1965) and can adjust plastically it can potentially perform as well as genetically specialised species which closely track the environment, provided environmental fluctuations remain within its tolerance range.

The wide ecological amplitude of *F. novae-zelandiae,* facilitated by biochemical diversity, a generalist life-history strategy and phenotypic plasticity as well as differentiation in some attributes, has enabled this species to adjust to environmental change at a range of spatial and temporal scales. In addition it has been able to take advantage of opportunities created by human disturbance. These characteristics are possibly widespread among New Zealand's indigenous long-lived herbs. Just as the generalist strategies prevalent in the floral biology of New Zealand plants are probably adaptations to an unpredictable assemblage of generalist pollinators (Lloyd, 1985), so could generalised life-histories and conservative levels of, at least demographic and morphological, adaptation, be a response to unpredictable or 'untrackable' environmental variation.

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APPENDIX 1: The taxonomic history of *F. novae-zelandiae*.

Species of fescue encountered by early botanists were initially all referred to a common European pasture grass, *Festuca duriuscula*. J. D. Hooker, in his 'Handbook of the New Zealand Flora' (1867), described *F. duriuscula* in New Zealand as: "very slender, densely tufted, glabrous. Culms 1-3 feet high . . . Leaves slender, involute, filiform or short and setaceous. Panicle 1-6 inches long, effuse or contracted . . . Spikelets few, 4-8 flowered, 1/4 to 1/3 inch long."

The name *F. duriuscula* appears to have been applied to a range of New Zealand *Festuca* species. Two specimens of *F. duriuscula* are illustrated in Buchanan's (1880) Manual of the Indigenous Grasses of New Zealand. One is small and slender, with short setaceous leaves and is most probably what Buchanan refers to as the sub-alpine form that resembles *F. ovina*. The other is more than twice the height, with a densely tufted habit and is more like the present-day *F. matthewsii*. Buchanan comments that New Zealand plants grouped under *F. duriuscula* showed a tendency to vary.

Further evidence of the polyphyletic nature of New Zealand *F. duriuscula* comes from records of its habitat and distribution. Hooker (1867) records it as abundant on the Alps, from Nelson to Otago, ascending to 4000 feet. Buchanan (1880) likewise describes it as "common in both Islands, from 1 - 4000 feet altitude." However previously, Buchanan (1868) recorded *F. duriuscula* in Otago as alpine, found above 4000 feet. In 1870, J. F. Armstrong recorded *F. duriuscula* as occurring on the Port Hills and at Sumner, on the North side of the range as well as "swamps". However, the Armstrongs' list of Canterbury indigenous grasses (1872) recorded *F. duriuscula* as "found all over the world in alpine pastures". J. B. Armstrong in 1880 recorded *F. duriuscula* as abundant in both the lowland and alpine zones.

The polyphyletic nature of New Zealand *F. duriuscula* was confirmed when Professor Edouard Hackel of Austria, described by Cheeseman as in the first rank of European agrostologists, examined New Zealand specimens of the genus *Festuca*. His conclusions formed the basis for Cheeseman's (1906) treatment of the genus. Those specimens that had previously been referred to *F. duriuscula* were now divided between *F. ovina* (two varieties) and *F. rubra*, with the comment that the true *F. duriuscula* probably did not exist in an indigenous state in New Zealand. To *F. rubra* was allocated the greater part of *F. duriuscula*, these plants undoubtedly being the smaller types described by Hooker (1867) and Buchanan (1880). Two new entities were described under *F. ovina*, *F. ovina* var *novae-zelandiae* and *F. ovina* var *matthewsii* (Hackel, 1903).

In 1915, in a paper concerning plants in the vicinity of the Cass Biological Station (Cockayne & Foweraker, 1916), *Festuca novae-zealandiae [sic]* (Hack.) Cockayne was included in the list of species with the note '= *F. ovina* L. var *novae-zealandiae [sic]* Hack.'. When Cheeseman updated his Manual he cited this reference by Leonard Cockayne as the authority for the elevation of the taxon to specific rank (Cheeseman, 1925). In his revised Manual Cheeseman (1925) also elevated *F. ovina* var. *matthewsii* to specific rank as *F. matthewsii*, with the comment: "This appears to me to be a perfectly distinct species, easily recognized by the large spikelets and curious pulvinate callus at the base of the leaf-blades."

APPENDIX 2:

Locations and accession numbers for representative specimens of all populations studied. Material is deposited in the University of Canterbury herbarium, Christchurch (CANU). Map references are for NZMS 260 series except HLF which is for NZMS 1.

Abbr.	Population	Map Ref.	Taxon	CANU
ANT	Anticrow	K34 900991	F. novae-zelandiae	35677
APS	Arthurs Pass	K33 923095	F. matthewsii	33928
BNK	Bankside	M36 423193	F. novae-zelandiae	35686
BRO	Broken River	K34 034863	'high alt' F. n-z.	35671
BRV	Bealey River	K33 925075	F. matthewsii	33927
CAH	Castle Hill	K34 055752	F. novae-zelandiae	35678
CAR	Carrington	K33 835042	F. matthewsii	35669
CBC	Craigieburn Cutting	K34 076841	F. novae-zelandiae	35660
CFL	Cass River Flats	K34 076955	F. novae-zelandiae	35681
CRV	Cass River	K34 071942	F. novae-zelandiae	35685
CSA	Cass Saddle 'A'	K34 027883	'high alt' F. n-z.	33921
CSS	Cass Saddle 'B'	K34 031888	F. novae-zelandiae	33920
CVS	Cass Valley	K34 053915	F. novae-zelandiae	33923
DEC	Deception River	K33 976113	F. matthewsii	35659
DIS	Discovery Stream	K33 066098	F. matthewsii	35667
GPS	Goat Pass	K33 980107	F. matthewsii	35658
GRE	Greenlaw	K33 852007	F. matthewsii	35674
HLF	Hallelujah Flat	S59 286284	F. novae-zelandiae	35662
KIL	Kilmarnock	K33 818042	F. matthewsii	35663
KLO	Klondike corner	K34 947985	F. novae-zelandiae	35664
KRV	Kowai River	L35 104660	F. novae-zelandiae	35687
LBR	lower Bealey River	K33 934051	F. matthewsii	35665
LHR	lower Hawdon River	K33 078032	F. novae-zelandiae	35682
LMR	lower Mingha River	K33 967045	F. novae-zelandiae	35668
LYN	Lake Lyndon	K35 048682	F. novae-zelandiae	35666
MBV	upper Mingha River	K33 982085	F. matthewsii	35673
MTH	Mt Horrible	K34 046968	'high alt' F. n-z.	33929
MTL	Mt Lyndon	K35 036676	'high alt' F. n-z.	35684
MTS	Mt Sugarloaf	K34 104965	F. novae-zelandiae	33922
OTR	Otira River	K33 904114	F. matthewsii	35657

APPENDIX 2 continued:

Locations and accession numbers for representative specimens of all populations studied. Material is deposited in the University of Canterbury herbarium, Christchurch (CANU). Map references are for NZMS 260 series except HLF which is for NZMS 1.

PEG	Pegleg Creek	K33 925115	F. matthewsii	33918
PPS	Porters Pass	K35 080673	'high alt' F. n-z.	33926
RED	Red Lakes	K35 978632	F. novae-zelandiae	33925
RIV	Riversdale	K34 076100	F. novae-zelandiae	35679
SLF	Sugarloaf Fan	K34 098959	F. novae-zelandiae	35688
SVH	Sudden Valley head	K33 034075	F. matthewsii	35676
SVY	Sudden Valley	K33 044049	F. matthewsii	35670
TOR	Mt Torlesse	L35 134697	F. novae-zelandiae	35680
UBR	upper Bealey River	K33 908094	F. matthewsii	35672
UHR	upper Hawdon River	K33 073075	F. matthewsii	35683
WAI	Waimakariri River	K33 841028	F. matthewsii	35675
WRV	White River	K33 810030	F. matthewsii	35689
WSH	Woolshed Hill	K33 093028	F. novae-zelandiae	33930
WSS	Woolshed Hill summit	K33 103038	'high alt' F. n-z.	35661