

Plant recruitment across alpine summits in south-eastern Australia

Submitted by

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Summary

This thesis investigated aspects of plant recruitment across an altitudinal gradient of mountain tops in the Victorian Alps, Australia, and provides a baseline for the patterns and processes of alpine plant recruitment in the absence of large-scale disturbance.

The patterns in alpine vegetation across the study sites were described in relation to abiotic environmental factors. Temperatures were lower and precipitation was higher at the high altitude sites. The vegetation did not differ significantly between the sites, although sites at low altitudes were shrubbier than those at high altitudes.

Analysis of the soil seed bank revealed high mean densities of germinable seed (80 to 1400 seeds m^{-2}) across the gradient of sites. The similarity between the seed bank samples and the standing vegetation was low (qualitative similarity: 0.08 to 0.2; quantitative similarity: 0.03 to 0.19).

In laboratory germination experiments, I found rapid and substantial germination. Final percent germination was above 90% for most species. One species, *Aciphylla glacialis*, showed evidence of dormancy mechanisms. In subsequent experiments, I found that innate primary seed dormancy in this species could be broken with cold-wet stratification.

There were no significant patterns in natural seedling recruitment across the altitudinal gradient. Similarities between the seedling flora and the standing vegetation were low (qualitative similarity: 0.18 to 0.45; quantitative similarity 0.04 to 0.09). Mean seedling density was best predicted by a combination of soil wilting point, altitude and plant litter. In some cases, seedling density was greater than 80 seedlings m^{-2} .

The relative importance of either negative (competitive) or positive (facilitative) interactions between seedlings with adjacent vegetation were investigated in relation to seed germination, seedling growth and seedling survival. Facilitative interactions were common at the higher altitude sites. At lower altitudes, facilitative and competitive interactions were common. Without close neighbours at high altitudes, seedlings were unlikely to survive into their second year.

An understanding of plant recruitment can provide a useful basis for predicting species responses to large-scale disturbance and climate change.

Statement of Authorship

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis submitted for the award of any other degree of diploma.

No other person's work has been used without due acknowledgment in the main text of the thesis.

This thesis has not been submitted for the award of any degree of diploma in any other tertiary institution.

Susanna Elizabeth Venn

31st August 2007

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Chapter 1 - Introduction: alpine plant recruitment and project goals

Summary

Alpine landscapes, above the climatic limits of tree species, are generally considered harsh and stressful places for plants. Low temperatures, snow cover, short growing seasons and frosts are some of the environmental factors that plants must contend with. As a consequence, recruitment from seed in alpine landscapes is expected to be uncommon. The maternal effort required to produce seeds on a low nutrient and low heat budget is high and the life expectancy for seedlings growing in alpine areas, where soil frost-heave, needle-ice and strong winds are common, is low. Hence, alpine plants are expected to be long-lived, perennial and recruit via vegetative, clonal regeneration. In the literature, however, there is an indication that this paradigm regarding alpine plant recruitment is changing.

Plant recruitment often follows disturbance which can create new opportunities for seed germination and seedling establishment in areas of bare ground. Australian species are particularly well suited to coping with large-scale disturbances, especially fire, and much of the research in Australian alpine ecosystems on plant recruitment has been in response to such disturbances. However, within Australian alpine landscapes, there is also an opportunity to study plant recruitment in the absence of large-scale disturbances. This research can provide a reference of background levels of seed accumulation in the soil seed bank and rates of seedling emergence, establishment and survival. Studies of this nature have been carried out overseas. However, the Australian alpine landscape is unusual; with soil covered mountain tops, comparatively mild winters and long growing seasons, all of which may provide suitable conditions for recruitment from seed. Hence, the motivation for this thesis.

The ‘first order’ research question in this thesis, “**What is the role of recruitment from seed among plants across a gradient of alpine mountain tops in Victoria?**” is presented, as well as several ‘second order’ research questions. These questions will be addressed in the thesis chapters. In answering the second order research questions, I aimed to link the life-history stages with the recruitment processes of alpine plant species, as depicted in the life-cycle model. The study is field based, with references to individual species and sites across the landscape.

Alpine plant recruitment

Background

Plant recruitment refers to ‘new growth’ or to ‘grow again’ (Wilkes and Krebs 1995). Successful plant recruitment is, therefore, the end product of the regeneration pathway (Welling and Laine 2002) from flowering and seed-set to germination and seedling establishment. Plant recruitment can be via sexual reproduction or asexual, vegetative, clonal regeneration. Plant recruitment therefore builds populations and maintains diversity within communities (Welling *et al.* 2004). Plant recruitment often follows regular environmentally determined patterns (such as seasons and photoperiod) or may be dependent upon, or triggered by, disturbances which disrupt the normal course of events or environmental characteristics (Grime 1979).

Alpine landscapes

Billings (1974, p 130) defined the alpine environment as “those physical and biological conditions occurring on mountains, above the regional climatic upper limits of tree species.” Climatic and environmental conditions common in alpine landscapes, similar to arctic tundra areas, present several hazards for successful plant recruitment (Urbanska and Schütz 1986). Extended periods of snow restricts the available growing season, the length of which can vary depending on altitude and latitude (Körner 1999). Additionally, frequent frosts, freezing temperatures and strong, desiccating winds contribute to the harsh conditions of an alpine environment (Bell and Bliss 1980). Immediately after snowmelt, freezing temperatures and high soil moisture levels can increase the occurrence of soil freeze-thaw processes, such as frost-heave and the formation of needle ice (Bliss 1962; Billings and Mooney 1968; Williams and Costin 1994; McDougall and Walsh 2007), which can both create localised areas of soil disturbance (Bliss 1971; Williams 1992; Chambers 1995; Inouye 2000). Later in the snow-free period, soils can dry beyond wilting point and into drought conditions (Bonde 1968; Bliss 1971; Billings 1974; Morgan 2004). In addition, areas of bare ground have been shown to heat to $>30^{\circ}\text{C}$ from the intense solar radiation at high elevations (Bliss 1962; Billings and Mooney 1968; Billings 1974; Körner 1999). Soils are typically rocky and acidic (pH 3-5), with low levels of soil organic matter that correspond with nitrogen availability (Körner 1999). Overall, nutrient availability can be very low at the highest elevations in comparison with more temperate regions (Körner 1999). Therefore, species growing in alpine regions must tolerate a range of climatic and environmental extremes.

Recruitment

In stressful environments, theory predicts that the vegetation will be dominated by long-lived perennials which emphasize the adult life-history stages at the expense of growth and fecundity (Grime 1977,1979). Therefore, if an alpine environment is considered stressful, alpine vegetation should be dominated by highly clonal, vegetatively spreading species (Billings and Mooney 1968), with few species predominantly reproducing from seed (Eriksson 1989; Callaghan *et al.* 1992). Indeed, most alpine and arctic regions are characterised by a lack of annual plants (Billings and Mooney 1968; Billings 1974), and research has suggested that seedling establishment is low due to soil heaving caused by frosts and subsequent needle ice (Bliss 1962,1971; Bell and Bliss 1980). Consequently, reproduction from seed is a high risk strategy in an alpine environment (Urbanska and Schütz 1986) due to the numerous environmental hazards that can affect all life-history stages in the regeneration pathway. The maternal effort required to produce seed by alpine plants, which are on a limited heat and nutrient budget, may also reduce the frequency of flowering and seed production (Urbanska and Schütz 1986; Körner 1999).

Recent research, however, has begun a shift in the paradigm regarding alpine plant recruitment. Körner (1998) suggests that the rate of carbon assimilation, biomass accumulation and growth rates of alpine plants are equivalent to those in more temperate ecosystems, when the length of the alpine growing season is taken into consideration. To achieve such growth rates, individual alpine plants and assemblages exhibit a wide range of special adaptations to de-couple their own microclimate from the ambient conditions. These include short stature, meristem-protecting leaf arrangements and leaf coverings such as waxes and hairs which insulate leaf tissues (Körner 1999). Common growth forms in alpine environments are caespitose or reduced rosettes and cushions (Bliss 1962; Chabot and Billings 1972; Körner 1999). By being close to the ground, forbs of this stature, as well as dwarfed shrubs, can escape strong winds and take advantage of the more favourable temperatures at ground level. Hence, alpine species may not experience the alpine environment as 'stressful' as a species from the lowlands may (Körner 1998). High rates of germination among alpine species are common (Amen 1966; Sayers and Ward 1966; Bliss 1971). However, early researchers presumed that subsequent seedling establishment was mostly unsuccessful (Bliss 1962; Billings and Mooney 1968). Further research has showed that seedling establishment may be more common and successful than previously thought (Jolls and Bock 1983; Chambers *et al.* 1990; Forbis 2003), and may also be the most common form of recruitment following many types of disturbance

in tundra regions (Chambers 1995). Hence, sexual plant recruitment may play an important role, in combination with vegetative regeneration, in the structure and functioning of alpine and arctic tundra communities (Welling *et al.* 2004).

Evidence for the old and new alpine plant recruitment paradigms is discussed briefly in the following sections, with respect to various life-history stages.

Flowering and Pollination

Almost all alpine and arctic plants are able to produce flower primordia at least one year before flowering (Sørensen 1941; Billings and Mooney 1968; Mark 1970; Billings 1974; Molau 1993). Pre-formed flower buds allow for fast spring flowering after snowmelt in the following growing season, which may be in response to snowmelt, temperature or photoperiod (Billings and Mooney 1968; Billings 1974; Galen and Stanton 1995; Venn and Morgan 2007). Early flowering species may have a low seed:ovule (relative reproductive success) ratio (mean 0.3) compared with late flowering species (Molau 1993). However, seed from early-flowerers have a higher chance of maturing during the growing season compared with seed from late-flowerers (Molau 1993; Körner 1999)

Many arctic tundra species are self-compatible, although they rely on pollinators as vectors for pollen transfer owing to a lack of autodeposition mechanisms within flowers (Molau 1993). Many flowers of herbaceous alpine perennials are white and yellow and tend to be pollinated by flies, bees, butterflies and moths (Mark 1970). Most graminoids are wind-pollinated (Billings 1974). Pollinator visitation rates tend to peak when ambient temperatures are high, corresponding to increased insect activity (Arroyo *et al.* 1982; Inouye and Pyke 1988). Over altitudinal gradients, Bingham and Orthner (1988) showed that pollinator visitation rates were significantly lower in alpine plant populations in comparison with analogous populations in the lowlands. However, in alpine populations, fewer pollinator visits are compensated for by more effective pollination during each visit. Reduced rates of pollination in alpine areas are rarely due to shortages of pollinators. Rather, ambient temperatures and other factors which affect pollinator activity such as internal flower style and pollen-tube problems, are more likely to cause reductions in pollination (Körner 1999).

Seed rain and seed bank dynamics

During favourable growing seasons, seed production among alpine plants can be large (Molau and Larsson 2000), although seeds in the seed rain may originate from either plants within the local community or from adjacent communities (Chambers 1995). Once on the soil surface, seeds are incorporated into the seed bank (entrapment) or are lost due to mortality or other causes such as secondary dispersal. Small-seeded species accumulate seed banks more effectively than large-seeded species (Thompson et al 1998, Welling et al 2004) and even strongly clonal species can accumulate seed banks (Eriksson 1992). Early research suggested that soil seed banks in alpine regions were either very small or non-existent (Billings and Mooney 1968; Bliss 1971). However, subsequent research in alpine and arctic areas has revealed that substantial seed banks do exist. A review by McGraw and Vavrek (1989) indicated that seed banks in alpine and arctic regions may be larger than previously assumed and of comparable size to seed banks in temperate regions. There is also evidence that seed bank size may change over altitudinal and latitudinal gradients (Thompson 1978). There may be a decrease in seed bank size as altitude or latitude increases, as plant productivity decreases with increasingly harsh conditions, leading to decrease in seed production and seed quality (Molau and Larsson 2000). Low floristic similarity between the seed bank, field seedlings and the standing vegetation may indicate that a persistent seed bank has little impact on vegetation structure (Welling *et al.* 2004).

Seed viability, dormancy and germination

Alpine seed viability is thought to be dependent on the conditions present during the previous and current year's growing seasons (Billings and Mooney 1968; Chambers 1989), especially if seed matures over several seasons. Most studies agree that seed from alpine species is generally viable, but seed production is also highly variable within species, and between and within years (Chambers 1989). Urbanska and Schütz (1986) report that seed viability among alpine plants can decrease with seed age, as can subsequent germination rates. However, seeds found in the soil seed bank may be of varying ages and therefore, seedlings emerging in a given year may not have come from the previous years' seed (Urbanska and Schütz 1986).

Seeds that persist in the seed bank may exhibit dormancy mechanisms (Chambers *et al.* 1990). However, seed dormancy among most alpine plants is fairly uncommon, occurring in perhaps only 20 to 40% of species (Bliss 1959; Amen 1966). Seed-coat inhibition is reported as the most likely cause of dormancy (Amen 1966). Only a few

species are reported to require a cold or wet treatment before germination (Amen 1966). The elapsed year or more between seed production and germination appears to be environmentally imposed (Billings and Mooney 1968; Billings 1974), ensuring that germination will only occur during the next period of favourable conditions (Körner 1999),

In laboratory conditions, alpine seed germination rates can be high, over 90% for some species, given adequate temperatures and soil moisture (Bliss 1959; Sayers and Ward 1966). However, under natural conditions, germination rates can be very low (Bell and Bliss 1980; Marchand and Roach 1980). Temperature thresholds for germination can be over 25°C for some species (Bliss 1959; Billings and Mooney 1968; Bell and Bliss 1980). If temperature requirements were lower, germination could be triggered in a season too cold for photosynthesis and adequate respiratory rates (Billings and Mooney 1968). Occasionally soil temperatures may become too hot. Mark (1965) recorded temperatures of up to 50 °C in bare ground patches, which rendered any seed present in the soil unviable. In contrast, Sørensen (1941) reported that seed germination occurred even though the seeds were frozen during half of every day during his experiment. In addition, Sayers and Ward (1966) showed that freezing soils overnight can reduce germination. Hence, alpine seed germination requirements can be extremely varied, even from year to year, from site to site, and within populations and individuals (Urbanska and Schütz 1986). As such, there appears to be no one alpine germination syndrome (Körner 1999).

Seedling emergence and survival

Many alpine species are highly clonal and are therefore expected to have low rates of seedling establishment (Callaghan *et al.* 1992). Although many seeds germinate, usually immediately after snowmelt (Urbanska and Schütz 1986), subsequent seedling establishment can take several years (Billings and Mooney 1968; Billings 1974). Mortality of seedlings has been attributed to needle ice and frost-heaving of the soil (Mark 1965; Brink *et al.* 1967; Billings and Mooney 1968; Bliss 1971; Billings 1973; Roach and Marchand 1984), as well as slow seedling development (Wager 1938; Bell and Bliss 1980). Many studies investigating seedling survival show that <50% of seedlings survive their first growing season (Bonde 1968; Jolls and Bock 1983; Roach and Marchand 1984). Under favourable conditions, however, such as warm ambient temperatures and sufficient soil moisture and nutrients (Sayers and Ward 1966; Chambers *et al.* 1990; Körner 1999), high seedling densities have been reported across the major

alpine and arctic tundra regions of the world (Freedman *et al.* 1982; Urbanska and Schütz 1986; Chambers *et al.* 1987; Kibe and Masuzawa 1994; Welling and Laine 2000b; Welling and Laine 2000a; Forbis 2003). Freedman *et al.* (1982) found seedling densities in the hundreds per m². Similarly, Forbis (2003) found high rates of seed germination in wet meadow communities, with emergent seedling densities up to 900 m⁻² and only 48% mortality of seedlings in their first year.

A safe site for seedling establishment refers to the immediate environment of the seedling, i.e. the soil micro-topography, moisture status, light conditions and temperature (Harper 1977), all of which can be influenced by adjacent vegetation and the disturbance history of the site. A common occurrence is the establishment of seedlings clumped together, sheltering in the lee of neighbours (Carlsson and Callaghan 1991; Moen 1993; Sturm *et al.* 2001; Callaway *et al.* 2002). These positive, or facilitative, plant interactions show that alpine plants can benefit from close neighbours. Neighbouring plants can reduce wind speed, increase the local temperature, aid in the accumulation of nutrients, reduce soil disturbance and, in some cases, help protect against herbivores (Carlsson and Callaghan 1991; Moen 1993; Sturm *et al.* 2001; Callaway *et al.* 2002). Plants living in stressful environments may therefore survive longer and show higher growth rates when surrounded by close neighbours. However, some species require bare ground gaps for germination and subsequent seedling establishment (Williams 1992). Following disturbances, that activate the soil seed bank or create bare-ground patches, seedling establishment can be the most common form of recruitment (Chambers *et al.* 1990; Chambers 1993,1995). In such microsites, seedling densities can be as high as those found in lower elevations (Jolls and Bock 1983; Forbis 2003).

Australian alpine regions

Landscapes

Alpine and sub-alpine areas in Australia (areas that regularly receive winter snow) are small and make up only 0.15% (11 700km²) of the continent (Costin *et al.* 2000). True alpine areas (areas above the climatic treeline) may have snow seasons of up to five months. This is more common in the highest areas of the Kosciuszko region, with some areas such as snowpatches on the lee-side of ridges, experiencing permanent snow in some years (Costin 1957; Costin *et al.* 2000). Alpine areas in Australia are considered particularly ancient; those on the mainland consist of an uplifted and faulted palaeoplain

which is cut across a complex bedrock and diversified by Tertiary sediments and volcanic deposits (Ollier and Wyborn 1989). All the major rock types are represented across the high mountain regions; acid granite, slate, basalt and limestone (Costin 1957). Glacial activity in the mountain regions appears to be restricted to the Pleistocene (Galloway 1989). Only on the highest regions of the eastern highlands, in the Snowy Mountains, New South Wales, is there evidence that small glaciers were present (Galloway 1989). This is where thirteen glacial cirques have been mapped. However, landforms and glacial deposits due to cold climates are more extensive in Tasmania. Evidence of periglacial activity, which arises from soil movements such as freeze-thaw processes, is widespread in areas above 900-1000 m. Solifluction deposits, comprising stony debris which coat most slopes, include textures ranging from boulders to fine material (Galloway 1989), giving the landscape a smooth appearance. In areas where boulders are abundant, the fine material may be washed out, leaving block-streams and block-fields (Galloway 1989). Active periglacial features are common but restricted to the areas near or above the treeline where vegetation is sparse or absent.

Soils

In comparison with the mountains of Europe, Australian mountains are characterised by relatively smooth knolls with well developed soils and few pointed, rocky peaks (Costin 1955,1957). Strong soil development in these regions is related to the mild glacial history, gentle slopes, a favourable climate for parent material weathering and vigorous biological activity in the soil (Costin 1957). Soils are not strongly differentiated according to rock type (Costin 1957). However, there are several well-defined soil groups in alpine areas including alpine humus soils, lithosols, gley podzols, acid marsh soils, snowpatch meadow soils and bog peats. The most widespread soil type is the alpine humus soil which occurs on well-drained terrain under optimal alpine conditions (Costin 1954,1957). This friable organic loam may be up to one metre deep. All alpine soils are relatively low in clay, high in organic matter, acidic (pH 4-5) and nutrient poor (Costin 1954,1957; Kirkpatrick 1983; Williams and Costin 1994). They are susceptible to erosion by water, wind, frost, fire and mechanical or biological soil disturbances (Costin 1954; Kirkpatrick and Dickinson 1984; Williams 1992).

Climate

Strong winds prevailing from the north-west to south-west are associated with most of the alpine precipitation, which falls predominantly as snow in winter and heavy thunderstorms in summer (Costin 1957). In the Victorian alpine zone, mean monthly precipitation during summer is around 60 mm (February), whereas in winter, rain and snow can contribute to over 300 mm (July) (Bureau of Meteorology, *unpublished data*). Ambient temperatures can reach above 30 °C in the summer months, with overnight temperatures below 0 °C (Williams 1987). Winter temperatures show reduced diurnal fluctuations, tending to hover between -10 °C and 8 °C (Williams 1987). Extreme temperatures outside these ranges can occur. For example, -20 °C was recorded overnight at Mt Hotham in November 1990 (Bureau of Meteorology, *unpublished data*). Frosts are frequent, with more than 100 per year, particularly in areas of cold air drainage such as sub-alpine frost hollows and grasslands surrounded by inverted treelines (Williams and Ashton 1987; Williams and Costin 1994; Wearne and Morgan 2001b). The length of snow lie varies across the landscape depending on topographic features and altitude. Across the Bogong High Plains, Victoria, snow cover may persist from June to September in an average year (Williams 1987), whereas on the higher peaks or in sheltered positions, such as in snowpatches on the lee-side of ridges, snow may persist well into October and November (Venn and Morgan 2007).

Vegetation

The recognition of the major floristic and structural groups of the Australian alpine vegetation began in the 1950s (Beadle and Costin 1952; Costin 1954). Since then, the major structural vegetation formations of the whole region have been revised and published in various forms (Costin 1962a, 1980; McDougall 1982; Kirkpatrick 1983; Walsh *et al.* 1986; Williams and Costin 1994; Kirkpatrick and Bridle 1999; Costin *et al.* 2000). The most recent revision is by McDougall and Walsh (2007) which provides a single classification of the treeless vegetation of Victoria, the Australian Capital Territory and New South Wales. They identified 56 plant communities, based on 1222 floristic quadrats, sampled from published data and new records (McDougall and Walsh 2007). Overall, the major structural forms have not changed and include heathlands, grasslands, open and closed herbfields, fens and bogs, and specialized formations such as snowpatches, feldmarks (in the Kosciuszko region) and bolster heaths (in Tasmania). The distribution of vegetation types is controlled by environmental determinants such as soil depth and type, soil moisture, topography and exposure to winds and frosts (Costin *et al.*

2000). Of the 710 native taxa recorded in the alpine regions by McDougall and Walsh (2007), the plant families with the most representatives are the Asteraceae (16.3%), Poaceae (10.6%), Cyperaceae (7.0%), Orchidaceae (4.4%), Apiaceae (3.7%) and Ericaceae (3.7%). Lesser represented families include the Myrtaceae, Juncaceae and Rubiaceae. Of the taxa recorded in their study, 30.6% exist only in the true, treeless alpine regions (McDougall and Walsh 2007).

Recruitment in Australian plants

Recruitment in response to disturbance

Plant communities tend not to exist in a stable state but rather, they change through space and time in response to natural and anthropogenic disturbances (Pickett and White 1985). Disturbances can disrupt the community structure by changing the availability of substrates, resources and local temperatures (Attiwill and Wilson 2003). In turn, this can affect plant recruitment. Disturbances such as fire, plant death or soil-loss can stimulate germination of seeds in the seed bank or seeds stored in the canopy as they respond to extreme heat, light or soil moisture. Newly created areas of bare ground after a disturbance may present opportunities for colonisation by seedling establishment, following the regeneration niche theory (Grubb 1977; Grime 1979). Subsequently, a different suite of species may establish in the area and repeated, small-scale disturbances may lead to cyclical patterns of vegetation change (Grime 1979).

Australian plant recruitment

In general, most Australian plant species are particularly well adapted to recruitment following disturbance, notably fire. All the major Australian vegetation types contain or are surrounded by flammable vegetation (Kemp 1981) and therefore, are likely to have burnt during historical times and are likely to burn again in the future. The biota, therefore, including the alpine, are variously adapted to particular fire regimes (Banks 1989). The evolution of the Australian flora with fire has resulted in specific, adaptive traits within species such as buried buds and lignotubers, axillary buds, tough bark and hard-seededness (Gill 1981). Notably, the widespread and sclerophyllous genus *Eucalyptus* is considered fire-tolerant but in some cases is also fire-promoting and fire-requiring, with seeds only germinating after a fire event (for example, *E. regnans*) (Ashton 1975). *Eucalyptus* species can promote fire with fibrous and stringy bark, tough

leaves containing volatile oils, open canopies and heavy litter-fall (Ashton 1981; Gill 1981). Hence, the Australian landscape has a predisposition to disturbance from fire and therefore, many Australian plant species have evolved adaptations to regenerate after fire and other similar large-scale disturbances.

Australian alpine plant recruitment

Among the studies of alpine plant recruitment in Australia, most consider successional regeneration responses after disturbances. The studies include vegetation responses to road and walking-track building (McDougall 2001; Johnston and Johnston 2004; Scherrer and Pickering 2006), fire (Kirkpatrick and Dickinson 1984; Wahren *et al.* 2001a; Kirkpatrick *et al.* 2002), cattle grazing and drought (Wahren *et al.* 1994; Scherrer and Pickering 2005). Disturbances which create gaps within the micro-topography of alpine plant communities are also important determinants of plant regeneration and cyclical processes (Williams and Ashton 1988). However, natural large-scale disturbance events in the Australian alpine landscape are infrequent; fire is likely to have only occurred in the region once or twice per century (Leigh *et al.* 1987). Few studies have investigated aspects of plant recruitment in the absence of disturbance. Of these, Pickering (1997b; 1997a; 2000) and Pickering and Hill (2002) explore the reproductive biology and breeding systems of several Australian alpine species within the *Ranunculus* and *Aciphylla* genera, and attempt to link patterns in reproductive effort with plant size and sex. There is, therefore, a large gap in the literature concerning natural recruitment mechanisms among alpine plants in the absence of disturbance.

Research focus and goals

Rationale

Ecological studies relating the environment with the patterns and processes of plant recruitment, across a relatively undisturbed landscape, have not been attempted among alpine species in Australia. Research of this nature can lead to a better understanding of the background levels of alpine plant recruitment and can be a basis for measuring plant responses following future large-scale disturbances such as fire and climate change. Similar research topics have been covered in studies from Europe, North and South America and New Zealand, while landscape-scale studies of alpine plant recruitment from Australia are non-existent. Alpine landscapes in Australia present unusual environments and conditions for plant reproduction, growth and survival which can be vastly different from those overseas. Hence, the motivation for this study.

Aims

The goal of this study was to answer the following ‘first-order’ focal research question:

What is the role of recruitment from seed among plants across a gradient of alpine mountain tops in Victoria?

In answering this question, I address four general hypotheses:

- 1) that the patterns in alpine vegetation across mountain tops are influenced by climatic and environmental parameters in a predictable manner;
- 2) that the patterns in the standing vegetation and plant recruitment processes across the mountain tops are influenced by climatic and environmental parameters;
- 3) that successful plant recruitment from seed is reduced at higher elevations as environmental and climatic parameters become unfavourable; and
- 4) that plant recruitment from seed is facilitated by close neighbouring plants at higher elevations, as close neighbours should buffer each other from the extremes of the environment.

Therefore,

I aimed to investigate the role, the importance and the success of recruitment from seed among alpine plants across mountain tops, across the range of altitude in Victoria.

Research questions, thesis chapters and the life-cycle model

To answer the first-order focal research question, I attempted to answer six ‘second-order’ research questions which are addressed in the chapters of the thesis (Box 1.1).

In Chapter 2, I describe the study sites and the patterns in climatic and environmental variables within and between the sites. I then focus on the patterns of the standing vegetation and how these patterns are related to the climatic and environmental variables. In Chapters 3-6, I explore the processes of alpine plant recruitment, those which link the life-history stages in the life-cycle model (Figure 1.1). Specifically, in Chapter 3 I investigate the role of the seed bank and its similarity with the standing vegetation, across the altitudinal gradient of sites. In Chapters 4 and 5, I investigate the seed germination requirements of several alpine species and compare germination rates within and between species. I single out one species with specific germination requirements, *Aciphylla glacialis*, for use as a case-study in Chapter 5. In Chapter 6, I explore the success of naturally occurring seedlings across sites and assess the similarity between the seedling flora and the standing vegetation. In Chapter 7, I investigate the role of neighbouring plants as facilitators for seed germination and seedling establishment. In Chapter 8, I synthesize the material presented in Chapters 2-7 and provide a summary of the answers to the second-order research questions and show how the results from Chapters 2-7 link the recruitment processes and life-history stages within the general life-cycle model of alpine plants. In addition, I integrate the results from Chapters 2, 3 and 6 to demonstrate the relative similarity in species between the seed bank, the seedling flora, and the standing vegetation. I then discuss the role of recruitment after disturbance in alpine ecosystems. I use a conceptual model to predict future responses in recruitment and changes in vegetation patterns with future disturbance and climate change.

Box 1.1. The second-order research questions with reference (in brackets) to the thesis chapters in which they are addressed.

- 1. Do climate and other environmental variables change across the altitudinal gradient of mountain tops?** (Chapter 2)
- 2. Are there patterns in the vegetation composition across an altitudinal gradient of mountain tops?** (Chapter 2)
- 3. Does the mountain top vegetation form a seed bank? If so, how similar is the species composition of the seed bank to that of the standing vegetation?** (Chapter 3)
- 4. What are the requirements for, and patterns in, seed germination for species which grow across the altitudinal gradient of mountain tops?** (Chapters 4 and 5)
- 5. Are there patterns in natural seedling emergence across the gradient of alpine sites? Are there similarities between the seedling flora and standing vegetation?** (Chapter 6)
- 6. Do interactions with neighbouring plants affect seed germination or seedling growth and survival? Do these patterns change across the altitudinal gradient?** (Chapter 7)

In answering the questions presented in Box 1.1, links between the stages in the plant life-cycle and regeneration pathway can be made. A schematic diagram of the relationships between life-history stages and recruitment processes are presented in the life-cycle model (Figure 1.1). The thesis chapters follow the same progression through the life-cycle model as would an individual plant, from seed production and germination through to seedling establishment and survival. In the final chapter, Chapter 8, I revisit this life-cycle model and show how the recruitment processes relate to the life-history stages.

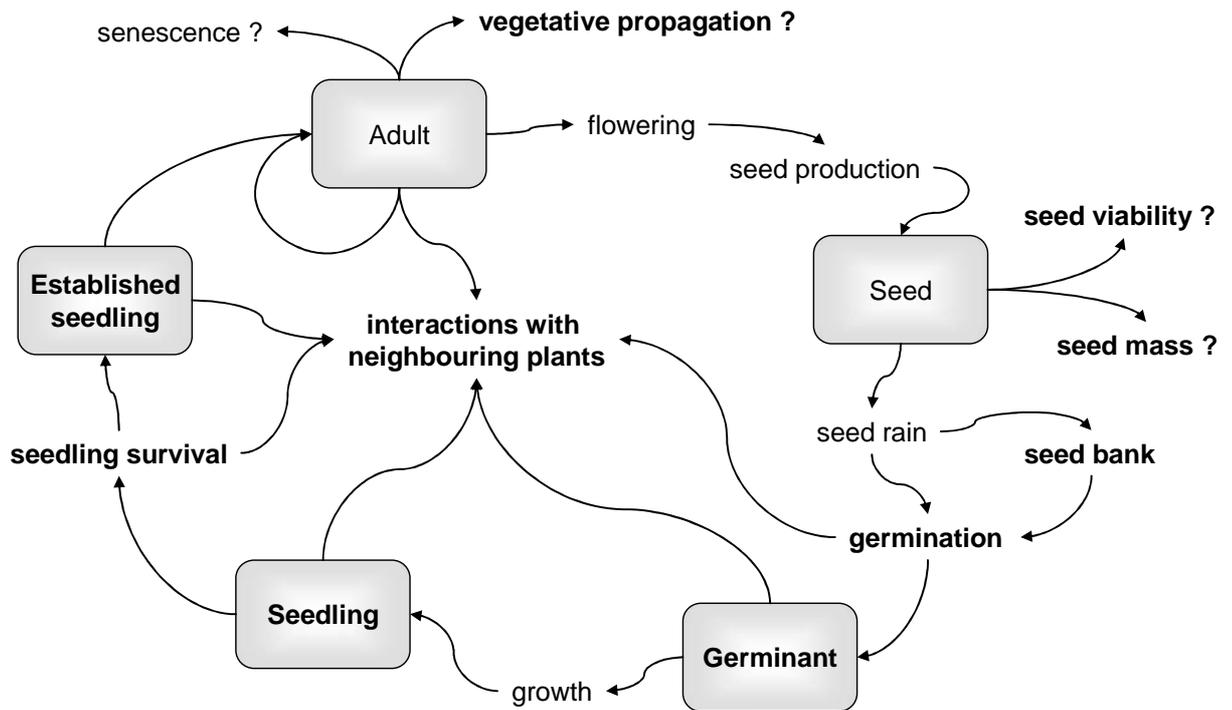


Figure 1.1. The life-cycle model. Life-history stages are represented by shaded boxes; recruitment processes link life-history stages with arrows. Properties of life-history stages are represented by question marks following the text. Mortality of individuals may occur during any stage or process of the life-cycle. Adult vegetation may also persist for many years without contributing seeds or seedlings to the life-cycle model. The time-frame over which the events in the model occur is not specified. The life-history stages, their properties and the recruitment processes which are addressed in this thesis are indicated by **bold** text.

Analytical approach

I used a gradient of alpine summits as study sites in order to assess the effect of climatic and environmental parameters on plant recruitment. This approach allowed for a greater difference in elevation from the lowest alpine site to the highest, than if I had used only one or two peaks and investigated plant recruitment from the summit to the treeline. In addition, study sites on the selected summits have a similar disturbance history. None had been burnt since 1939 and cattle grazing had been discontinued at all sites. Using the summit area of each site also held wind and weather patterns relatively constant across sites, as well as the vegetation type.

Scale of the study

The patterns and processes of plant recruitment are assessed at three spatial scales: individual species, within sites, and across the landscape. However, not all chapters in the thesis deal with plant recruitment across all three scales. Studies using individual species became valuable when comparing specific germination requirements and interactions between close neighbouring vegetation, as including the whole suite of available species in these studies would have clouded important, species-specific responses. The general patterns in recruitment processes or life-history stages within each site allowed for valuable comparisons across sites. Thus, the general patterns in plant recruitment across the altitudinal gradient could be detected.

Thesis style

The data chapters in this thesis, Chapters 2-7, are prepared in the style of research papers suitable for publication. Each chapter starts with a brief summary, similar to an abstract, followed by an introduction, methods, results, discussion and conclusion section. This format results in some repetition, especially in the introduction and methods sections when describing research rationale and study sites. However, this format has the advantage of producing discrete studies, whilst addressing the overall project goal and second-order research questions. When necessary, relevant ideas and results are referred to between chapters. This helps to link the chapters and produces a coherent, flowing thesis. The formatting style follows that of the *Australian Journal of Botany*. However, table, figure and appendix numbers also include the chapter number.

Chapter 2 - The relationship of alpine vegetation with climatic and environmental factors across an altitudinal gradient in Victoria, south-east Australia

Summary

In this chapter, I first describe the study sites, which are a series of mountain peaks in the Victorian alpine zone. I then examine the patterns in climatic and environmental factors across the gradient of sites which include temperatures, frosts, soil wilting point, soil pH and organic matter content. I show that several climatic parameters, estimated using BIOCLIM, are significantly related to altitude. In addition, total nitrogen content, organic carbon and the concentration of copper in the soil showed a significant trend with altitude. I then examine the patterns in vegetation across the altitudinal gradient of sites.

Mean species richness showed a significant decline with altitude. The percent abundance of shrub species also showed a decline with altitude, whereas forb species showed a significant increase with altitude. Using NMDS and ordination, quadrats sampled from Mt Bogong, Mt Hotham, Mt Buller and Mt Stirling tended to clump together strongly. The vector for altitude appeared to drive the patterns seen in the ordination diagrams. These results were further supported by cluster analysis, single-factor ANOSIM tests and subsequent pairwise comparisons. In an all sub-sets modelling procedure, I showed that a combination of climatic parameters including precipitation variables, temperature variables, total soil nitrogen and organic carbon are important characteristics which can drive patterns seen in the vegetation across the altitudinal gradient.

I conclude with a discussion of the potential for this study to be useful in a space-for-time analysis, with the emphasis on predicting future vegetation patterns with climate change.

Introduction

The Australian Alps are characterised by relatively smooth knolls with well developed soils and few pointed, rocky peaks (Costin 1955,1957). Alpine and sub-alpine areas in Australia (areas that regularly receive winter snow) are small and make up only 0.15% (11 700km²) of the continent (Costin *et al.* 2000). In true alpine areas, an altitudinal range from the tree-line to the summit of a given peak will be no more than 400 m. Alpine vegetation patterns and plant community dynamics in the Australian Alps have been researched almost continuously for several decades. In the 1950s, floristic surveys were conducted by Costin (1957), followed by more rigorous and widespread assessments of plant and soil interactions (Carr and Turner 1959), small-scale vegetation patterns in relation to environment (Williams 1987; Wahren 1997; Wahren *et al.* 2001b; Wahren *et al.* 2001c), as well as community dynamics (Williams 1992) and their relationships with environmental factors (Kirkpatrick and Bridle 1998; Wearne and Morgan 2001a). Vegetation maps and extensive species lists for various regions have also been produced (McDougall 1982; Walsh *et al.* 1986; McDougall and Walsh 2007).

In Victoria, obvious vegetation patterns exist across the alpine landscape as plant communities respond to topography and local climate (Williams and Ashton 1987; Wahren *et al.* 2001c). Climate and environmental factors such as temperature, precipitation and soil nutrient availability, are expected to change across altitudinal gradients (Costin *et al.* 2000) and hence, the patterns in vegetation composition are also expected to change across altitudinal gradients (Billings and Mooney 1968; Körner 1999; Costin *et al.* 2000).

In this study I aimed to: (1) quantify the change in climatic and environmental variables across an altitudinal gradient; (2) quantify the differences in vegetation patterns across the same gradient; and (3) investigate whether any differences in vegetation patterns can be correlated with patterns in climatic and environmental variables across the altitudinal gradient. I used a series of mountain peaks to form the altitudinal gradient, whilst keeping the plant community type relatively constant. Any changes in vegetation composition across the gradient can therefore be interpreted as a response to climatic and environmental variables which are particular to each site, rather than to topographic features which may drive differences in plant communities across landscapes (Costin *et al.* 2000). The mountain top vegetation in Victoria is characterised by low, open herbfields dominated by *Poa* spp., *Celmisia* spp. and Asteraceae species, with interspersed shrubs such as *Grevillea australis*, *Prostanthera cuneata*, *Podolobium alpestre* and *Hovea montana*. The relative proportions of species in the current

assemblage are therefore expected to change as climatic and environmental variables change across the altitudinal gradient.

If the patterns in environmental and vegetation characteristics are correlated, gradient studies of this nature may be useful in predicting future vegetation patterns resulting from climate change. The gradient of sites can be used as a chronosequence in a 'space-for-time' analysis (Pickett 1989). In this study, the current patterns observed at the lower mountain tops may resemble those at higher sites in the future, assuming that climate variables change as predicted across altitudinal gradients. This hypothesis is supported by research from the Swiss Alps and elsewhere in Europe, which has showed that warmer temperatures over recent decades can already be correlated with migrations in vegetation (Grabherr *et al.* 1994; Walther *et al.* 2002; Walther *et al.* 2005) as the effects of climate, the major limiting factor for species at high altitudes, is diminished. Hence, vegetation that currently exists at lower altitudes may have the opportunity to migrate to higher altitudes in coming decades, assuming migration corridors and habitat niches are available (Huggett 1995). Species are therefore expected to track a shifting climatic envelope (Walther *et al.* 2002; Klanderud and Birks 2003), sorting themselves according to their tolerance ranges and to extreme weather events (Huggett 1995). In addition to describing patterns and potential interactions between vegetation, environment and climate, this study may also lend insight into potential vegetation change over the coming decades.

Methods

Study sites

The study was carried out in the Alpine National Park in the north-east region of Victoria, approximately 350 km from Melbourne, Australia. The area comprises several high peaks, including Victoria's highest mountain, Mt Bogong (1986 m), which may be covered by snow for four to five months of the year. The mean annual rainfall of this region is high compared to adjacent lowland areas, over 1800 mm (LCC 1982), with much of this precipitation falling as snow on the high peaks during winter. Average air temperatures follow seasonal variations with typical daily minimums and maximums of 2 and 27 °C in summer and -6 and 12 °C in winter (Bureau of Meteorology, *unpublished data*). Frosts are frequent and can occur at any time of year (Williams 1987).

The study sites are located within this mountainous region and I selected eight true alpine summit areas which represent an altitudinal gradient ranging from Mt Speculation (1668 m) to Mt Bogong (Hooker Plateau at 1970 m) (Figure 2.1, Table 2.1). All sites are within 40 km of each other, with most less than 10 km apart (Figure 2.1). All sites are classed as 'Steep Alpine Mountains' after Costin (1957) and all contain alpine herbfield vegetation and occasionally understorey species found in sub-alpine woodland. The underlying geology of the area is varied. Many sites exhibit upper Devonian sedimentary siltstones, mudstones and sandstones, while others exhibit younger Devonian granites (LCC 1982) (Table 2.2). Despite this geological variation, in these regions parent material rarely influences soil type (Costin 1955) and all soils are considered to be of the 'alpine humus' type, highly acidic (pH 4 to 5) and with a gravelly or skeletal structure (Costin 1962b; LCC 1982). Cattle are currently excluded from all sites, but grazing has occurred to varying degrees in the past (Lawrence 1999, A. Markwick, pers. comm.) (Table 2.1). None of the sites examined have been burnt since 1939 or, in some cases, well before this time.

Each site represents the top 5 m contour of the selected summit, with the boundary at either the 5 m contour or at 50 m from the centre of the site, whichever was reached first. The centre of the site was determined as the highest point of the peak. In cases where the highest point exhibited signs of excessive trampling, an adjacent knoll or high point was used. Due to the nature of varying slopes, the sites vary in shape and size, ranging from approximately 612 to 2500 m² (Table 2.1), and all were rounded with a flat top and steeply sloping sides (Figure 2.2, Figure 2.3).

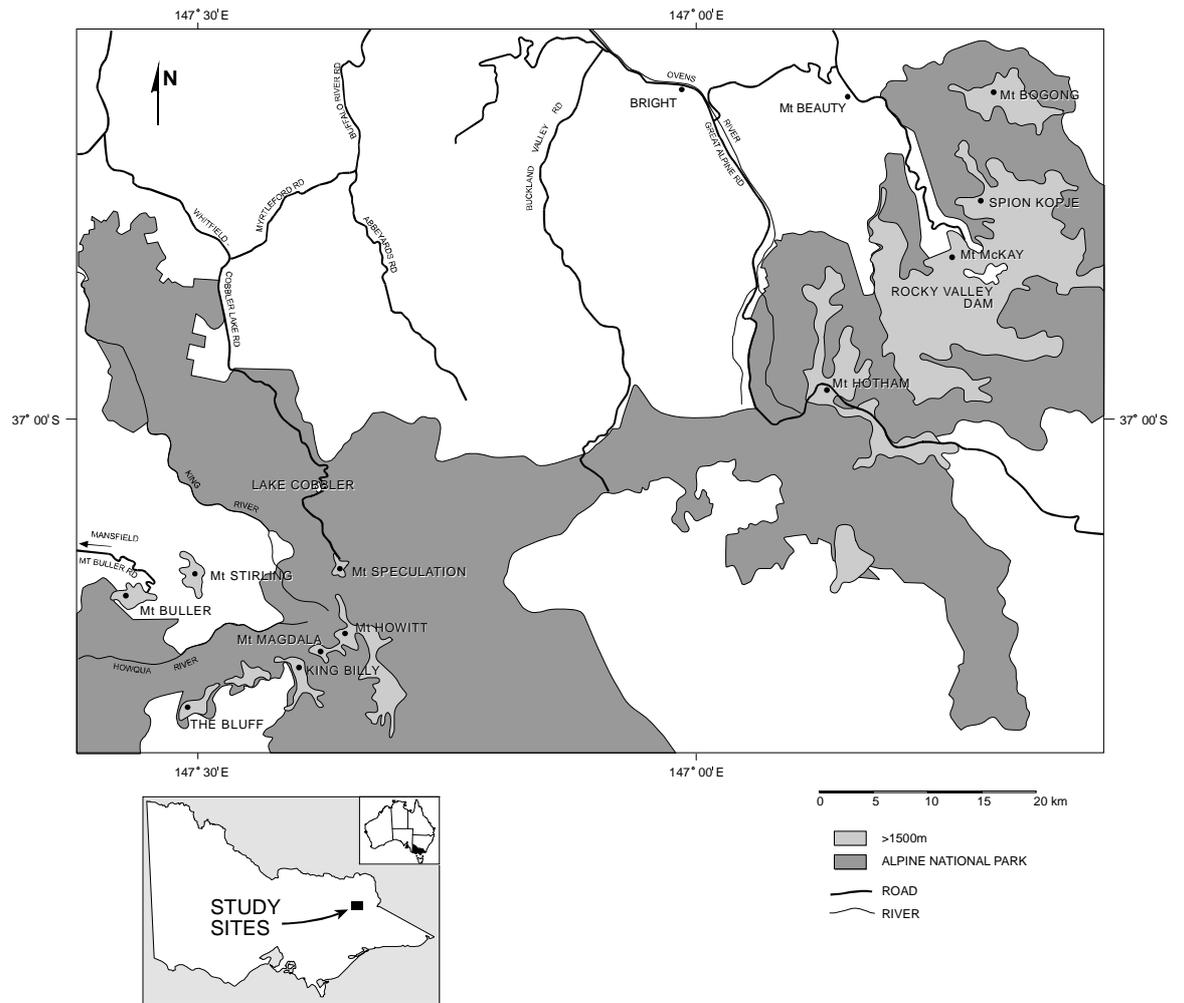


Figure 2.1. The study sites, within the Alpine National Park in north-east Victoria, south-eastern Australia.

Table 2.1. The eight study site locations, altitude (m a.s.l.), size (m²) and cattle grazing history

Study site	Location		Altitude (m a.s.l.)	Site size approx (m ²)	Cessation of cattle grazing
	latitude	longitude			
Mt Speculation	37°07'30"	146°38'40"	1668	1197	1960
King Billy (2)	37°12'45"	146°36'15"	1696	2418	inaccessible to cattle
Mt Magdala	37°15'30"	146°37'15"	1725	1710	1989
The Bluff (South Knob)	37°14'30"	146°28'50"	1725	1742	1992
Mt Stirling (Stanley's Knob)	37°07'50"	146°29'50"	1748	1260	1993
Mt Buller (West Knob)	37°08'45"	145°26'15"	1762	612	1960
Mt Hotham	36°58'35"	147°07'30"	1860	2500	1958
Mt Bogong (Hooker Plateau)	36°44'27"	147°17'15"	1970	2500	1956

Table 2.2. The geology and parent materials of the eight study sites (Land Conservation Council 1982).

Site	Geology and parent materials
Mt Speculation Mt Magdala The Bluff	} Upper Devonian sedimentary (lacustrine) siltstones, sandstones, mudstones and conglomerates.
Mt Buller Mt Hotham	} Ordovician sedimentary (marine) siltstones, sandstones, carboniferous shales
King Billy	→ Extrusive Tertiary (Oligocene) basalts
Mt Stirling	→ Middle Devonian intrusive granite, granodiorite, diorite, hornblende porphyrite
Mt Bogong	→ Ordovician metamorphic gneiss, poliated granite and phyllite schist



Figure 2.2. The study sites at Mt Bogong, Mt Hotham, Mt Stirling and Mt Buller, Victoria, Australia.

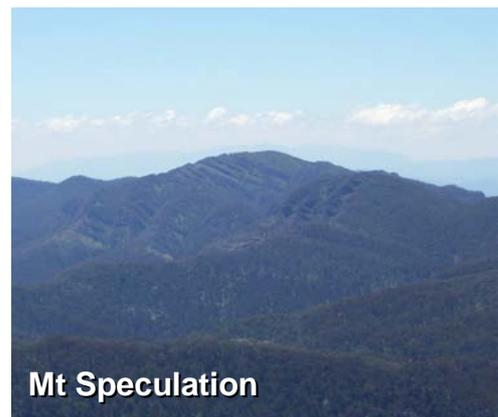


Figure 2.3. The study sites at The Bluff, Mt Magdala, King Billy and Mt Speculation, Victoria, Australia.

Climatic and environmental variables

Climatic variables

Air temperatures were measured bi-hourly with T-Tec data loggers (Temperature Technology, Henley Beach, SA) at The Bluff, King Billy and Mt Speculation between February 2004 and April 2006. The temperature probes were housed in Stevenson screens mounted on stakes at 1 m height. The data set is incomplete due to occasional equipment failure and theft. Data for Mt Hotham and Mt Buller were provided by the Bureau of Meteorology.

Temperature data were converted to mean monthly 'growing degree-days' (GDDs). GDDs were calculated as a measure of the accumulated amount of heat (in degrees Celsius) above a base temperature to represent a cumulative index of energy available for growing plants, according to the formula:

$$\text{GDDs} = [(\text{maximum daily temperature} + \text{minimum daily temperature}) / 2] - \text{base temperature}$$

The daily GDDs were then summed for each month. I chose 0 °C as a conservative base growing temperature as this value encompasses the variability shown by alpine plants in their absolute base growing temperature (Bliss 1962; Körner 1998; Brown *et al.* 2006) and is consistent with other studies of alpine vegetation/temperature relations (Walker *et al.* 1994; Dirnböck *et al.* 2003). GDDs are a useful way to analyse temperature data as one value can be obtained for each month, and values for each site can be easily compared.

Other mean climate variables were estimated using the BIOCLIM bioclimatic prediction system of the ANUCLIM software package (Houlder *et al.* 2000). These values are derived by the software by incorporating the variables of latitude, longitude, altitude and solar radiation, with long-term data from local climate stations. The climate variables estimated by BIOCLIM are presented in Appendix 2.1.

I measured the impact of frost events on soil stability using vertical displacement pins (Brown *et al.* 2000) at Mt Bogong, Mt Hotham and King Billy. This method records the height that frozen soil reaches during a frost event, and frost-heave is inferred from the change in height of a rubber washer on a 5 mm stainless steel rod. The rods were inserted to a depth of 10 cm into the soil (Figure 2.4). A rubber washer sits above a wooden disc, which are both forced to slide up the rod when pushed by freezing soil. The rubber washer stays in place, gripping the rod after a frost event, and the distance it moved from the surface can later be measured. The wooden disc slides back down the

rod to the soil surface as the soil thaws. The rods are reset after frosts by pushing the rubber washer back to the soil surface. Ten vertical displacement pins were erected areas of naturally occurring bare ground and ten in intact vegetation at the three sites. Frost-heave measurements were made at three times over the 2005/06 growing season.



Figure 2.4. Vertical displacement pins on naturally occurring bare ground (left) and intact vegetation (right).

Soil properties

The wilting point of soil (water content at 1500 kPa) at each site was determined with a presoaked ceramic pressure plate in a sealed pressure vessel (Soil Moisture Equipment Co., Santa Barbara, California) on two replicate samples from each site according to the method of Dane and Topp (2002). Saturated soil samples were subject to 1500 kPa pressure within the pressure vessel until moisture leaving each sample had reached equilibrium. Samples were then weighed, dried at 105 °C for 48 hrs and re-weighed to determine the soil water content (soil moisture) at wilting point.

Several soil characteristics were also recorded at each site. Twenty soil samples, of approximately 500 g, were dug randomly from the top 10 cm at each site. The samples were bulked and divided for analysis. Soil pH was analysed with an electronic pH meter on samples that were air dried, sieved to 2 mm and mixed in a 1:5 soil:water suspension, following the method of Rayment and Higginson (1992). Organic matter content was measured as loss on ignition by heating oven-dried (105 °C) sub-samples to 550 °C in a muffle furnace, following the method of Carter (1993). Remaining soil material from each site was sieved to 2 mm and analysed for key plant nutrients, minerals and trace

metals by CSBP Soil and Plant Nutrition Laboratory Ltd., Bibra Lake, Western Australia (Appendix 2.2).

Vegetation sampling

The vegetation of the eight sites was sampled from a total of 160, 1 m² randomly stratified quadrats (20 per site), during the summer growing season of 2004 and 2005. Landscape positions and aspects were equally represented by the random placement of quadrats. This quadrat size was chosen to be comparable with other alpine vegetation surveys (Wahren *et al.* 1994; Wahren 1997). Within each quadrat, the cover of every vascular species, bare ground, rock and plant litter was estimated to the nearest 5%. Individual plants were identified to species level, except in some cases where plants of the *Craspedia* and *Poa* genera were only identified to genus level, due to the lack of distinguishing flower parts present. Nomenclature follows Ross and Walsh (2003).

In addition to sampling the vegetation within the 20 quadrats at each site, I recorded the percent cover of vegetation as life-forms (herbs, graminoids and shrubs), bare ground, litter and rock using line transects. Line intercepts of herbs, graminoids and shrub species were recorded every 10 cm along four transect lines that ran from the centre to the edge of each site on each aspect. An abundance estimate of each life form, bare ground, litter and rock was calculated as a percentage of the total recorded.

Data analysis

The change in climatic and environmental variables (those estimated from the BIOCLIM analysis, soil nutrients, minerals and grazing history) across the altitudinal gradient were analysed using multiple linear regression. Variables which showed strong trends with altitude were then used in an all sub-sets modelling procedure, the Schwarz-Bayesian information criterion (BIC), following the formula:

$$\text{BIC} = n[\ln(\text{SS}_{\text{Residual}})] + (p+1)\ln(n) - n\ln(n)$$

where n = number of observations and p = number of predictors. This technique made clear which combination of these independent variables and altitude best fit the regression model (Quinn and Keough 2003). Variables that are auto-correlated with others were not used in the analysis. For example, 'precipitation in the driest quarter' is auto correlated with 'mean annual precipitation', and hence only one of these variables could be considered in the statistical model.

Non-metric multi-dimensional scaling (NMDS) was used to analyse the relationships in vegetation patterns within and between sites. NMDS is an iterative search for a ranking and placement of n entities on k dimensions (axes) that minimizes the stress of the k -dimensional configuration. The calculations are based on an $n \times n$ distance matrix calculated from the $n \times p$ -dimensional main matrix, where n is the number of rows and p is the number of columns in the main matrix. How good the dissimilarity matrix is can be determined by the stress value (Kruskal 1964; McCune and Mefford 1999). “Stress” is a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original p -dimensional space and distance in the reduced k -dimensional ordination space. Stress values below 0.2 are recommended (Clarke 1993) as values above this threshold may mislead interpretations. Dissimilarities between all pairs of quadrats were calculated using the Bray-Curtis dissimilarity coefficient, previously noted as a robust measure in recovering ecological distance over a range of models and stochastic variations in the data (Bray and Curtis 1957; Quinn and Keough 2003). The resultant ordination diagrams were fitted with the environmental characteristics as vectors, enabling the variables which display more significant or apparent trends across the ordination to be identified, as well as their direction and influence in relation to the floristic data. Ordinations presented here are in three dimensions and have stress values below 0.2.

To further define groups (sites) by their similarities, I used cluster analysis. The best dendrogram following the analysis (one with clearest separation of groups and least amount of chaining) was based on a Jaccard distance measure and a flexible-clustering linkage method (beta at -0.95) (Sneath and Sokal 1973).

The difference between sites was analysed by the analysis of similarities (ANOSIM) procedure (Clarke 1993; Quinn and Keough 2003). This procedure is analogous to an ANOVA comparing between-group and within-group variation. The ANOSIM procedure tests the null hypothesis that there are no differences between *a priori* defined groups, or that the average rank of dissimilarities between all possible pairs of objects in different groups are the same as the average of the rank of dissimilarities between pairs of objects in the same groups (Quinn and Keough 2003). All ANOSIM procedures for percent-cover and presence-absence data used permutation / randomization methods on a similarity matrix to randomly allocate objects to groups and then generate the distribution of R under the null hypothesis that all random allocations are equally likely (Clarke 1993; Quinn and Keough 2003). The R distribution is scaled between pairs of objects in the same group with values between -1 and 1. Differences between groups

would be suggested by R values greater than zero where objects are more dissimilar between groups than within groups. R values of zero indicate that the null hypothesis is true. $R=1$ indicates that all samples within groups are more similar to each other than to those in different groups (Clarke 1993; Wahren 1997; Quinn and Keough 2003). Only ten randomly selected quadrats from each site were used in the analysis due to the computational limitations of the software.

The dominant character species for each site, and the species that are useful in discriminating between sites, were explored using the SIMPER procedure (Clarke 1993). This procedure utilizes the similarity and dissimilarity indices between all pairs of samples to identify typical species within a site, as well as important species that distinguish between sites (Clarke 1993; Wahren *et al.* 1999).

Linear regression was used to model the change in percentage of life forms across the altitudinal gradient using the line intercept results.

Ordinations, cluster analysis and dendrograms were performed using PC-ORD (McCune and Mefford 1999). ANOSIM and SIMPER routines were performed using the PRIMER 5 package (Plymouth Routines in Multivariate Ecological Research 5.1.2. 2000). SYSTAT version 10 (Copyright SPSS Inc., 2000) was used for all other statistical analyses.

Results

Climatic and environmental variation across the altitudinal gradient

Temperatures and growing degree days

Temperature measurements throughout 2004, 2005 and 2006 revealed strong patterns in monthly mean ambient temperatures in relation to the altitude of each site. Generally, the higher altitude sites (1750 m and above) were several degrees cooler than lower altitude sites. Daily overnight temperatures were around 3 to 5 °C cooler at the higher altitudes compared to the lower altitudes. The highest daily maximum temperatures were recorded at Mt Speculation, where summer daytime temperatures were regularly above 30 °C, the maximum recorded during the period of measurement being 37 °C on February 18th 2006. The lowest daily temperatures recorded across all sites in winter were routinely around -5 °C. The timing of snowmelt, recorded when the loggers were released from snow, represented a major shift from the constant ambient conditions in winter, to regular diurnal temperature fluctuations. Snow melted approximately one month later at Mt

Bogong than at King Billy. Frost events, measured as ambient temperatures below 0 °C, were 1.3 times more frequent at Mt Bogong than at King Billy.

Temperature measurements, converted into accumulated monthly growing degree days, revealed that the low altitude sites accumulated more heat over the duration of study than the high altitude sites (Figure 2.5). This was most pronounced during spring and autumn. A low altitude site can often be twice as warm as a high altitude site during these months and therefore, plants at low altitudes can have twice the amount of heat energy available for their growth than those at high altitudes. Mt Bogong, Mt Hotham and Mt Buller accumulated negative growing degree days over winter, represented as zero in Figure 2.5.

Climatic variables estimated with BIOCLIM

Nine climatic variables, estimated by BIOCLIM, were significantly related to altitude. Seven of these are shown in Table 2.3. Maximum temperatures of any particular period tend to be higher at the low altitude sites, and lower at the high altitude sites. Precipitation is also significantly greater at the high sites during both wet and dry periods.

Frost heave

A strong frost event can cause the soil to heave several centimetres. Frost heave of this nature was significantly stronger in areas of bare ground compared to intact vegetation (Log+1 transformed data, $P = 0.000$) (Figure 2.6). There was also a significant effect of site, pooling over treatment (Log+1 transformed data, $P = 0.040$), although there was no interaction between site and treatment (two way ANOVA, $F = 1.829$, $P = 0.164$). There were no significant differences within treatments across sites.

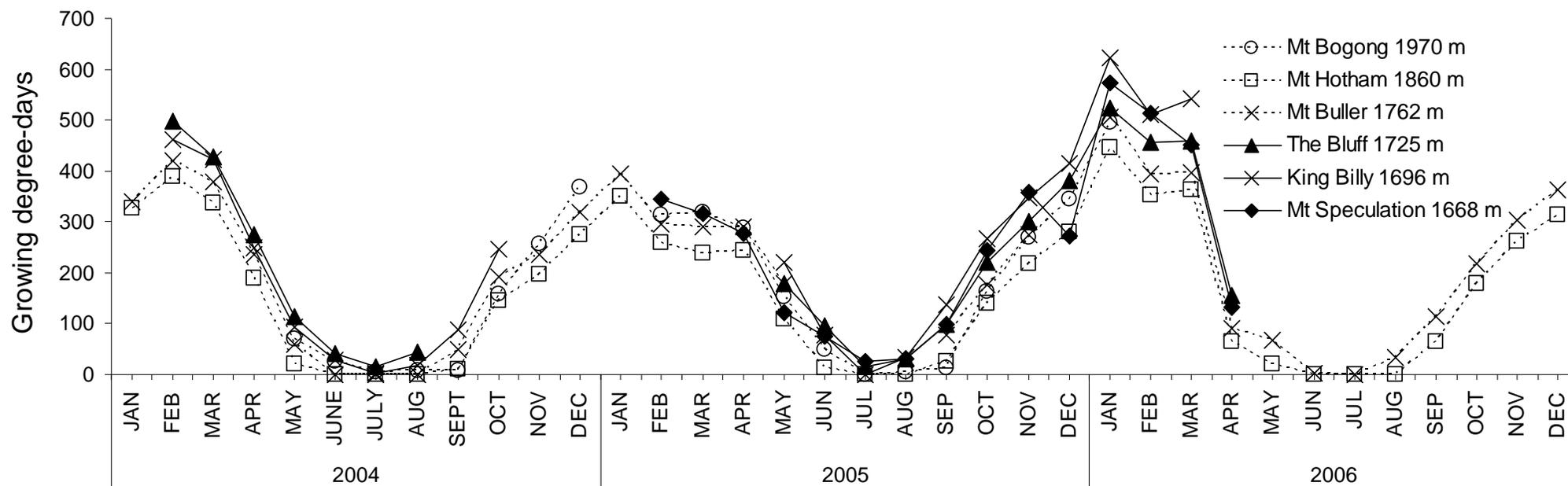


Figure 2.5. Accumulated monthly growing degree days (GDDs) ($^{\circ}\text{C}$) for six sites during 2004, 2005, and 2006. Negative values of accumulated degrees are displayed as zero. Gaps in the data were due to logger failure or theft.

Table 2.3. Seven climatic variables from the BIOCLIM output for each mountain top site. Maximum Temperature of Warmest Period, Minimum Temperature of Coldest Period (measured as the highest/lowest temperatures respectively of any weekly maximum temperature); Precipitation of the Wettest and Driest Periods (measured as the precipitation of the wettest/driest week); Precipitation of the Wettest Quarter and Precipitation of the Driest Quarter (measured as wettest/driest consecutive 13 weeks determined to the nearest week); and the annual mean precipitation (Houlder *et al.* 2000). The fit (R^2) of the linear regression analysis of each variable with site altitude is shown in the column Altitude R^2 . Significant linear relationships with altitude ($P < 0.05$) are marked with an asterisk.

BIOCLIM variables	Mt Bogong	Mt Hotham	Mt Buller	Mt Stirling	Mt Magdala	The Bluff	King Billy	Mt Speculation	Altitude R^2
Max Temperature of Warmest Period (°C)	15.6	16	16.1	16.2	16.2	16.2	16.4	16.8	-0.76*
Min Temperature of Coldest Period (°C)	-4.4	-3.9	-3.1	-3	-2.9	-2.9	-2.8	-2.7	-0.96*
Annual Precipitation (mm)	2615	2350	1757	1769	1827	1756	1788	1802	0.89*
Precipitation of Wettest Period (mm)	85	75	55	55	58	55	56	57	0.88*
Precipitation of Driest Period (mm)	25	24	18	19	20	19	19	19	0.83*
Precipitation of Wettest Quarter (mm)	922	816	589	595	616	589	604	614	0.88*
Precipitation of Driest Quarter (mm)	370	342	276	277	286	276	279	277	0.90*

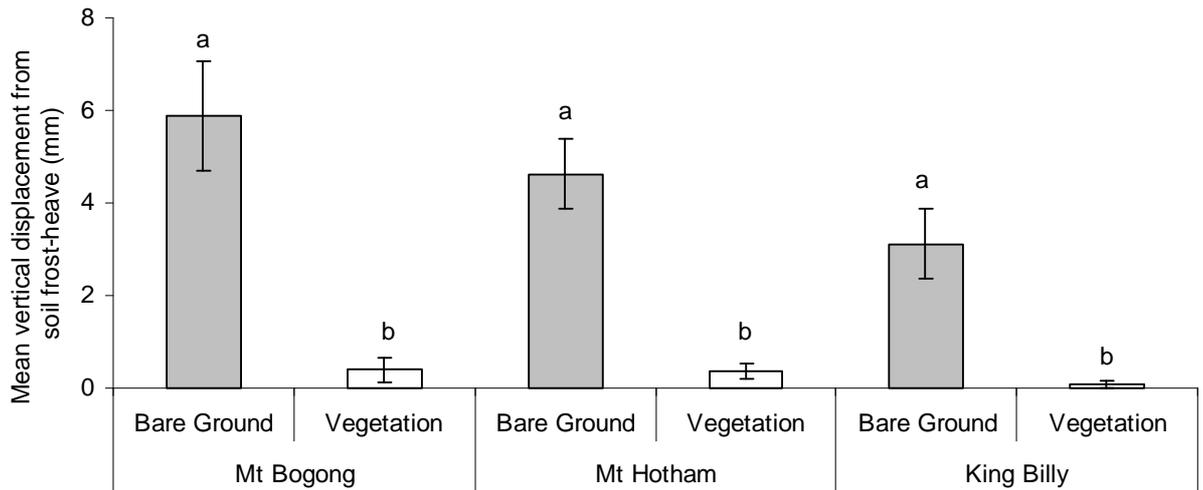


Figure 2.6. Mean (± 1 standard error) vertical displacement (mm) of rubber washers on vertical displacement pins in bare ground and intact vegetation at three sites, Mt Bogong (1970 m), Mt Hotham (1860 m) and King Billy (1696 m) during the 2005/2006 growing season. $N = 10$ for each treatment at each site. Different labels (a or b) above columns indicate significant differences ($P < 0.05$). Higher mean vertical displacement indicates stronger and higher frost-heave of the soil.

Soil properties

The wilting point of soils from the sites across the gradient was varied and showed no trends with altitude ($R^2 = 0.00$, $P > 0.05$) (Figure 2.7). Values ranged between 9.7 % soil moisture at The Bluff and 34 % at King Billy.

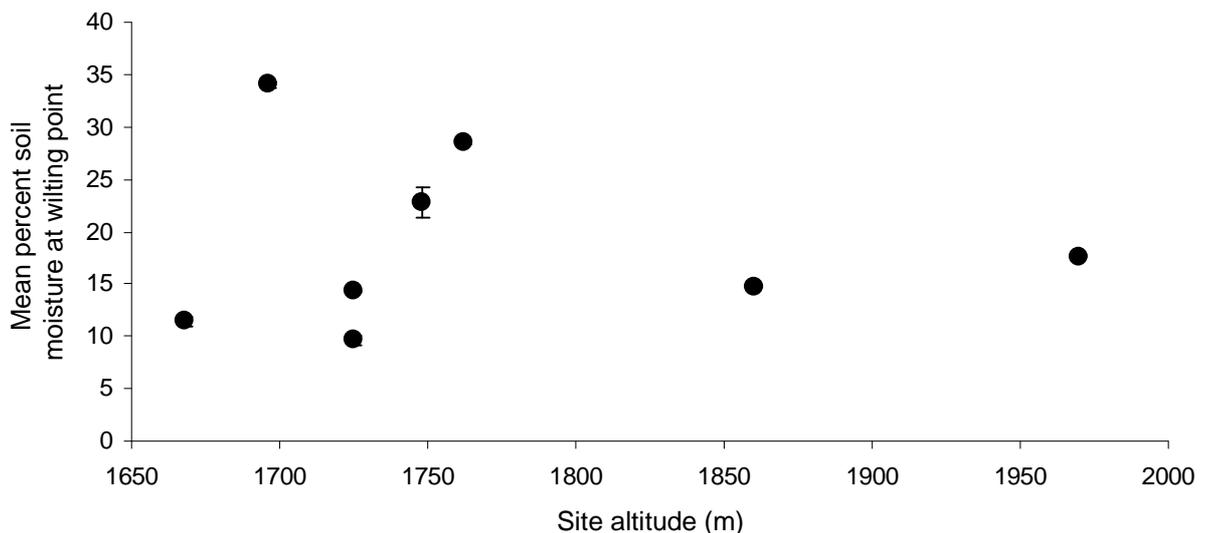


Figure 2.7. Mean (± 1 standard error) percent soil moisture at wilting point (1500 kPa) at sites across the altitudinal gradient.

Soil pH, organic carbon, nutrients and trace elements varied across sites (Appendix 2.2) and few showed trends with altitude. Total soil nitrogen appeared to strongly decrease with altitude ($R^2 = 0.73$, $P = <0.001$), as did organic carbon content ($R^2 = 0.96$, $P = <0.001$). Of the trace elements, extractable copper showed an increasing trend with altitude ($R^2 = 0.78$, $P = <0.001$). These values, and those in Appendix 2.2, should be used with caution as they are derived from only one (bulked) soil sample from each site, and hence there is no available measure of variability.

Soil organic matter (%) ranged from 11, at Mt Hotham and Mt Speculation, to 39% at King Billy. The difference in soil organic matter between sites was significant (1 way ANOVA, $F = 171.24$, $P = 0.00$), and although there was a significant relationship with site altitude, this had poor predictive power ($R^2 = 0.179$, $P = 0.00$).

Modelling of climate and soil properties

All sub-sets modelling indicated which combination of variables vary the most predictably with altitude (Appendix 2.3). Max (Maximum temperature of the warmest period), Min (Minimum temperature of the coldest period), Precip (Precipitation of Driest Quarter), total nitrogen, organic carbon and copper concentration were considered in the analysis. Of these, the best combinations include Max, Min, Precip and total nitrogen, or Max, Min, Precip and organic carbon. Therefore, climate and soil variables can be equally important as driving characteristics across the altitudinal gradient.

Vegetation patterns across the altitudinal gradient

Across the eight sites, a total of 76 species were recorded. There were between 13 and 30 species recorded at each site (Table 2.5). Mean species richness, based on the 20 quadrats per site, showed a significant decline with altitude ($R^2 = 0.62$, $P = 0.019$). The percent abundance of the different life-forms, from the line intercept data, showed a significant increase in forbs with altitude (linear regression, $R^2 = 0.72$, $P < 0.01$), a decline in shrubs (linear regression, $R^2 = 0.36$, $P = 0.111$) and no trend in graminoid abundance across the gradient (linear regression, $R^2 = 0.00$, $P = 0.84$) (Figure 2.8). The number of shrub species recorded also declined significantly with altitude (linear regression, $R^2 = 0.529$, $P = 0.041$).

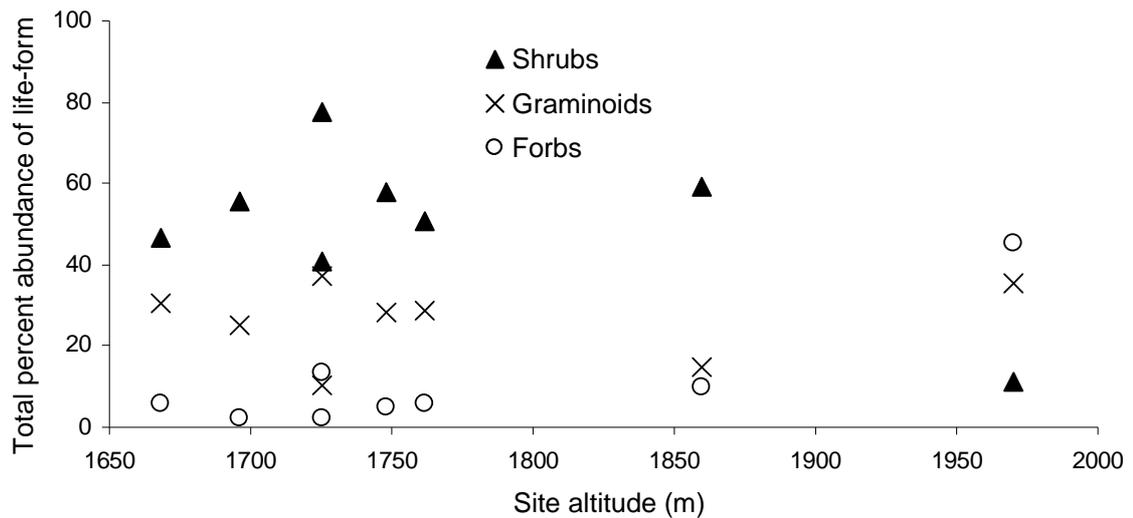


Figure 2.8. Percent abundance of shrubs, graminoids and forbs across the altitudinal gradient of sites from line intercept data.

The clearest separation between sites was seen in the ordinations based on presence/absence data (Figure 2.9.). Of all the environmental characteristics fitted as vectors to the ordination diagrams, altitude explained the most variation in the positioning of quadrats in ordinal space. However, altitude can only explain a low proportion of this variation ($R^2 = 0.35$). Altitude *per se* can never drive floristic patterns as it is not an environmental or climatic variable; however, it can represent a gradient in several variables which vegetation responds to. Hence, the floristic variation within and between sites may be driven by the combination of environmental and climatic variables which do change predictably with altitude, as well as parameters that are specific to each site. Quadrats from within Mt Bogong, Mt Hotham, Mt Buller and Mt Stirling tended to clump together strongly, which is most obvious in the axis 1 vs 3 configuration, indicating that floristic variation within these sites is more similar than across sites.

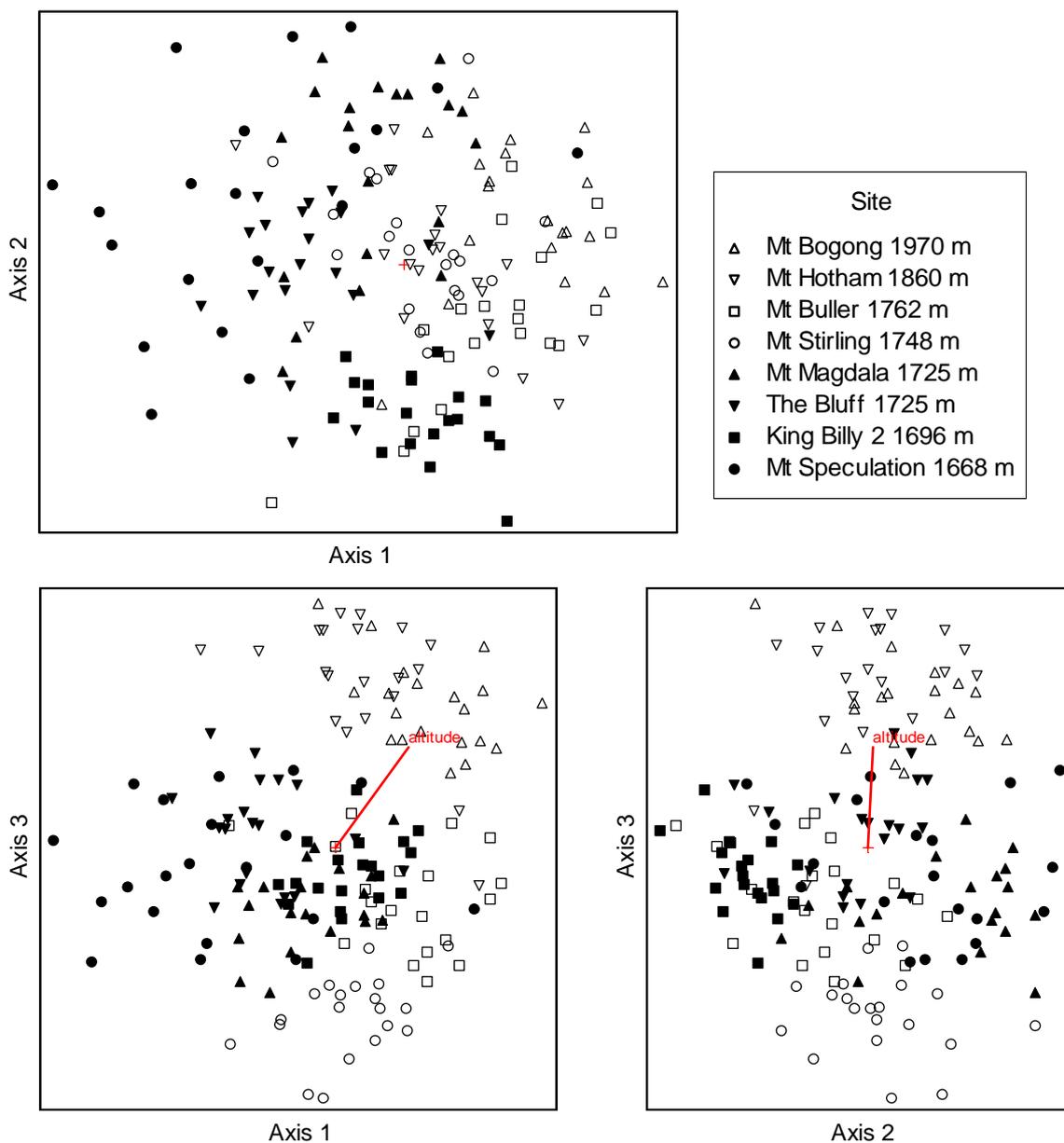


Figure 2.9. Position of samples from each site within the three dimensional NMDS configuration based on presence/absence data and vector of maximum correlation ($R^2 = 0.35$) representing site altitude. Stress: 0.18.

The patterns in the ordination diagrams are supported by cluster analysis, depicted as a dendrogram in Figure 2.10. Sites separated clearly, with the higher altitude sites (Mt Bogong and Mt Hotham), showing the most separation. This is consistent with the patterns seen in the ordination diagrams. Quadrats from Mt Magdala were the most inconsistent with respect to site grouping, which was also apparent in the ordination diagrams.

Single-factor ANOSIM tests and subsequent pairwise comparisons further support the results seen in the ordination and the dendrogram. The composition of vegetation at every site is significantly different from every other (ANOSIM, $\log_{10} + 1$ transformation, with 5000 permutations, percent cover; global $R = 0.711$, $P < 0.001$, presence/absence;

global $R = 0.697$, $P > 0.001$). In percent-cover pairwise comparisons of vegetation composition between sites, most R values were between 0.6 and 1.0, indicating that sites are mostly dissimilar from each other. The quadrats from Mt Bogong and Mt Stirling showed very high dissimilarity, ($R = 1.0$, $P < 0.05$) indicating the vegetation is more similar within these sites than between them. The quadrats from Mt Magdala and Mt Speculation showed the reverse trend with a relatively low value ($R = 0.305$, $P = 0.2$) indicating these sites have many species in common in similar abundances. In pairwise comparisons using presence/absence data, there was more variation between sites (R between 0.2 and 0.9). Comparisons between The Bluff and Mt Magdala, Mt Hotham and Mt Bogong, and Mt Speculation and Mt Magdala showed higher similarities between pairs of sites than all other comparisons performed in the ANOSIM procedure ($R = 0.372$, $P = 0.1$; $R = 0.244$, $P = 0.3$; $R = 0.249$, $P = 0.6$ respectively). It is interesting to note that The Bluff and Mt Magdala are at the same altitude (1725 m) and Mt Hotham and Mt Bogong are the two highest sites (1970 m and 1860 m respectively).

The species which contribute to the similarities and dissimilarities between sites are shown in Table 2.4. The lower elevation sites (Mt Speculation, King Billy, Mt Magdala and The Bluff) contain more shrub species (eg. *Hovea montana*, *Podolobium alpestre*, *Grevillea australis*, *Prostanthera cuneata*) than the higher elevation sites (Mt Buller, Mt Hotham and Mt Bogong). Graminoid species (including the *Poa* and *Carex* genera) were typical throughout all sites as was the forb species *Stelleria pungens*. The higher elevation sites were typically characterised by many forb species, notably *Celmisia pugioniformis* and *Craspedia* spp. These species are present at lower elevation sites, but did not occur within the top five most abundant species for those sites.

The mean similarities of quadrats within sites are shown in Table 2.5. Quadrats from all sites are more than 30 % similar to each other when based on percent cover and presence/absence data. However, the low values indicate high variability within each site.

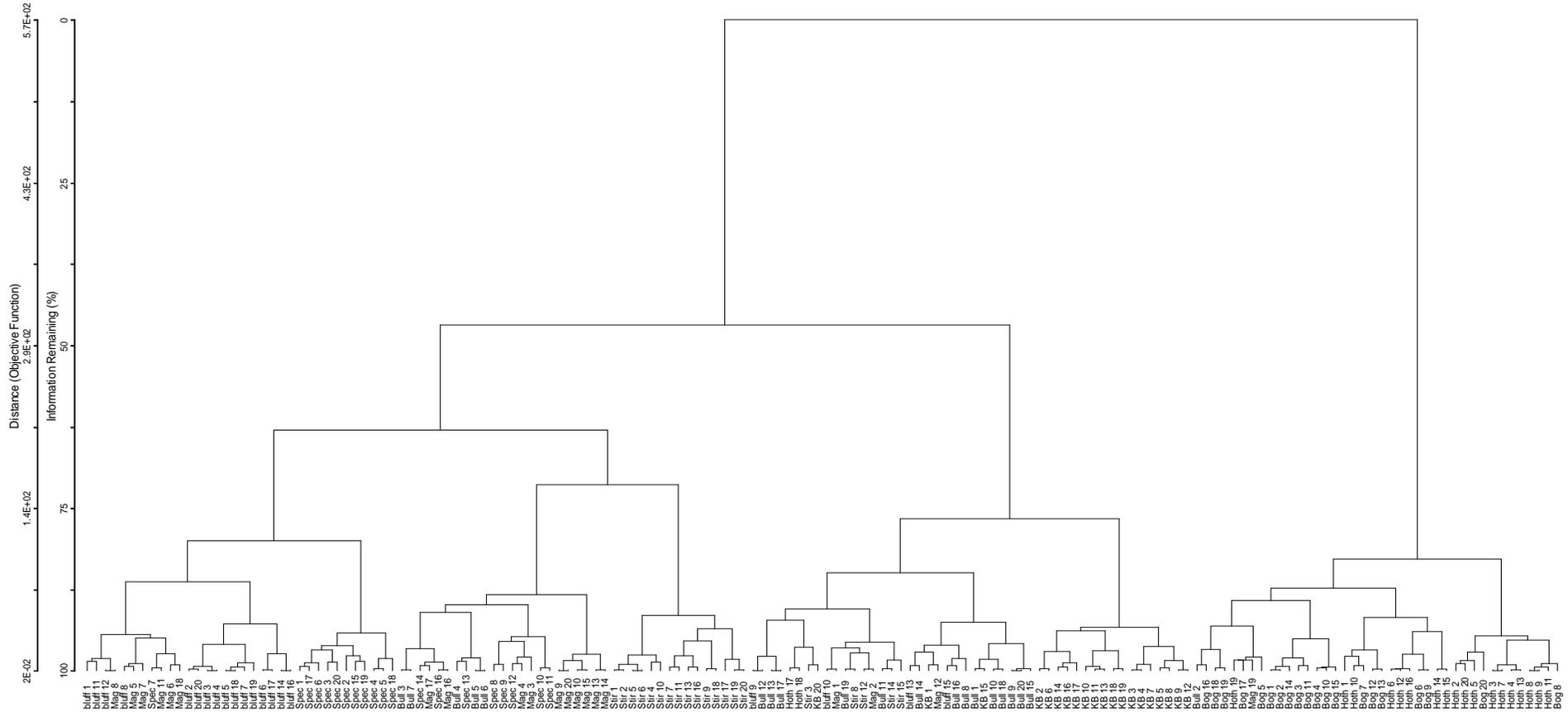


Figure 2.10. Dendrogram of the twenty quadrats from each site based on presence/absence data, a Jaccard's distance measure and a flexible-clustering linkage method (beta at -0.95). The change in information context (% information remaining and Euclidean distance) is shown on the vertical axis as a measure of group dissimilarity. Percent linkage = 0.51.

Table 2.4. Mean abundance (%) of the top five species at the eight study sites in Victoria, and the mean similarity between quadrats within each site. Sites: SP, Mt Speculation (1668 m); KB, King Billy (1969 m); MA, Mt Magdala (1725 m); BL, The Bluff (1725 m); ST, Mt Stirling (1748 m); BU, Mt Buller (1762 m); HO, Mt Hotham (1860 m); BO, Mt Bogong (1970 m). Mean Similarity, mean contribution of that species to the group; Similarity / SD, mean similarity divided by the standard deviation of each species' contribution to the mean similarity among groups; Cov, percent cover data; P/A, presence/absence data; *denotes exotic species.

Site	Species	Mean Abundance		Mean Similarity		Similarity / SD		Contribution %		Cumulative %
		Cov	P/A	Cov	P/A	Cov	P/A	Cov	P/A	
SP	<i>Hovea montana</i>	26.5	0.8	8.73	6.71	1.12	1.21	25.25	17.4	25.25
SP	<i>Podolobium alpestre</i>	23	0.6	5.82	3.73	0.65	0.68	16.83	9.67	42.08
SP	<i>Poa phillipsiana</i>	15	0.5	3.72	2.42	0.52	0.52	10.76	6.36	52.84
SP	<i>Carex breviculmis</i>	2.8	0.8	3.56	6.53	1	1.23	10.31	16.93	63.15
SP	<i>Stelleria pungens</i>	4.1	0.7	3.52	4.79	0.84	0.9	10.19	12.43	73.33
KB	<i>Poa fawcettiae</i>	55	0.9	14.99	7.24	1.75	1.95	29.67	12.18	29.67
KB	<i>Podolobium alpestre</i>	17.5	0.8	7.16	5.33	1.17	1.26	14.18	8.96	43.85
KB	<i>Microseris</i> sp. 2	7.6	0.9	7.12	7.18	1.62	1.94	14.1	12.07	57.95
KB	<i>Grevillia australis</i>	12.15	0.7	3.78	4.26	0.66	0.92	7.49	7.17	65.43
KB	<i>Carex breviculmis</i>	2.5	1	3.7	8.84	1.87	11.23	7.32	14.86	72.76
MA	<i>Hovea montanus</i>	33.5	0.9	11.49	8.97	1.77	1.88	26.72	18.53	26.72
MA	<i>Stelleria pungens</i>	16.5	0.7	5.78	5.31	0.88	0.91	13.43	10.96	40.15
MA	<i>Microseris</i> sp. 2	4.7	0.9	5.03	8.59	1.42	1.91	11.69	17.74	51.84
MA	<i>Poa phillipsiana</i>	15.5	0.6	4.37	3.8	0.69	0.7	10.15	7.84	61.99
MA	<i>Carex breviculmis</i>	3.7	0.8	3.7	6.78	1.06	1.23	8.59	14	70.58
BL	<i>Poa fawcettiae</i>	62	0.9	19.07	8.27	1.89	1.92	33.54	13.24	33.54
BL	<i>Hovea montanus</i>	24.5	0.9	12.66	8.18	1.66	1.92	22.27	13.09	55.81
BL	<i>Celmisia pugioniformis</i>	11.5	0.6	4.53	3.3	0.67	0.7	7.97	5.28	63.78
BL	<i>Prostanthera cuneata</i>	11	0.6	4.41	3.25	0.67	0.7	7.75	5.19	71.54
BL	<i>Microseris</i> sp. 2	1.8	1	4.11	10.21	4.66	9.5	7.23	16.33	78.76
ST	<i>Hovea montanus</i>	25.1	0.9	10.73	10.45	1.4	1.84	21.61	18.08	21.61
ST	<i>Stelleria pungens</i>	8	1	10.67	13.19	6.52	5.81	21.49	22.82	43.1
ST	<i>Poa heimata</i>	40	0.7	8.39	6.11	0.86	0.9	16.91	10.58	60
ST	<i>Grevillia australis</i>	17.5	0.8	7.57	7.57	1.12	1.24	15.26	13.1	75.27
ST	<i>Acetosella vulgaris</i> *	4.1	0.7	4.03	6.34	0.84	0.9	8.11	10.98	83.38
BU	<i>Poa fawcettiae</i>	55.5	0.8	15.78	7.86	1.16	1.22	37.28	14.99	37.28
BU	<i>Stelleria pungens</i>	4.2	0.8	4.82	7.46	1	1.21	11.39	14.22	48.66
BU	<i>Podolobium alpestre</i>	9.5	0.6	3.97	4.01	0.66	0.68	9.37	7.64	58.03
BU	<i>Microseris</i> sp. 2	2.6	0.9	3.66	9.13	1.61	1.91	8.64	17.4	66.67
BU	<i>Craspedia</i> sp.	2.6	0.6	2.94	3.9	0.64	0.69	6.94	7.44	73.61
HO	<i>Poa fawcettiae</i>	34	1	18.4	12.57	6.65	13.59	35.46	24.74	35.46
HO	<i>Celmisia pugioniformis</i>	13.5	0.9	11.44	0.91	1.84	1.95	22.05	19.51	57.52
HO	<i>Kunzea mulleri</i>	32	0.7	9.05	5.76	0.86	0.92	17.44	11.33	74.96
HO	<i>Grevillia australis</i>	7	0.5	3.08	2.93	0.52	0.53	5.93	5.77	80.89
HO	<i>Craspedia</i> sp.	2.6	0.6	2.99	4.19	0.64	0.7	5.76	8.25	86.65
BO	<i>Poa fawcettiae</i>	54	1	28.22	16.29	3.55	3.76	54.88	33.69	54.88
BO	<i>Celmisia pugioniformis</i>	20.5	0.7	9.53	7.52	0.82	0.87	18.54	15.56	73.42
BO	<i>Craspedia</i> sp.	6.6	0.9	8.09	11.71	1.15	1.87	15.73	24.21	89.15
BO	<i>Carex breviculmis</i>	2.35	0.7	2.85	6.68	0.73	0.91	5.54	13.81	94.68
BO	<i>Asperula gunnii</i>	1.2	0.4	0.78	1.58	0.36	0.39	1.51	3.26	96.2

Table 2.5. Mean similarity (percent) of quadrats within each site based on percent cover (Cov) and presence/absence (P/A) data, with total number of species recorded at each site. Sites: SP, Mt Speculation; KB, King Billy; MA, Mt Magdala; BL, The Bluff; ST, Mt Stirling; BU, Mt Buller; HO, Mt Hotham; BO, Mt Bogong.

Site	Mean similarity (%)		Species richness
	within sites		
	Cov	P/A	
SP	34.58	38.55	30
KB	50.31	59.48	19
MA	43.02	48.42	19
BL	56.86	62.51	23
ST	49.63	57.79	13
BU	42.32	52.45	20
HO	51.87	50.79	14
BO	51.42	48.35	21

Discussion

Vegetation patterns with climatic and environmental parameters

Climatic and environmental factors vary predictably across the altitudinal gradient of sites sampled. Collectively, the sites show high degrees of floristic variation and no single climatic or environmental factor can adequately explain the patterns in vegetation across sites. Rather a combination of variables is more useful. Other factors not examined in this study, such as past fire frequency or other disturbances, such as cattle grazing intensity, may contribute to the variation in the vegetation amongst sites. However, these sites have a very similar fire-history; none have been burnt in recent decades as the last recorded alpine fire being in 1939, where discrete burn patterns across the landscape were not recorded. Over time, such variables (fire history, grazing etc) would also form part of the complex environmental gradient.

The combination of lower temperatures, increased precipitation, decreasing total nitrogen and decreasing soil organic carbon appeared to be the most important variables with increasing altitude, as indicated by the fit of the regression models in the BIC analysis. Related climatic variables, such as frosts, are also more likely at the higher altitude sites, owing to the lower temperatures. In a separate study, I recorded 31 frost events (air temperatures below 0 °C) at King Billy (1696 m), and 41 frost events at Mt Bogong (1970 m) during the snow-free season in 2005/06 (see Chapter 7). In addition to

cooler temperatures, growing season length can be up to a month shorter at the higher sites, as seen in the abrupt increase in growing degree days in Figure 2.5.

The vegetation patterns across sites appear to be driven by altitude, as seen in the ordination diagrams, as altitude can represent a gradient in environmental and climatic factors. These factors therefore appear to correlate with the patterns in floristic variation. The vegetation at Mt Bogong and Mt Hotham, the highest sites, show a distinct suite of species. In addition, there is a decrease in shrub abundance at the higher sites and a decrease in the total number of shrub species. Hence, the distinct assemblage of species common to Mt Bogong and Mt Hotham is likely to be a direct result of these species being able to adapt to the climatic constraints, such as extended snow cover and lower temperatures (Körner 1999). Similar floristic patterns in alpine vegetation are often seen across altitudinal gradients elsewhere in Australia (Costin 1957; Kirkpatrick and Bridle 1998; Costin *et al.* 2000) and around the world (Körner 1999). Changes in species' ranges and tolerance of various climatic conditions can be related to growth form. Small, rosettes and clumped graminoids are able to protect meristematic regions from frosts and low temperatures by housing them deep within the centre of the plant (Körner 1999). In comparison, the aerial, unprotected position of buds and shoots in shrub species can restrict them from growing at altitudes where detrimental conditions are present.

The vegetation assemblage at each site was distinctive. However, variation within each site was evident as generally quadrats were no more than 20 -30 % similar. This variation adds to the inconsistencies among sites seen in the ordinations and cluster analysis, and may explain why each site appears only partially influenced by the environmental and climatic variables. Overall, the vegetation assemblage on each Victorian mountain top exhibits a high degree of local variation and only a small amount of overlap in composition between mountains (sites), consistent with the broad-scale patterns found by Walsh *et al.* (1986).

Common overlapping species between the lowest sites were *Hovea montanus* and *Podolobium alpestre* (both shrubs). Common overlapping species between some of the high sites include *Poa fawcettiae* and *Celmisia pugioniformis*. Although *Poa* and *Celmisia* are sporadically present at lower sites, they are not ranked highly as driving species, as indicated by the similarity tables. The presence of some species across the entire gradient, such as *Asperula gunnii*, *Carex breviculmis*, and *Grevillea australis*, suggests a wide ecological tolerance and the potential capacity to withstand changing environmental/climatic conditions in the future (Wearne and Morgan 2001a). There was a significant decrease in mean species richness with altitude, consistent with European

mountain studies where, across much larger environmental gradients, species richness nearly always decreases with altitude (Körner 1999). Overall, my analysis shows greater shrub abundance and species richness at lower altitudes. In contrast, very few shrub species contribute to the total composition at higher altitudes. These patterns are also consistent with patterns seen in mountain studies in south-eastern Australia, Tierra del Fuego and Europe (Kirkpatrick and Bridle 1998; Körner 1999; Mark *et al.* 2001).

Predicting future vegetation patterns in Victoria

This study across an altitudinal gradient can be used in a space-for-time analysis in order to predict future patterns in vegetation and floristic variation. The change in abundances of species life-forms across the altitudinal gradient showed straightforward, linear responses with altitude. However, the floristic variation within these sites was not linear, nor easily predictable. Hence, a space-for-time analysis across these sites may be limited to life-forms and predicting the general patterns in species abundances (Pickett 1989).

The climate change predictions for the Australian alpine zone reveal that higher temperatures, decreased snowfall, and earlier snow-melt are likely scenarios for the future (Hennessey *et al.* 2003). In addition, the snow line is predicted to rise (Hennessey *et al.* 2003) which would leave the lowest alpine sites virtually snow-free for most of the winter and considerably lengthen the growing season. Flow-on effects to the vegetation may include a change in the timing of species' growing optima and phenological events (Galen and Stanton 1993; Venn and Morgan 2007) and hence, potential changes in the timing of seed production and seedling establishment. In addition, with changes in climate across the altitudinal gradient, there is the likelihood that species may initiate migration, expand or contract their current range. Grabherr *et al.* (1994) report species migrations in the Swiss Alps over the last century up to 4 m per decade in response to a temperature rise of 0.7 °C, although most species can only move < 1 m per decade (Grabherr *et al.* 1994; Klanderud and Birks 2003; Walther *et al.* 2005). Therefore, alpine species are unlikely to track the changes in climate as quickly as these changes occur (Körner 1999). Dispersal mechanisms among most alpine plants are unlikely to limit range expansions, as occasionally seed from sub-alpine species can be found at higher altitudes (see Chapter 3). However, other climatic factors associated with warming temperatures, such as unexpected early season frosts (Bannister *et al.* 2005), are likely to suppress expansion, contraction or migration of those species by acting on seedling establishment (Inouye 2000). In places where snow melt occurs unexpectedly early, plants may experience more severe temperatures as they are 'left out in the cold' without the insulative

protection of snow cover (Bannister *et al.* 2005). Nonetheless, if frosts are minimal, the lower mountains in this altitudinal gradient may slowly support species previously considered sub-alpine, and the higher alpine areas may support an increased number of shrub species.

Range expansions and subsequent changes to current species dynamics in alpine systems are more likely following disturbances which can prompt regeneration (Kirkpatrick and Dickinson 1984; Wahren *et al.* 2001a). Disturbances such as fire, herbivory and soil disruptions act to create instant opportunities for regeneration from seed (Williams 1992), potentially altering species dynamics which can lead to changes in vegetation patterns. As climate-change in the Australian alpine region is likely to induce such disturbances more frequently (Hennessey *et al.* 2003), there is every likelihood that species will respond in combination with warming temperatures. Such disturbances and future changes in the Australian alpine landscape will be discussed further in Chapter 8.

Conclusions

At the higher altitudes in this study, floristic composition appears to be driven by low temperatures and high precipitation. These factors may also be related to the reduction in total soil nitrogen and organic carbon. Environmental characteristics such as previous grazing history, soil pH and mineral composition showed no predictive trends with the altitudinal gradient. Vegetation at the high altitude sites was the most similar in composition, whereas the floristic composition of the low altitude sites showed high degrees of variation within and between sites. All sites were significantly different from one another in terms of floristic variation. Shrub and forb species tended to drive differences between the lower and higher altitude sites. Applied as a space-for-time chronosequence to predict future vegetation patterns with a changing climate, the results indicate that shrub abundance may increase at high sites in future decades, and low sites may support vegetation not previously considered alpine.

Appendices

Appendix 2.1. The 35 climatic variables estimated by BIOCLIM bioclimatic prediction system of the ANUCLIM software package (Houlder *et al.* 2000). The variables subsequently used in the BIC analysis were chosen from these nine (shaded) variables which showed strong linear relationships with altitude.

Climate parameters estimated by BIOCLIM	Mt Bogong	Mt Hotham	Mt Buller	Mt Stirling	The Bluff	Mt Magdala	King Billy	Mt Speculation
	1970 m	1860 m	1762 m	1748 m	1725 m	1725 m	1696 m	1668 m
Annual Mean Temperature	3.9	4.5	4.9	5	5	5	5.2	5.5
Mean Diurnal Range(Mean(period max-min))	6.3	6.4	6.2	6.3	6.3	6.4	6.5	6.6
Isothermality 2/7	0.31	0.32	0.33	0.33	0.33	0.33	0.34	0.34
Temperature Seasonality (C of V)	1.71	1.67	1.63	1.63	1.61	1.6	1.61	1.63
Max Temperature of Warmest Period	15.6	16	16.1	16.2	16.2	16.2	16.4	16.8
Min Temperature of Coldest Period	-4.4	-3.9	-3.1	-3	-2.9	-2.9	-2.8	-2.7
Temperature Annual Range (5-6)	20	20	19.2	19.2	19.1	19.1	19.2	19.4
Mean Temperature of Wettest Quarter	-1.9	-1.3	-0.6	-0.5	-0.4	-0.3	-0.2	-0.1
Mean Temperature of Driest Quarter	10.1	10.5	10.6	10.7	10.6	10.6	10.9	11.2
Mean Temperature of Warmest Quarter	10.1	10.5	10.7	10.8	10.7	10.7	11	11.3
Mean Temperature of Coldest Quarter	-1.9	-1.3	-0.8	-0.7	-0.6	-0.6	-0.4	-0.2
Annual Precipitation	2615	2350	1757	1769	1756	1827	1788	1802
Precipitation of Wettest Period	85	75	55	55	55	58	56	57
Precipitation of Driest Period	25	24	18	19	19	20	19	19
Precipitation Seasonality(C of V)	34	32	27	28	27	28	28	29
Precipitation of Wettest Quarter	922	816	589	595	589	616	604	614
Precipitation of Driest Quarter	370	342	276	277	276	286	279	277
Precipitation of Warmest Quarter	373	346	278	278	278	286	279	278
Precipitation of Coldest Quarter	921	814	586	587	585	607	596	608
Annual Mean Radiation	13.4	13.4	13.8	13.8	13.8	13.7	13.8	13.8
Highest Period Radiation	21.9	22	22.3	22.4	22.4	22.4	22.5	22.6
Lowest Period Radiation	5.3	5.3	5.4	5.4	5.4	5.4	5.4	5.4
Radiation Seasonality (Cof V)	46	46	46	46	46	47	47	47
Radiation of Wettest Quarter	7.2	7.1	8	8	8	7.9	8	7.5
Radiation of Driest Quarter	19.2	19.4	19.5	19.5	19.5	19.4	19.5	19.5
Radiation of Warmest Quarter	19.7	20	20.1	20.1	20.1	20	20.1	20.2
Radiation of Coldest Quarter	6.9	6.8	7.2	6.9	7.1	6.8	6.8	6.9
Annual Mean Moisture Index	1	1	0.98	0.98	0.98	0.99	0.98	0.98
Highest Period Moisture Index	1	1	1	1	1	1	1	1
Lowest Period Moisture Index	0.98	0.96	0.88	0.88	0.88	0.9	0.88	0.85
Moisture Index Seasonality (C of V)	0	1	4	4	4	3	4	5
Mean Moisture Index of High Qtr. MI	1	1	1	1	1	1	1	1
Mean Moisture Index of Low Qtr. MI	0.99	0.98	0.93	0.93	0.93	0.94	0.93	0.91
Mean Moisture Index of Warm Qtr. MI	0.99	0.99	0.94	0.94	0.95	0.95	0.94	0.93
Mean Moisture Index of Cold Qtr. MI	1	1	1	1	1	1	1	1

Appendix 2.2. Soil nutrients, trace elements, minerals and extractable ions and from soils at each site. Key: P, K, S: Phosphorus, Potassium, Sulphur (mg/kg). Cu, Zn, Mn, Fe: Copper, Zinc, Manganese, Iron (mg/kg) extracted using diethylenetriaminepentacetic acid (DPTA). Ca, Mg, Na, K₂, Al: extractable ions of Calcium, Magnesium, Sodium, Potassium and Aluminium (meq/100g). Total N: total nitrogen (%); pH: soil pH analysed with H₂O and pH electrode; OC: Organic carbon content (%). All analysis except pH was undertaken by CSBP Soil and Plant Nutrition Laboratory Ltd. Bibra Lake, Western Australia.

Element	Mt Bogong	Mt Hotham	Mt Buller	Mt Stirling	Mt Magdala	The Bluff	King Billy	Mt Speculation
P	32	28	167	121	48	23	48	14
K	135	211	418	117	231	134	290	82
S	9.2	11.2	25.5	7	11.8	6.7	6.2	8
Cu	1.29	0.78	0.6	0.39	1.3	0.37	0.37	0.47
Zn	1.31	2.32	5.26	2.47	4.98	1.8	0.87	0.78
Mn	31.87	92.9	15.87	10.79	87.85	27.52	7.2	7.08
Fe	181.98	180.26	431.74	182.02	316.06	243.31	131.13	159.83
Ca	0.25	2.65	4.07	1.43	2.05	1.25	3.28	0.63
Mg	0.24	0.87	1.71	0.49	0.72	0.4	1.31	0.37
Na	0.02	0.07	0.04	0.07	0.03	0.03	0.07	0.02
K ₂	0.36	0.54	1.06	0.33	0.52	0.33	0.64	0.18
Al	4.4	3.16	5.54	8.72	5.43	3.97	4.63	8.16
Total N	0.46	0.38	1.4	1.09	0.59	0.46	1.77	0.38
pH	4.8	5.3	4.5	4.9	4.6	4.7	5.0	4.9
OC	5.47	7	10	10	8.52	6.46	10	6.12

Appendix 2.3. Comparisons between different numbers of predictors using the Schwarz-Bayesian Information Criterion (BIC) following multiple regression analysis against site altitude. *denotes the best predictors (smallest BIC values). Max, Maximum Temperature of Warmest Period; Min, Minimum Temperature of Coldest Period; Precip, Precipitation of Driest Quarter; N, Total nitrogen; OC, Organic carbon content (%); Cu, Copper concentration, extracted with DPTA. Low BIC values, (**bold**, marked with an asterisk*) indicate the best, more parsimonious models (Quinn and Keough 2003).

Independent variable	No. predictors	SS residual	R ²	P	F-ratio	BIC
Max	1	124812.11	1.00	0.00	1401.31	81.40
Min	1	377913.93	0.99	0.00	458.12	90.26
Precip	1	115398.10	1.00	0.00	1516.20	80.77
N	1	6693373.74	0.73	0.00	19.26	113.26
OC	1	1114937.74	0.96	0.00	150.65	98.92
Cu	1	5468120.58	0.78	0.00	25.15	111.64
Max, Min	2	4351.84	1.00	0.00	17307.31	56.63
Max, Precip	2	13336.62	1.00	0.00	5645.48	65.59
Max, N	2	117500.51	1.00	0.00	638.12	83.00
Max, OC	2	107551.91	1.00	0.00	697.42	82.29
Max, Cu	2	121362.35	1.00	0.00	617.72	83.26
Min, Precip	2	67417.76	1.00	0.00	1114.39	78.55
Min, N	2	371600.49	0.99	0.00	199.72	92.21
Min, OC	2	286031.41	0.99	0.00	260.37	90.11
Min, Cu	2	350640.80	0.99	0.00	211.84	91.74
Precip, N	2	115384.04	1.00	0.00	649.88	82.85
Precip, OC	2	109483.76	1.00	0.00	685.06	82.43
Precip, Cu	2	107737.81	1.00	0.00	696.21	82.30
N, OC	2	576255.34	0.99	0.00	127.73	95.72
N, Cu	2	2021182.77	0.92	0.00	34.27	105.76
OC, Cu	2	653999.16	0.97	0.00	112.19	96.73
Max, Min, Precip	3	2867.48	1.00	0.00	14593.32	55.37
Max, Min, N	3	4142.98	1.00	0.00	10099.98	58.32
Max, Min, OC	3	3966.78	1.00	0.00	10548.68	57.97
Max, Min, Cu	3	3959.90	1.00	0.00	10567.01	57.95
Max, Precip, N	3	13248.37	1.00	0.00	3157.28	67.62
Max, Precip, OC	3	13227.04	1.00	0.00	3162.38	67.60
Max, Precip, Cu	3	12154.81	1.00	0.00	3441.49	66.93
Max, N, OC	3	104383.02	1.00	0.00	399.27	84.13
Max, N, Cu	3	107359.20	1.00	0.00	388.16	84.35
Max, OC, Cu	3	97195.53	1.00	0.00	428.92	83.56
Min, Precip, N	3	67392.31	1.00	0.00	619.34	80.63
Min, Precip, OC	3	67117.76	1.00	0.00	621.88	80.60
Min, Precip, Cu	3	60871.87	1.00	0.00	685.86	79.81
Min, N, OC	3	206984.31	0.99	0.00	200.53	89.61
Min, N, Cu	3	326246.45	0.99	0.00	126.61	93.25
Min, OC, Cu	3	234585.26	0.99	0.00	176.74	90.61
Precip, N, OC	3	96912.21	1.00	0.00	430.18	83.53
Precip, N, Cu	3	105734.60	1.00	0.00	394.14	84.23
Precip, OC, Cu	3	96118.26	1.00	0.00	433.74	83.47
N, OC, Cu	3	480456.66	0.98	0.00	85.44	96.34
Max, Min, Precip, N	4	2454.36	1.00	0.00	10230.01	56.21*
Max, Min, Precip, OC	4	1938.00	1.00	0.00	12952.85	54.32*
Max, Min, Precip, Cu	4	2717.40	1.00	0.00	12953.85	57.02
Max, Precip, N, OC	4	13226.52	1.00	0.00	1897.50	69.68
Max, Precip, N, Cu	4	11453.93	1.00	0.00	1898.50	68.53
Max, Precip, OC, Cu	4	11589.62	1.00	0.00	2165.64	68.62
Max, N, OC, Cu	4	96437.28	1.00	0.00	259.38	85.57
Min, Precip, N, OC	4	65553.72	1.00	0.00	382.05	82.49
Min, Precip, N, Cu	4	59836.47	1.00	0.00	418.65	81.76
Percip, N, OC, Cu	4	89987.60	1.00	0.00	278.04	85.02
Max, Min, Precip, N, OC, Cu	6	1377.56	1.00	0.00	6075.78	55.75

Chapter 3 - The soil seed bank at alpine summits in Victoria in relation to the standing vegetation

Summary

In this chapter, I describe the nature of the germinable seed bank from study sites across an altitudinal gradient in Victoria. I describe the density of species, life-form abundances and seasonal differences. I examine the similarity of species in the seed bank within each site and compare the similarity of seed bank species with the species of the standing vegetation. I group species in the seed bank and the standing vegetation according to regeneration class, in an attempt to assess how frequently species of a particular class are present and whether the dominance of species in each regeneration class changes across an altitudinal gradient.

The density of germinable seeds from seed bank samples showed no significant differences between seasons, nor a significant relationship with altitude. Species richness in seed bank samples was dependent upon site. I suggest that the seed banks at these sites are persistent. The similarity between seed bank samples and the immediate standing vegetation was low. Of the seeds that germinated in the seed bank samples, the percentage of these species that were also present in the local standing vegetation was between 30-65%. The species in seed banks across all sites were no more, or less similar to each other than to other sites, based on NMDS and ordination. At all sites, there were more species from the seed bank that fit into the 'mostly seed' class. Species in the standing vegetation were equally classed as 'mostly seed' and 'mostly vegetative'. Across the regeneration classes of seed bank species, there were no significant trends with altitude. The proportion of species from the standing vegetation in the 'obligate seedling' class appeared to increase with altitude.

I discuss my results, with reference to the international literature, on the topics of transient and persistent seed banks, changes across altitudinal gradients, and how regenerative strategies of species influence seed bank composition.

Introduction

Early research suggested that soil seed banks in alpine regions were either very small or non-existent (Billings and Mooney 1968; Bliss 1971). It was assumed that the cold and harsh conditions in such regions would limit seed production and therefore, limit additions to the seed bank. Consequently, seedling establishment was also thought to be rare. Thus, vegetative regeneration by rhizomes was thought to be the predominant means of regeneration in these habitats. However, reproduction from the seed bank can be an important mechanism of plant re-establishment following disturbances in alpine environments (Grubb 1977), and subsequent research in alpine and arctic areas has revealed that substantial seed banks do exist.

A review by McGraw and Vavrek (1989) indicated that seed banks in alpine and arctic regions may be larger than previously assumed and of a comparable size to seed banks in temperate regions. Estimates of the size of seed banks from undisturbed alpine / sub-alpine habitats range up to 7000 seeds per m² (Chambers 1993; Diemer and Prock 1993). However, germination requirements and microsite characteristics seem to limit germination and seedling establishment under natural conditions (Wager 1938; Bell and Bliss 1980; Welling *et al.* 2004). There is also evidence that seed bank size may change over altitudinal and latitudinal gradients (Thompson 1978). At higher altitudes and latitudes, seed production and seed rain may decrease in comparison with that observed at lower altitudes and latitudes, where environmental conditions are more favourable to plant productivity (Milton 1939; Fox 1983; Miller and Cummins 1987). Thus, there may be a decrease in seed bank size with increasing altitude or latitude as plant productivity responds to increasingly stressful conditions and subsequent inputs into seed banks decline. On the other hand, cool and stable soil conditions, with low decomposition rates in harsh climates are likely to aid the preservation of seeds stored in the soil (Fox 1983), allowing seed stores to build up over time.

Seed banks can be classed as either *transient* or *persistent* (Thompson and Grime 1979). In transient seeds banks, seeds typically remain within the top soil layers and can germinate quickly, usually within one year (Welling *et al.* 2004). Species with persistent seed banks have viable seed that may become buried under the surface soil layers, potentially inducing dormancy, and germination of accumulated seeds may not occur for several years (Welling *et al.* 2004). Therefore, species with transient seed banks are usually adapted to exploit the gaps created by predictable disturbances (Thompson and Grime 1979) whereas persistent seed banks can act as a genetic memory of a population (Simpson *et al.* 1989). In some cases, even in arctic areas, buried seeds can persist in the

soil for centuries (McGraw *et al.* 1991). Hence, without regular disturbances, the germination of seed in persistent seed banks may play an important role in future community dynamics and the structure of plant populations.

The composition of the seed bank and the standing vegetation provide an indication of the potential for regeneration from seeds in a particular environment (Diemer and Prock 1993). Fox (1983) found a positive correlation between biomass of established species and seed bank size in the Alaskan tundra and others have also shown that the seed bank species are mostly represented in the established vegetation (Molau and Larsson 2000; Cooper *et al.* 2004). However, in some cases, similarity between the seed bank and the standing vegetation can be low (Freedman *et al.* 1982; Welling *et al.* 2004). If environmental factors at high altitudes do indeed reduce the potential for plants to contribute to seed banks, the similarity between the composition of the established vegetation and the seed bank might be expected to decrease with altitude (Diemer and Prock 1993). Long periods without disturbance and a lack of suitable environmental factors to cue regeneration from seed banks, in combination with high mortality of seeds and seedlings, can also contribute to low similarity between the standing vegetation and soil seed banks at high altitudes (Roach 1983; Welling and Laine 2000b).

Alpine vegetation is regarded as highly sensitive to the impacts of climate and environmental changes (Grabherr *et al.* 1994; Arft *et al.* 1999). Following such events, community composition may be mediated by the seed rain and the seed bank (Molau and Larsson 2000). Hence, a better understating of the role of alpine seed banks in community dynamics is crucial for predicting the potential redistribution of plant species in these landscapes in future decades.

In the current study, I examine the variation in species richness and density of viable seeds in soil seed banks across an altitudinal gradient of mountain summits within the Victorian alpine zone. I compare the species composition of the established standing vegetation with that of the seed bank, and attempt to relate similarities and differences to altitude. Annual inputs into seed banks are compared across sites from samples collected during either spring or autumn and therefore, the species contributing to either persistent or transient seed banks are quantified. I also classify the species in the seed bank and standing vegetation according to their predominant regeneration strategy. I can then establish which species are more or less likely to contribute to soil seed banks based on their strategy, and investigate whether the abundances of species in different strategies change across the altitudinal gradient.

Methods

Study sites

The soil and vegetation sampling was conducted on eight alpine summits in Victoria, Australia (Table 2.1 in Chapter 2). These summits represent a gradient in environmental variables from more favourable conditions at Mt Speculation (1668 m), where winter snow cover is usually marginal, to Mt Bogong (1986 m) where frosts are common all year round (Williams 1987) and where snow cover may last for four to five months of the year. All summits have been free from major disturbances such as bushfires since at least 1939, but have been grazed by cattle to various degrees in the past (Table 2.1 in Chapter 2). All summits are within the Alpine National Park, approximately 350 km from Melbourne, and are within 40 km of each other with most less than 10 km apart (Figure 2.1 in Chapter 2). Mean annual rainfall of this region is relatively high compared to adjacent lowland areas, over 1800 mm (LCC 1982), with much of this precipitation falling as snow on the high peaks during winter. Average air temperatures follow seasonal variations, with typical daily minimums and maximums of 2 and 27 °C in summer and -6 and 12 °C in winter (Bureau of Meteorology, *unpublished data*). However, at the high sites, temperatures can be up to ten degrees lower during summer, frosts are more frequent and severe and snow cover can last up to a month longer (Chapter 2). All sites are classed as 'Steep Alpine Mountains' after Costin (1957) and all contain tall alpine herbfield vegetation. The underlying geology of the area is varied (Table 2.2 in Chapter 2). Despite the variation, in these regions parent material rarely influences soil type and all soils are considered alpine humus, with a gravelly and skeletal structure (Costin 1962b; LCC 1982) and are acidic, ranging from pH 4 to 5.

Sampling and laboratory methods

Twice during the 2004/2005 growing season at each site, I randomly placed twenty 1 m² quadrats within which I recorded all vascular plant species to the nearest 5%. I then collected three soil cores of 4 cm diameter to a depth of 10 cm within each quadrat, which were bulked. The first round of sampling occurred in spring (from October to December), before the onset of flowering and seeding of the standing vegetation. The second round of sampling occurred in autumn (from March to April), after the seed dispersal from adult plants had finished. Collecting seed seasonally allowed me to characterise the soil seed bank when seed densities should be minimal, after the flush of early spring germination, but before the commencement of flowering and seed inputs in

the current season when seed densities may be potentially at their maximum. Hence, the difference in seed density between samples from these two seasons should reflect the nature of a functioning seed bank in terms of persistence or transience.

Soil samples collected in the field during both seasons were returned to the laboratory, air dried, and sieved to 2 mm to remove gravel and plant material such as roots and shoots. Seeds larger than 2 mm were identified during this process and returned to the sample. Soil samples were then moistened by spraying with tap water, placed in air-tight plastic bags and cold-stratified in dark conditions at 2 °C for two months. After this period, samples were then spread evenly over 2 cm of autoclaved sand in 130 × 75 mm rectangular trays and re-located to the glasshouse. All samples were automatically watered twice daily with a fine spray-mist, and kept at warm ambient temperatures (12 to 30 °C). Soil samples were equal in their volume, but varied in weight due to differences in soil composition and compaction.

Soil samples were censused for germinants every six to eight weeks until the number of germinants per tray plateaued, at around 30 weeks. During each census, seedlings were identified and removed. In cases where I was unable to identify seedlings, individuals were transplanted into separate pots, and were allowed to grow until they were identifiable. Seedlings that died before they were identified were recorded as unidentified monocot or dicot. At approximately 15 weeks into the study, moss growing on the samples was removed and the soil was deliberately disturbed to encourage further germination of seeds. Known nursery weeds from the glasshouse environment were removed and not recorded in the analysis

Data analysis

The density of germinable seed per m², estimated from the three bulked soil samples of known volume per quadrat, at sites across the altitudinal gradient, were analysed by linear regression. Site and seasonal differences between seed density was analysed using two-way ANOVA on un-transformed and square-root transformed data.

Similarity analyses between the density of germinable seed and the standing vegetation within the same quadrat were carried out based on Jaccard's qualitative similarity index and the quantitative similarity ratio (Jongman *et al.* 1987; Welling and Laine 2000b), for both the seasons, before and after flowering. The qualitative similarities were calculated according to the equation:

$$SJ = c/(A + B - c)$$

where A is the total number of species in the mature vegetation, B is the total number of species of seedlings, and c is the number of species shared by the standing vegetation and the seedling vegetation (Welling and Laine 2000b).

As quantitative data from species abundances always have many zeros (i.e. some species are absent from several sites and quadrats), I used a quantitative index which gives different weights to the presence or absence of a species, with regard to differences in abundance when the species is present (Jongman *et al.* 1987). The quantitative similarities, or similarity ratio (see Ball 1966 in Jongman *et al.* 1987), were calculated according to the equation:

$$SR_{ij} = \sum_k Y_{ki} Y_{kj} / (\sum_k Y_{ki}^2 + \sum_k Y_{kj}^2 - \sum_k Y_{ki} Y_{kj})$$

where Y_{ki} is the abundance of the k th species in the mature vegetation, Y_{kj} is the abundance of the k th species in the seedling vegetation, and $Y_{ki} Y_{kj}$ is the abundance of species shared by the mature and seedling vegetation (Welling and Laine 2000b). As per Welling and Laine (2000b), I transformed the mature and seedling vegetation values to comparable percentages, so sums of the number of seedlings and percent cover of mature vegetation were both 100 at each site. For both indices, values closer to 1 indicate a closer similarity between standing and seedling vegetation, and values closer to 0 indicate low similarity.

The variation in mean quantitative and qualitative values between sites across the gradient were then analyzed using two-way ANOVA and Bonferroni post-hoc tests on un-transformed and square-root transformed values (Quinn and Keough 2003). In addition to using the aforementioned similarity indices, I also compared the number of species that are shared between the standing vegetation and the germinable seed bank using simple percentage values, and compared these across sites with one-way ANOVA on un-transformed and square-root transformed values. Predictable changes in the similarity indices, and the percentage similarity between seed bank and standing vegetation across the altitudinal gradient, were investigated with linear regression.

I used ordination to investigate the differences and similarities in the germinable seed bank across sites. I analysed absolute values of seedling emergence and presence/absence of each species in the seedling flora. Quadrats were ordinated by global non-metric multidimensional scaling (NMDS). This method is well suited to data that are non-normal or are on arbitrary or discontinuous scales. NMDS is an iterative search for a ranking and placement of n entities on k dimensions (axes) that minimizes the stress of the k -dimensional configuration. The calculations are based on an $n \times n$ distance matrix calculated from the $n \times p$ -dimensional main matrix, where n is the number of rows and p

is the number of columns in the main matrix. How good the dissimilarity matrix is can be determined by the stress value (Kruskal 1964; McCune and Mefford 1999). Stress values below 0.2 are recommended (Clarke 1993), as values above this threshold may yield misleading interpretations. Dissimilarities between all quadrats were calculated using the Bray-Curtis dissimilarity coefficient, previously noted as a robust measure in recovering ecological distance over a range of models and stochastic variations in the data (Quinn and Keough 2003).

I divided the species found in the seed banks and the standing vegetation into one of four regeneration classes. Species were classed by their capability and frequency with which they reproduce by seed or are able to spread vegetatively under natural conditions. The groups were: obligate seeder (OS, no ability to regenerate vegetatively); mostly seed (MS, the species rarely regenerate vegetatively, although it has the ability to do so); mostly vegetative (MV, the species rarely reproduces by seed although it has the ability to do so); and vegetative reproduction (VR, reproduction by vegetative means consistently maintains populations of the species). The frequencies of species in particular groups were used in comparisons between the seed bank and the standing vegetation, and across sites.

All statistical analyses were performed using SYSTAT version 10 (Copyright SPSS Inc., 2000), except the ordinations, which were performed using PC-ORD (McCune and Mefford 1999).

Results

Germination from seed bank samples

The total germinable seed bank from the eight alpine sites was composed of 41 species from 25 families, of which Asteraceae (eight species), Poaceae (five species) and Myrtaceae (three species) were the most common. Twenty-three of the seed bank species were herbs, nine were shrubs, seven were graminoids, and one fern, moss and tree species were also recorded. In contrast with the patterns of life-forms recorded across the altitudinal gradient in Chapter 2, here there were no significant relationships between the life-form of seed bank species with altitude. Forb species were the most common in all samples, followed by graminoid and shrub species. There were no significant differences between the occurrences of particular life forms from either spring or autumn samples. Species richness in the seed bank varied across sites from 18 species at Mt Hotham to

nine at Mt Stirling and The Bluff. There was a significant relationship between species richness and altitude for samples collected during autumn, although this relationship has poor predictive power ($R^2 = 0.061$, $P = 0.002$). Results from independent t-tests showed no significant differences between the species richness of samples between seasons at any site; nor were there any significant differences in total individuals per sample, between seasons. Two-way ANOVA of species richness indicated a significant interaction between site and season (site \times season, $F = 2.288$, $P = 0.028$). Species richness was also dependent on site ($F = 3.594$, $P = 0.001$), but not season ($F = 0.247$, $P = 0.619$).

The density of germinable seeds varied between sites (Figure 3.1). However, within each site, there were no significant differences in density between seasons, except at Mt Speculation (t-test, $P = 0.041$). Seed bank density was independent of the interaction between site and season ($F = 1.018$, $P = 0.418$), and season alone ($F = 0.791$, $P = 0.375$), but was dependent on site ($F = 21.329$, $P = 0.000$).

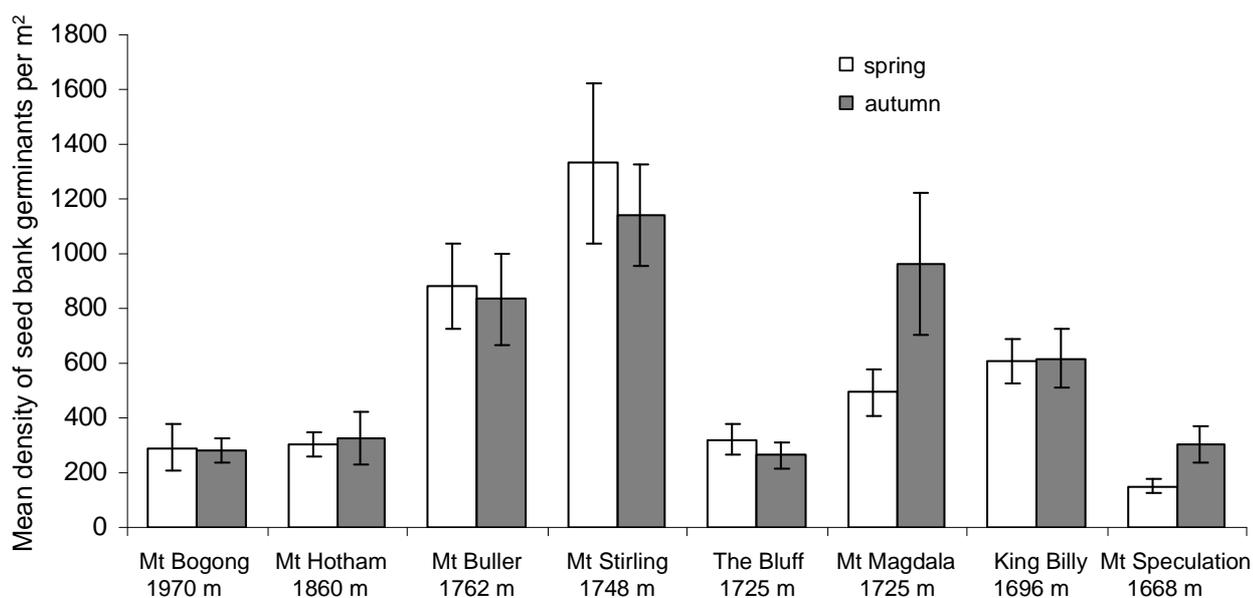


Figure 3.1. Mean (± 1 standard error) density of germinants from the soil seed bank (per m^2) at each site across the altitudinal gradient from samples collected before flowering (spring) and after flowering (autumn).

No species consistently contributed significantly more seed during either season, autumn or spring (based on paired t-tests) and hence, none of the species in this study can be classed as having a transient seed bank. Occasionally, some species' contribution to the seed bank between seasons was significantly different at a particular site, but this was never consistent across the gradient, nor was there any relationship with altitude. Individual species' contribution to overall density values are shown in Tables 3.1 and 3.2.

The overall density of germinable seeds from both seasons showed no predictive relationships with altitude. However, this analysis did show that the relationship was significant for samples collected during autumn ($R^2 = 0.061$, $P = 0.059$).

The similarity between the standing vegetation and the seed bank, based on qualitative and quantitative data, was generally low at all sites (Figure 3.2). The number of species shared between the standing vegetation and the seed bank, based on Jaccard's qualitative (SJ) similarity, was dependent on site (two-way ANOVA, $F = 3.505$, $P = 0.001$), but not season, nor the interaction between site and season (season, $F = 1.184$, $P = 0.277$; site \times season, $F = 1.105$, $P = 0.360$). The quantitative similarity between the seed bank and the standing vegetation, based on the similarity ratio (SR), which incorporates the abundance of species in every sample, was also dependent on site, but not season nor their interaction (two-way ANOVA; site, $F = 2.359$, $P = 0.023$; season, $F = 0.496$, $P = 0.482$; site \times season, $F = 0.935$, $P = 0.480$).

At most sites, the qualitative similarity between the standing vegetation and the seed bank was higher than the quantitative similarity. This indicates that although there may be some similarity in species between the two life-history stages, the relative abundances of these species are largely dissimilar. This may be due to the occurrence of common species in the standing vegetation which grow in a sparse manner, such as *Carex* and *Luzula* species. The number of individuals of these species may be high, but their percent cover is rarely over 10%. Hence, high numbers of individuals in the seed bank of such species can lead to poor correlations when based on abundance between the seed bank and standing vegetation.

Table 3.1. Seed density per m² (mean ± 1 standard error), family, life-form and regeneration class from soil seed bank samples collected during the spring of the 2004/2005 growing season, from eight alpine sites in Victoria. * denotes exotic species. Species names follow Ross and Walsh (2003). MS, mostly seed; MV, mostly vegetative; OS, obligate seeder; VR, vegetative reproduction maintains populations.

Species	Family	Life form	Regeneration class	Sites							
				Mt Bogong mean ±1se	Mt Hotham mean ±1se	Mt Buller mean ±1se	Mt Stirling mean ±1se	Mt Magdala mean ±1se	The Bluff mean ±1se	King Billy mean ±1se	Mt Speculation mean ±1se
<i>Acetosella vulgaris</i> *	Polygonaceae	Forb	MS	16.7 ± 11.7	10.0 ± 5.5	363.3 ± 85.6	1063.3 ± 296.0	180.0 ± 81.7	70.4 ± 22.6	83.3 ± 21.6	
<i>Asperula gumii</i>	Rubiaceae	Forb	MV				6.7 ± 4.6	16.7 ± 16.7			3.3 ± 3.3
<i>Baeckea ramosissima</i>	Myrtaceae	Shrub	MV	3.3 ± 3.3	6.7 ± 4.6		3.3 ± 3.3				13.3 ± 10.4
<i>Brachyscome rigidula</i>	Asteraceae	Forb	MV	10.0 ± 10.0			13.3 ± 10.4		3.3 ± 3.3		
<i>Brachyscome spathulata</i>	Asteraceae	Forb	MS			3.3 ± 3.3					3.3 ± 3.3
<i>Carex breviculmis</i>	Cyperaceae	Graminiod	MS	153.3 ± 81.8	33.3 ± 13.2	193.3 ± 71.6	86.7 ± 20.0	116.7 ± 29.4	100.0 ± 37.9	156.7 ± 34.3	36.7 ± 14.1
<i>Chionogentias muelleriana</i>	Gentianaceae	Forb	MS		3.3 ± 3.3						
<i>Crassula sieberiana</i>	Chenopodiaceae	Forb	VR			3.3 ± 3.3			6.7 ± 4.6	6.7 ± 4.6	
<i>Epilobium</i> sp.	Onagraceae	Forb	MS	3.3 ± 3.3	16.7 ± 8.2	3.3 ± 3.3	3.3 ± 3.3	3.3 ± 3.3		3.3 ± 3.3	3.3 ± 3.3
<i>Erigeron nitidus</i>	Asteraceae	Forb	MS	3.3 ± 3.3						20.0 ± 9.8	
<i>Eucalyptus pauciflora</i>	Myrtaceae	Tree	MS		3.3 ± 3.3			6.7 ± 6.7		3.3 ± 3.3	
<i>Exocarpus nanus</i>	Santalaceae	Shrub	MS								
<i>Geranium potentilloides</i>	Geraniaceae	Forb	MV		10.0 ± 5.5						
<i>Gonocarpus montanus</i>	Haloragagaceae	Forb	MV			3.3 ± 3.3	3.3 ± 3.3				3.3 ± 3.3
<i>Goodenia hederacea</i>	Goodeniaceae	Forb	MV	6.7 ± 4.6		3.3 ± 3.3				3.3 ± 3.3	
<i>Hovea montana</i>	Fabaceae	Shrub	MV				3.3 ± 3.3	6.7 ± 6.7			
<i>Hydrocotyle</i> sp.	Apiaceae	Forb	MV		6.7 ± 4.6	6.7 ± 6.7					3.3 ± 3.3
<i>Hypochaeris radicata</i> *	Asteraceae	Forb	OS	20.0 ± 7.0	23.3 ± 16.9	6.7 ± 4.6	6.7 ± 4.6	13.3 ± 6.1	20.0 ± 8.5	20.0 ± 7.0	6.7 ± 4.6
<i>Juncus</i> sp.	Juncaceae	Graminiod	OS								
<i>Kunzea muelleri</i>	Myrtaceae	Shrub	MV		3.3 ± 3.3						
<i>Leptonella</i> sp.	Asteraceae	Forb	MS				3.3 ± 3.3				
<i>Luzula modesta</i>	Juncaceae	Graminiod	MS	16.7 ± 9.5	23.3 ± 13.9	166.7 ± 74.4	103.3 ± 33.7	36.7 ± 17.1	40.0 ± 18.4	110.0 ± 26.6	26.7 ± 12.2
<i>Lycopodium fastigiatum</i>	Lycopodiaceae	Moss	VR								
<i>Neopaxia australasica</i>	Portulacaceae	Forb	MS			13.3 ± 10.4	3.3 ± 3.3				
<i>Ozothamnus hookeri</i>	Helichrysum	Shrub	MS		3.3 ± 3.3						
<i>Poa costiniana</i>	Poaceae	Graminiod	MS	23.3 ± 12.1	13.3 ± 10.4	40.0 ± 14.8	3.3 ± 3.3	43.3 ± 13.9	20.0 ± 8.5	30.0 ± 14.9	3.3 ± 3.3
<i>Poa fawcettiae</i>	Poaceae	Graminiod	MS	20.0 ± 7.0	43.3 ± 16.2	10.0 ± 5.5	6.7 ± 4.6	20.0 ± 8.5	26.7 ± 12.2	70.0 ± 18.4	23.3 ± 7.3
<i>Podolobium alpestre</i>	Fabaceae	Shrub	MV		10.0 ± 10.0	16.7 ± 13.6		10.0 ± 10.0		13.3 ± 7.8	3.3 ± 3.3
<i>Polystichum proliferum</i>	Dryopteridaceae	Fern	OS					3.3 ± 3.3			
<i>Stelleria pungens</i>	Caryophyllaceae	Forb	MV					3.3 ± 3.3			
<i>Tasmania xerophila</i>	Winteraceae	Shrub	VR					3.3 ± 3.3			
<i>Trisetum spicatum</i>	Poaceae	Graminiod	MS		6.7 ± 4.6						
unidentified dicot	N/A	N/A	N/A	6.7 ± 4.6	13.3 ± 6.1	33.3 ± 10.3	13.3 ± 7.8	20.0 ± 10.9	30.0 ± 16.4	53.3 ± 13.3	6.7 ± 4.6
unidentified forb	N/A	N/A	N/A		3.3 ± 3.3	10.0 ± 7.3	6.7 ± 4.6	3.3 ± 3.3	3.3 ± 3.3	20.0 ± 8.5	6.7 ± 6.7
unidentified shrub	N/A	N/A	N/A	6.7 ± 6.7	53.3 ± 20.3	6.7 ± 4.6		3.3 ± 3.3	3.3 ± 3.3	13.3 ± 7.8	3.3 ± 3.3
<i>Viola betonicifolia</i>	Violaceae	Forb	OS					3.3 ± 3.3	3.3 ± 3.3		

Table 3.2. Seed density per m² (mean ± 1 standard error), family, life-form and regeneration class from soil seed bank samples collected during the autumn of the 2004/2005 growing season, from eight alpine sites in Victoria. * denotes exotic species. Species names follow Ross and Walsh (2003). MS, mostly seed; MV, mostly vegetative; OS, obligate seeder; VR, vegetative reproduction maintains populations.

Species	Family	Life form	Regeneration class	Sites							
				Mt Bogong mean ±1se	Mt Hotham mean ±1se	Mt Buller mean ±1se	Mt Stirling mean ±1se	Mt Magdala mean ±1se	The Bluff mean ±1se	King Billy mean ±1se	Mt Speculation mean ±1se
<i>Acetosella vulgaris</i> *	Polygonaceae	Forb	MS	25.9 ± 12.7	23.3 ± 13.9	373.3 ± 90.5	753.3 ± 196.2	436.7 ± 260.4	73.3 ± 26.9	106.7 ± 41.4	40.7 ± 38.7
<i>Asperula gunnii</i>	Rubiaceae	Forb	MV				16.7	11.7			
<i>Asterolasia trymalioides</i>	Rutaceae	Shrub	VR			3.3 ± 3.3					
<i>Baeckea ramosissima</i>	Myrtaceae	Shrub	MV								3.3 ± 3.3
<i>Brachyscome rigidula</i>	Asteraceae	Forb	MV	3.3 ± 3.3		26.7 ± 13.2	13.3 ± 10.4	16.7 ± 10.7	3.3 ± 3.3	43.3 ± 30.7	20.0 ± 13.8
<i>Brachyscome spathulata</i>	Asteraceae	Forb	MS								0
<i>Carex breviculmis</i>	Cyperaceae	Graminiod	MS	113.3 ± 35.9	133.3 ± 72.9	150.0 ± 33.1	150.0 ± 48.8	200.0 ± 54.1	40.0 ± 17.0	106.7 ± 31.1	63.3 ± 15.7
<i>Cotula alpina</i>	Asteraceae	Forb	MS		3.3 ± 3.3	3.3 ± 3.3					
<i>Crassula sieberiana</i>	Chenopodeaceae	Forb	VR			176.7 ± 176.7		16.7 ± 13.6	3.3 ± 3.3		3.3 ± 3.3
<i>Epilobium</i> sp.	Onagraceae	Forb	MS		3.3 ± 3.3	3.3 ± 3.3	3.3 ± 3.3		16.7 ± 11.7		
<i>Erigeron nitidus</i>	Asteraceae	Forb	MS							6.7 ± 4.6	
<i>Eucalyptus pauciflora</i>	Myrtaceae	Tree	MS					6.7 ± 6.7			
<i>Exocarpus nanus</i>	Santalaceae	Shrub	MS					3.3 ± 3.3			
<i>Geranium potentilloides</i>	Geraniaceae	Forb	MV		13.3 ± 7.8					26.7 ± 11.2	
<i>Gonocarpus montanus</i>	Haloragagaceae	Forb	MV		3.3 ± 3.3					3.3 ± 3.3	10.0 ± 7.3
<i>Goodenia hederacea</i>	Goodeniaceae	Forb	MV							3.3 ± 3.3	
<i>Hovea montana</i>	Fabaceae	Shrub	MV				10.0 ± 10.0				
<i>Hydrocotyle</i> sp.	Apiaceae	Forb	MV			3.3 ± 3.3	3.3 ± 3.3			6.7 ± 6.7	
<i>Hypochaeris radicata</i> *	Asteraceae	Forb	OS	3.3 ± 3.3	6.7 ± 6.7	10.0 ± 5.5	3.3 ± 3.3	13.3 ± 7.8	6.7 ± 4.6	23.3 ± 10.0	3.3 ± 3.3
<i>Juncus</i> sp.	Juncaceae	Graminiod	OS	3.3 ± 3.3	3.3 ± 3.3			3.3 ± 3.3			6.7 ± 4.6
<i>Kunzea muelleri</i>	Myrtaceae	Shrub	MV		6.7 ± 6.7						
<i>Leptorhynchos squamatus</i>	Asteraceae	Forb	VR		3.3 ± 3.3						
<i>Luzula modesta</i>	Juncaceae	Graminiod	MS	30.0 ± 14.1	16.7 ± 9.5	46.7 ± 18.8	96.7 ± 24.4	80.0 ± 24.9	23.3 ± 10.0	143.3 ± 36.9	16.7 ± 8.2
<i>Lycopodium fastigiatum</i>	Lycopodiaceae	Moss	VR					3.3 ± 3.3			
<i>Neopaxia australasica</i>	Portulacaceae	Forb	MS	3.3 ± 3.3				3.3 ± 3.3		3.3 ± 3.3	
<i>Pimelea axiflora</i>	Thymelaeaceae	Shrub	MV		10.0 ± 7.3			16.7 ± 9.5		3.3 ± 3.3	
<i>Poa costiniana</i>	Poaceae	Graminiod	MS	13.3 ± 10.4	20.0 ± 20.0	6.7 ± 4.6	3.3 ± 3.3	50.0 ± 15.2	43.3 ± 16.2	36.7 ± 13.2	56.7 ± 24.8
<i>Poa fawcettiae</i>	Poaceae	Graminiod	MS	53.3 ± 14.2	46.7 ± 20.0	6.7 ± 4.6	3.3 ± 3.3	60.0 ± 17.4	26.7 ± 11.2	63.3 ± 28.8	46.7 ± 20.0
<i>Podolobium alpestre</i>	Fabaceae	Shrub	MV			13.3 ± 13.3	6.7 ± 4.6			3.3 ± 3.3	10.0 ± 7.3
<i>Polystichum proliferum</i>	Dryopteridaceae	Fern	OS	10.0 ± 5.5	10.0 ± 10.0	6.7 ± 4.6	10.0 ± 5.5			16.7 ± 10.7	3.3 ± 3.3
<i>Prasophyllum alpestre</i>	Orchidaceae	Geophyte	OS					3.3 ± 3.3			
<i>Scleranthus</i> sp.	Caryophyllaceae	Forb	MV	3.3 ± 3.3						3.3 ± 3.3	
<i>Stackhousia monogyna</i>	Stackhousiaceae	Forb	MS					3.3 ± 3.3			
unidentified dicot	N/A	N/A	N/A	16.7 ± 6.6	20.0 ± 9.8	3.3 ± 3.3	66.7 ± 39.6	30.0 ± 13.2	26.7 ± 10.1	10.0 ± 5.5	23.3 ± 8.8
unidentified forb	N/A	N/A	N/A					6.7 ± 4.6			
unidentified shrub	N/A	N/A	N/A				3.3 ± 3.3	6.7 ± 4.6			
<i>Viola betonicifolia</i>	Violaceae	Forb	OS	3.3 ± 3.3				3.3 ± 3.3		6.7 ± 4.6	

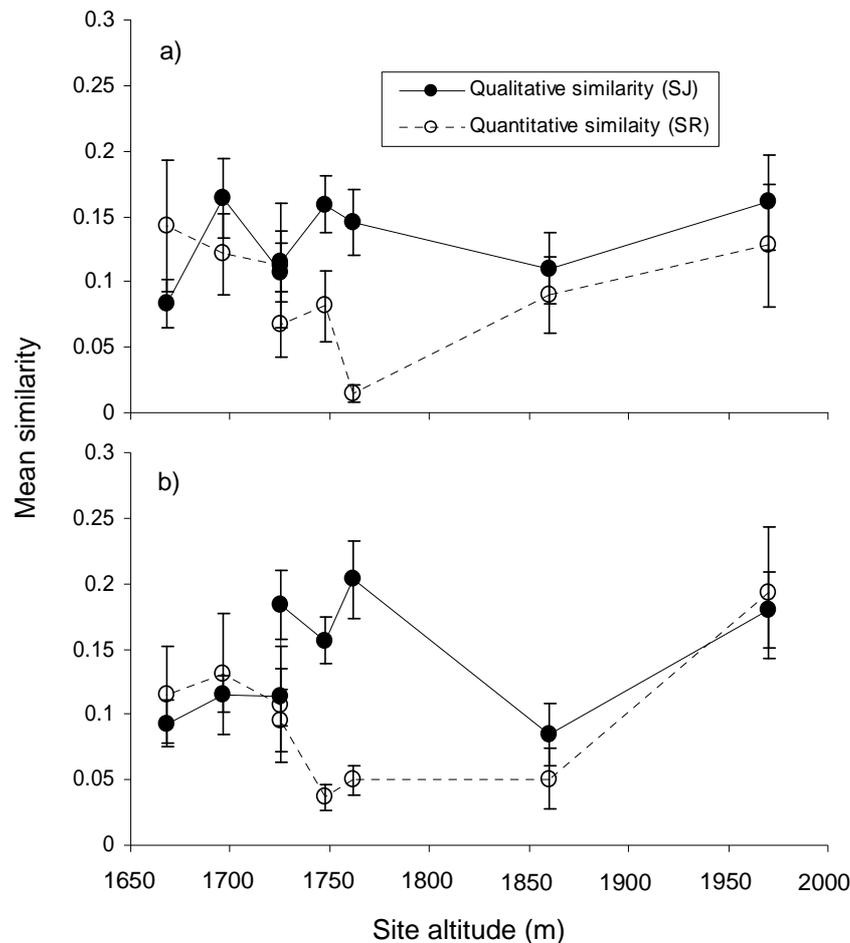


Figure 3.2. Mean (± 1 standard error) similarity of seed bank samples to standing vegetation across sites of varying altitude (m) during (a) the spring collection and (b) the autumn collection.

The percentage of species shared between the standing vegetation and the seed bank, based on the total number of species for each sample and the corresponding quadrat, was low at all sites. Values ranged from 8 to 15% and were dependent on site (two-way ANOVA; $F = 3.462$, $P = 0.001$), but independent of season and the interaction between site and season ($F = 0.471$, $P = 0.493$; $F = 1.276$, $P = 0.262$ respectively). Of the seeds that germinated in the seed bank samples, the percentage of these species that were present in the local standing vegetation was relatively high (i.e. 30 - 65%). However, two-way ANOVA showed no significant differences between site, season, or the interaction between these sources of variation. There was also no significant predictive relationship with altitude based on these data.

The similarity in seed bank samples between sites was interpreted from ordination diagrams. Based on presence/absence data, in two dimensions, there were no distinct patterns along either axis of the ordination (Appendix 3.1). The lowest stress value obtained during the calculations was 0.3 and therefore, interpretations of the diagram should be made with caution. In this configuration, sites appeared to be arranged

randomly and individual sites showed no indication that they were more or less similar to other sites, nor did quadrats from individual sites appear to clump together. A useful ordination diagram could not be produced from the abundance data, due to the very high abundances of some species at some sites.

The number of species in each regeneration class varied across the altitudinal gradient (Figure 3.3). At all sites, in the seed bank there were more species in the ‘mostly seed’ class. This pattern was only partially reflected across sites in the standing vegetation, where species from the ‘mostly seed’ and ‘mostly vegetative’ classes were most common. Species in the ‘vegetative regeneration’ class were poorly represented across the gradient of sites in both the seed bank and in the standing vegetation. There was no significant predictive relationship between the numbers of species in each class across the altitudinal gradient. However, the proportion of species, compared to the total number of species, from the standing vegetation in the ‘obligate seeding’ class, appeared to increase with altitude ($R^2 = 0.55$, $P = 0.034$). There were no other trends with altitude based on the proportion of species in each class from either the seed bank or standing vegetation.

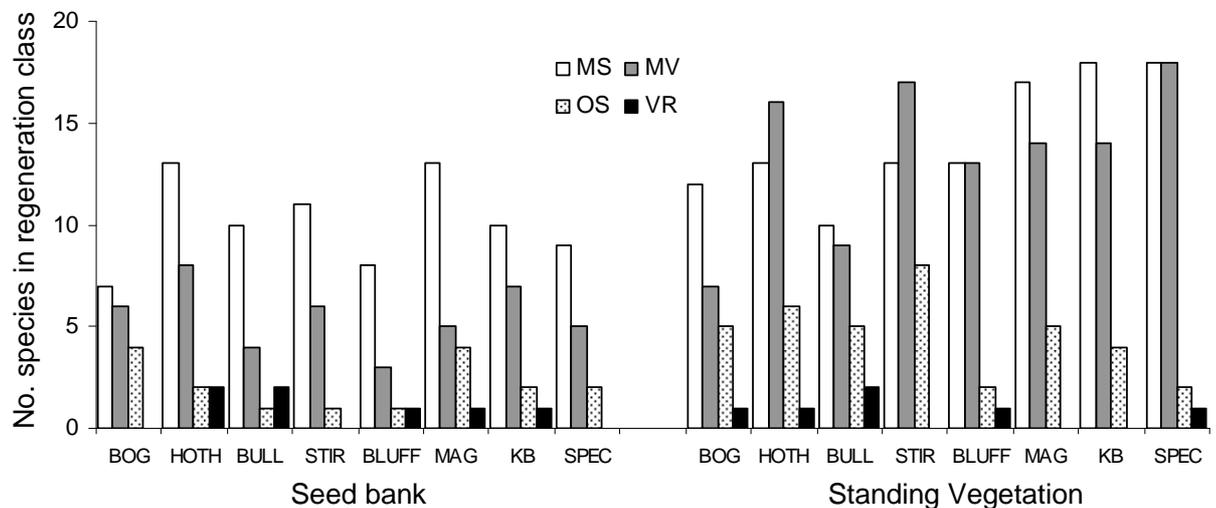


Figure 3.3. The number of species at each site from across the altitudinal gradient according to their regeneration class, from the seed bank and the standing vegetation. Sites: BOG, Mt Bogong (1970 m); HOTH, Mt Hotham (1860 m); BULL, Mt Buller (1762 m); STIR, Mt Stirling (1748 m); BLUFF, The Bluff (1725 m); MAG, Mt Magdala (1725 m); KB, King Billy (1696 m); SPEC, Mt Speculation (1668 m). Key: MS, mostly seed regeneration; MV, mostly vegetative regeneration; OS, obligate seeder with no apparent vegetative regeneration potential; VR, vegetative regeneration can maintain populations.

Discussion

Limitations

The seedling emergence techniques used in this study have documented the size of the germinable seed bank and therefore, may underestimate the true size of the seed bank, as the conditions for germination of all species may not have been met. However, the disturbance caused during the experiment (when moss was removed from each tray), the cold stratification treatment applied prior to sowing, the diurnal temperature and light variations in the glasshouse, and the 30+ week germination period are likely to have promoted emergence of all but the most deeply dormant seeds. Some seeds may also require a longer period than 30 weeks to germinate, although the numbers of seeds germinating after this time were too few to warrant continuing the experiment.

Seed bank density and composition

In this study, an appreciable seed bank was found in soils from mountain tops across the Victorian alpine zone. To my knowledge, this is the first seed bank study conducted in alpine regions in Australia. The range in density of germinable seeds in the seed bank found in this study (180 to >1400 per m²) is within the range found in the sub-arctic of Finland (Welling *et al.* 2004) and the high arctic islands in Norway (Cooper *et al.* 2004), the high alpine region of the Chilean Andes (Arroyo *et al.* 1999) and tundra habitats in northern Alaska (Fox 1983; Roach 1983), among others. However, the density of seeds in this study are mostly below that found in high arctic islands of Canada (Freedman *et al.* 1982) and tussock grasslands in the mountains of Argentina (Funes *et al.* 2003), and above the values found in the high exposed areas of the Cairngorm Mountains in Scotland (Miller and Cummins 2003). The wide variability in the density of seeds across the sites in this study is not surprising, as seed banks are typically variable both spatially and temporally (McGraw and Vavrek 1989).

In this study, soil seed bank species richness was site dependent. However, there were no trends in seed bank species richness across the altitudinal gradient. In contrast, Funes *et al.* (2003) found significant trends of increasing species richness across a gradient of altitude from 1200 to 2200 m. They also found that seed density increased with altitude. Consistent with my study, many others have reported high proportions of herbaceous and graminoid species in seed bank samples (Diemer and Prock 1993; Welling *et al.* 2004). Species from these life forms also tend to be the most prominent among seedlings (see Chapter 6).

Seed bank dynamics, persistence and transience

I took soil samples in spring and autumn, allowing me to characterise the soil seed bank in terms of persistence or transience. In a transient seed bank, the annual seed inputs from the previous season should have already germinated, whereas in a persistent seed bank, annual seed inputs from previous seasons should accumulate. I found no significant differences in parameters measured in the seed bank such as the density and number of individuals and species, neither specific life forms nor proportion of species from specific regeneration classes, between autumn and spring collections. Nor did any species consistently contribute more seeds to the seed bank in either season. Therefore, the seed banks and the alpine species across this altitudinal gradient are predominantly persistent.

Seasonal changes in seed bank parameters may not have been significantly different because the seeds from transient species, had not yet germinated at the time of spring sampling, leaving the soil samples to resemble that of a persistent seed bank. However, alpine species are renowned for germinating quickly after snowmelt (Billings and Mooney 1968; Bliss 1971), and I am confident that the majority of seeds in the soil that were cued to germinate during that season, had already done so before the spring sampling (see Chapter 6). Additionally, I did not record which species flowered and produced viable seed during the year of study, hence, transience in the system may have been overlooked due to annual fluctuations in seed production.

Persistent seed banks may contain seeds that have since become dormant (Roach 1983) as they have been worked down into the lower layers of the soil profile, perhaps by freeze-thaw processes (Chambers 1995). Hence, the large number of species not represented in the seed bank, which do occur as adults at each site, may have been deeply dormant and their dormancy was not broken by the cold-stratification treatment. Other species may not be represented in the persistent seed bank if they contribute too few seeds to the seed rain, or germinate immediately after dispersal, therefore indicating transience (McGraw and Vavrek 1989; Molau and Larsson 2000). The latter explanation is unlikely in alpine species, as the cues for seed germination are predominantly immediately after snowmelt (Amen 1966; Billings and Mooney 1968) (also see Chapter 4).

Consistent with my study, Arroyo *et al.* (1999) found predominantly persistent seed banks in the central Chilean Andes. They discovered only nine species of buried germinable seeds that gave a seed bank size of 899 seeds per m², but a higher percentage of species that were shared by the standing vegetation and seed bank vegetation (31%) than found in the current study. Close similarity between the persistent seed banks and the standing vegetation is not expected (McGraw and Vavrek 1989) as cold-climate seed

banks are characterised by low turnover rates and the climate can act in maintaining seed viability and persistence in the soil (Cavieres and Arroyo 2000). Persistent seed banks may also be more common with increasing altitude. Funes *et al.* (2003) found seed banks in all alpine sites above 1200 m in Argentina to be persistent, and the proportion of species that contributed to the persistent seed banks increased with altitude, whereas the proportion of species that contributed to transient seeds banks decreased. However, these trends may not be related to environmental variables. Thompson and Grime (1979) suggest that seed bank strategy is independent of environment and is more likely an inherent characteristic of a species.

Seed bank similarity with the standing vegetation

The germinable seed bank showed little similarity with the standing vegetation at all sites across the altitudinal gradient. Neither qualitative nor quantitative similarity values varied predictably across the altitudinal gradient of sites, and therefore site-specific factors may be driving the patterns in similarity between these two life-history stages. Occasionally some samples showed complete dissimilarity with the immediate standing vegetation; however, there was never complete dissimilarity in the mean Jaccard's qualitative index or the quantitative similarity ratio values. The mean values obtained in this study (0.01 to 0.24) are comparable with those found by Welling *et al.* (2004), using the same index, who reported values of 0.05 to 0.24. Low correlation between the seed bank and the standing vegetation is common in alpine systems (Diemer and Prock 1993; Arroyo *et al.* 1999; Funes *et al.* 2003), especially where persistent seed banks exist in relatively long-undisturbed sites (Chambers 1993). Almost all species that were represented in the total seed bank were also present in the local standing vegetation. Only two species that did not occur in the local proximity of the sites were recorded. These species, the shrubby *Tasmannia xerophylla* and the tree *Eucalyptus pauciflora*, are usually restricted to the sub-alpine vegetation. Hence, dispersal and subsequent incorporation into the germinable seed banks at higher altitudes may promote the potential upslope migration of some subalpine species with a warming climate in future decades.

Low similarity between the germinable seed bank and the standing vegetation for some species may indicate limited seed dispersal (Roach 1983; Chambers 1995), short lived seeds, germination failures, low seed abundance (McGraw and Vavrek 1989; Molau and Larsson 2000), or that species in the standing vegetation no longer exist in the vicinity of their buried seeds. If these processes continue for long periods, the relative

proportions of particular species in different recruitment phases will ultimately diverge. Hence, long-term undisturbed persistent seed banks may either have no influence on, or may drive community composition and structure away from the current assemblage (Chambers 1995; Welling *et al.* 2004), as opposed to maintaining the current assemblage.

The composition of the seed banks across sites was very similar, whereas the patterns in the standing vegetation across the same sites (see Chapter 2) showed some separation with altitude. Hence, the distribution of species in the standing vegetation may be responding to environmental factors which are not currently being expressed in the seed bank. These factors, such as cold temperatures, extreme diurnal fluctuations and frosts, which drive plant community patterns in alpine areas (Billings and Mooney 1968), may be contributing to the dissimilarity of seed banks and standing vegetation. Such environmental factors can govern the success of reproductive outputs, potentially leading to poor seed production and viability (Körner 1999) and therefore, lower inputs into germinable seed banks. Environmental factors can be site-specific (see Chapter 2) and hence, this leads to specific differences in the patterns between standing vegetation and seeds banks, rather than predictive trends across altitudinal gradients. Low species richness among seed bank samples may also have contributed to the similarity of seed banks across sites (Morgan 1998).

Seed banks across altitudinal gradients

A decrease in the density of seeds at higher altitudes may be expected, as shorter growing seasons and harsh conditions may select for species which put less effort into sexual reproduction and have lower productivity rates, thus making reduced contributions to seed banks (Johnson 1975; Fox 1983). Several studies have shown evidence for this, for example, Milton (1939), Thompson (1978), Fox (1983) and Molau and Larsson (2000). Welling *et al.* (2004) showed a strong negative correlation between seed bank density and altitude ($R^2 = 0.810$, $P < 0.05$). Alternatively, the predominantly persistent seed banks at high altitudes may accumulate seeds, leading to higher densities over time. In this study, there was a gradient of environmental conditions corresponding to the difference in altitude between the sites (see Chapter 2). However, as there is only 302 m difference between the lowest and highest site, the environmental gradient may not have been strong enough to produce differences in plant contributions to the germinable seed bank and thus, seed bank characteristics did not vary predictably with altitude.

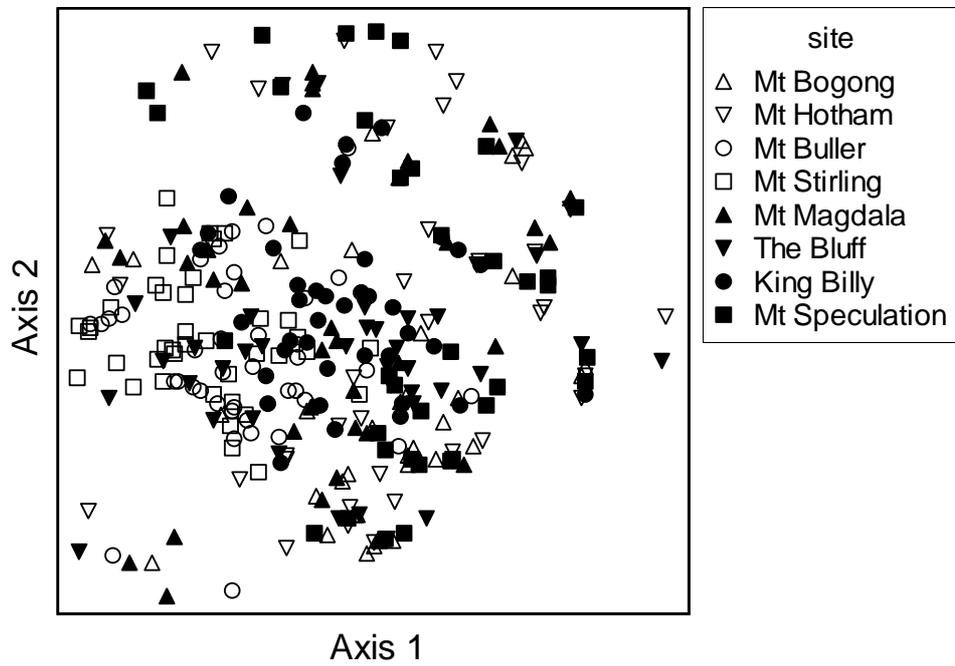
Regeneration strategies and seed banks

Reproductive traits will influence a species' inherent ability to reproduce from seed and therefore, influence the structure and composition of the seed bank (Freedman *et al.* 1982; Chambers 1993). Obligate seeding species appear the most likely to contribute to seed banks. Surprisingly, however, clonal plants can accumulate sizeable seed banks, although seedling recruitment may be rare (Welling *et al.* 2004,2005). Few studies have attempted to quantify alpine seed bank species with regard to their regeneration strategies. In this study, most of the seed bank species were classed as MS (mostly seeders), closely followed by MV (mostly vegetative spreaders). The seed banks and the standing vegetation were also dissimilar in their relative proportions of species in the different regeneration classes. Although, the regeneration strategies of the species in the standing vegetation are expected to influence the composition of the seed bank (Freedman *et al.* 1982; Chambers 1993). These discrepancies between the seed bank and standing vegetation can be caused by species which have the ability to reproduce by seed, but seldom do. For example, many clonal species which rely mostly on vegetative spreading for reproduction (classified here as MV or VR) can still have effective seed dispersal and accumulate persistent seeds banks (Welling *et al.* 2004). In addition, many long lived, perennial species from the standing vegetation, which tend to be in either the MV or VR class, were absent from the seed bank, consistent with the findings of Bakera (1989). Similarly, some annual species were common in the seed bank (e.g. *Acetosella vulgaris*, typically classed as MS or OS), but these species were not always present in the standing vegetation, perhaps due to unfavourable conditions during the period of survey. The analysis of regeneration classes was based purely on the number of species, rather than proportions of species in each life-history phase. Hence, common species in the seed bank such as *Carex breviculmis*, *Luzula modesta*, and *Poa* spp., which would have contributed significantly to the MS classes, appear to be underrepresented. In addition, these species are often not the dominant species in the standing vegetation. The use of regeneration classes therefore re-emphasizes the difference between the composition of the seed bank and the standing vegetation. However, among the species in this study, regeneration strategy did not appear to limit certain species from accumulating in the seed bank.

Conclusions

The density of seeds across germinable seed bank samples from Victorian mountain tops was comparable with studies from alpine areas of North and South America and sites in the arctic tundra. The seed banks were made up of predominantly persistent seeds, as there was no difference between samples collected in spring and autumn, which would have indicated a transient strategy. The qualitative (floristic) and the quantitative (abundance) similarity between the seed bank samples and the standing vegetation was low. Environmental factors that predominate across the altitudinal gradient of sites sampled, which can drive patterns in above ground vegetation, do not appear to strongly influence the characteristics of the seed bank flora. Many species in the seed bank were classed as ‘mostly seeders’; however, this was not reflected in the standing vegetation. Therefore, across alpine summits in Victoria, the seed bank does not appear to play a major role in maintaining the current structure and composition of plant communities, nor do the regeneration strategies of species appear to strongly influence the composition of the seed bank. However, the seed bank may play a role in successional processes after disturbance in this region. Continuing alpine seed bank research in this part of Victoria should include the response of seed banks to fire, a likely disturbance in this region. Possible responses of alpine vegetation to disturbances, including the role of the seed bank, will be discussed in Chapter 8.

Appendices



Appendix 3.1. Ordination diagram based on presence/absence data for seed bank species across sites. Stress: 0.3.

Chapter 4 - Laboratory germination characteristics and seed mass of alpine species from the Victorian Alps

Summary

In this chapter, I explore the differences in seed mass and germination characteristics among ten alpine species from different elevations within the Victorian alpine zone. I used laboratory techniques to simulate germination during early spring (cool treatment) and summer (warm treatment) under standard moisture regimes and diurnal light fluctuations. No seeds were pre-treated in the experiments and all were tested for viability. I weighed all seeds before subjecting them to experimental conditions.

Across different altitudes, seed mass varied within each species, but only two of the ten species showed a significant relationship between seed mass and altitude of seed origin. Within each species, mean seed mass showed no significant correlations with final percent germination.

Final percent germination was high among seeds from all species with some species having >90% germination. Seeds of *Aciphylla glacialis* did not germinate under either treatment. Germination lag-times were short and germination speeds (T_{50}) were fast. Germination lag-times were significantly longer in the cool treatment compared to the warm treatment. Most species had reached their final percent germination after 20 days. Although the final percent germination values between seeds of different elevations were similar, the probability of germination was often higher in seed that originated from lower elevations.

I discuss my results in relation to the international literature on alpine and arctic seed germination characteristics. I discuss how various germination strategies affect alpine species which grow across altitudinal gradients and how subsequent seedling establishment among alpine plants may be influenced by seed mass and particular germination syndromes.

Introduction

Reproduction by seed in alpine areas has historically been considered a rare event (Billings and Mooney 1968). The short, cold growing seasons, large diurnal temperature fluctuations in summer and regular frosts with consequent soil heave are likely to hinder all phases of sexual reproduction (Bliss 1962; Brink *et al.* 1967; Billings and Mooney 1968; Bliss 1971; Bell and Bliss 1980; Körner 1999; Inouye 2000). Hence, the probability of successful sexual regeneration in alpine areas is thought to be low, and it has been widely accepted that plant dispersal and regeneration in alpine areas is largely through vegetative means such as rhizomes and re-sprouting (Bliss 1962; Billings and Mooney 1968; Bliss 1971). Despite this apparent lack of sexual regeneration under natural conditions, there is evidence that many alpine plants flower readily (Körner 1999) and produce hundreds of viable seeds (Sayers and Ward 1966; Chambers *et al.* 1987) that can contribute to extensive soil seed banks (Freedman *et al.* 1982; Cooper *et al.* 2004) and under laboratory conditions, germinate easily (Amen 1966; Sayers and Ward 1966; Bliss 1971; Kibe and Masuzawa 1994).

The stages of seedling emergence and subsequent establishment are the periods with the highest risk of mortality at all elevations (Urbanska and Schütz 1986; Körner 1999). Under the pressure of natural selection, therefore, patterns in seed germination are expected to vary with environmental factors in order to maximize seedling survival (Cavieres and Arroyo 2000). Environmental factors, such as soil moisture, the current and previous season's temperature, and the length of the snow season can act as selective pressures affecting the timing of alpine seed germination (Mooney and Billings 1961; Amen 1966; Chambers 1989; Cavieres and Arroyo 2000; Giménez-Benavides *et al.* 2005). These factors can vary predictably across an altitudinal gradient (see Chapter 2) and hence, germination patterns may be expected to vary accordingly and thus, explain the abundance and altitudinal distribution of alpine species (Chambers *et al.* 1990). However, studies comparing germination patterns across species within habitats have indicated that germination characteristics can partly be a function of life history traits (Baskin and Baskin 1971; Grime *et al.* 1981; Washitani and Masuda 1990). This therefore makes the relationship between germination and habitat type difficult to ascertain (Meyer *et al.* 1990). Within species and genera, however, differences in germination characteristics between habitats have been detected (Meyer *et al.* 1990; Schütz and Rave 1999; Giménez-Benavides *et al.* 2005), although results from different species are inconsistent. Hence, an overall 'alpine germination syndrome' is unlikely to exist (Körner 1999).

Very few studies have compared the effect of environmental factors on alpine seed germination within habitat type and species. Vera (1997) showed that seeds of *Calluna vulgaris* and *Erica cinerea* collected from the highest altitudes in the Cantabrian Mountains, North Spain, had the highest percent germination but it is unclear whether habitat type was consistent between seed collections.

In the current study, I examined the variation in seed germination between populations within species across an altitudinal gradient. I held habitat type constant by using seed from the peaks of mountains that vary in altitude, but where tall open herbfield is the habitat type across mountains. This approach also holds other aspects of species life-history relatively constant, making differences in germination characteristics in relation to the environmental factors across the gradient easier to detect (Cavieres and Arroyo 2000).

The main objectives of this study were to 1) characterise seed mass and germination responses within several alpine species across an altitudinal gradient, and 2) to compare seed mass and germination responses of each species between sites and experimental treatments.

Methods

Study sites

The study was conducted with seeds from ten alpine species from four families collected across eleven alpine sites. The study sites (Table 2.1 in Chapter 2) represent a gradient in environmental conditions from the ‘warm and favourable conditions’ at Mt Speculation (1668 m) where winter snow cover is usually marginal, to Mt Bogong (1986 m) where conditions are ‘less favourable’; here, frosts are common all year round (Williams and Ashton 1987) and the growing season is four months at most. All sites are within the Alpine National Park, approximately 350 km from Melbourne and are within 40 km of each other, with most less than 10 km apart (Figure 2.1 in Chapter 2). In addition to the sites used in Chapter 2, I also used seed collected from Spion Kopje (1880 m, 36°50’00’’S, 147°19’30’’E), Mt McKay (1840 m, 36°52’35’’S, 147°14’30’’E) and Mt Howitt (1738 m, 37°10’30’’S, 146°38’50’’E). Mean annual rainfall of this region is relatively high compared to adjacent lowland areas, over 1800 mm (LCC 1982), with much of this precipitation falling as snow during winter. Average air temperatures follow seasonal variations with typical daily minima and maxima of between 2 and 27 °C in

summer and -6 and 12 °C in winter (Bureau of Meteorology *unpublished data*). Frosts are frequent and can occur at any time of year (Williams 1987). The growing season spans approximately seven months from snowmelt, usually the end of September, until late April, when the first substantial snowfalls of the winter begin. Key climatic parameters for the study sites, derived from long-term data by BIOCLIM are shown in Table 2.3 in Chapter 2. All sites are classed as ‘Steep Alpine Mountains’ after Costin (1957), are above the natural tree-line and are dominated by tall alpine herbfield vegetation. The lower peaks also contain species typical of adjoining sub-alpine woodland (Costin 1957). The underlying geology of the sites varies (Table 2.2 in Chapter 2). Despite such variation, the parent material in these regions rarely influences soil type and all soils are considered alpine humus, with a gravelly or skeletal structure (Costin 1962b; LCC 1982) and are acidic, ranging from pH 4 to 5.

Study species and seed collection

Ten study species were chosen on the basis of their conspicuous abundance in at least two of the study sites and whether ample seed was available for collection. From the Apiaceae, I chose *Aciphylla glacialis*. From the Asteraceae, I chose *Brachyscome rigidula*, *Brachyscome spathulata*, *Leucochrysum albicans* sub. sp. *albicans*, *Microseris* sp. 2, *Olearia phlogopappa* var. *subrepanda* and *Xerochrusym subundulatum*. From the Junceaceae, *Luzula acutifolia* was selected and from the Poaceae, *Trisetum spicatum* and *Rytidosperma nudiflora*. Seeds from these species were collected by hand over two months during the summer of 2003/2004. I took care that seed was mature and easily detached from the remaining stalks or inflorescences. The seed was placed in paper bags, transported to the laboratory and left to dry in a purpose built heated drying box, set at 17 °C, for two weeks. Seed was then stored in dry conditions with naphthalene crystals, to deter insects, at room temperature until the experiments began.

Germination trials

Each seed was assessed for viability prior to the germination experiments, by squeeze tests and inspection on a light box, to ascertain that each embryo was filled. Seed mass was determined by weighing to four decimal places. Twenty random seeds from each species were arranged on moist seed germination paper (A.S.C. seed filter paper, 1 mm thick, 84 mm diameter) in petri dishes, with eight replicates per species in each of the two temperature treatments. Petri dishes were sealed with laboratory Parafilm to prevent moisture loss. The germination trials were conducted in Thermoline Refrigerated

Incubators, with a bank of fluorescent tubes providing a light intensity of 48 microeinsteins $\text{m}^{-2} \text{s}^{-1}$. Eight replicates of each species were subjected to a ‘cool’ treatment (12/10°C with 14/10 hours day length, representing late winter/early spring conditions) and a ‘warm’ treatment (20/10°C with 12/12 hours day length, representing mid summer). Petri dishes were randomly placed in the incubators, checked every 2 to 4 days during the ‘day’ part of their cycle and re-randomised upon return to the incubator. Seeds were considered germinated when the radicle had emerged from the seed coat.

The germination trials were staggered due to space limitations and equipment failure. Seeds from all species were placed in the cool treatment on the 21st October 2004. *Brachyscome rigidula* seeds were placed in the warm treatment on the 29th October 2004. The remaining seeds did not start their warm treatment until the 5th July 2005 and hence, were stored for an extra nine months compared with their counterparts in the cool treatment. Too few seeds of *Rytidosperma nudiflora* were collected to allow this species to be included in the warm treatment. At the end of each test period, ungerminated seeds were scored for fungal attack and again for viability. Seeds deemed unviable or killed by fungus were removed from the analysis and scores of final percent germination in each petri dish were adjusted accordingly.

Data analysis

Germination characteristics were only compared within a species, rather than across species. I used multi-factorial ANOVA with Bonferroni post-hoc tests to compare seed mass across sites. I used linear regression to investigate the relationship between seed mass and altitude for species which were collected from three or more sites.

I describe the germination lag-time time, the number of days until seeds from each species first germinate, and the germination speed (T_{50}), the number of days until 50% of the final germination has occurred.

I used multi-factorial ANOVA with Bonferroni post-hoc tests to compare the final percent germination within and between the cool and warm treatments.

I used the Kaplan-Meier (K-M) product limit estimation function (Kaplan and Meier 1958; Lee 1992) to model the probability of germination during the experiment. Modelling the germination curves in this manner reveals the germination ‘journey’ that a group of seeds take on their way to reaching their final percent germination. This method also gives a mean probability of germination score at each sampling time which can be compared across sites within each species. The method uses germination data from every seed, in the form of elapsed time (days) to germination (right censored data) and also data

for seeds which did not germinate (non-censored data) (Giménez-Benavides *et al.* 2005). The values in the probability of germination curves are then constructed by subtracting the K-M values (0 to 0.9) from 1. Comparisons of paired germination probability curves across sites were then tested by non-parametric Log-rank tests, which provide a Mantel's χ^2 statistic and *P*-value. The shape of the probability of germination curves were remarkably similar to the percent germination curves and are therefore not presented (see Figure 5.3, in Chapter 5, for an example of germination probability curves). SYSTAT version 10 (Copyright SPSS Inc., 2000) was used for all statistical analyses.

Results

Seed mass

For some species, seed mass varied significantly across sites of different elevations (Figure 4.1). Overall, there were few trends between seed mass and altitude. However, *Olearia phlogopappa* var. *subrepanda* and *Leucochrysum albicans* sub sp. *albicans* both showed significant linear relationships between seed mass and altitude ($R^2 = 0.69$, $P < 0.001$; $R^2 = -0.17$, $P = 0.032$ respectively).

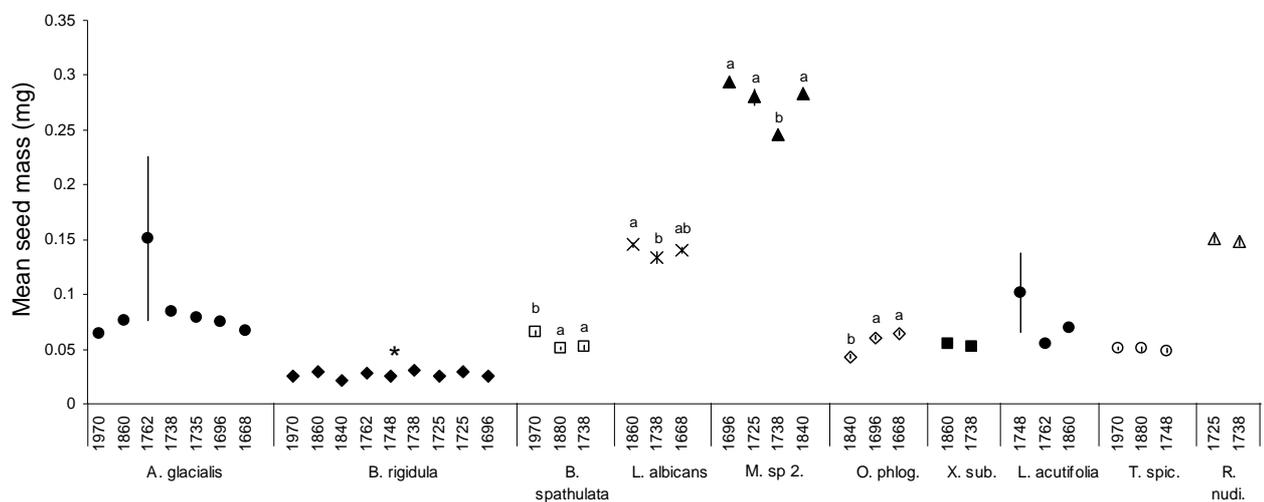


Figure 4.1. Mean (± 1 standard error) seed mass and altitude for each species. Different labels (a, b or ab) above data points signify the Bonferroni significant differences within each species. Data points without labels showed no significant differences between sites. * Significant differences in seed mass between sites of *B. rigidula* in Appendix 4.1. For full species names see Appendix 4.2.

Germination characteristics

Germination lag-times, the time until the first germination of any seeds of each species was recorded, were short (2-19 days), especially for the forbs from the Asteraceae in the cool treatment (Table 4.1). The shrub *Olearia phlogopappa* var. *subrepanda* showed significantly longer lag times in both treatments than other species from the same family. The graminoid species showed consistently longer lag times than Asteraceae species in both treatments. Seeds of *Aciphylla glacialis* failed to germinate in both treatments and therefore germination speed and lag times are not available. All species showed significantly longer lag times (6 – 21 days) in the warm treatment than in the cool treatment (except *O. phlogopappa* var *subrepanda*).

Germination speed (T_{50}) was particularly fast in the Asteraceae species in both treatments. Some species reached T_{50} at the first or second sample interval (Table 4.1).

Table 4.1. Germination speed (T_{50}) and germination lag-time (lag) for seeds in cool (12/10°C) and warm (20/10°C) treatments of ten species from various altitudes across the Victorian alpine zone. Dashes (-) indicate seed unavailability. No *Aciphylla glacialis* seeds germinated in either treatment, therefore germination lag and speed data is not available.

Species	Site and altitude (m) of seed origin	Cool treatment		Warm treatment	
		lag (days)	T_{50} (days)	lag (days)	T_{50} (days)
<i>Aciphylla glacialis</i>	Mt Bogong (1970)	N/A		N/A	
	Mt Hotham (1860)	N/A		N/A	
	Mt Buller (1762)	N/A		N/A	
	Mt Howitt (1738)	N/A		N/A	
	Mt Magdala (1725)	N/A		N/A	
	King Billy (1696)	N/A		N/A	
	Mt Speculation (1668)	N/A		N/A	
<i>Brachyscome rigidula</i>	Mt Bogong (1970)	2	2	6	8
	Mt Hotham (1860)	2	2	6	8
	Mt McKay (1840)	2	8	6	8
	Mt Buller (1762)	2	2	6	8
	Mt Stirling (1747)	2	8	6	8
	Mt Howitt (1738)	2	2	6	8
	Mt Magdala (1725)	2	2	6	8
	The Bluff (1725)	2	2	6	8
	King Billy (1696)	2	2	6	8
<i>Brachyscome spathulata</i>	Mt Bogong (1970)	2	8	11	14
	Spion Kopje (1880)	2	8	11	14
	Mt Howitt (1738)	2	8	11	14
<i>Leucochrysum albicans</i> subsp. <i>albicans</i>	Mt Hotham (1860)	2	2	8	6
	Mt Howitt (1738)	2	2	-	-
	Mt Speculation (1696)	2	2	6	6
<i>Microseris</i> sp. 2	Mt McKay (1840)	2	2	6	14
	Mt Howitt (1738)	2	2	6	11
	Mt Magdala (1725)	2	8	6	11
	King Billy (1696)	2	2	6	11
<i>Olearia phlogopappa</i> var. <i>subrepanda</i>	Mt McKay (1840)	19	28	17	39
	King Billy (1696)	19	35	21	37
	Mt Speculation (1668)	19	28	21	30
<i>Xerochrysum subundulatum</i>	Mt Hotham (1860)	2	8	6	11
	Mt Speculation (1668)	2	8	6	11
<i>Luzula acutifolia</i>	Mt Hotham (1860)	15	23	17	24
	Mt Buller (1762)	10	12	14	17
	Mt Stirling (1747)	12	19	14	21
<i>Trisetum spicatum</i>	Mt Bogong (1970)	8	10	-	-
	Spion Kopje (1880)	8	10	11	11
	Mt Stirling (1747)	2	8	11	11
<i>Rytidosperma nudiflora</i>	Mt Magdala (1725)	8	10	-	-
	Mt Howitt (1738)	10	19	-	-

The germination curves for each species reflect the short germination lag times and rapid germination speeds (Figure 4.2). For most species, few seeds had germinated after 20 to 30 days, by which time the final percent germination values has mostly already been attained. Final germination was above 90% for many species, with little or no significant differences between sites within each species (Figure 4.3). There were no significant differences between final percent germination for any species at any site between the cool and warm treatments (paired t-tests, $P = >0.05$)

Within each species, the probability of seed germination between pairs of sites, over the course of the experiment, was often significantly different (Table 4.2 and Table 4.3), even though final mean percent germination was often the same among each pair. These pairwise comparisons between sites, within species and treatments, showed that seeds from lower elevations were more likely to germinate than those from higher elevations (Table 4.2 and 4.3). Of all the pairwise comparisons which showed significant differences in germination probabilities, 75% indicated that germination probability was higher in seed which originated from lower elevations. However, around half of all comparisons showed either no significant differences, or in some cases, that seed from a higher mountain peak had a significantly higher germination probability.

Within species, seed from the lower mountain peaks generally had a higher probability of germination in the cool treatment compared to the warm treatment (Table 4.4). However, seed from higher mountain peaks showed no trends in germination probability

Comparisons of seed properties

Within each species, mean seed mass showed no significant correlations with final percent germination. Neither lag-time nor germination speed were correlated with final percent germination using the Pearson/Spearman rank correlation co-efficient.

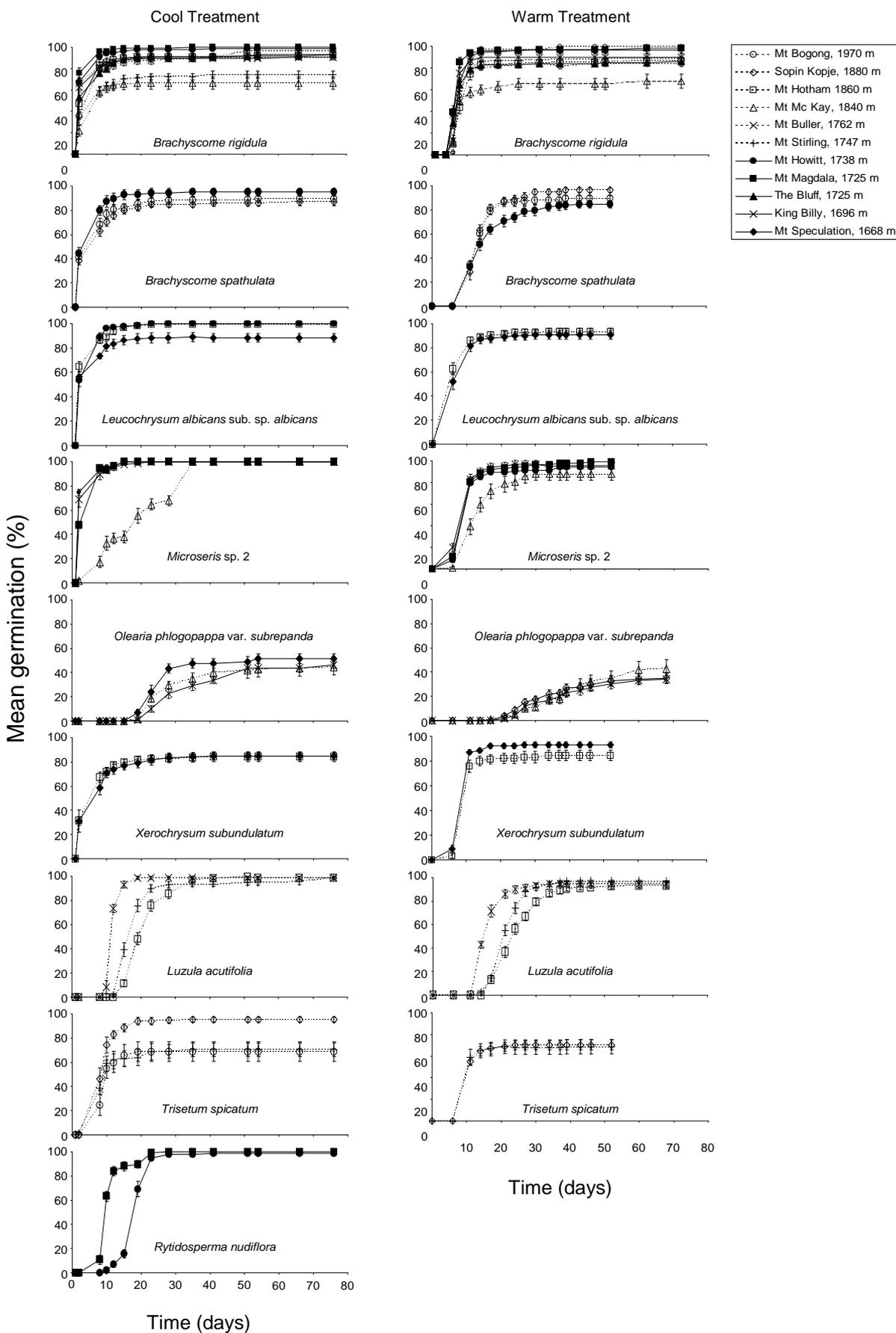


Figure 4.2. Mean (± 1 standard error) percent germination curves for the cool (12/10 °C) and warm (20/10 °C) treatments against time (days) for seeds from species from the eleven sites. No seeds from *Aciphylla glacialis* germinated in either treatment during the experiment and therefore no germination curves are available for this species.

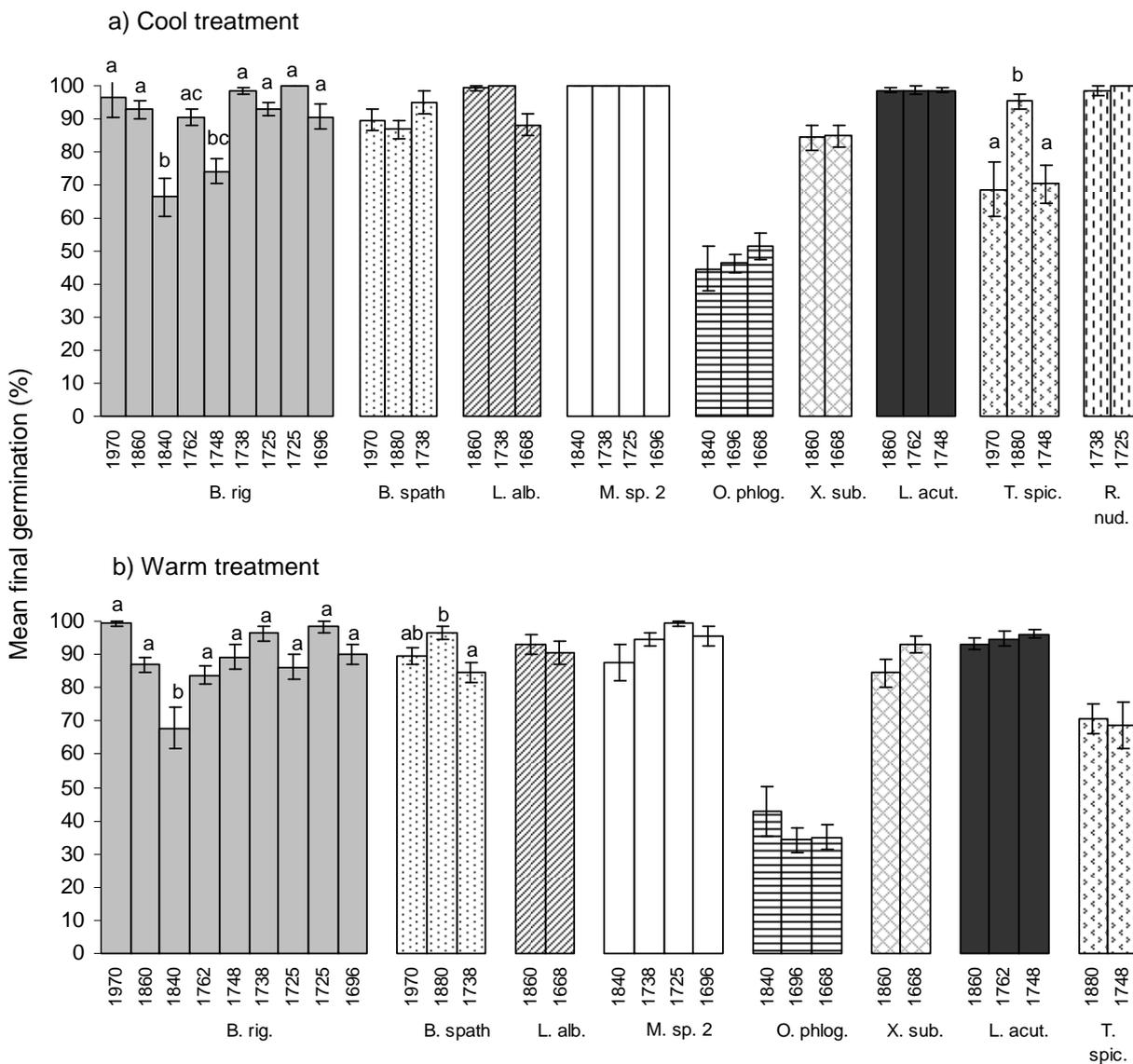


Figure 4.3. Mean (\pm standard error) final percent germination for (a) the cool (12/10 °C) and (b) the warm (20/10 °C) treatments. Different labels (a, b, or ab) above columns signify the Bonferroni significant differences within each species. Species columns without labels showed no significant differences between sites. No *Aciphylla glacialis* seed germinated under either treatment, zero mean final percent germination values are not presented. For full species names see Appendix 4.2.

Table 4.2. Pairwise comparisons of the probability of seed germination between sites, within each species, based on the probability of germination curves, explained by Mantel's χ^2 in the cool treatment. Significant differences are indicated by an asterisk(s). *** denotes $P \leq 0.001$, ** denotes $P \leq 0.01$, * denotes $P < 0.05$. Overall greater probability of germination between each pair is indicated in brackets with greater than (>) symbol between site names. Site name abbreviations and site altitudes are shown in Appendix 4.3. For full species names see Appendix 4.2.

Species	Pairwise comparisons by site (Mantel's χ^2).									
<i>B. rigidula</i>	BO v HO 0.054	BO v MK 25.098*** (BO>MK)	BO v BU 1.482	BO v ST 15.573*** (BO>ST)	BO v HW 27.857*** (HW>BO)	BO v BL 1.6881	BO v MA 2.762	BO v KB 0.946	HO v MK 26.993*** (HO>MK)	HO v BU 1.229
	HO v ST 16.816*** (HO>ST)	HO v HW 24.576*** (HW>HO)	HO v BL 1.397	HO v MA 4.592* (MA>HO)	HO v KB 0.755	MK v BU 19.355*** (BU>MK)	MK v ST 1.176	MK v HW 81.675*** (HW>MK)	HO v BL 1.397	MK v MA 16.293*** (MA>MK)
	MK v BU 19.355*** (BU>MK)	MK v ST 1.176	BU v HW 6.036* (HW>BU)	BU v BL 0.000	BU v MA 6.122* (MA>BU)	BU v KB 0.106	ST v HW 67.136*** (HW>ST)	ST v BL 25.438*** (BL>ST)	ST v MA 10.172*** (MA>ST)	ST v KB 14.709*** (KB>ST)
	HW v BL 14.505*** (HW>BL)	BL v MA 4.751* (BL>MA)	BL v KB 0.153	MA v KB 6.839** (MA>KB)						
<i>B. spathulata</i>	BO v SP 0.817	BO v HW 4.516* (HW>BO)	SP v HW 9.207** (HW>SP)							
<i>L. albicans</i>	HO v HW 0.239	HO v SP 14.667*** (HO>SP)	HW v SP 10.084*** (HW>SP)							
<i>M. sp.2.</i>	MK v HW 150.736*** (HW>MK)	MK v MA 132.109*** (MA>MK)	MK v KB 122.454*** (KB>MK)	HW v MA 10.519*** (MA>HW)	HW v KB 1.546	MA v KB 2.989				
<i>O. phlog</i>	MK v KB 0.482	MK v SP 1.540	KB v SP 3.959*** (SP>KB)							
<i>X. sub.</i>	HO v SP 0.409									
<i>L. acutifolia</i>	HO v BU 142.356*** (BU>HO)	HO v ST 14.235*** (HO>ST)	BU v ST 103.516*** (BU>ST)							
<i>T. spicatum</i>	BO v SP 42.294*** (SP>BO)	BO v ST 4.418* (ST>HO)	SP v ST 16.790*** (SP>ST)							
<i>R. nudiflora</i>	MA v HW 120.749*** (MA>HW)									

Table 4.3. Pairwise comparisons of the probability of seed germination between sites, within each species, based on the probability of germination curves, explained by Mantel's χ^2 in the warm treatment. Significant differences are indicated by an asterisk(s). *** denotes $P \leq 0.001$, ** denotes $P \leq 0.01$, * denotes $P < 0.05$. Overall greater probability of germination between each pair is indicated in brackets with greater than (>) symbol between site names. Site name abbreviations and site altitudes are shown in Appendix 4.3. For full species names see Appendix 4.2.

Species	Pairwise comparisons by site (Mantel's χ^2).									
<i>B. rigidula</i>	BO v HO 11.474*** (BO>HO)	BO v MK 35.964*** (BO>MK)	BO v BU 0.000	BO v ST 1.859	BO v HW 5.189	BO v BL 0.005	BO v MA 40.230*** (BO>MA)	BO v KB 8.704** (KB>BO)	HO v MK 8.244** (HO>MK)	HO v BU 11.834*** (HO>BU)
	HO v ST 2.152	HO v HW 18.112*** (HW>HO)	HO v BL 4.361	HO v MA 55.283*** (MA>HO)	HO v KB 17.400*** (KB>HO)	MK v BU 31.295*** (BU>MK)	MK v ST 15.394*** (ST>MK)	MK v HW 32.885*** (MK>HW)	HO v BL 4.361	MK v MA 68.968*** (MA>MK)
	MK v BU 31.295*** (BU>MK)	MK v ST 15.394*** (ST>MK)	BU v HW 0.299	BU v BL 2.691	BU v MA 13.773*** (MA>BU)	BU v KB 0.273	ST v HW 6.003	ST v BL 0.522	ST v MA 32.159*** (MA>ST)	ST v KB 7.667** (KB>ST)
	HW v BL 1.627	BL v MA 19.390*** (MA>BL)	BL v KB 3.337	MA v KB 4.101						
<i>B. spathulata</i>	BO v SP 0.793	BO v HW 3.241	SP v HW 10.046** (SP>HW)							
<i>L. albicans</i>	HO v SP 1.737									
<i>M. sp 2.</i>	MK v HW 22.017*** (HW>MK)	MK v MA 43.228*** (MA>MK)	MK v KB 29.767*** (KB>MK)	HW v MA 4.152* (MA>HW)	HW v KB 2.420	MA v KB 29.767*** (KB>MA)				
<i>O. phlog.</i>	MK v KB 1.516	MK v SP 0.537	KB v SP 0.288							
<i>X. sub.</i>	HO v SP 9.975** (SP>HO)									
<i>L. acutifolia</i>	HO v BU 53.221*** (BU>HO)	HO v ST 10.418*** (ST>HO)	BU v ST 38.660*** (ST>BU)							
<i>T. spicatum</i>	SP v ST 0.000									

Table 4.4. Pairwise comparisons of the probability of seed germination between the cool and warm treatments, within each species and site, based on the probability of germination curves, explained by Mantel's χ^2 . Significant differences are indicated by an asterisk(s). *** denotes $P \leq 0.001$, ** denotes $P \leq 0.01$, * denotes $P < 0.05$. Overall greater probability of germination between each pair is indicated in brackets with greater than (>) symbol between treatments; C, cool; W, warm. Site name abbreviations and site altitudes are shown in Appendix 4.3. For species names abbreviations, see Appendix 4.2.

Species	Pairwise comparisons by treatment (Mantel's χ^2) within site										
	BO	SP	HO	MK	BU	ST	HW	BL	MA	KB	SP
<i>B. rigidula</i>	9.530** (W>C)	N/A	28.467*** (C>W)	1.123	12.642*** (C>W)	1.307	63.904*** (C>W)	19.470*** (C>W)	8.077** (C>W)	5.931	N/A
<i>B. spathulata</i>	37.019	14.496*** (W>C)	N/A	N/A	N/A	N/A	36.807*** (C>W)	N/A	N/A	N/A	N/A
<i>L. albicans</i>	N/A	N/A	50.367*** (W>C)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	12.439*** (W>C)
<i>M. sp 2.</i>	N/A	N/A	N/A	0.066	N/A	N/A	230.211*** (C>W)	N/A	156.251*** (C>W)	120.186*** (C>W)	N/A
<i>O. phlogopappa</i>	N/A	N/A	N/A	1.291	N/A	N/A	N/A	N/A	N/A	3.055,	10.739*** (C>W)
<i>X. subundulatum</i>	N/A	10.290*** (W>C)	30.974*** (C>W)	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
<i>L. acutifolia</i>	N/A	N/A	12.676*** (C>W)	N/A	68.135*** (C>W)	34.598*** (C>W)	N/A	N/A	N/A	N/A	N/A
<i>T. spicatum</i>	N/A	69.643*** (C>W)	N/A	N/A	N/A	8.666*** (C>W)	N/A	N/A	N/A	N/A	N/A

Discussion

General interpretation of results

Mean seed mass did not differ significantly across the altitudinal gradient for most species, nor were there significant trends between seed mass and final percent germination for any species at any site. In the germination experiments, where no seed was pre-treated, high mean percent germination was common at all sites across the altitudinal gradient, with seven of the nine species showing >90% germination in one or more sites. *Aciphylla glacialis* seeds did not germinate under either treatment. Apart from *A. glacialis*, the only species not to reach high final percent germination was *O. phlogapappa* var. *subrepanda* (shrub) which showed mean final percent germination of 40-55% in both treatments. Dormancy mechanisms were not apparent as seed from all species germinated within the time period of the experiment, except for *A. glacialis* seeds. Possible dormancy mechanisms of *A. glacialis* are explored in Chapter 5.

Germination lag times were short in both treatments for all species, between 2 and 11 days for most of the Asteraceae, and up to 21 days for grass, rush and shrub species. Short lag times indicate opportunistic germination strategies which enable germination to occur as soon as suitable conditions are present. This strategy is characteristic of alpine species (Bell and Bliss 1980) and may be indicative of species with a transient seed bank. However, my results suggested that persistent seed banks are present across the mountain-top sites (Chapter 3), as samples from spring and autumn were not consistently different within any species. The species used in the current study were rarely found in the seed bank samples and hence, there may be different strategies operating among different species at different life-history stages i.e. opportunists and those that “wait”.

Neither germination lag-time, nor germination speed (T_{50}), were significantly correlated with final percent germination. However, these parameters can be important characteristics under natural conditions where seed germination may be limited to brief periods in the summer when sufficient soil water coincides with favourable ambient temperatures (Bliss 1971). I demonstrated that the overall germination ‘journeys’ encountered in this study were 1) early rapid germination and 2) late rapid germination. The germination journey that a group of seeds took was modelled using Kaplan-Meier probability curves. The comparisons between pairs of sites showed that the germination probability of seeds from lower altitudes, within species and treatments, was often higher than that of seeds from high altitudes. This result is not consistent among species, however, and was often caused by exceptionally low germination of seeds from

Mt McKay (1840 m), for reasons that remain unknown. However, roughly half the comparisons showed no difference in germination probability between high and low elevations.

When comparing the germination probability between the cool and warm treatments, seeds of five species had a higher germination probability in the cool treatment. The cool treatment simulated field conditions present at the start the growing season (early spring). Therefore, high germination probabilities in this treatment support the predominance of opportunistic germination strategies under natural conditions. This was more common for seeds from lower altitudes. The use of germination probability curves, therefore, can be a useful tool for comparing the germination probability of seeds over set time periods and across treatments (Giménez-Benavides *et al.* 2005).

Overall, I showed that the germination response of Victorian alpine seeds is fairly consistent across the two temperature regimes among naturally co-occurring species. Few differences in germination characteristics across the altitudinal gradient exist within species.

Seed mass and reproductive success

In my study, I found no trends relating seed mass to germination probability or success. My results are consistent with the findings of Molau (1993) who reported that relative reproduction success does not correlate well with resource allocation to reproduction, seed number, seed weight or germinability among seeds from arctic tundra species. Large seeds are more likely to have extra reserves available for germination and subsequent seedling emergence and survival (Holm 1994; Westoby *et al.* 1996; Vera 1997; Leishman *et al.* 2000; Pickering 2000; Pickering and Hill 2002). Large seeds, therefore, would be advantageous for plants growing at high altitudes in order to compensate for the various environmental stresses (Vera 1997; Pickering and Arthur 2003). However, large seeds require more maternal investment and therefore, at higher elevations or in more stressful environments, some species may adopt the conservative strategy of producing large but few seeds to compensate for the environmental stresses (Molau 1993). These species would be identified as *K*-strategists along the *r/K* continuum (MacArthur and Wilson 1967), which is the group most arctic and alpine flowering plants tend to fall into (Molau 1993).

However, within a species, examples of seed mass increasing with altitude are rare. Rather, there tends to be a high degree of variability in seed mass across an altitudinal range (Vera 1997; Moles *et al.* 2003; Pluess *et al.* 2005). Over a large

altitudinal gradient (1255 m, which is more than four times the size of the altitudinal gradient in this study), Lord (1994) found that mean seed mass of *Festuca novae-zelandiae* increased significantly with altitude. The size of flowers and other reproductive structures do not usually change with altitude (Fabbro and Körner 2004) and consequently, seed mass may also remain unchanged across altitudes. However, between congeneric, closely-related species the seed mass of alpine species may be higher than that of their lower dwelling temperate counterparts (Pluess *et al.* 2005). This could be investigated for *Brachyscome rigidula*, and *Microseris* sp. 2 in future studies as they occur at high altitudes above the treeline and in sub-alpine areas.

Germination characteristics

Final percent germination results in this experiment were within (or above) the ranges of other alpine plant germination studies using similar day/night temperature regimes and without seed pre-treatments (Bliss 1959; Amen 1966; Sayers and Ward 1966; Chabot and Billings 1972; Bell and Bliss 1980; Urbanska and Schütz 1986; Mariko *et al.* 1993; Kibe and Masuzawa 1994; Giménez-Benavides *et al.* 2005; Wesche *et al.* 2006). Optimum temperatures for alpine seed germination are notoriously variable but in many cases maximum germination occurs between 20 to 30 °C (Billings and Mooney 1968; Marchand and Roach 1980). Below these temperatures, percent germination can decline rapidly (Chabot and Billings 1972). A high temperature requirement for germination among alpine seeds may act as an important cue under natural conditions, ensuring seeds germinate during the warmer months following snowmelt (Billings and Mooney 1968; Chabot and Billings 1972). However, I found no significant difference in final percent germination between the two temperature treatments for any species. A likely explanation may be the small difference in temperature regimes between the cool and warm treatments.

In general, few alpine seeds show any forms of innate dormancy (only one species in my study, *Aciphylla glacialis*) and hence, dormancy may be controlled by the environment and low winter temperatures (Billings and Mooney 1968). This is exacerbated by the high temperature germination requirement (Chabot and Billings 1972), again ensuring developmental processes operate predominantly during favourable conditions (Billings and Mooney 1968). In the experiments, I simulated natural conditions by alternating the day and night temperatures, as diurnal temperature fluctuations have been found to significantly increase final percent germination rates compared with constant temperatures (Sayers and Ward 1966; McDonough 1969).

However, I did not simulate winter conditions prior to the germination trials which may account for the lack of germination in *Aciphylla glacialis*.

I found quick lag times and fast germination for seeds under both temperature regimes. These characteristics are indicative of seedling emergence at the very start of the growing season (see Chapter 6), corresponding with favourable environmental conditions immediately after snowmelt and limiting the risks associated with germination to a few weeks (Billings and Mooney 1968). Most seeds from all species in this experiment had reached 90% of their germination within 20 days, which may indicate that under natural conditions, the available ‘window’ for seed germination in the Victorian alpine zone is small and germination usually occurs quickly. I found no variations in lag-times and germination speeds from seeds collected across the altitudinal gradient. However, across regions with much stronger environmental gradients, seeds from high alpine areas or stressful habitats (i.e., snowpatch) can show significantly faster germination rates (Mariko *et al.* 1993; Lord 1994; Vera 1997; Shimono and Kudo 2005). This strategy takes advantage of every opportunity for germination, regardless of the probability of successful seedling establishment (Bell and Bliss 1980).

In contrast, species with intermittent or “cautious” germination syndromes may spread germination over extended periods, thereby restricting seedling establishment to rare intervals of favourable weather during the snow-free period (Bell and Bliss 1980; Schütz 2002) and protecting seedlings from the hazards of emerging too early during extended winters or in exposed locations (Meyer *et al.* 1990). Under natural conditions, seeds with this germination strategy may remain buried in the soil for many years before the right combination of external conditions coincide, prompting germination. Mark (1965) found *Chionochoa rigida* seeds germinated after four years in the laboratory, which may indicate such a strategy. In contrast, the species in this study, except perhaps *O. phlogopappa* var. *subrepanda* and *L. acutifolia*, tended to have an opportunistic germination strategy, with quick lag-times, fast germination and high final percent germination during the experimental period.

Conclusions

High rates of seed germination among co-existing species indicate many opportunities for seedling emergence. However, the strong risk of seedling mortality in alpine environments may enforce strategies that ensure germination is cued with favourable ambient conditions. In my experiments, I found few trends in germination characteristics between the cool and warm treatments, although germination probability was often higher among seeds in the cool treatment which originated from lower elevations. The seeds of the study species are likely to be opportunistic in their germination and therefore germinate immediately after snowmelt under natural conditions. I found few differences in final percent germination in seeds from different altitudes, possibly because the gradient used in this study was small. To fully understand the germination strategies of alpine plants, these laboratory germination trials are compared with patterns of seedling recruitment, emergence and establishment under natural conditions in Chapter 6.

Appendices

Appendix 4.1. Matrix of *P*-values which indicate any significant differences ($P < 0.05$) in seed mass of *Brachyscome rigidula*, based on log-transformed data, after the Bonferroni adjustment, between sites of varying elevation (m, **bold** type).

	1668	1696	1725	1738	1748	1762	1840	1970
1668	1.000							
1696	0.000	1.000						
1725	0.000	0.022	1.000					
1738	0.000	0.000	0.550	1.000				
1748	0.000	1.000	0.108	0.001	1.000			
1762	0.000	0.024	1.000	1.000	0.088	1.000		
1840	0.000	0.221	0.000	0.000	0.066	0.000	1.000	
1970	0.000	1.000	0.358	0.003	1.000	0.241	0.022	1.000

Appendix 4.2. Abbreviations of species names used in Figures 4.1 and 4.3 and Tables 4.2, 4.3 and 4.4.

Abbreviation	Species name
B. rig	<i>Brachyscome rigidula</i>
B. spath	<i>Brachyscome spathulata</i>
L. alb	<i>Leucochrysum albicans</i> sub. sp. <i>albicans</i>
M. sp. 2	<i>Microseris</i> sp. 2
O. phlog	<i>Olearia phlogopappa</i> var. <i>subrepanda</i>
X. sub	<i>Xerochrysum subundulatum</i>
L. acut	<i>Luzula acutifolia</i>
T. spic	<i>Trisetum spicatum</i>
R. nudi	<i>Rytidosperma nudiflora</i>

Appendix 4.3. Abbreviations of site names used in Tables 4.2, 4.3 and 4.4.

Abbreviation	Site name (m)
BO	Mt Bogong (1970)
SK	Spion Kopje (1880)
HO	Mt Hotham (1860)
MK	Mt McKay (1840)
BU	Mt Buller (1762)
ST	Mt Stirling (1748)
HW	Mt Howitt (1738 m)
BL	The Bluff (1725)
MA	Mt Magdala (1725)
KB	King Billy (1696)
SP	Mt Speculation (1668)

Chapter 5 - Case study: seed germination of *Aciphylla glacialis* (Mountain Celery)

Summary

In this chapter, I investigate the germination characteristics of *Aciphylla glacialis* (Apiaceae). This species failed to germinate under the experimental conditions that nine other alpine species from the same region found favourable (see Chapter 4). I used seeds collected during the summer growing seasons of 2004 and 2005 from eight mountain tops in the Victorian alpine zone which form an altitudinal gradient of 302 m. I subjected the seeds to a cold-wet stratification treatment in an attempt to overcome what appeared to be seed dormancy in the experiments described in the previous chapter.

After approximately 15 weeks of the cold-wet stratification treatment, *A. glacialis* seeds began to germinate. Germination rates were fast among seeds from the mid to high altitude sites, as was the final percent germination. Final percent germination was lowest at Mt Speculation (1668 m) and Mt Bogong (1970 m) from seeds collected in 2004. In 2005, the lowest values were also from Mt Bogong. Between years, there was no significant difference between final percent germination for seed from any site. Across the altitudinal gradient, there were no significant relationships between altitude and any germination characteristics. Between sites, there were several significant differences in germination probability. However, there was no overall trend in germination probability between high and low sites.

I also discuss the role of seed dormancy mechanisms in relation to the alpine environment and speculate about the role of altitudinal gradients in relation to seed germination in this species.

Introduction

Seed germination, dormancy and environment

Seed germination and seedling emergence under natural conditions are often highly seasonal (Baskin and Baskin 1988). In alpine areas, where the changes in ground level temperatures are predictable due to the timing of snowmelt, temperature can provide a reliable seasonal germination cue for seeds located at or near the soil surface. In Chapter 4, I found that nine species from the Victorian alpine zone have high rates of germination, as do many species in alpine areas from the northern hemisphere (Amen 1966; Bliss 1971). Optimum temperatures for seed germination among alpine species worldwide are high, often between 10 and 30 °C (Amen 1966; Bell and Bliss 1980; Schütz 2002). Many seeds also germinate opportunistically whenever suitable ambient conditions are present (Bell and Bliss 1980; Körner 1999). Seed dormancy is therefore considered rare in these ecosystems (Amen 1966; Bliss 1971) and germination immediately following snowmelt, coinciding with abundant soil moisture and warmer ambient temperatures, is very common (Bliss 1962; Billings and Mooney 1968; Körner 1999).

Cold-wet stratification, as experienced over winter in an alpine landscape, may be required to break seed dormancy in the few alpine species that use such internal physiological mechanisms to restrain germination (Baskin and Baskin 1988; Probert 1992). This stratification may also be responsible for the timing of seedling emergence in these species. Photoperiodism also affects the seeds of many alpine species, ensuring that growth does not commence in periods which, by ‘evolutionary experience’, would be fatal for an emerging seedling (Körner 1999). Hence, there are various strategies to ensure that germination occurs in spring or early summer when conditions are most favourable for the survival of seedlings in the alpine zone.

Relationships between germination syndrome, habitat and geographical distribution have been difficult to ascertain (Baskin and Baskin 1988), even at the species level (Meyer *et al.* 1990), as germination characteristics can, in part, be a function of life history traits (Baskin and Baskin 1971; Grime *et al.* 1981; Washitani and Masuda 1990). However, if the aspects of life-history, habitat and distribution are relatively similar, different adaptations to environmental factors within species can be discerned more clearly (Meyer *et al.* 1990) as natural selection should favour seed germination patterns that promote seedling establishment (Cavieres and Arroyo 2000). Germination characteristics, therefore, are expected to vary predictably across an altitudinal and

environmental gradient. Evidence suggests that seed viability and seedling vigour may decrease within a species as altitude increases, due to environmental constraints such as short growing seasons, low temperatures and harsh conditions at high altitudes (Amen 1966; Billings and Mooney 1968). Therefore, germination strategies may be partly a function of life-history traits and partly due to habitat characteristics.

Characteristics of the Aciphylla genus

In this study, I aimed to investigate the germination behaviour of a locally common, but regionally rare, alpine forb which grows across an altitudinal gradient in Victoria. The focal species is the Mountain Celery, *Aciphylla glacialis* (F.Muell.) Benth. (Apiaceae). It is one of only three *Aciphylla* species found in Australia, all of which are restricted to alpine and sub-alpine regions. *A. simplicifolia* is uncommon in Victoria and mostly restricted to the high alpine areas of New South Wales (Costin *et al.* 2000), and the Tasmanian endemic, *A. procumbens* is restricted to bolster heath, heath and alpine sedge-land (Kirkpatrick 1997). The other forty species of this genus are found in New Zealand, where they occur over a wide range of habitats from lowland grasslands to alpine areas (Raven 1973).

As a dioecious, obligate out-crossing genus, *Aciphylla* species are dependent on pollinators for fertilization and are therefore likely to experience severe competition, both within and between species, for the few pollinators that are active at high altitudes (Inouye and Pyke 1988; Pickering 2000). The sex ratio of populations of *A. glacialis* are strongly male biased, with an overall ratio of female to male plants of 1:1.49, with males producing four times more flowers than females and therefore attracting and competing with females for pollinators with large floral displays (Pickering 2000). However, there is generally no change in the number of flowers with altitude for both male and female plants among the same sized populations (Pickering and Hill 2002). The proportion of biomass that females allocate to reproduction in *A. simplicifolia* can be 80% more than males based on the average weight of the inflorescences (Pickering and Arthur 2003) and nearly all female flowers produce fruit.

The great investment into reproduction by female *Aciphylla* plants is assumed to lower their survival and growth, especially at the higher alpine sites where the conditions for the accumulation of biomass are limited. The costs associated with female function at high altitudes could therefore result in females flowering less frequently (Pickering and Arthur 2003). At lower altitudes, resources are potentially more abundant (longer snow-free period, warmer temperatures), which could result in an equal flowering ratio between

males and females. Phenotypic differences in relation to environmental effects are also common in this genus, making *A. glacialis* a good model species for investigating the differences in germination across an altitudinal gradient. To my knowledge, no published germination studies exist for any *Aciphylla* species in Australia.

Chapter focus

Following the results in Chapter 4, when *A. glacialis* seeds did not germinate under laboratory conditions simulating early spring and summer, I ask: Can seed dormancy of *A. glacialis* be overcome by cold-wet stratification? Which dormancy syndrome does the behaviour of *A. glacialis* exhibit? Does the altitude of seed origin or the year of seed collection influence the germination characteristics?

Methods

Seed collection and study sites

Seed from *Aciphylla glacialis* (hereafter referred as *Aciphylla*) populations was collected during 2004, between January and March, from seven alpine peaks in Victoria, and again from three of the peaks in 2005. Seed was kept in dry, dark, stable conditions until the germination trials began in mid 2005. The peaks represent a gradient of 302 m in altitude from Mt Speculation (1668 m) to Mt Bogong (1986 m) (see Table 2.1 in Chapter 2). In addition to the sites used in Chapter 2, seed was also collected from Mt Howitt (1738 m, 37°10'30"S, 146°38'50"E), however, seed was not collected from Mt Stirling or The Bluff. All sites are within 40 km of each other, with most less than 10 km apart (Figure 2.1 in Chapter 2).

Mean annual rainfall of this region is relatively high compared to adjacent lowland areas, over 1800 mm (LCC 1982), with much of this precipitation falling as snow during winter. Average air temperatures follow seasonal variations with typical daily minimums and maximums of 2 and 27 °C in summer, and -6 and 12 °C in winter (Bureau of Meteorology *unpublished data*; Chapter 2). Frosts are frequent and can occur at any time of year (Williams 1987). The growing season spans approximately seven months from snowmelt, usually the end of September, until late April, when the first substantial snowfalls of the winter begin. All sites are classed as 'Steep Alpine Mountains' after Costin (1957), are above the natural tree-line and are dominated by tall alpine herbfield vegetation. The lower peaks also contain species typical of adjoining sub-alpine

woodland (Costin 1957). The underlying geology of the area varies (see Table 2.2 in Chapter 2). Despite this variation, the parent material in these regions rarely influences soil type and all soils are considered alpine humus, with a gravelly or skeletal structure (Costin 1962b; LCC 1982) and are acidic, ranging from pH 4 to 5.

Germination trial

Filled seeds were selected by visually assessing each seed using a light box and by gently squeezing each seed. Seeds from each site were then weighed in multiples of ten on an electronic balance, to three decimal places to determine seed mass. In a prior experiment, described in Chapter 4, *Aciphylla* seeds did not germinate under conditions that nine other alpine species found favourable (cool treatment: 12/10°C with 14/10 hours day length and warm treatment: 20/10°C with 12/12 hours day length). Thus, in this experiment, I sought to pre-treat the *Aciphylla* seeds with cold-wet stratification. I arranged 20 replicates of ten seeds from each site in petri dishes on a bed of moist cotton wool with an anti-fungal treatment (10 ml of Mancozeb solution). Petri dishes were then sealed with Parafilm to prevent moisture loss and kept at 2 °C in the dark. Seeds were exposed to daylight for a few minutes whilst they were being monitored for germination, every two to three weeks. Germination was considered to have occurred when the radical emerged from the seed coat, and petri dishes were monitored every one to two weeks after the first germination of seeds occurred. The experiment was terminated at 205 days when germination rates across sites had stabilised and incidences of fungal attack had become more frequent. The final values of germination were adjusted to represent percent germination of the viable seeds present, i.e. those that had not succumbed to fungus attack or were in fact unfilled at the start of the experiment.

Data analysis

Mean seed mass was compared across the sites of seed origin with a factorial ANOVA and Bonferroni post-hoc tests. Final percent germination was expressed as a percentage of viable seeds that germinated during the course of the trial. Germination lag-time was the time in weeks for germination to begin, and germination speed (T_{50}) was measured as the time in days taken to reach 50% of final germination. The final percent germination of seeds was compared between sites using ANOVA and Bonferroni post-hoc tests.

The shape of each percent germination curve, the germination ‘journey’ by which the group of seeds at every site take to reach the final germination score, were compared by modelling the germination curves as a probability of germination, using the Kaplan-

Meier (K-M) product limit estimation function (Kaplan and Meier 1958; Lee 1992; Giménez-Benavides *et al.* 2005), as in Chapter 4.

Linear regression, and in some cases Pearson/Spearman's rank correlations, were performed across populations between combinations of final percent germination, lag-time, germination speed, altitude of seed origin and seed mass.

SYSTAT version 10 (Copyright SPSS Inc., 2000) was used for all statistical analyses.

Results

Germination characteristics

Seeds from all elevations and years showed some germination under the experimental conditions (Figure 5.1). Across all sites, the mean final percent germination was 39 to 95% for seeds collected in 2004, and 30 to 95% for seeds collected in 2005 respectively. Seeds from Mt Hotham had the highest mean final percent germination in both years (95.5 ± 1.53). Comparisons across sites, of seeds collected in 2004, revealed that seeds from Mt Bogong and Mt Speculation (the highest and lowest sites respectively) had significantly lower mean final percent germination ($P < 0.05$) than seeds from all other sites (Figure 5.2). Of the seeds collected in 2005, those from Mt Bogong also had significantly lower mean final percent germination ($P < 0.05$) than the other sites (Figure 5.2). There were no significant differences between years in the final percent germination of seeds from Mt Bogong, Mt Hotham and Mt Buller ($P > 0.05$). Linear regression showed that there was no significant relationship between final mean percent germination and altitude.

The germination lag-time for all sites was approximately 15 weeks from the start of the experiment. As an exact date was not determined, lag-time is not included in the statistical analyses. Germination speed (T_{50}) varied across the gradient (Table 5.1). However, there was no significant relationship between T_{50} and the altitude of seed origin. T_{50} did, however, show a strong relationship with final percent germination ($R^2 = 0.81$, $P = 0.000$) indicating that fast germination speeds correlate with high final germination. Linear regression showed that there was no significant relationship between T_{50} and altitude of seed origin ($P > 0.05$).

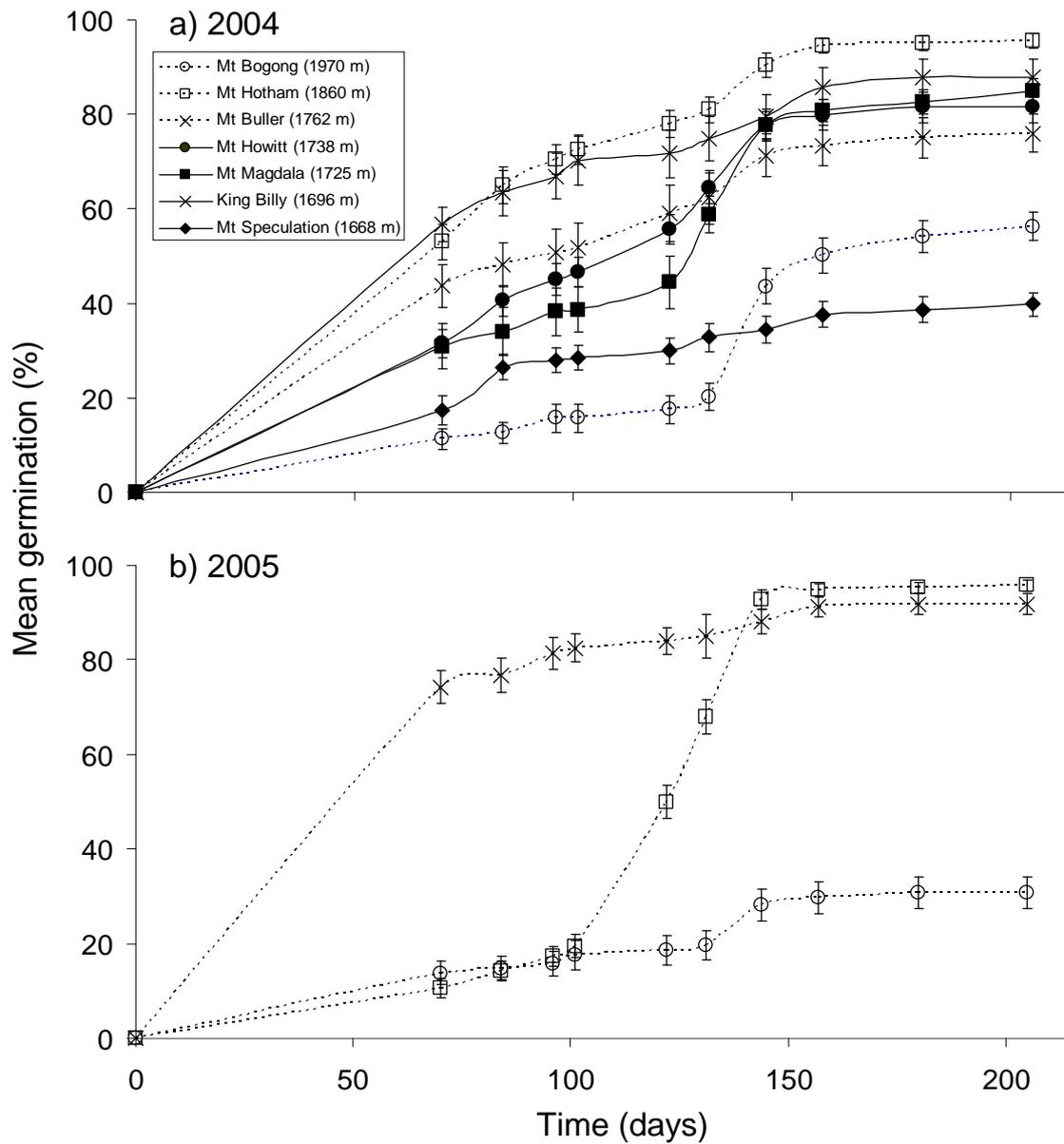


Figure 5.1. Mean percent germination (± 1 standard error) of *Aciphylla glacialis* seed collected from the seven alpine sites in (a) 2004 and (b) 2005, over the duration of the experiment (days).

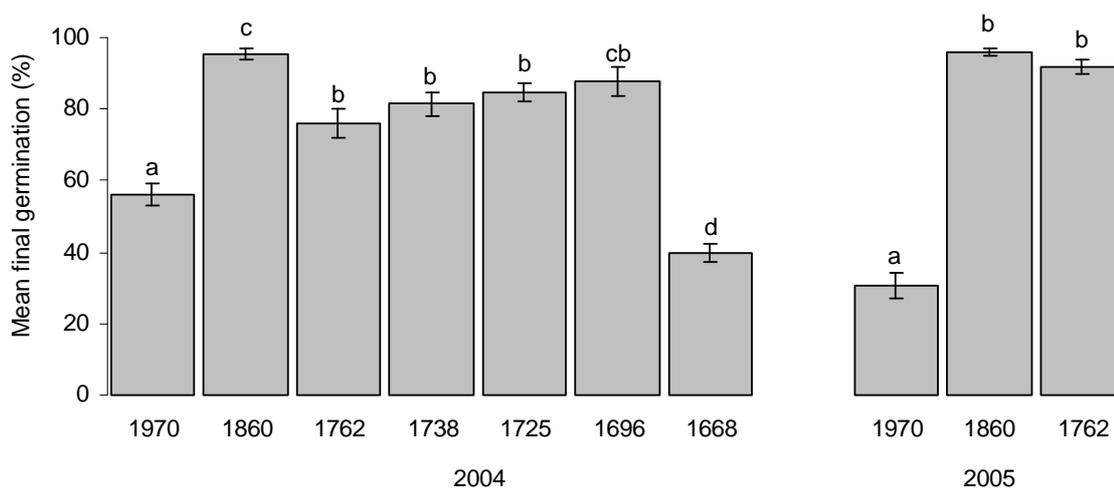


Figure 5.2. Mean final percent germination (± 1 standard error) of *Aciphylla glacialis* seed collected in 2004 and 2005 from different elevations (m). Different labels (a - d) above columns signify the Bonferroni significant differences within each year.

Table 5.1. Germination speed (T_{50}) of *Aciphylla glacialis* seeds from the seven sites, at various altitudes (m), collected in 2004 and 2005

Site of seed origin	Altitude (m)	Year of collection	T_{50} (days)
Mt Bogong	1970	2004	157
Mt Hotham	1860	2004	70
Mt Buller	1762	2004	96
Mt Howitt,	1738	2004	122
Mt Magdala	1725	2004	131
King Billy	1696	2004	70
Mt Speculation	1668	2004	205
Mt Bogong	1790	2005	205
Mt Hotham	1860	2005	122
Mt Buller	1762	2005	70

The probability of germination over time (Figure 5.3) indicates that there are few trends with altitude of seed origin; however, there are several significant differences between curves of different sites (Table 5.2). Of the 23 pairwise comparisons of germination probability by site over both years, nine of these showed that the higher altitude site of the pair had a greater overall probability of germination during the course of the experiment. Eleven showed that a lower site had a high germination probability. Hence, there were no overall trends in seed germination probability with altitude of seed origin.

The probability of germination over time between years was also significantly different for Mt Bogong, Mt Hotham and Mt Buller. Seeds collected in 2004 from Mt Bogong and Mt Hotham were more likely to germinate than seed collected in 2005 (Mantel's $\chi^2 = 16.264$, $P = 0.000$; Mantel's $\chi^2 = 34.267$, $P = 0.000$ respectively). In contrast, seed from Mt Buller collected in 2005 had a higher probability of germination than that from 2004 (Mantel's χ^2 , 34.025; $P = 0.000$).

Across seed from all sites, there were no significant relationships between seed mass and final percent germination, germination speed, germination probability, year or altitude of seed origin (see Chapter 4).

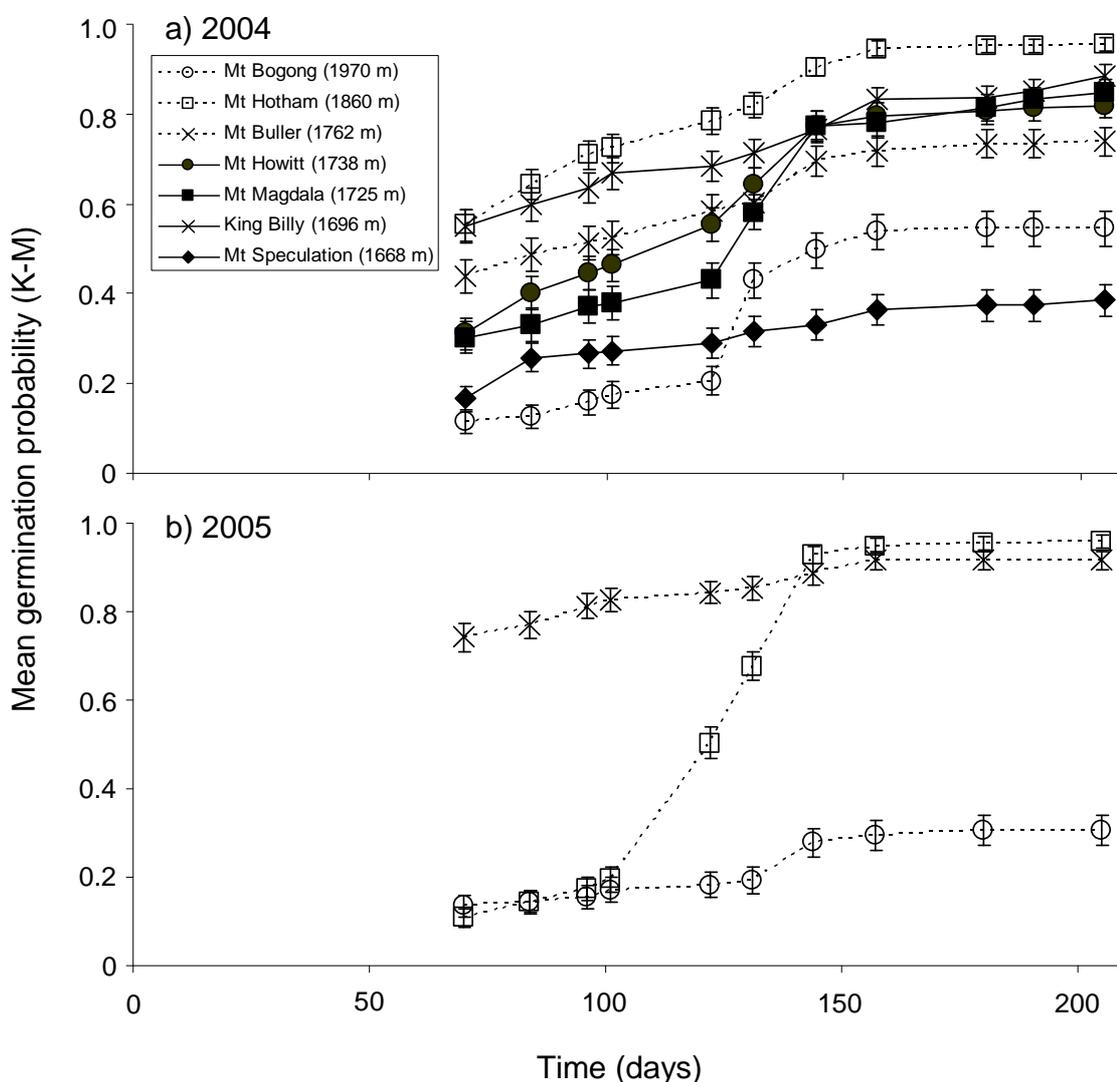


Figure 5.3. Mean probability of germination (± 1 standard error) of *Aciphylla glacialis* seed collected from the seven alpine sites in (a) 2004 and (b) 2005 based on Kaplan-Meier models over the duration of the experiment (days).

Table 5.2. Pairwise comparisons of the probability of *Aciphylla glacialis* seed germination between sites, based on the probability of germination curves, explained by Mantel's χ^2 , from seed collected in 2004 and 2005. Significant differences are indicated by an asterisk(s). *** denotes $P \leq 0.001$, ** denotes $P \leq 0.01$, * denotes $P < 0.05$. Overall greater probability of germination between each pair is indicated in brackets with greater than (>) symbol between site names. Site name abbreviations are as follows: BO, Mt Bogong (1970 m); HO, Mt Hotham (1860 m); BU, Mt Buller (1762 m); HW, Mt Howitt (1738 m); MA, Mt Magdala (1725 m); KB, King Billy (1696 m).

Year / Site						
2004	HO	BU	HW	MA	KB	SP
BO	153.986*** (HO>BO)	30.323*** (BU>BO)	52.243*** (HW>BO)	53.297*** (MA>BO)	80.893*** (KB>BO)	4.540*** (BO>SP)
HO		33.978*** (HO>BU)	28.733*** (HO>HW)	35.362*** (HO>MA)	7.264** (HO>KB)	164.768*** (HO>SP)
BU			0.838	0.685	10.988*** (KB>BU)	50.047*** (BU>SP)
HW				0.201	5.811* (KB>HW)	67.260*** (HW>SP)
MA					6.203* (KB>MA)	70.067*** (MA>SP)
2005	HO	BU				
BO	160.512*** (HO>BO)	195.719*** (BU>BO)				
HO		41.276*** (BU>HO)				

Discussion

General interpretation of results

Aciphylla seeds did not germinate under the laboratory conditions that seeds from nine co-occurring alpine species found favourable, as found in Chapter 4. This indicates that *Aciphylla* seeds may experience innate primary seed dormancy. In the current study, I showed that this dormancy may be broken by a low temperature stratification, which represents a natural dormancy breaking mechanism (Probert 1992) and implies that this species is a strict spring germinator. Consequently, the few observations of *Aciphylla* seedlings emerging in the field were restricted to spring and early summer (see Chapter 6).

The lag-time for *Aciphylla* seeds to germinate from all populations was around 15 weeks, during which conditions were kept at a constant dark 2 °C. Fifteen weeks roughly correlates with the length of a typical Victorian winter, taking into account inter-annual variability in snowfall (Hennessey *et al.* 2003). I therefore suggest that this germination lag-time is a direct result of evolutionary experience of these species growing in the Victorian alpine zone.

In this study, I observed considerable variation in germination characteristics between populations from different altitudes. However, final percent germination showed no significant trends with altitude, nor did seed germination probability. Therefore, germination in this species is likely to be a function of inherited seed traits (Grime *et al.* 1981; Washitani and Masuda 1990) and does not show strong adaptations to the changes in environmental factors found across sites. *Aciphylla* seeds also appear to act independently of ambient conditions and thus, the timing of germination may be reliant on seed dormancy alone. This restrictive germination pattern may protect *Aciphylla* seeds from the hazards of early germination (Meyer *et al.* 1990), especially if snow melts unusually early, leaving plants ‘out in the cold’ when overnight spring frosts are common (Bannister *et al.* 2005). The high rates of germination in this study, 70 - 90%, are within the range of alpine species from around the world (Sayers and Ward 1966; Bell and Bliss 1980; Mariko *et al.* 1993; Körner 1999).

High final percent germination was significantly related to fast germination speeds. Inherently fast rates of germination following snowmelt may be important during the early phases of seedling growth (Sayers and Ward 1966). This ensures that seedlings establish during periods of favourable weather and ample soil moisture (see Chapter 6)

and therefore, species capable of rapid germination have an early-season survival advantage.

The variation in germination characteristics between years from Mt Bogong, Mt Hotham and Mt Buller were statistically undetectable. Hence, the 2005 seeds followed the same patterns in percent germination as those from 2004. Seeds from Mt Hotham showed the highest final germination of all sites in both years. Such consistency between years is unusual for alpine species, as slight increases in temperatures during the seed maturation period can lead to improved seed germinability (Körner 1999). The timing of snowfall, snowmelt and ambient temperatures were not particularly unusual compared to the long-term trends in either 2004 or 2005 and therefore, the similarities in germination may be a result of the predictable environmental conditions that prevail at these sites annually.

Dormancy mechanisms

Dormancy makes intuitive sense in a landscape where winters are cold and severe. However, Billings and Mooney (1968) suggest that the protective layer of snow over winter may serve to insulate seeds sufficiently and hence, they need never fully evolve specific seed dormancy syndromes. Hence, most alpine species lack a seed dormancy mechanism (see Chapter 4) and the elapsed year or more between seed production and germination is an environmentally imposed cue (Amen 1966). However, non-dormant species may germinate in mid-winter if the snow melts unexpectedly, and therefore experience high mortality rates (Amen 1966).

Innate seed dormancy is most frequently imposed by seed coat inhibition among alpine species (Amen 1966; Urbanska and Schütz 1986). This mechanism can spread germination over an extended period and thereby encompass several periods of favourable growth. Thus, germination of some innately-dormant species may occur intermittently over many years, even if growing season conditions are favourable for seedling emergence (Mark 1965; Billings and Mooney 1968). Seed coat inhibition can be broken by scarification of seeds. Under natural conditions, abrasion of buried seeds by frost heave or strong winds at the soil surface, blowing seeds over rocky substrates, may induce the required scarification (Amen 1966; Billings and Mooney 1968). In future studies, deliberate scarification of *Aciphylla* seeds in combination with a chilling treatment, could confirm whether seed coat inhibition occurs in this species.

Cold stratification and cold-wet stratification are techniques used to break seed dormancy of many species from cold climates (Amen 1966; Sayers and Ward 1966;

Cavieres and Arroyo 2000). In my experiment, the length of the cold-wet stratification period required for germination (lag-time) was not precisely recorded. However, other studies clearly show that seeds originating from high elevations require longer stratification periods (Billings and Mooney 1968; Dorne 1981; Cavieres and Arroyo 2000). Cavieres and Arroyo (2000) showed that *Phacelia secunda* seed from 1600 m needed only one month cold stratification, whereas seed from 3400 m needed three months. This pattern may not be apparent in *Aciphylla* seeds as the altitudinal distribution of this species is relatively small and adaptations to differences in snow season length across the gradient may be minimal or undetectable.

Altitudinal gradients

I did not find a relationship between germination characteristics and the altitude of seed origin, possibly because the altitudinal gradient of sites which support *Aciphylla* populations was too small. Elsewhere, the variation in germination characteristics between populations across environmental gradients is common, especially amongst species that respond to variation in habitat. For example, the shrub *Artemisia tridentata*, which grows across a wide environmental range in North America from desert to montane sites, showed strong habitat related differences in seed germination patterns (Meyer *et al.* 1990). Thompson (1973) compared the germination requirements for *Silene vulgaris* across a wide geographical range and found that the temperature range for seed germination was broad across several habitats. However, within a habitat, germination characteristics between populations were remarkably similar (Thompson 1973). Some researchers have suggested that the highest percent germination and shortest germination speed may come from seeds which originate from the highest elevations, when compared to seed of the same species from lower elevations (Mariko *et al.* 1993; Holm 1994; Vera 1997). Vera (1997) showed *Calluna vulgaris* seeds that germinated in the high mountains in Spain also had the highest survival rate as seedlings at the highest altitudes. Large seeds at the highest altitudes may also have the highest survival rates as seedlings (Holm 1994). In Chapter 4, I found no significant relationship between *Aciphylla* seed mass and altitude, nor was there any significant difference between seed mass from high altitude or low altitude sites. Seed germination rates were significantly lower at Mt Bogong and Mt Speculation when compared to the other sites. Hence, *Aciphylla* may be near its upper and lower distributional limits at these sites. Pickering and Arthur (2003) speculated that the growth and fecundity of female *A. simplicifolia* plants may be limited at higher altitudes due to the high maternal investments made during seed production, in

combination with stressful environmental conditions. However, I found no general trends between altitude and final percent germination or germination probability for *Aciphylla* seeds. Therefore, any limitations that the female plants may be experiencing across the altitudinal gradient are not being translated into reductions in seed germinability.

Conclusions

In laboratory experiments, *Aciphylla glacialis* seeds showed germination responses typical of seeds with an innate primary dormancy syndrome. This is an effective way to ensure that spring germination is cued at the end of the winter snow season in an alpine landscape. Final percent germination was high, up to 95%, and no differences in germination were found in seeds collected in different years. Fast germination speeds were significantly related to high final percent germination. These germination characteristics of *Aciphylla* did not show significant trends across the altitudinal gradient of sites within the Victorian alpine zone.

Chapter 6 - Natural seedling recruitment in the Victorian alpine zone

Summary

Having found that seed banks exist in Victorian alpine areas (Chapter 3) and that many species have germinable seeds (Chapters 4 and 5), in this chapter I investigate seedling recruitment under natural conditions. I explore three aspects of seedling recruitment: (1) the abundance of seedlings across the altitudinal gradient of sites; (2) the survival and establishment rates of seedlings over two growing seasons and; (3) the patterns in seedling establishment in relation to the altitudinal gradient. I also investigate the similarity between the seedling flora and the standing vegetation, and the similarity of the seedling flora within and between mountain tops. In addition, I measure the ambient temperatures during the period of field research and the soil moisture in relation to wilting point.

Seedlings were common at all study sites. There were no significant trends in mean seedling emergence with altitude in either growing season. However, mean seedling emergence was significantly higher at four of the seven sites during the 2005/06 growing season. Seedling emergence was best predicted by a combination of altitude, plant litter and soil wilting point. Most seedlings emerged early in the growing season across all sites. Many seedlings survived to become established plants (37 - 61%), however, there was no significant relationship between the percentage of established seedlings and altitude. Seedling mortality was high, (31 - 57%), although there was no significant relationship between mortality and altitude. Most mortality occurred in the early sample period, immediately after snowmelt. Forb seedlings were most common, mostly from the Asteraceae family, while fewer graminoid and shrub seedlings were recorded. Often seedlings emerged in bare ground patches, even at the higher sites where temperatures are cooler and frosts are more common. The similarity between the seedling flora and the standing vegetation was low. The similarity of seedling species within each site was also low. However, there was some similarity in the seedling species among sites alike in altitude.

I also compare my results with similar studies of natural seedling emergence from the international literature. I discuss the role of seedlings in terms of alpine plant recruitment across altitudinal gradients. I discuss how similarities or dissimilarities with the standing vegetation may influence community structure and function. I also give a

brief outline of the potential role of seedling recruitment following disturbances in alpine areas.

Introduction

Alpine environments are characterised by snow cover for several months of the year, short growing seasons, frost, soil-heaving from needle ice (Bliss 1962; Brink *et al.* 1967; Billings and Mooney 1968), late-season soil drought (Bliss 1962; Billings and Mooney 1968; Bonde 1968) and large diurnal temperature fluctuations in summer (Körner 1999). When Bliss (1971) reviewed the available literature, he reported that alpine seed germination rates were low and as a consequence, seedlings were uncommon and seedling mortality was high. Bliss (1971) suggested that stressful environmental conditions were responsible and proposed that needle ice and soil drought were the two most important controls on seedling establishment. Hence, it was assumed that a vegetative reproductive strategy predominated in arctic and alpine areas (Billings and Mooney 1968; Bliss 1971), and that only some years are suitable for seed germination and seedling establishment (Bliss 1962; Körner 1999). Ecological theory regarding stressful environments supports these ideas and suggests that alpine plants will exhibit a life-history strategy that emphasises the adult stages, at the expense of growth and fecundity (Grime 1977). Alpine plants are therefore traditionally viewed as ‘stress tolerant’ (Grime 1979) and the vegetation is dominated by long-lived perennials (Billings and Mooney 1968). An extreme example of this is a clonal *Carex* species from the central Alps, Switzerland that is reported to be around 2000 yrs old (Steinger and Körner 1996).

Despite the apparent reliance on clonal regeneration among alpine plants, there is evidence that many alpine plants flower readily (Körner 1999), produce hundreds of viable seeds (Sayers and Ward 1966; Chambers *et al.* 1987) that can contribute to extensive soil seed banks (Freedman *et al.* 1982; Cooper *et al.* 2004) and germinate easily (Kibe and Masuzawa 1994). Under field conditions, high seedling densities have been reported in North American arctic (Freedman *et al.* 1982) and alpine areas (Chambers *et al.* 1987). Freedman *et al.* (1982) found seedling densities in the hundreds per m². More recently, researchers have quantified seedling establishment and survival across a variety of plant communities in arctic Finland (Welling and Laine 2000b; Welling and Laine 2000a), alpine Switzerland (Urbanska and Schütz 1986) and North America (Forbis 2003), challenging the widely held view that seedling establishment is a rare event in

these regions. For example, Forbis (2003) found high rates of seed germination in wet-meadow communities, with emergent seedling densities up to 900 m² and 48% mortality in the first year.

In the current study, I tracked seedlings emerging under natural conditions across a range of elevations in the Victorian alpine zone. Having already discerned that seed banks exist in Victorian alpine areas (Chapter 3) and that many species have germinable seeds (Chapters 4 and 5), here I aim to discern whether seedling recruitment is occurring under natural conditions.

Methods

Study area and study sites

The study was conducted in the Alpine National Park in the north-east region of Victoria, approximately 350 km from Melbourne, Australia. The area comprises several high peaks, including Victoria's highest mountain, Mt Bogong (1986 m), which may be covered by snow for four to five months of the year. The mean annual rainfall is around 1800 mm (LCC 1982), with much of this precipitation falling as snow during winter. For the duration of the study period, however, drought conditions prevailed over much of south-eastern Australia and rainfall was well below average. At some sites rainfall was only 30% of the long-term average, during what are usually the wettest months (Bureau of Meteorology *unpublished data*). Average air temperatures follow seasonal variations with typical daily minimums and maximums of between 2 and 27 °C in summer and -6 and 12 °C in winter. Frosts are frequent and can occur at any time of year (Williams 1987). The growing season spans approximately seven months from snowmelt, usually the end of September, until late April, when the first substantial snowfalls of the winter begin. Key climatic parameters for the study sites, derived from long-term data by BIOCLIM are shown in Table 2.3, Chapter 2.

The study sites are located within this mountainous region and consist of seven true alpine summit areas. The summits represent a gradient of elevation of alpine sites; Mt Speculation (1668 m), King Billy (1696 m), The Bluff (1725 m), Mt Stirling (1748 m), Mt Buller (1762 m), Mt Hotham (1860 m) and Mt Bogong (1970 m) (Table 2.1 in Chapter 2). All sites are within 40 km of each other, with most less than 10 km apart (Figure 2.1 in Chapter 2). All sites are classed as 'Steep Alpine Mountains' after Costin (1957), are above the natural tree-line and are dominated by tall alpine herbfield

vegetation. The lower peaks also contain species typical of adjoining sub-alpine woodland (Costin 1957). The underlying geology of the area varies (Table 2.2 in Chapter 2). Despite such geological variation, in this region parent material rarely influences soil type and all soils are considered to be of the 'alpine humus' type and are highly acidic (pH 4 to 5) (Costin 1962b; LCC 1982). Cattle are currently excluded from all sites, but grazing has occurred to varying degrees in the past (Lawrence 1999) (Table 2.1 in Chapter 2). None of the sites in this study have been burnt since 1939 or, in some cases, well before this time.

At each summit, the study site was defined as the area that is enclosed by the 5 m contour from the peak, or the area within 50 m from the peak of the summit, whichever was reached first. The sites therefore vary in shape and size, due to the nature of varying slopes, ranging from approximately 612 to 2500 m² (Table 2.1 in Chapter 2). The sites are all rounded with a flat top and steeply sloping sides (Figure 2.2 and Figure 2.3 in Chapter 2). The centre of the site was determined as the highest point of the peak. I avoided summits heavily impacted by recreation.

Sampling design

During the first growing season of the study (austral spring 2003 to austral autumn 2004), 20 permanent quadrats, each 0.5 × 1 m², were arranged in a stratified random manner around each site; with five quadrats placed on each aspect. Initially, I recorded all species in the standing vegetation and the presence of bare ground, rock and litter in each of the fifty 10 × 10 cm grids within each quadrat. The total percent cover of all vascular species was estimated to the nearest 5%. At this time, the seedlings of all species growing in each quadrat were recorded and each seedling was marked with a coloured paper-clip.

Thereafter, three times over the following two growing seasons (at early-, mid- and late-season sampling intervals), I monitored those initially recorded seedlings and new emergents. During the second growing season (2004/05), the early-season sampling interval was between November 23, 2004 and January 30, 2005; the mid-season sampling interval was between February 15 and April 6, 2005; and the late-season sampling interval was between April 5 and May 4, 2005. During the third growing season (2005/06), the early-season sampling interval was between November 4, 2005 and January 3, 2006; the mid-season sampling interval was between January 11 and March 2, 2006; and the late-season sampling interval was between March 17 and April 27, 2006. During these intervals, lower altitude sites were generally visited first, due to earlier snow melt and hence, an earlier start to the growing season.

Seedlings were monitored until they were deemed to be substantially developed or established, i.e. they had reached reproductive maturity or were big enough to withstand potentially detrimental environmental pressures such as frost, wind, extreme temperatures or herbivory. Seedlings were identified to species level where possible. However, several graminoids and some species of the Asteraceae family are difficult to identify until they reach reproductive maturity or a certain size, by which time many had died.

Environmental variables

Air temperatures were measured bi-hourly with T-Tec data loggers (Temperature Technology, Henley Beach, SA) at The Bluff, King Billy and Mt Speculation between February 2004 and April 2006. The temperature probes were housed in Stevenson screens mounted on stakes at 1 m height. The data set is incomplete due to occasional equipment failure and theft. Data for Mt Hotham and Mt Buller were provided by the Bureau of Meteorology.

Temperature data were converted to mean monthly growing degree-days (GDDs). GDDs were calculated as a measure of the accumulated amount of heat (in degrees Celsius) above a base temperature to represent a cumulative index of energy available for growing plants, according to the formula:

$$\text{GDDs} = [(\text{maximum daily temperature} + \text{minimum daily temperature}) / 2] - \text{base temperature}$$

The daily GDDs were then summed for each month. I chose 0 °C as a conservative base growing temperature (the temperature above which plants can perform metabolic functions) as alpine plants are generally varied in their absolute base growing temperature and this value encompasses this variability (Bliss 1962; Körner 1998; Brown *et al.* 2006). Additionally, a base temperature of 0 °C is consistent with other studies of alpine vegetation/temperature relations (Walker *et al.* 1994; Dirnböck *et al.* 2003). GDDs are a useful way to analyse temperature data as one value can be obtained for each month, and values for each site can be easily compared.

Percent soil moisture was measured in every plot at every sampling interval using a theta-probe and HH2 reader (Measurement Engineering Australia, Pty, Ltd). Readings were calibrated against gravimetrically determined soil moisture measurements.

The wilting point of soil (water content at 1500 kPa) at each site was determined with a presoaked ceramic pressure plate in a sealed pressure vessel (Soil Moisture Equipment Co., Santa Barbara, California) for two replicate samples from each site

according to the method of Dane and Topp (2002). Saturated soil samples were subject to 1500 kPa pressure within the pressure vessel until moisture leaving each sample had reached equilibrium. Samples were then weighed, dried at 105 °C for 48 hrs and re-weighed to determine the soil water content (percent soil moisture) at wilting point.

Statistical analysis

Relationships between seedling density and environmental predictors such as altitude, litter, bare ground and the wilting point of soil were analysed with linear regression and Pearson's correlation coefficient on actual and log-transformed values. Different combinations of environmental predictors that are likely to show a relationship with seedling density across the altitudinal gradient were then used in a Schwarz-Bayesian Information Criterion (BIC) analysis, to find the smallest sub-set of useful predictors which best fit the regression model, according to the formula:

$$\text{BIC} = n[\ln(\text{SS}_{\text{Residual}})] + (p+1)\ln(n) - n\ln(n)$$

where n = number of observations and p = number of predictors. This technique makes clear which combination of these independent parameters and the dependant variable best fit the regression model (Quinn and Keough 2003). Relationships between seedling life-form and altitude, bare ground, litter and soil moisture were examined with linear regression and the BIC. Differences between seedling density within each site between 2004/05 and 2005/06 were analysed with paired t-tests. Differences between seedling emergence across each year, at early-season, mid-season and late-season intervals, were examined with ANOVA. The differences between soil moisture measurements across the season were not statistically compared as each value recorded is not independent; i.e. particularly wet or dry soil during the early-season sample interval may influence measurements taken later in the year; nor were measurements taken simultaneously across sites.

Similarity analyses between the emerging seedlings and the standing vegetation within the one quadrat were undertaken based on qualitative and quantitative Jaccard's similarity indices (Jongman *et al.* 1987; Welling and Laine 2000b). The qualitative similarities (SJ) were calculated according to the equation:

$$\text{SJ} = c/(A + B - c)$$

where A is the total number of species in the standing vegetation, B is the total number of species of seedlings, and c is the number of species shared by the standing vegetation and the seedling vegetation (Welling and Laine 2000b). The quantitative similarities (the similarity ratio, SR) were calculated according to the equation:

$$SR_{ij} = \sum_k Y_{ki} Y_{kj} / (\sum_k Y_{ki}^2 + \sum_k Y_{kj}^2 - \sum_k Y_{ki} Y_{kj})$$

where Y_{ki} is the abundance of the k th species in the standing vegetation, Y_{kj} is the abundance of the k th species in the seedling vegetation, and $Y_{ki} Y_{kj}$ is the abundance of species shared by the standing and seedling vegetation (Welling and Laine 2000b). As recommended by Welling and Laine (2000b), I transformed the standing and seedling vegetation values to comparable percentages, so sums of the number of seedlings and percent cover of standing vegetation were both 100 at each site. For both indices, values closer to 1 indicate a closer similarity between standing and seedling vegetation. The variation in mean quantitative and qualitative values for each site were then analyzed using one-way ANOVA and Bonferroni post-hoc tests (Quinn and Keough 2003).

I used ordination to investigate the similarities in seedling species within and between sites. Environmental variables (percent litter, bare ground and rock, years since cattle grazing, soil pH, soil organic matter, soil wilting point and site altitude) were fitted as vectors to the ordinations to enable the variables which display more significant or apparent trends across the ordination to be identified, as well as their direction and influence in relation to the floristic data of the seedling quadrats. I analysed absolute values of seedling emergence and presence/absence of each species in the seedling flora. Quadrats were ordinated by global non-metric multidimensional scaling (NMDS). This method is well suited to data that are non-normal or are on arbitrary or discontinuous scales. NMDS is an iterative search for a ranking and placement of n entities on k dimensions (axes) that minimizes the stress of the k -dimensional configuration. The calculations are based on an $n \times n$ distance matrix calculated from the $n \times p$ -dimensional main matrix, where n is the number of rows and p is the number of columns in the main matrix. How good the dissimilarity matrix is can be determined by the stress value (Kruskal 1964; McCune and Mefford 1999). “Stress” is a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original p -dimensional space and distance in the reduced k -dimensional ordination space. Stress values below 0.2 are recommended (Clarke 1993) as values above this threshold may mislead any interpretations. Dissimilarities between all quadrats were calculated using

the Bray-Curtis dissimilarity coefficient, previously noted as a robust measure in recovering ecological distance over a range of models and stochastic variations in the data (Bray and Curtis 1957; Quinn and Keough 2003). Ordinations presented here are in three dimensions and have a stress value of 0.21 so they should be interpreted with caution.

The differences in seedling species within and between sites were analysed by the analysis of similarities (ANOSIM) procedure (Clarke 1993; Quinn and Keough 2003). This procedure is analogous to an ANOVA comparing between-group and within-group variation. The ANOSIM procedure tests the null hypothesis that there are no differences between *a-priori* defined groups of community samples or, that the average rank of dissimilarities between all possible pairs of objects in different groups are the same as the average of the rank of dissimilarities between pairs of objects in the same groups (Quinn and Keough 2003). All ANOSIM procedures for percent cover and presence-absence data used permutation/randomisation methods on a similarity matrix to randomly allocate objects to groups and then generate the distribution of R , under the null hypothesis that all random allocations are equally likely (Clarke 1993; Quinn and Keough 2003). The R distribution is scaled between pairs of objects in the same groups, with values between -1 and 1. Differences between groups would be suggested by R values greater than zero, where objects are more dissimilar between groups than within groups. R values of zero indicate that the null hypothesis is true. $R=1$ indicates that all samples within groups are more similar to each other than to those in different groups (Clarke 1993; Wharen 1997; Quinn and Keough 2003).

The dominant character species for each site, those that are useful in discriminating between sites, were explored using the SIMPER procedure (Clarke 1993). This procedure utilises the similarity and dissimilarity indices between all pairs of samples to identify typical species within a site, as well as important species that distinguish between sites (Clarke 1993; Wharen *et al.* 1999).

Ordinations were performed using PC-ORD (McCune and Mefford 1999). ANOSIM and SIMPER routines were performed using the PRIMER 5 package (Plymouth Routines in Multivariate Ecological Research 5.1.2. 2000). SYSTAT version 10 (Copyright SPSS Inc., 2000) was used for all other statistical analyses.

Results

Environmental variables

Climate

Temperature measurements throughout 2004, 2005 and 2006 revealed strong patterns in relation to elevation of site and monthly mean ambient temperatures. On most days, the high elevation sites were several degrees lower than the low elevation sites. Overnight temperatures were also generally around 3 to 5 °C lower at the high elevations. The highest temperatures were recorded at Mt Speculation, where summer daytime temperatures were often above 30 °C. The lowest temperatures recorded across all sites were in winter and were routinely around -5 °C. The timing of snowmelt represented a major shift from the mostly constant ambient conditions of winter, to regular diurnal temperature fluctuations.

Temperature measurements converted into accumulated monthly GDDs revealed that the accumulated degrees at lower elevation sites are indeed higher (Figure 6.1), which therefore represents more energy available to plants growing at these sites. The accumulated monthly GDDs follow seasonal variations across the year, with many sites experiencing negative accumulated degrees over winter. During the spring and autumn months, when temperatures change rapidly, there may be almost twice as much energy available to plants growing at low sites, compared with plants growing at high sites.

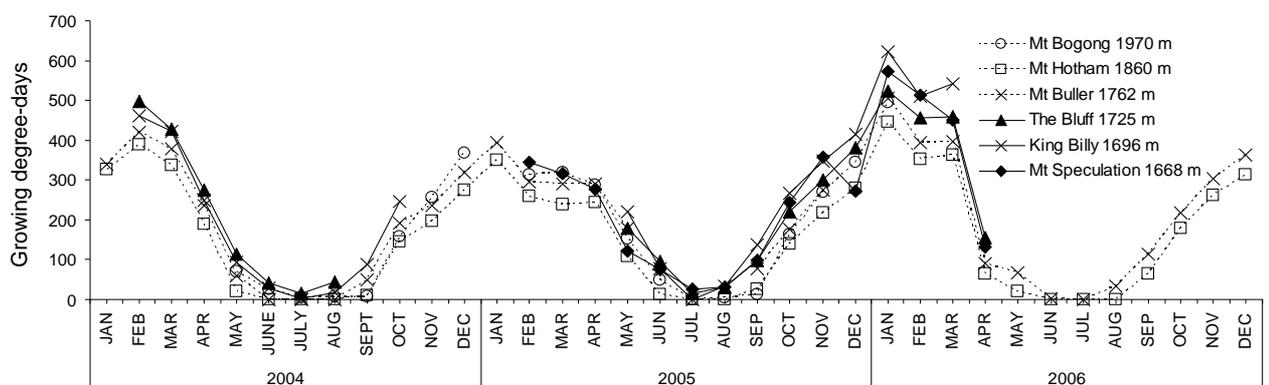


Figure 6.1. Accumulated monthly growing degree days (°C) for six of the seven study sites during 2004, 2005, and 2006. Negative values of accumulated degrees are displayed as zero. Gaps in the data were due to logger failure or theft. These data are also presented in Figure 2.5 in Chapter 2.

Rain and snowfall during the duration of the study were particularly low and well below the long-term average. Some sites did not receive any precipitation at all during the summer months. For example, during December 2005 and January 2006, Mt Buller received no measurable rainfall although the long-term mean is between 82 and 123 mm for these months (Bureau of Meteorology *unpublished data*). Soils were consequently dry during the study period.

Soils

Soil moisture during the 2004/05 season was lower than the 2005/06 season, with mean percent soil moisture ranging from 15 to 30% (Figure 6.2). Soils were particularly dry at Mt Buller, Mt Stirling and King Billy during 2004/05, where mean values did not reach above wilting-point during the growing season. There were few differences between mean percent soil moisture between early-, mid- and late-season sample intervals in 2004/05. During the 2005/06 growing season, mean percent soil moisture within each site showed strong patterning between season intervals, with early- and late-season sample intervals being mostly between 20 and 30%. Soils sampled at all sites during the mid-season of 2005/06 were much drier and never above 15% soil moisture.

The soil moisture values measured throughout the two growing seasons are not independent; i.e. high values may be due to a rain event before sampling and so they have limited value for further statistical analysis. Coincidentally, a peak of very high soil moisture recorded at King Billy during the early-season in 2005/06 corresponded with a very high number of seedlings emerging at that time. During the mid- and late-season sample intervals in 2005/06, very few seedlings emerged, which appeared to correspond with very low soil moisture values recorded at that time.

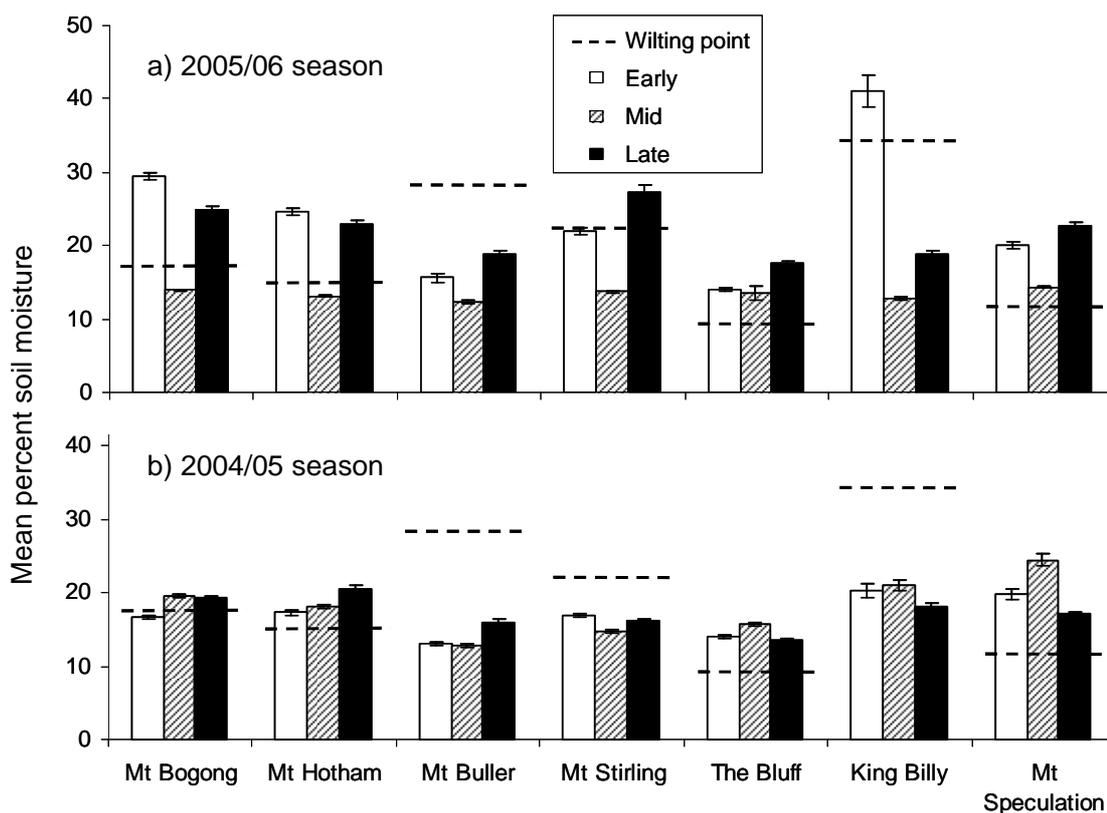


Figure 6.2. Mean (± 1 standard error) percent soil moisture within seedling plots at each site during the three sample intervals (early-, mid- and late-season) over two growing seasons during the study, (a) 2005/06 and (b) 2004/05. Wilting point for each site is represented with a horizontal dashed line.

Seedling emergence

Seedlings were common at all study sites. At Mt Bogong, Mt Hotham, The Bluff and Mt Speculation, significantly more seedlings emerged during the 2005/06 summer than the 2004/05 summer (Figure 6.3). The highest mean seedling densities were found at King Billy (2004/05: 70 ± 13 per m^2 ; 2005/06, 83 ± 22 per m^2). On one occasion, more than 200 seedlings were found in a $0.5 m^2$ plot at this site. At all other sites, pooling over year, the mean density of seedlings was between 7 and 40 per m^2 .

All subsets modeling identified that the combination of altitude, litter and soil wilting point best predicted seedling emergence for both growing seasons.

Independently, however, these predictors are less useful. For example, linear regression analysis revealed only a slight negative, insignificant trend between seedling density and altitude for both mean and log-transformed values (Figure 6.3). This trend was slightly more pronounced in the 2005/06 growing season ($R^2 = 0.27$, $P = 0.23$). Pearson's correlation procedure also revealed no correlation between seedling density and altitude.

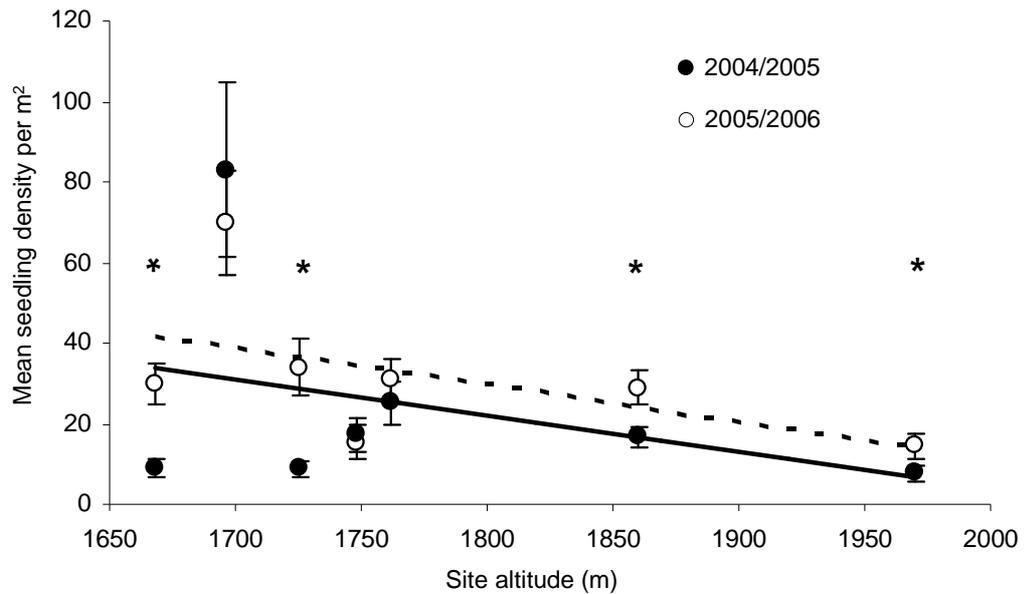


Figure 6.3. Mean (± 1 standard error) seedling density per m^2 of new seedlings during the 2004/05 (closed circles) and 2005/06 (open circles) growing seasons, across the altitudinal gradient. Significant differences in seedling density within sites between the seasons are indicated with an asterisk. Regression lines indicate linear regression analysis between site altitude and seedling density during the 2004/05 summer (solid line, $R^2 = 0.12$, $P = 0.44$); and the 2005/06 summer (dashed line, $R^2 = 0.27$, $P = 0.23$).

Mean seedling emergence differed significantly between sites ($F = 24.29$, $P = 0.000$), growing season ($F = 41.36$, $P = 0.000$) and sample intervals ($F = 111.27$, $P = 0.000$). There was also a significant interaction between these three sources of variation ($F = 3.38$, $P < 0.000$). At most sites mean seedling emergence was highly significantly different between sample intervals (early-, mid- and late-season) and growing season (2004/05 and 2005/06) (Figure 6.4, Table 6.1). A strong pattern emerged during the 2004/05 growing season showing progressively fewer seedlings emerging at each site from the early- to late-season sample intervals. This pattern was weaker in the 2005/06 growing season, where seedling emergence at some sites during the late-season sample interval was higher or equal to that in the early-season sample interval. Hot and dry conditions during the middle of the 2005/06 growing season may have contributed to these results.

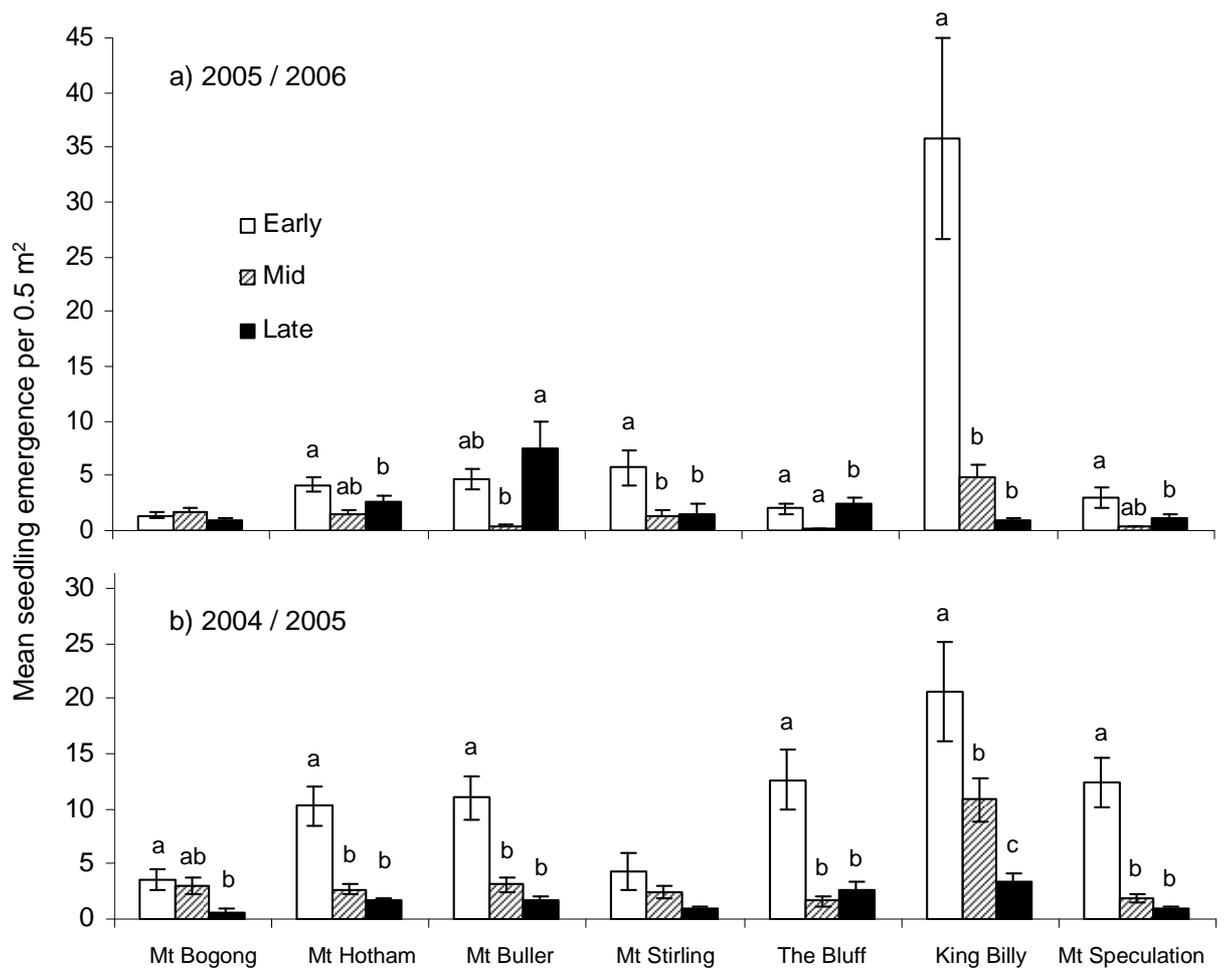


Figure 6.4. Mean seedling emergence (± 1 standard error) per 0.5 m² quadrat for each study site during (a) 2005/06 and (b) 2004/05, during the early-, mid- and late-season sample intervals of each growing season. Different labels (a, b or ab) above columns signify significant differences within each site based on Bonferroni post-hoc analysis. Columns without labels showed no significant differences between sample intervals.

Table 6.1. Two-way ANOVA comparing new seedling emergence at the seven alpine sites between sample intervals (early, mid late), growing seasons (2004/05 and 2005/06) and their interaction. All data were log-transformed +1 prior to analysis to minimise the heterogeneity of variance. Significant P -values ≤ 0.05 , ≤ 0.01 and ≤ 0.001 are indicated by asterisks *, ** and *** respectively.

Site (m)	Source of variation	df	MS	F	P
Mt Bogong (1970)	Sample interval	2	4.52	9.59	0.000***
	Growing season	1	1.86	3.95	0.049*
	Sample interval \times Growing season	2	0.81	1.725	0.183
	Error	114	0.47		
Mt Hotham (1860)	Sample interval	2	10.34	24.54	0.000***
	Growing season	1	2.54	6.03	0.016**
	Sample interval \times Growing season	2	2.64	6.28	0.003**
	Error	114	15.31		
Mt Buller (1762)	Sample interval	2	12.56	17.91	0.000***
	Growing season	1	2.52	3.60	0.060
	Sample interval \times Growing season	2	7.13	10.17	0.000***
	Error	114	0.70		
Mt Stirling (1748)	Sample interval	2	5.23	6.39	0.002**
	Growing season	1	0.13	0.16	0.686
	Sample interval \times Growing season	2	0.69	0.85	0.432
	Error	114	0.82		
The Bluff (1725)	Sample interval	2	13.14	22.11	0.000***
	Growing season	1	12.68	21.32	0.000***
	Sample interval \times Growing season	2	3.44	5.79	0.004**
	Error	114	0.59		
King Billy (1696)	Sample interval	2	33.72	35.86	0.000***
	Growing season	1	4.81	5.12	0.026*
	Sample interval \times Growing season	2	3.27	3.47	0.034*
	Error	114	0.94		
Mt Speculation (1668)	Sample interval	2	17.57	40.20	0.000***
	Growing season	1	9.33	21.36	0.000***
	Sample interval \times Growing season	2	3.45	7.91	0.001**
	Error	107	0.43		

Seedling survival

The percentage of seedlings that became established plants (as defined in the Methods section) was between 37 and 61% across all sites and years (Table 6.2). The highest mortality recorded was among seedlings from King Billy, which is also where the highest densities of seedling were found. Using linear regression, however, there was no significant relationship between the percentage of established seedlings and the altitude ($R^2 = 0.10$, $P = 0.469$).

Table 6.2. The percentage of seedlings that became established and seedling mortality across all quadrats within each site.

Site (m)	Established seedlings (%)	Mortality (%)
Mt Bogong (1970)	44.7	35.9
Mt Hotham (1860)	40.5	42.1
Mt Buller (1762)	55.7	35.2
Mt Stirling (1748)	46.8	42.9
The Bluff (1725)	44.4	50.5
King Billy (1696)	37.4	56.6
Mt Speculation (1668)	61.3	30.9

The rate of seedling mortality (%), combining data from both seasons, was similar to that of seedling establishment (%); from 31% at Mt Speculation to 57% at King Billy (Table 6.2). The percentages of established seedlings and mortality in Table 6.2 do not account for lost seedlings or those which were still alive but not yet considered ‘established’ at the end of the study, and hence these values do not equal 100%. Using linear regression, there was no statistical relationship between seedling mortality (%) and altitude ($R^2 = 0.06$, $P = 0.56$).

In the 2004/05 growing season, most seedling mortality was recorded early in the season at the higher sites (Mt Bogong, Mt Hotham, Mt Buller), indicating that death occurred during or soon after winter. At the lower sites, the most seedling mortality was recorded during the mid-season sample interval when soils were at their driest (Figure 6.2). In the 2005/06 growing season, most deaths occurred during the mid-season interval across all sites. Again, these deaths appeared to correspond with very dry soils at this time.

By the mid- and late-season sample intervals of the 2005/06 growing season, very few previously recorded seedlings were still alive. These remaining seedlings were at Mt Bogong and Mt Hotham, the highest sites. The seedlings that most commonly died were forbs from the Asteraceae, including *Microseris* sp. 2., *Erigeron nitidus* and *Craspedia* spp. *Acetosella vulgaris* (exotic) was also amongst the forb seedlings that commonly died. Most of the shrub seedlings lived beyond the duration of the study. These were mostly *Grevillea australis*. Graminoid seedlings also generally became established plants.

Seedling life forms

Emerging seedlings were classified by life-form and grouped as either forb (which includes geophytes), shrub or graminoid (which includes sedges and rushes). At every site, forb and graminoid seedlings were recorded. Forb seedlings were the most common across all sites. Shrub seedlings were recorded at every site except Mt Bogong and The Bluff. During both years, the relationship between mean seedling emergence of each life-form and altitude was generally weak and non-significant (2004/05: forbs $R^2 = 0.18$, $P = 0.34$; graminoids $R^2 = 0.34$, $P = 0.16$; shrubs $R^2 = 0.18$, $P = 0.33$. 2005/06: forbs $R^2 = 0.11$, $P = 0.45$; graminoids $R^2 = 0.12$, $P = 0.44$; shrubs $R^2 = 0.23$, $P = 0.27$).

During both seasons, the percentage of forb seedlings increased with altitude, though this trend was not significant (2004/05: $R^2 = 0.32$, $P = 0.18$; 2005/06 $R^2 = 0.15$, $P = 0.37$). The percentage of shrub and graminoid seedlings at each site both showed slight decreasing (non-significant) trends with altitude (2004/05: shrubs $R^2 = 0.30$, $P = 0.20$; graminoids $R^2 = 0.28$, $P = 0.21$; 2005/06: shrubs $R^2 = 0.23$, $P = 0.27$; graminoids $R^2 = 0.06$, $P = 0.59$).

Within each site, shrub and graminoid seedlings were often seen growing on bare ground patches, especially at the lower altitude sites (Table 6.3); however, there were no significant trends relating bare ground and seedling emergence with altitude. Even at the higher altitude sites, where cooler temperature and frosts are more common, many forb seedlings grew in bare ground patches. Here, the insulating effects of close vegetation would be minimal (see Chapter 7). Many of these seedlings died after only one sampling interval.

Table 6.3. Comparison of seedling life-forms (%) that emerged in bare ground patches at each site.

Site (m)	Forbs	Shrubs	Graminoids
Mt Bogong (1970)	44.5	0	35
Mt Hotham (1860)	29	15	26.9
Mt Buller (1762)	7.9	17	12
Mt Stirling (1748)	2.3	37.5	46.2
The Bluff (1725)	20.2	100	20.6
King Billy (1696)	13.9	42.6	29
Mt Speculation (1668)	13	7.1	16.8

Similarities within and between sites

Overall, the similarity between the standing vegetation and the seedling vegetation at most sites was low (Table 6.4). Qualitative similarity was higher than quantitative similarity. This indicates that the species of the emerging seedlings are likely be the same as that in the standing vegetation, but high cover-values in the standing vegetation of a particular species are unlikely to be matched by high seedling densities of that species. There was statistically significant variation between the similarity values from the seven sites (qualitative similarity: $F = 4.90$, $P = 0.043$; quantitative similarity, square-root transformed: $F = 2.24$, $P = 0.00$). A Bonferroni post-hoc analysis was used to determine which sites differed from each other in qualitative similarity. The variation in quantitative similarity (SR) within each site was low and therefore no individual sites differed from one another, based on square-root transformed values (Table 6.4).

Table 6.4. Mean (± 1 standard error) qualitative and quantitative similarities (using Jaccard's similarity index and the similarity ratio) for the seven study sites. Labels (a,b or ab) signify significant differences between sites, based on Bonferroni post-hoc analysis. No significant differences in quantitative similarity (SR) were found between sites.

Site (m)	Qualitative similarity (SJ)	Quantitative similarity (SR)
Mt Bogong (1970)	0.32 \pm 0.04 ^{ab}	0.05 \pm 0.02
Mt Hotham (1860)	0.45 \pm 0.04 ^a	0.06 \pm 0.02
Mt Buller (1762)	0.37 \pm 0.04 ^a	0.09 \pm 0.03
Mt Stirling (1748)	0.18 \pm 0.04 ^b	0.05 \pm 0.03
The Bluff (1725)	0.32 \pm 0.04 ^{ab}	0.04 \pm 0.02
King Billy (1696)	0.34 \pm 0.04 ^{ab}	0.04 \pm 0.01
Mt Speculation (1668)	0.36 \pm 0.02 ^a	0.09 \pm 0.02

Based on species presence-absence data, the seedling species within each site were often similar to those between sites. Often sites did not clump together strongly in the ordination diagrams (Figure 6.5). However, strong separation along Axis 3 indicates that the higher and lower sites do not often share seedling species and that similar species are common within these two broad groupings of sites. Seedlings recorded at Mt Stirling, Mt Speculation and Mt Bogong appear to be the most dissimilar from all other sites, and from each other. None of the environmental variables fitted to the ordination as vectors were significant at the 0.05 level, nor were they above R^2 of 0.1. Ordinations using quantitative (percent cover) data were discarded as suitable stress values were not obtained in less than three dimensions.

Analysis using ANOSIM showed that there were no significant differences between sites based on presence/absence data ($R = 0.49$, $P = 0.1$). Subsequent pairwise contrasts based on presence/absence data also showed no difference between each pair of sites.

Exploration of species composition of sites using SIMPER showed that the similarity among seedling quadrats from each site were between 35.8 and 44.1% (Table 6.5). The contributions from individual species to the total similarities are also given in Table 6.5. The typical species of a site were those which were found in high numbers consistently among quadrats, and which also had high mean similarity values between quadrats at the each site. Typical species across all sites were *Carex* spp., *Poa* spp., *Microseris* sp. 2, and *Acetosella vulgaris* (exotic). At most sites, there were seedling species specific to that site; however, these were recorded infrequently.

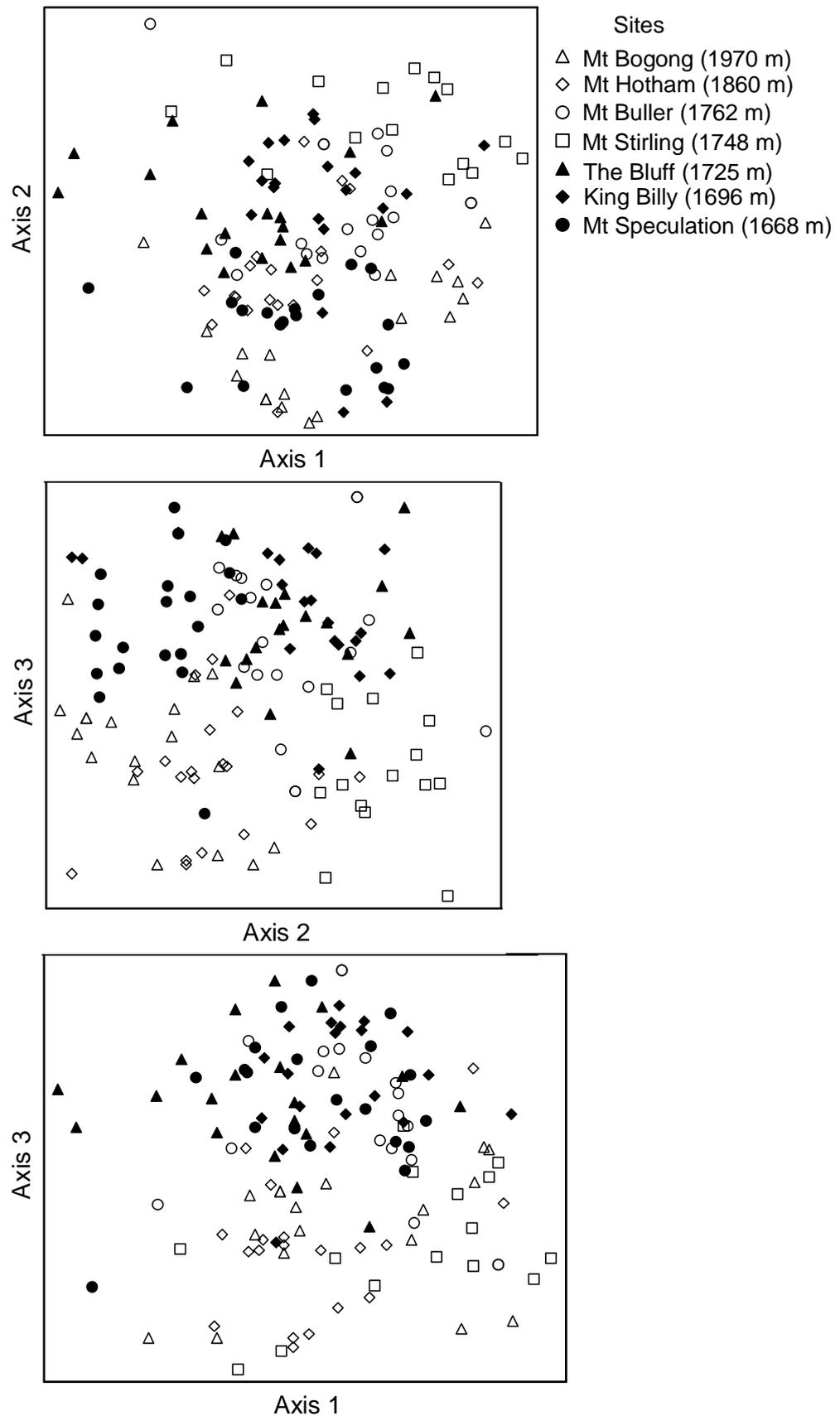


Figure 6.5. The position of seedling quadrats from each site within the three dimensional NMS configuration based on presence/absence data. Open shapes indicate sites above 1725 m (high sites), closed shapes indicate sites at or below 1725 m (low sites). Stress: 0.21.

Table 6.5. The mean similarity (%) of quadrats within each site; the number of seedling species recorded at each site; the top five typifying seedling species of each site; the mean abundance (%) within each quadrat of each of these species; the mean similarity of individual species contributions within each site; standard deviation of each species contribution to the mean similarity; contribution of each species (%) to the mean abundance at each site. Asterisks denote exotic species.

Site (m)	Mean similarity (%) within sites	No. species recorded	Typifying species	Mean abundance (%)	Mean similarity	Similarity / SD	Contribution (%)
Mt Bogong (1970)	41.37	9	<i>Carex</i> sp.	0.78	16.43	1.11	39.72
			<i>Craspedia</i> sp.	0.61	9.33	0.73	22.56
			<i>Acetosella vulgaris</i> *	0.39	4.07	0.39	9.85
			<i>Celmisia</i> sp.	0.33	2.62	0.32	6.32
			<i>Ranunculus muelleri</i>	0.33	2.57	0.32	6.21
Mt Hotham (1860)	39.31	21	<i>Erigeron nitidulus</i>	0.80	9.16	1.27	23.30
			<i>Poa</i> sp.	0.65	5.82	0.82	14.80
			<i>Carex</i> sp.	0.60	5.21	0.72	13.24
			<i>Craspedia</i> sp.	0.55	4.53	0.59	11.52
			<i>Celmisia</i> sp.	0.55	4.18	0.63	10.64
Mt Buller (1762)	44.05	13	<i>Microseris</i> sp.2	0.79	11.79	1.14	26.76
			<i>Trisetum spicatum</i>	0.68	9.02	0.85	20.49
			<i>Poa</i> sp.	0.63	8.33	0.74	18.92
			<i>Acetosella vulgaris</i> *	0.47	4.82	0.49	10.94
			<i>Carex</i> sp.	0.53	4.40	0.59	10.00
Mt Stirling (1748)	36.85	11	<i>Acetosella vulgaris</i> *	0.79	16.79	1.05	45.57
			<i>Hypochoeris radicata</i>	0.57	8.34	0.62	22.64
			<i>Poa</i> sp.	0.50	5.27	0.53	14.29
			<i>Grevillea australis</i>	0.36	2.14	0.35	5.81
			<i>Wahlenbergia</i> sp.	0.29	1.27	0.26	3.46
The Bluff (1725)	36.70	16	<i>Microseris</i> sp. 2	0.84	13.18	1.33	35.91
			<i>Carex</i> sp.	0.63	6.40	0.78	17.43
			<i>Asperula gunnii</i>	0.53	4.04	0.59	11.00
			<i>Brachyscome spathulata</i>	0.47	3.46	0.51	9.43
King Billy (1696)	42.10	24	<i>Stellaria pungens</i>	0.42	3.39	0.41	9.23
			<i>Carex</i> sp.	0.90	10.33	1.61	24.54
			<i>Trisetum spicatum</i>	0.75	6.67	1.00	15.85
			<i>Microseris</i> sp. 2	0.70	6.47	0.87	15.36
			<i>Viola</i> sp.	0.75	6.18	1.04	14.68
Mt Speculation (1668)	35.80	26	<i>Austrostipa</i> sp.	0.45	2.43	0.45	5.76
			<i>Carex</i> sp.	0.95	17.35	2.11	48.45
			<i>Poa</i> sp.	0.60	6.45	0.70	18.01
			<i>Microseris</i> sp. 2	0.45	2.64	0.47	7.39
			<i>Trisetum spicatum</i>	0.35	1.78	0.34	4.96
<i>Lomandra longifolia</i>	0.25	1.26	0.23	3.51			

Discussion

General interpretation of results

Seedling emergence in the Victorian alpine zone is previously undescribed. Only Williams (1992) and Williams and Ashton (1988) have attempted to describe the seedling recruitment dynamics of shrubs, forbs and graminoids in a sub-alpine environment. These studies were also linked to the responses of vegetation to disturbance. I found seedlings to be common at all mountain top sites. Seedling emergence was dependent on site, season and year, with significant differences between seasons and years within each site. There was a slight, non-significant trend for higher seedling densities at lower altitudes during both growing seasons. Such trends might be expected because lower altitudes present fewer obstacles for recruitment than the higher alpine peaks, where cold and short growing seasons favour vegetative persistence (Jolls and Bock 1983). Most seedlings were forbs from the Asteraceae family. A higher percentage of forbs and graminoids were found at the higher elevations than shrubs. I found several seedlings growing in bare ground patches, although many of these did not survive more than one or two sample intervals.

Survival of seedlings was high across sites, with many seedlings reaching reproductive maturity or an equivalent 'established-adult' stage within the two growing seasons of this study. There was no correlation between the ability of seedlings to survive and altitude, although some of the longest surviving seedlings (more than four sample intervals) were found at the highest sites (Mt Bogong, Mt Hotham). At the highest altitudes, many seedlings appeared to die during, or immediately after, winter. In this instance, many seedlings were found dead during the early-season sampling interval after snowmelt. At the lower altitude sites, very dry soils during the mid-season may have influenced seedling mortality.

Percent soil moisture was generally low at all sites, with some sites never reaching mean values above wilting point. Soil moisture typically corresponded poorly to the density and timing of seedling emergence and was therefore not a useful predictor. However, particularly low percent soil moisture values during the mid-season sample interval of 2005/06 did corresponded with very low rates of seedling emergence across most sites. In addition, unusually high soil moisture immediately following snowmelt in 2005/06 at King Billy corresponded with very high mean seedling emergence.

The seedling species were not particularly similar to the species in the standing vegetation at any site. However, the occurrence of the same species in the seedling flora

as in the standing vegetation (qualitative similarity) was higher than the occurrence of those species being equal in abundance (quantitative similarity). Using presence/absence data, the seedling flora did not differ significantly across sites. Seedling species at Mt Stirling, Mt Speculation and Mt Bogong showed the highest degree of within-site similarity. There were no relationships between seedling species and altitude, soil pH, time since cattle removal or soil organic matter in the three-dimensional ordination.

Seedling emergence

Environmental determinants

The altitudinal gradient provides a gradient of environmental conditions with more frequent frosts (Chapter 7), stronger soil heave from needle ice (Chapters 2 and 7), and cooler temperatures occurring at the higher elevations. I therefore expected lower rates of seedling emergence at the higher elevations, where there are numerous environmental hazards at every stage of seedling recruitment (Billings and Mooney 1968; Urbanska and Schütz 1986). However, my results only partly support this hypothesis, as I found few statistically significant trends of seedling emergence, or seedling life-forms, varying with altitude. All sub-sets modelling revealed that the combination of altitude, litter and soil wilting point best predicted seedling emergence. Altitude *per se* can never be an environmental determinant on its own, rather it can represent a suit of climatic and environmental variables that can vary predictably across an altitudinal gradient (see Chapter 2). Hence, seedling emergence is dependent on several climatic and environmental characteristics.

None of the environmental variables (vectors) fitted to the ordination of seedling samples were significant. This indicates that these variables do not change predictably at each site, nor do they appear to drive the patterns in seedling species at each site

Altitudinal gradients

There was not a strong relationship between seedling density and altitude in this study. Mean seedling densities in this study were between 7 and 40 seedlings per m² for each season. In contrast, a strong decrease in seedling density across an altitudinal gradient was reported by Jolls and Bock (1983), where mean values of seedling densities ranged from 25 to 50 per m² in montane and sub-alpine areas, and from 0 and 2 seedlings per m² in treeline and dry-alpine sites. In their study, the altitudinal range from tree-line to the highest alpine site was 242 m, comparable to this study where the range between the

lowest site (at the tree-line) and highest site was 302 m. These densities of seedlings reported by Jolls and Bock (1983) and those that I report here, are well-below the range found on the Niwot Ridge, Colorado, by Forbis (2003), where seedling densities varied enormously between community type, but in the wet-meadow, were over 750 seedlings per m² in 1998. Freedman *et al.* (1982) reports high seedling densities from 13 to 5916 per m² across community types which germinated from large seed banks on a high arctic island in Canada. The highest of these were found in disturbed areas including vehicle tracks (Freedman *et al.* 1982). In addition, Jolls and Bock (1983) initially described the occurrence of alpine seedlings to be so rare and patchily distributed that they went undetected with random sampling. However, in small patches of emerging seedlings, densities exceeded that of lower elevations, with seedlings possibly responding to small-scale environmental patterns in microsites (Jolls and Bock 1983). Hence, if the availability of microsites is sufficient, germination at high altitudes may match or even exceed that at lower altitudes. My study occasionally revealed very high seedling emergence in plots adjacent to very low seedling emergence; for example, on one occasion at the King Billy site, there were over 200 seedlings in one plot and only 5 in an adjacent plot.

Such a large range in arctic and alpine seedling emergence rates across sites and elevations indicates the extent to which species respond to site-specific environmental pressures and disturbance histories. The number of seedlings found above the treeline in this study may be a product of the high numbers of obligate-seeding and mostly-seedling species that were found in the seed bank and the standing vegetation (see Chapter 3). The seedlings which make up the top five most common species at each site all come from obligate seeding species, which cannot regenerate clonally or by rhizomes underground.

Similarity with standing vegetation

My results indicate few similarities between the standing and the seedling vegetation. I showed mean qualitative similarity values (Jaccard's) between 0.18 and 0.45 and mean quantitative similarity values (similarity ratio) was between 0.05 and 0.09. A similar result was found by Welling and Laine (2000b) in an analogous study in sub-arctic of Finland where across community types mean Jaccard's qualitative similarity values ranged between 0.1 and 0.42, and quantitative similarity values ranged between 0.05 and 0.40.

Similarities between mature vegetation and seedlings and the seed-bank are determined by life-history strategies (Chambers 1993) and restrictions through the

regeneration pathway (Urbanska and Schütz 1986; Körner 1999; Welling *et al.* 2005). Many factors can reduce the similarity between the seedling flora and the standing vegetation including the high mortality of seeds in the seed bank and emerging seedlings (Freedman *et al.* 1982; Körner 1999). Körner (1999) suggests that only half the species in the mature vegetation may be represented in emergent seed banks, with the other half having either deeply dormant seeds, low seed production or high mortality. Such low floristic similarity between the standing and seedling vegetation supports the hypothesis that clonal or vegetative growth may play a crucial role in the maintenance and structure of alpine vegetation (Welling and Laine 2000b) and although seedlings are common, they may not be driving the patterns in the standing vegetation. The similarity between species in the seed bank, the seedling flora and the standing vegetation are explored in Chapter 8.

Seedling establishment and survival

Establishment and mortality rates

In this study, 45% of seedlings survived to established juvenile stages and sometimes to reproductive adult stages. This is a substantial number and may reflect that seedling survival is not as limited by environmental factors in alpine regions as previously thought. At alpine summits, many seedlings died within one or two sample intervals of being recorded in this study, consistent with previous studies which found that up to 70% of alpine and arctic seedlings died in their first year (Wager 1938; Urbanska and Schütz 1986). Drought is often cited as the major factor contributing to seedling death in alpine and arctic areas (Billings and Mooney 1968; Bonde 1968; Bell and Bliss 1980; Körner 1999; Forbis 2003), and may account for up to 100% of seedling mortality (Bell and Bliss 1980). In addition, Morgan (2001) found that seedling recruitment was rarely successful in temperate grasslands in Australia, primarily because summer drought caused almost complete mortality. However, I recorded seedlings surviving after periods of intense soil drought well below wilting point.

I also found high mortality following winter, possibly indicating that these seedlings may not have attained critical carbohydrate thresholds or a critical biomass during the previous summer (Wager 1938; Schütz 2002). Galen and Stanton (1999) report that seedlings which produce at least one true leaf are significantly more likely to survive until the next growing season than those which do not. They found that winter survival rates declined from 77% for seedlings with at least one true leaf to 55% for seedlings with only cotyledons at the end of the first growing season. Therefore, the

timing of seed germination is critical for seedling survival. Environmental pressures on life-history stages in alpine plants will usually act to ensure that germination and seedling establishment occurs soon after snowmelt, as I found here. This is when the conditions are most suitable and ample time is available for growth before the subsequent winter (Chambers 1995).

Survival strategies across different altitudes

I found no clear relationship between seedling survival and altitude. This is consistent with the work of Jolls and Bock (1983) who suggested that more extreme environments may not necessarily be more stressful for the species that persist there. However, other studies have found trends of decreasing seedling survival with increasing altitude. On Mt Fuji in Japan, Maruta (1983) reported that *Polygonum cuspidatum* seedlings growing at 2500 m had only 3% survival compared with 63% survival at 1400 m. In contrast, Vera (1997) found that large-seeded species growing at the highest altitudes showed the highest seedling survival when grown under laboratory conditions.

When the longevity of alpine species is taken into account, alpine and lowland species may not differ in their seedling survival probabilities (Forbis 2003; Forbis and Doak 2004), indicating that the alpine environment can strongly shape life-history, but does not alter the shape or strength of evolved life-history trade-offs. Longevity is an appropriate strategy in environments with high inter-annual variation in climate and where frequent sexual reproduction is generally limited by the environment (Grime 1979; Bell and Bliss 1980). Longer-term survival of a species may be achieved through apomixis. Clonality in this form, as an alternative to sexually produced seeds, can facilitate the survival of new, vigorous and well-adapted biotypes (Bliss 1962). These can also benefit from the same dispersal mechanisms as individuals from sexually produced seeds.

The role of seedlings in community level dynamics and responses to disturbance

Reproduction by seed is an important characteristic for species which are responding to abrupt changes in climate. Species are expected to track changing climatic envelopes (Walther *et al.* 2002; Klanderud and Birks 2003) and doing this via sexual reproduction may be faster and more effective than clonal regeneration, especially if long-distance dispersal is required (Forbis 2003). However, cloned individuals derived from hardy, mature mother plants may be more robust in the face of early-season frosts (Inouye 2000),

a scenario predicted for regions where snowmelt in future decades is likely to occur several weeks earlier than at present (Bannister *et al.* 2005).

Large-scale disturbances likely to affect alpine areas in Victoria include soil erosion, cattle grazing and trampling, tourism and fire. Alpine species with the ability to re-sprout or flower en-mass after disturbances are more likely to be abundant and successful, and therefore more likely to control the nature of succession over the following 20 years, dominating the vegetation and reducing the overall vegetation heterogeneity (Kirkpatrick and Dickinson 1984; Wahren *et al.* 2001a). However, seedlings may also be abundant in the post-fire landscape, benefiting from the profusion of nutrients provided by the ash-bed and the lack of competitors (Gill 1981) although, re-sprouting species are expected to grow faster and out-compete species recruiting from seed. Investigation into the role of large-scale disturbance such as fire, in relation to alpine seed germination requirements and subsequent seedling survival, is discussed further in Chapter 8.

Conclusions

Seedling establishment among alpine plants in the Victorian alpine zone is common. Seedling densities are within the ranges of those reported from alpine regions elsewhere in the world. As few relationships with seedling emergence, density and survival were found with altitude, the factors controlling seedling establishment may be similar across sites. Recruitment from seed in alpine areas can be a successful regeneration strategy, as up to 40% of seedlings survived or established to robust stages within two growing seasons. Knowledge of current alpine seedling dynamics at high altitude sites will be useful as a base-line for future alpine plant recruitment studies, particularly in the face of a changing climate and potential large-scale disturbances.

Chapter 7 - Are facilitative interactions between alpine plants during the early life-history stages more important at high altitudes?

Summary

In this chapter, I investigate the role of above-ground facilitative and competitive interactions among germinating seeds and transplanted seedlings of three alpine species, along an altitudinal gradient. The species I chose were *Aciphylla glacialis* (Apiaceae), *Brachyscome rigidula* (Asteraceae) and *Trisetum spicatum* (Poaceae). Seeds and seedlings were transplanted into small cleared (vegetation removed) or control (vegetation intact) plots. The ‘high’ sites in the study (Mt Bogong and Mt Hotham) had lower air and soil temperatures, more frequent frosts, and stronger soil frost-heave events than the ‘low’ sites and hence, facilitative interactions of the target species with the neighbouring vegetation was expected at these sites.

Seed germination showed few trends with respect to site and treatment. Using the Relative Neighbour Effect index, I found that positive (facilitative) and neutral interactions were more common across all sites. At the lower sites, positive, neutral and negative (competitive) interactions were detected. Seedling survival probability curves revealed that seedlings planted at high elevations had a higher probability of surviving into their second year with close neighbouring vegetation.

The findings in this chapter highlight the importance of alpine seed germination and seedling establishment. The current suite of alpine vegetation and community patterns may not respond solely to environmental pressures, but switch between responding positively and negatively towards close neighbours. Should the balance of plant interactions change in coming decades as the climate changes, the composition of the vegetation in alpine areas may also change. Current plant interactions that are overwhelmingly facilitative may become less so as harsh ambient conditions at high altitudes diminish.

Introduction

Along gradients of increasing environmental stress, plant productivity is predicted to be highest in the least stressful environment (Grime 1979). Here, individual plants compete for resources such as light, water and nutrients, and are able to grow to the point where they are limited by competing neighbours (Wilson and Keddy 1986). At the stressful end of the gradient, plants may be more limited by abiotic pressures than resource availability or competition from nearby plants (Callaway *et al.* 2002). Many experimental studies in a variety of ecosystems have demonstrated strong shifts from competitive interactions in favorable and productive environments, to facilitative interactions where the abiotic environment is severe (see Callaway (1995) for a review). By definition, facilitation, or positive interactions between plants, occurs when one species enhances the survival, growth or reproduction of another (Klanderud and Totland 2005), whereby the environmental factor(s) constraining plant growth are alleviated by the physical presence of a neighbouring plant. This may be through the amelioration of the abiotic environment by insulating the substrate, providing shade, buffeting against strong winds, or protecting from frosts (Callaway 1995; Choler *et al.* 2001). Competition involves a struggle between individuals to acquire limited resources (Callaway 1997), while the importance of competition is the relative degree to which negative interactions contribute to the overall decrease in growth rate, metabolism, fecundity and survival of an individual below its optimal condition (Brooker and Callaghan 1998). Until recently, plant interaction studies have been dominated by competition experiments. Experimentation in benign environments may render little evidence for facilitative interactions as, although they do exist, they are probably masked by the relatively greater impact of competition (Brooker and Callaghan 1998).

Alpine environments are particularly suited to studies of facilitation as the severity of the abiotic environment is the primary limit to plant growth (Billings and Mooney 1968; Körner 1999; Olofsson *et al.* 1999). The Australian alpine landscape is no exception, with the highest peaks (>1800 m) dominated by stressful conditions such as strong winds, frequent frosts, extended snow cover and cool summer temperatures (Williams 1987). The lower alpine peaks (1500-1700 m) have potentially more favorable conditions for plant growth because the snow season is shorter, frosts are less common, and growing seasons are warmer and longer (see Chapter 2).

Across the alpine landscape in Australia, I suggest that facilitative interactions between close neighbouring plants are more likely to occur at the highest elevations, where the benefactor and beneficiary plants are closely and positively associated. At

lower elevations, where plants may be less limited by their environment, I expect to see fewer positive associations between close neighbouring plants and individuals performing better without close neighbours.

There is a knowledge gap in the alpine plant literature regarding the interactions of alpine plants at the very early life-history stages. The role of seed germination and seedling survival in alpine areas has been largely neglected (Billings and Mooney 1968; Bliss 1971; Billings 1973) and, although many alpine species are clonal and historically thought to rarely reproduce by seed, seed germination, seedling emergence, growth and survival are all critical to many species' longevity and migration capabilities in the face of global warming (Körner 1999). In a natural alpine setting, seedlings are expected to grow better clumped together, sheltering in the lee of neighbours, as many authors have found for adult individuals (Carlsson and Callaghan 1991; Sturm *et al.* 2001; Callaway *et al.* 2002). Such positive interactions have been discovered in numerous alpine locations around the world on adult plants (summarized by Callaway *et al.* 2002), with the overriding outcome that most plants benefit from close neighbours, and that facilitation is the dominant inter-plant interaction in high mountain environments. Neighbouring plants can change micro-habitats by reducing wind speeds, increasing local temperatures, aiding in the accumulation of nutrients, reducing soil-heave from frosts and, in some cases, helping to protect against herbivores (Carlsson and Callaghan 1991; Moen 1993; Sturm *et al.* 2001). However, this may not always be the case. Williams (1992) showed on the Bogong High Plains, Victoria, that several species of forbs and shrubs were able to colonise bare ground gaps in alpine grasslands and herbfields without the facilitative buffering effect of adjacent vegetation. In addition, as I showed in Chapter 6, seedlings of all life-forms can emerge in bare ground gaps regardless of altitude or ambient temperatures.

In the current study, I experimentally investigated the role of competitive and facilitative interactions with regard to seed germination, seedling growth and seedling survival along a natural altitudinal gradient in the Victorian alpine zone. This natural gradient can also be used in a 'space-for-time' substitution (Pickett 1989) in order to predict the consequences of global warming on alpine seeds and seedlings.

Specifically, I ask: "Does the presence of close neighbouring plants enhance (facilitate) the seed germination, seedling growth and seedling survival of alpine plants at the highest altitude sites in comparison with the lower altitude sites?"

Methods

Study sites and species

The study was conducted in the Alpine National Park in north-east Victoria, approximately 350 km from Melbourne, Australia. The area comprises several high peaks, including Victoria's highest mountain, Mt Bogong 1986 m, which can be covered by snow for four to five months of the year. The mean annual rainfall is >1800 mm (LCC 1982) with much of this precipitation falling as snow on the high peaks during winter. Average air temperatures follow seasonal variations with typical daily minimums and maximums of between 2 and 27 °C in summer and -6 and 12 °C in winter. Frosts are frequent and can occur at any time of year (Williams 1987). The growing season spans approximately seven months from snowmelt, usually the end of September, until late April, when the first substantial snowfalls of the winter begin.

I chose sites on four mountain peaks to represent a gradient of elevation from high to low: Mt Bogong (1970 m), Mt Hotham (1860 m), Mt Magdala (1725 m) and King Billy (1696 m) (Figure 2.1, Table 2.1 in Chapter 2). All sites are classed as 'Steep Alpine Mountains' after Costin (1957), are above the natural tree-line and are dominated by tall alpine herbfield vegetation (McDougall 1982; Walsh *et al.* 1986). The low peaks, being closer to the tree-line, also include shrub species that are common in sub-alpine woodland (Costin 1957). The underlying geology of the area varies (LCC 1982) (Table 2.2 in Chapter 2). Despite such geological variation, in these regions parent material rarely influences soil type and all soils are considered to be of the 'alpine humus' type and are acidic (pH 4 to 5) (Costin 1962b; LCC 1982). Cattle are currently excluded from all sites, but grazing has occurred to varying degrees in the past (Lawrence 1999) (Table 2.1 in Chapter 2). None of the sites examined have been burnt since 1939 or, in some cases, well before this time.

I chose three study species, *Aciphylla glacialis* (Apiaceae), *Brachyscome rigidula* (Asteraceae) and *Trisetum spicatum* (Poaceae), hereafter referred to as *Aciphylla*, *Brachyscome* and *Trisetum*. All species are locally abundant at each site and their occurrence has been confirmed at most of the other mountain peaks in the region (Walsh *et al.* 1986; McDougall and Walsh 2007). Additionally, I found high levels of germination in these species in prior laboratory tests (Chapters 4 and 5). All seeds used in sowing experiments were pre-tested for filled embryos with a light-box and squeeze tests.

Climate and environmental variables

Soil and air temperatures were measured hourly with TinyTag data loggers (Hastings Data Loggers, Port Macquarie, QLD) at one high sites (Mt Bogong, 1970 m) and one low site (King Billy, 1696 m) during the 2005/2006 growing season. The data set is incomplete due to occasional equipment failure and theft. The soil temperature probes were inserted into cleared (vegetation removed) and control (vegetation intact) plots at 10 cm depth. The air temperature probes were housed in a Stevenson screen mounted on a stake at 1 m height.

Temperature data were converted to mean monthly growing degree-days (GDDs). GDDs were calculated as a measure of the accumulated amount of heat (in degrees Celsius) above a base temperature to represent a cumulative index of energy available for growing plants, according to the formula:

$$\text{GDD} = [(\text{maximum daily temperature} + \text{minimum daily temperature}) / 2] - \text{base temperature.}$$

The daily GDDs were then summed for each month. I chose 0 °C as a conservative base growing temperature as alpine plants are generally varied in their absolute base growing temperature and this value encompasses this variability (Bliss 1962; Körner 1998; Brown *et al.* 2006). Additionally, a base temperature of 0 °C is consistent with other studies of alpine vegetation/temperature relations (Walker *et al.* 1994; Dirnböck *et al.* 2003). GDDs are a useful way to analyse temperature data as one value can be obtained for each month, and values for each site can be easily compared.

I measured the impact of frost events on soil stability using vertical displacement pins (Brown *et al.* 2000) at Mt Bogong, Mt Hotham and King Billy. This method records the height that frozen soil reaches during a frost event, and frost-heave is inferred from the change in height of a rubber washer on a 5 mm stainless steel rod. The rods were inserted to a depth of 10 cm into the soil (see Figure 2.4 in Chapter 2). A rubber washer sits above a wooden disc, which are both forced to slide up the rod when pushed by freezing soil. The rubber washer stays in place, gripping the rod after a frost event, and the distance it moved from the surface can later be measured. The wooden disc slides back down the rod to the soil surface as the soil thaws. The rods are reset after frosts by pushing the rubber washer back to the soil surface. Ten vertical displacement pins were erected in areas of naturally occurring bare ground and ten in intact vegetation at three sites. Frost-heave measurements were made at three intervals over the 2005/06 growing season.

Soil moisture (%) was measured in cleared (vegetation removed) and control (vegetation intact) plots over the 2004/05 and 2005/06 growing seasons at every sample interval using a Theta-Probe and HH2 reader (Measurement Engineering, Australia, Pty, Ltd). Readings were calibrated against gravimetrically determined soil moisture measurements from the four sites.

Experimental design

I investigated the role of above-ground facilitation at two critical life history phases, the seed germination and seedling stages, across a gradient of alpine sites. I chose not to include below-ground interactions in my study, as the factors that drive plant community patterns in Australian alpine landscapes are thought to be predominantly above-ground processes, i.e. frosts, wind, cold air drainage into frost hollows and snowmelt patterns (Williams and Ashton 1987).

Seed germination

The first experiment tested for the effects of neighbouring plants on seed germination. At each site, 24 cleared (vegetation removed) plots were created by clipping above-ground vegetation to ground level within a 225 cm² plot. Twenty-four adjacent control plots (vegetation left intact) of the same size were paired with each cleared plot, within approximately 0.5 m. The plots were arranged in a stratified-random manner around each site, with an equal number of plots on each aspect. Towards the end of the growing season in 2003/04, I planted 10 seeds into eight cleared and eight control plots for each of the study species at each site. Seed was sourced from populations local to each site collected two to four months prior to planting. Germinants were recorded three times over the growing seasons of 2004/05 and 2005/06. Individual germinants in each plot were identified with a coloured paper-clip.

In the first growing season, the early-season sample interval was between November 24, 2004 and January 14, 2005 (austral spring); the mid-season sample interval was between January 31 and March 19, 2005 (austral summer); and the late-season sample interval was between April 7 and April 27, 2005 (austral autumn). In the second growing season, the early-season sample interval was between November 5 and November 18, 2005; the mid-season sample interval was between January 11 and January 26, 2006; and the late-season sample interval was between March 16 and April 13, 2006.

Seedling growth and survival

The second experiment tested for the effects of neighbouring vegetation on seedling growth and survival. At each site, 24 cleared plots (for each species) were created by clipping above-ground vegetation to ground level from a 225 cm² plot, as in the seed germination experiments. Adjacent control plots of the same size were paired with each cleared plot and arranged in a stratified-random manner around each site, with an equal number of plots on each aspect. One seedling was planted into plot. Seedlings had been grown from seed collected during the 2003/04 and 2004/05 growing seasons; the seed was germinated in Melbourne at La Trobe University, in controlled glasshouse conditions and seedlings were grown outside in the shadehouse. During April 2005, seedlings of *Aciphylla*, *Brachyscome* and *Trisetum* were transported and planted at their sites of seed origin into cleared and control plots. There were insufficient seedlings to plant each species at each site. Thus, *Aciphylla* seedlings were not planted at Mt Bogong and *Brachyscome* seedlings were not planted at Mt Hotham.

At the time I established the experiments, I counted the number of leaves for every *Aciphylla* and *Trisetum* seedling and measured the height of every *Brachyscome* seedling. The ongoing performance of planted seedlings with and without neighbours was quantitatively assessed by counting the leaves on *Aciphylla* and *Trisetum* seedlings and measuring heights of *Brachyscome* seedlings, at three intervals (early, mid and late) over the 2005/06 growing season.

Data analysis

Seed germination

To examine whether facilitative interactions with close neighbours are indeed occurring at the higher elevation sites, I investigated the interaction of site (Mt Bogong, Mt Hotham, Mt Magdala or King Billy) and treatment (cleared or control) on seed germination using two-way ANOVA. After attempting to transform the data to meet the assumptions of ANOVA, as non-germination results (zeros) were very common throughout the data set, I ranked the mean germinations in each treatment for each site, and performed the ANOVA on these ranks, following the method used by Kepner and Robinson (1988). Non-parametric tests were not appropriate as none give an interaction term, which would demonstrate an interaction between site and treatment and hence, any facilitative or competitive effects on seed germination. Each site was compared against every other site

for each species, in order to determine an interaction between site and treatment. A significant interaction indicates that the effect of neighbours on seed germination may depend on the site.

Seedling transplant growth

I calculated the relative competitive intensity between pairs of seedlings, with and without neighbours at high and low sites, using the Relative Neighbour Effect (RNE) index (Markham and Chanway 1996; Brooker *et al.* 2005):

$$\text{RNE} = (P_{\text{Cl}} - P_{\text{Co}}) / P_{\text{Cl}}$$

where ‘ P_{Cl} ’ refers to the performance of seedlings grown in cleared plots, ‘ P_{Co} ’ refers to the performance of seedlings grown in control plots. The RNE index allows for the expression of the intensity of both facilitative and competitive interactions, with positive values indicating a stronger competitive effect. To make more intuitive sense, I present the RNE values in reverse, so that a positive value indicates a positive interaction (facilitation) and a negative value indicates a negative interaction (competition), as per Callaway *et al.* (2002). I calculated the term for ‘performance’ in the RNE index using the number of leaves for *Aciphylla* and *Trisetum* seedlings, and height (cm) for *Brachyscome*, for the seedlings in paired cleared and control plots.

I present the overall mean RNE value for seedlings from each pair of cleared and control plots, for each site at three intervals across the growing season in 2005/2006. By using the RNE index, I can therefore assume that differences in leaf number or height of seedlings, between pairs of cleared and control plots, constitute a relevant indicator of the direction and strength of a biotic interaction between the seedlings and the neighbouring plants. In my analysis, a death in any pair of seedlings was removed from the calculations to give a conservative estimate of competitive or facilitative interactions with neighbouring plants. Towards the end of the growing season, many *Aciphylla* seedlings had died, leaving too few pairs remaining on which to calculate meaningful RNE values. Hence, no values for the last sample interval for this species are presented. Among *Brachyscome* and *Trisetum* seedlings, the variability in RNE values tend to increase toward the end of the growing season, again due to a decrease in the sample size following seedling deaths. The differences between RNE values at each site, within each species and sample interval, were compared with independent t-tests.

Seedling transplant survival

I investigated the probability of survival of planted seedlings in cleared and control plots at all sites using the Kaplan-Meier (K-M) product limit estimation function (Kaplan and Meier 1958; Lee 1992). This is a non-parametric, step function commonly used in medical trials but it is equally applicable to ecological data where the distribution of the statistical population is unknown. Survival times are broadly defined as the time to the occurrence of a given event, in this case, death. The method uses survival data from every seedling in the form of elapsed time (sample intervals) until death (right censored data) and also data for seedlings which did not die (non-censored data) (Giménez-Benavides *et al.* 2005).

Unlike the RNE values used to assess the effect of neighbours on plant performance, which includes the interaction between cleared and control plots, there is no one metric that can be calculated to compare the effect of neighbours on survivorship over the course of the experiment. Simply comparing survival curves does not infer any differences in effect-size between cleared and control plots across the course of the experiment. Therefore, for each species, I performed multiple two-factor ANOVAs on the proportion of seedlings alive on each aspect of each site. I assessed the effects of treatment (cleared plot or control plot) by site (each mountain) and the interaction between them. In this analysis, the point of interest is the interaction term. A significant interaction indicates that the effect of neighbours on seedling survival may depend on site. Where the interaction terms were significant, plots of means were examined to determine the direction of the interaction.

SYSTAT version 10 (Copyright SPSS Inc., 2000) was used for all statistical analyses.

Results

Environmental variables

Air and soil temperatures

Over most of the growing season, air temperatures were high at King Billy (1696 m) with daytime maximum temperatures regularly between 20 and 30 °C and overnight temperatures rarely below 10 °C (between January and March). At Mt Bogong (1970 m) during the same period, maximum daytime temperatures were between 15 and 20 °C and overnight temperatures always below 10 °C and often below 0 °C. Overall, in the summer months following snowmelt, air temperatures at King Billy were up to 100 degree days warmer than Mt Bogong. Air temperatures at Mt Bogong stayed cooler for longer, mostly due to the extended snow-lie at this site.

Soil temperatures at King Billy and Mt Bogong followed the patterns of the air temperatures, with higher soil temperatures at the lower site (Figure 7.1). Soil temperatures were generally higher in the control plots than in the cleared plots. This difference was most striking at King Billy (Figure 7.1).

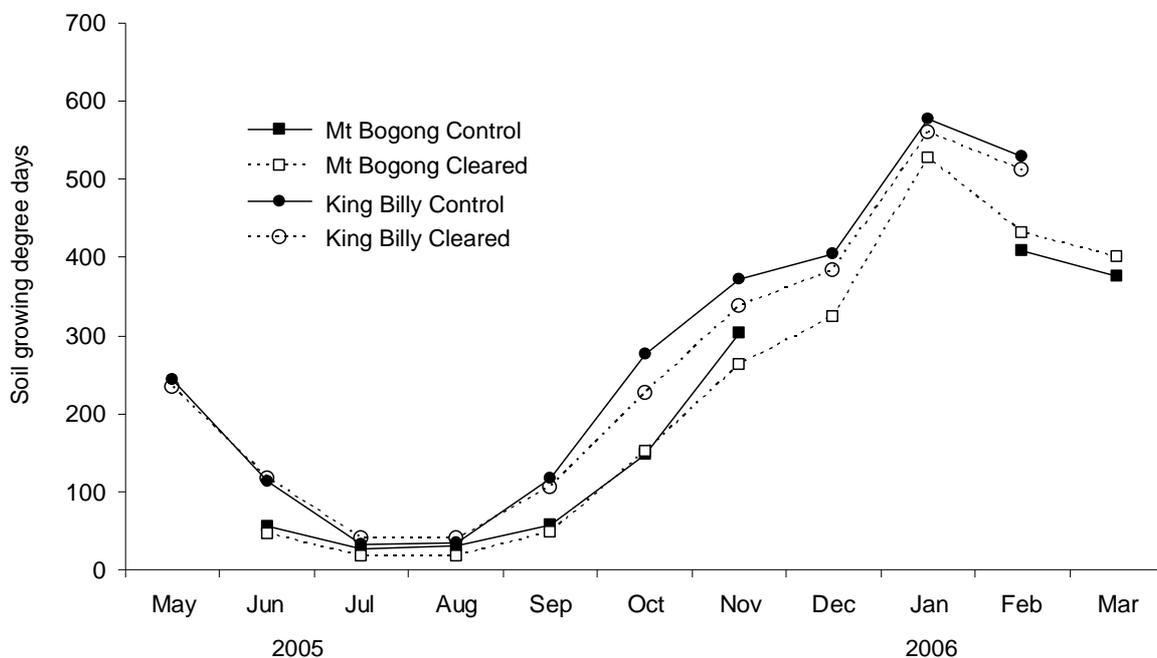


Figure 7.1. Soil temperatures, converted to monthly growing degree days, recorded during 2005 and 2006 in cleared (vegetation removed, dashed line, open symbol) and control (vegetation intact, solid line, closed symbol) plots at King Billy (circles) and Mt Bogong (squares).

Frost heave

I recorded 31 frost events (air temperatures below 0 °C) at King Billy (1696 m), and 41 frost events at Mt Bogong (1970 m) during the snow-free season in 2005/06. Snow thawed almost a month later at Mt Bogong than at King Billy. Frost-heave was recorded regularly throughout the 2005/06 growing season using the vertical displacement pins at three of the study sites (Figure 7.2). Frost events caused strong soil frost-heave mostly early in the growing season at these three sites. Frost-heave was more frequent in areas of bare ground. Frost-heave was also significantly stronger in areas of bare ground compared with areas of intact vegetation (Figure 7.2; Log+1 transformed data, $P = 0.000$). There was also a significant effect of site, pooling over treatment (Log+1 transformed data, $P = 0.040$), although there was no interaction between site and treatment (two way ANOVA, $F = 1.829$, $P = 0.164$) (Figure 7.2).

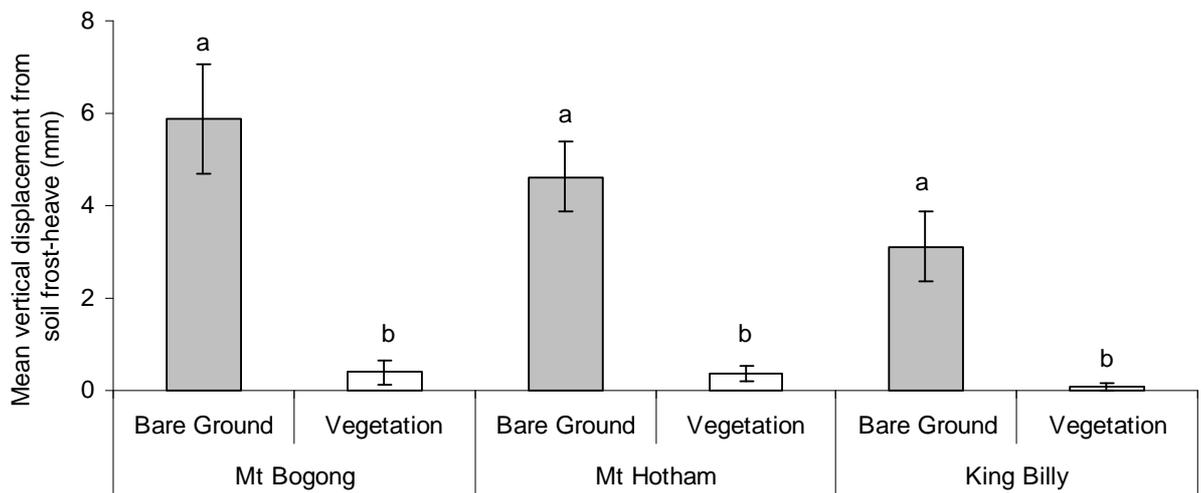


Figure 7.2. Mean (± 1 standard error) vertical displacement of rubber washers on vertical displacement pins (mm) in bare ground (grey bars) and vegetated (white bars) areas at three sites, Mt Bogong (1970 m), Mt Hotham (1860 m) and King Billy (1696 m) during the 2005/2006 growing season. $N = 10$ for each treatment at each site. Different labels (a or b) above columns indicate significant differences ($P < 0.05$). Higher mean vertical displacement at indicates stronger and higher frost-heave of the soil. These data are also presented in Figure 2.6 in Chapter 2.

Soil moisture

For approximately half the comparisons, soil moisture between cleared and control plots showed no significant differences within the same sample interval at the same site (Figure 7.3). However, on 12 occasions, soil moisture was significantly higher in the cleared plots than the control plots, based on independent t-tests ($P < 0.05$). During the 2004/05 growing season, at all three sample intervals, soil moisture was significantly higher in cleared plots than controls at Mt Bogong. At Mt Hotham, cleared plots were significantly wetter during the mid- and late-sample intervals, as at King Billy during the mid-sample

interval. During the 2005/06 growing season, soil moisture in cleared plots was significantly higher than in control plots in the late-sample interval across all sites, and in the early-sample interval at Mt Magdala and King Billy. Differences in percent soil moisture between sample intervals (early, mid and late) within the same growing season were not compared as they are not strictly independent, i.e., particularly wet soil early in the season may influence measurements taken later on.

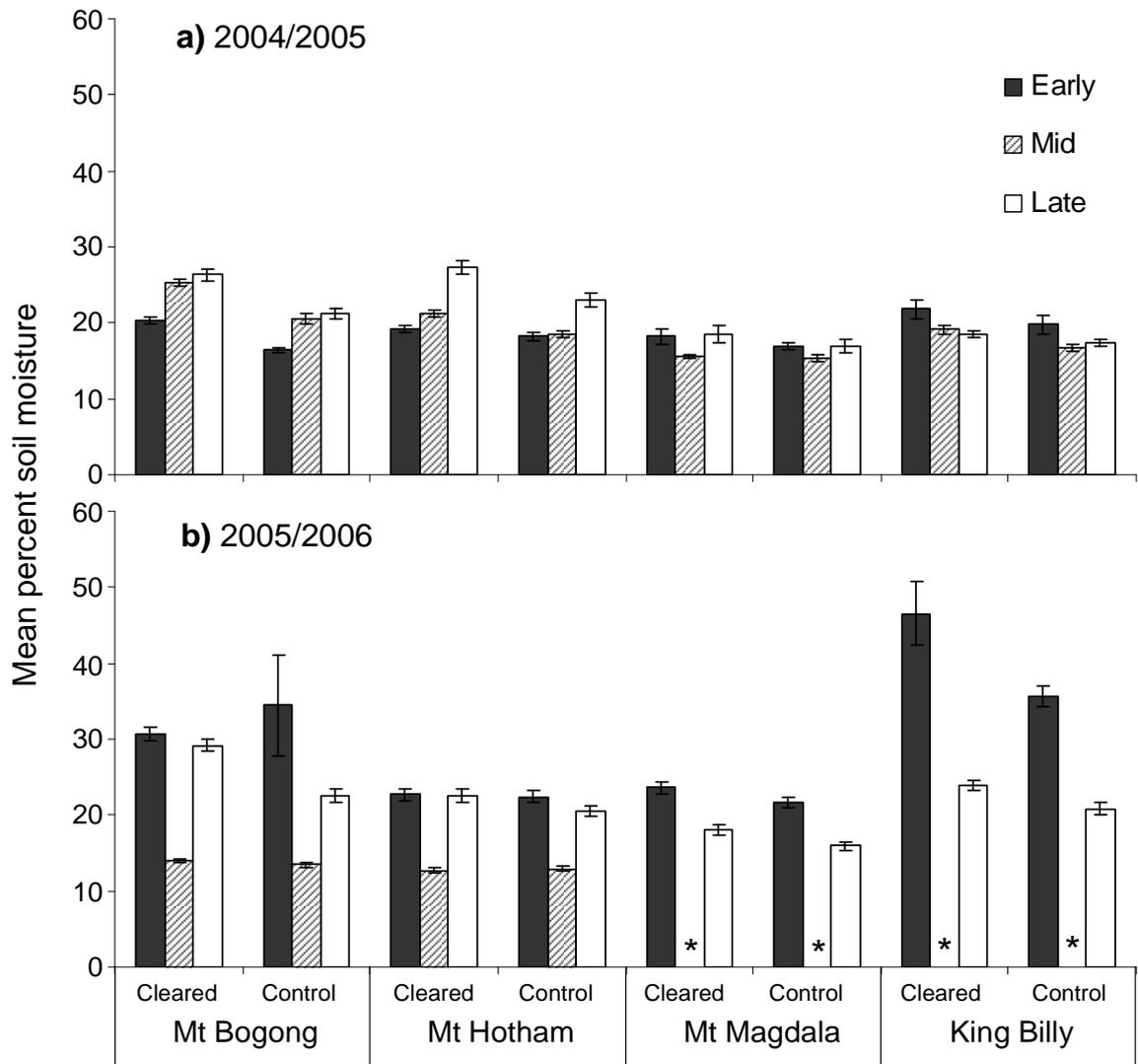


Figure 7.3. Mean percent soil moisture (± 1 standard error) for soil in cleared and control plots at the four alpine sites, at three sample intervals (early mid and late-season) for (a) the 2004/05 growing season and (b) the 2005/06 growing season. *No measurements were taken during the mid sample interval at Mt Magdala and King Billy during the 2005/06 growing season.

Seed and Seedling Experiments

Seed germination

Of the few seeds that germinated across all species and plots (Figure 7.4), more than 70% germinated early in the first growing season after sowing. Of the *Aciphylla* and *Trisetum* seeds, only four and two seeds respectively germinated in the second growing season. *Trisetum* seeds only germinated at King Billy, with no significant difference ($P > 0.05$) in mean germination between in cleared and control plots, based on independent t-tests. There was no germination of *Aciphylla* seed at Mt Bogong. Few *Aciphylla* seeds germinated in cleared plots at Mt Hotham (Figure 7.4). There was a significant difference in mean *Aciphylla* germination in cleared plots between Mt Hotham and King Billy, and between Mt Hotham and Mt Magdala (Figure 7.4, t-tests: $P < 0.05$ respectively). No significant difference in germination of *Aciphylla* seed was found in control plots between any sites. *Brachyscome* seeds germinated equally well in cleared and control plots across all sites, with no significant differences between treatments or sites.

Two-way ANOVAs between sites, within each species, based on germination rank, revealed no significant interactions for any comparison. Therefore, I conclude that the effect of neighbours on seed germination is independent of site. Often, *Aciphylla* and *Trisetum* seed germination was significantly dependent on site alone; however, this is likely due to the complete lack of, or minimal, germination at some sites. Hence, neither competitive nor facilitative interactions between close neighbouring vegetation appear to influence seed germination at these sites.

Seedling survival from germinated seeds was low. Most seeds lived between one and three sampling intervals, i.e. one growing season. Independent t-tests showed no significant differences ($P > 0.05$) between survival for seedlings in cleared and control plots at high and low peaks, the exception being *Aciphylla* seedlings at low sites which survived on average two sample intervals in control plots and only one sample interval in cleared plots ($P < 0.05$). Seedling survival times from these seeds were not compared formally in the two-way ANOVA method, comparing site and treatment, owing to the low numbers of survivors.

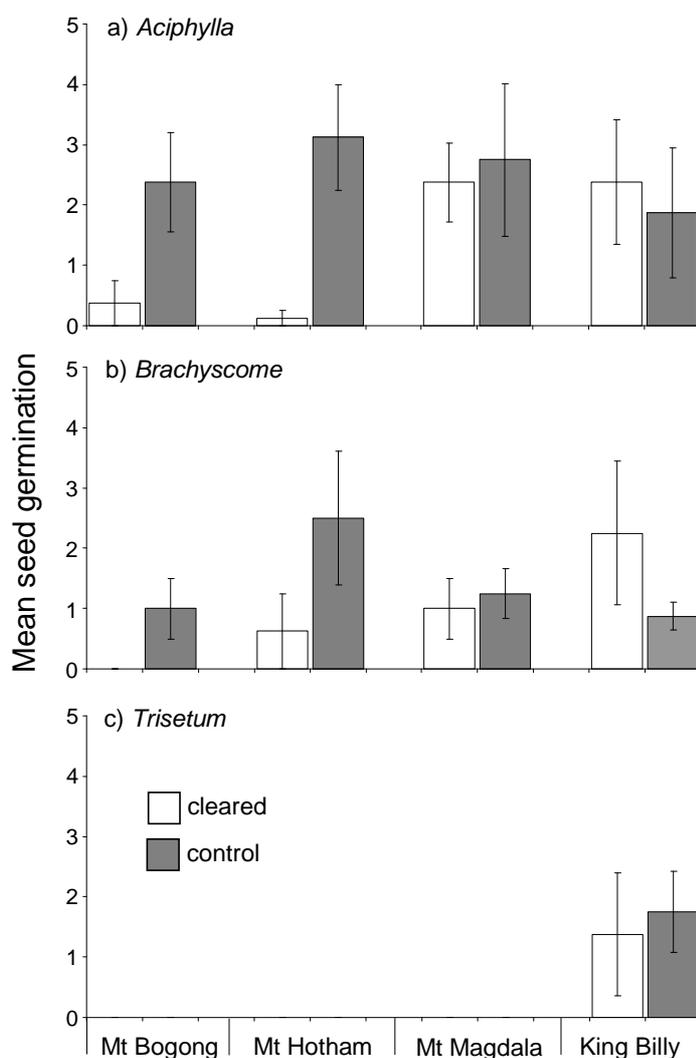


Figure 7.4. Mean (± 1 standard error) seed germination for (a) *Aciphylla*, (b) *Brachyscome* and (c) *Trisetum* seed in cleared and control plots at the four sites. Data is pooled across the 2004/05 and 2005/06 growing seasons. N = 10 seeds in each plot. There were eight plots of each treatment at each site.

Seedling transplant growth

Seedlings appear to be strongly influenced by the effects of neighbouring vegetation.

Across all elevations, facilitative interactions between seedlings and neighbouring vegetation were common, particularly in *Aciphylla* and *Brachyscome* (Figure 7.5).

Seedlings produced more leaves and grew taller when surrounded by intact vegetation.

At the lower elevations, *Trisetum* seedling growth was higher overall in the cleared plots, indicating a negative or competitive interaction with close neighbouring plants. By contrast, facilitative effects, or no apparent effects at some sample intervals, were common among *Aciphylla* and *Brachyscome*.

The mean RNE values from pairs of seedlings at each site indicated that facilitative, positive interactions may be occurring at all elevations between *Aciphylla* and *Brachyscome* seedlings and adjacent vegetation over the duration of the growing season

(Figure 7.5). However, *Trisetum* seedlings appear to show a significant switch from facilitative effects at high elevations (Mt Bogong and Mt Hotham) to competitive interactions at the lower elevations (Mt Magdala and King Billy), most obviously occurring during the mid-sample interval (Figure 7.5).

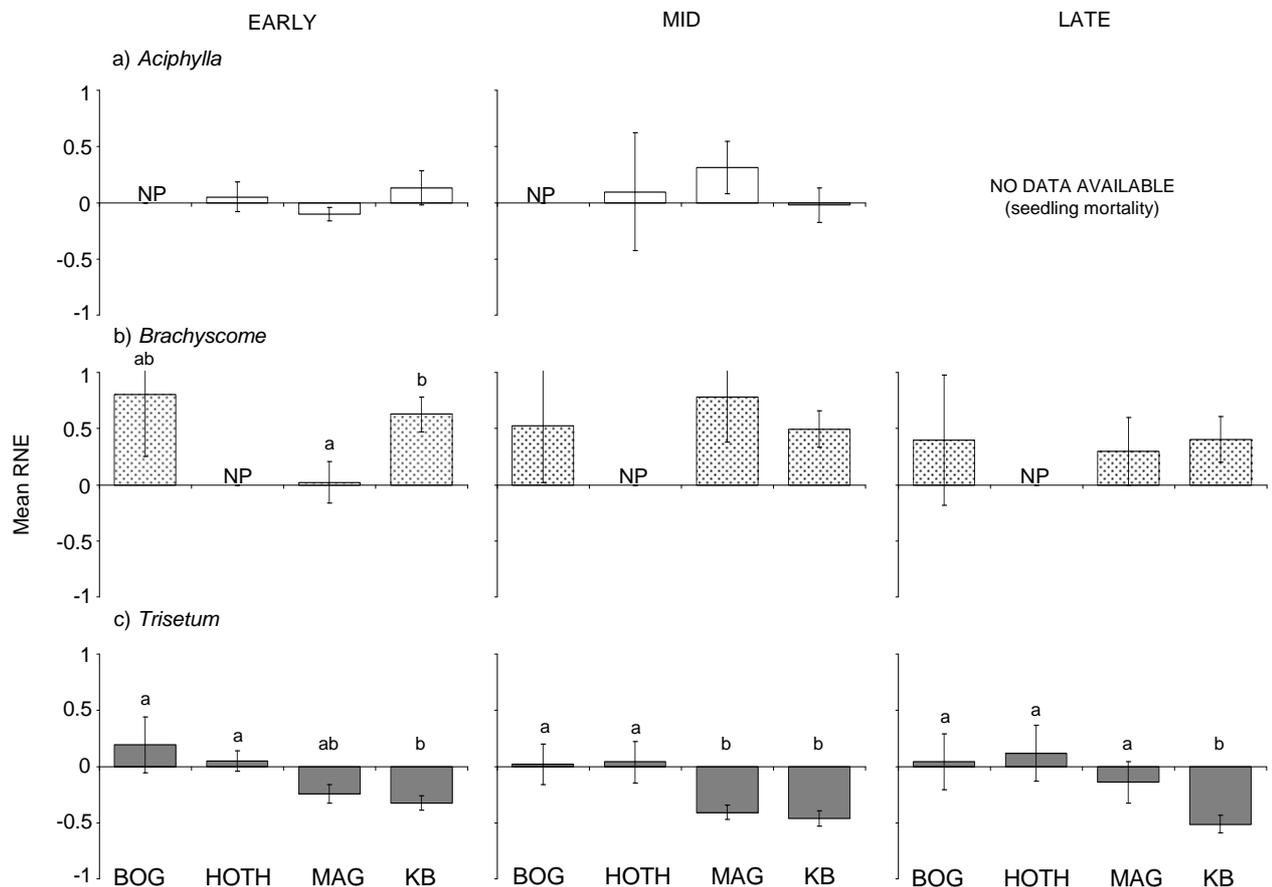


Figure 7.5. Mean Relative Neighbour Effect (RNE) (± 1 standard error) for (a) *Aciphylla*, (b) *Brachyscome* and (c) *Trisetum*, for pairs of planted seedlings at Mt Bogong, 1970 m (BOG); Mt Hotham, 1860 m (HOTH); Mt Magdala, 1725 m (MAG); and King Billy, 1696 m (KB), across three sample intervals (early, mid and late) during the 2005/06 growing season. Positive values indicate a facilitative interaction; negative values indicate a competitive interaction. Different labels above columns indicate significant differences between sites during that particular sample interval for each species using Bonferroni post-hoc tests. *Aciphylla* seedlings were not planted (NP) at Mt Bogong, *Brachyscome* seedlings were not planted (NP) at Mt Hotham.

Seedling transplant survival

The survival of seedlings without close neighbouring vegetation was reduced. The seedlings transplanted into cleared plots at high elevations (particularly *Aciphylla* and *Brachyscome*), were the least likely to survive into their second year. Over one growing season, the probability of survival of *Aciphylla* and *Brachyscome* seedlings declined dramatically during the mid- and late-season sample intervals (Figure 7.6). *Trisetum* seedlings maintained a high survival probability over the duration of the experiment, regardless of treatment. *Aciphylla* seedlings planted into cleared plots at Mt Hotham showed a sharp decrease in survival probability over the season compared to all other plots. Overall, if seedlings were able to produce several leaves during the growing season, their probability of survival was greatly increased, regardless of the presence or absence of surrounding vegetation. Therefore, growth influences survival. However, as revealed by using the RNE index, the effect of clearing close vegetation can decrease growth.

I used ANOVA to compare the proportion of survivors on each aspect of every site, using data from the mid- and late-sample intervals of the 2005/06 growing season between all possible pairs of sites, within each species. The only significant interactions between site and treatment were during the mid sample interval for *Brachyscome* between King Billy and Mt Bogong ($F_{\text{treatment} \times \text{site}} = 6.318$, d.f. = 1, $P = 0.027$) and between Mt Magdala and Mt Bogong ($F_{\text{treatment} \times \text{site}} = 5.706$, d.f. = 1, $P = 0.034$) (Figure 7.7). Both of these comparisons indicated higher survival of seedlings grown in cleared plots at the lower site (King Billy or Mt Magdala), and a high proportion seedlings surviving when grown in control plots at the higher site (Mt Bogong) (Figure 7.7). Therefore, at these particular sites, *Brachyscome* seedling survival may depend on the proximity of close neighbours.

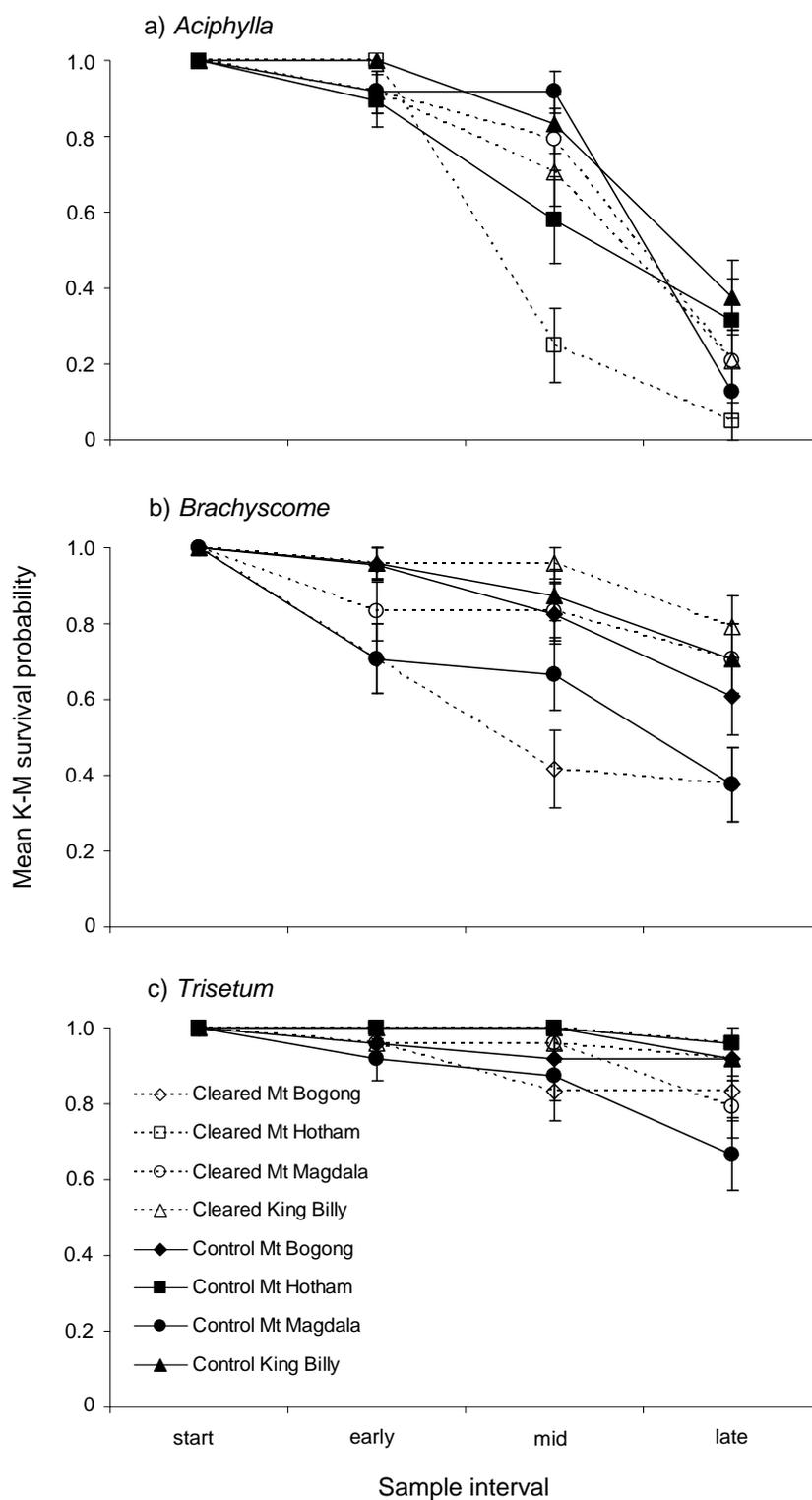


Figure 7.6. Mean (± 1 standard error) Kaplan-Meier (K-M) survival probability curves for (a) *Aciphylla*, (b) *Brachyscome* and (c) *Trisetum* seedlings, at different sample intervals (early, mid and late) during the 2005/06 growing season. Seedlings were planted into cleared plots (dashed lines and open symbols) and control plots (solid lines and closed symbols) at the four different elevation sites. The experiment began (start) before snowfalls of 2005, when all seedlings were alive.

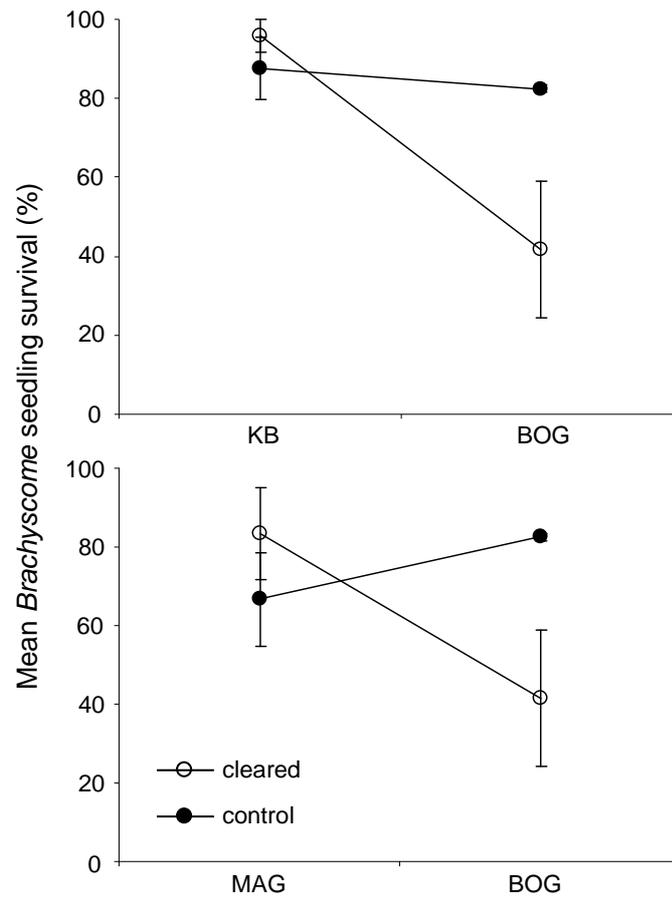


Figure 7.7. Mean (± 1 standard error) percentage of surviving *Brachyscome* seedlings at the mid sample interval of the 2005/06 growing season in cleared and control plots for (a) King Billy, 1696 m (KB) and (Mt Bogong, 1970 m (BOG) and (b) Mt Magdala, 1725 (MAG) and Mt Bogong, 1970 m (BOG). Crossed lines between points demonstrate the interaction of site and treatment on *Brachyscome* survival.

Discussion

General interpretation of results

The data indicate that facilitative plant interactions, at the early life-history stages in these three study species, may be of only minor importance in the Victorian alpine zone. Plant interactions tended not to influence seed germination anywhere across the gradient. Experiments on seedling growth and survival indicated that plant interactions across the gradient are mostly neutral, with facilitative interactions occurring only occasionally over the course of the experiment. Competitive interactions were only found at the lower elevations based on the relative growth rates of *Trisetum* seedlings. I suggest, therefore, that facilitative interactions between close neighbouring plants can occasionally occur across the gradient of alpine sites in Victoria. The conditions at lower altitude sites may not be particularly favourable compared to higher elevation sites and therefore, a balance between positive and negative plant associations are expected there.

During the course of data analysis from these experiments, 75 independent comparisons were made between the sites; comparisons which included the effect-size between the cleared and control plots (t-tests of RNE values between sites), or comparisons that produced an interaction term between site and treatment (two-way ANOVAs on seedling survival and seed germination data between sites). Of these, 17% indicated that facilitation or, in some cases, 'less competition' was in fact occurring at a high elevation site when compared to a low elevation site. Although the gradient of sites chosen in this study is not particularly large, about 270 m in elevation, I also found that plant interactions can switch from facilitation at the higher peaks to competition at the lower peaks; this is shown clearly by the relative growth of *Trisetum* seedlings in Figure 7.5. Overall however, the weak differences seen in competitive and facilitative effects between seedlings and their neighbours may simply reflect the small altitudinal gradient of the sites used.

With decreasing altitude, the unfavourable environmental factors such as frosts and low temperatures diminished and thus, the buffering effect of close neighbouring plants from frost-heave and cool temperatures may also become less important. In addition to the decrease in ambient temperatures associated with an increase in elevation, I found that intact vegetation can also be important in diminishing the effects of frost heave. Significantly stronger frost-heave was shown in cleared plots compared to control plots where vegetation acted as an insulative barrier to the soil. Wetter soils, also likely contributors to frost-heave, were more common in the cleared plots, potentially increasing

the occurrence and strength of frost-heave. I also found that intact vegetation can contribute to the amount of heat trapped at the soil surface, potentially creating a more favorable micro-climate for germinating seeds and emerging seedlings. This was most pronounced at the lowest site, King Billy (1696 m).

Seed germination

A significant interaction in seed germination between site and treatment would indicate that the effect of site and treatment are not independent and hence, facilitative or competitive interactions between neighbouring plants may be occurring. However, I found no consistent pattern of seed germination with either treatment that interacted with site across the alpine gradient. My results suggest that, at small-scales, further amelioration of environmental conditions by close neighbouring vegetation did not influence seed germination significantly, especially during the first or second growing season. My results contradict those of Gough (2006) who found seed germination at higher elevations required the presence of close, buffering vegetation. However, low mean germination rates of planted seed are not uncommon (Aguiar and Sala 1994; Gough 2006) and more than two thirds of the seeds planted in this experiment failed to germinate. None of the study species are hard-seeded and so, it is unlikely that any frost-heave occurring in the cleared plots would have increased germination rates through seed-coat scarification (Bliss 1962; Amen 1966).

Facilitative effects can change temporally over a plant's lifetime. Aguiar and Sala (1994) found that the facilitative effects of close neighbours (grass and shrub species) were important for providing shelter for seed germination and young plants. Then, as the seedlings developed into adults, the positive effects of aerial protection provided by shrubs became less important than the below-ground competition for resources. Their results further demonstrate that the facilitative effects of close neighbours may be important at the early life-history stages when the germinant is most susceptible to harsh or stressful environmental conditions. In my experiment, it appears, the conditions were not favourable for germination in either the cleared or the control plots. Few seeds germinated in the low elevation control or cleared plots where I expected that the most favourable conditions would occur.

None of the species used in this study are notably dependent on gaps in the vegetation (analogous to cleared plots) for germination. Over time, such gap-dependent species may switch their interactions with neighboring plants, and a species that acts as a beneficial neighbour on one side, may act as a competitor on the other, providing too

much shade, cooling ambient conditions and restricting seed germination (Olofsson *et al.* 1999).

Seedling growth and survival

Over the last decade or so, many studies have emphasized the beneficial effects of close neighbouring plants on the growth and survival of alpine plants, suggesting that abiotic factors such as low temperatures, wind and soil disturbances limit plant growth more than resource availability (Callaway 1995; Kikvidze 1996; Callaway 1997; Choler *et al.* 2001; Pugnaire and Luque 2001; Callaway *et al.* 2002; Klanderud and Totland 2005). In contrast to my methodology, previous studies have focused on removing vegetation around the target, naturally occurring, adult individuals and measuring final biomass or number of leaves as an indication of the strength of the relationship between the target plant and its surroundings. The methodology used in this study enabled me to focus on, and experiment with, the early life history stages of seed germination, seedling growth and seedling survival.

Collectively, most plant-plant interaction studies across biomes show strong support for the hypothesis that facilitative effects are likely to occur in environments where abiotic stress or consumer pressure is high. In this study, I found mixed results where predominantly the interactions between the planted seedlings and their neighbours were either neutral or facilitative across the altitudinal gradient. Rarely were the interactions competitive. *Trisetum* seedlings were the only species to show strong competitive interactions anywhere across the gradient of sites, at the lower elevation summits of King Billy and Mt Magdala. These sites are likely to be where physical stress and possible consumer pressures are low (Pugnaire and Luque 2001). However, over time, individual seedlings may respond differently to environmental variables and close neighbours. In the early sample intervals, many of the seedling transplants without neighbours at the higher sites had similar survival probabilities as their equivalents at lower sites. It was not until the later sample intervals that the direction of plant interactions became clearer. Therefore, at any point in time, the direction of the interaction can only be interpreted as the net balance of any possible interactions; the sum of all the direct and indirect, positive and negative influences between the target individual and the surrounding vegetation (Pugnaire and Luque 2001).

Over time, with increased shelter or with ambient conditions becoming more favourable, neighbouring plants which once facilitated each other's growth, may begin to compete below-ground for water and nutrients. Hence, if a neighbour is to be facilitative,

the advantages of the association must be sufficiently large to compensate for below-ground competition and generate a net benefit for the co-existing species (Carlsson and Callaghan 1991). The survival of *Brachyscome* seedlings showed a significant interaction between sites of high and low altitude with treatment. Seedlings were more likely to survive in the low altitude environment (Mt Magdala or King Billy) if they were planted without neighbours. Survival of *Brachyscome* at the high elevation (Mt Bogong) was weakly dependent on treatment as it tended to survive in control plots. Overall, however, close neighbours at high elevation sites in Victoria may not always act as beneficiaries, nor may the environmental conditions at these sites always be constraining to plant growth.

Further evidence for facilitative interactions at early life-history stages

Studies on the very early life-history stages of alpine plants, in relation to competitive and facilitative interactions, have been relatively few both in the Australian and the international literature. In the Snowy Mountains, Australia, Wilson (1993) showed that neighbours promoted survival in one species, but suppressed growth in all other study species. He also showed that the degree of below-ground competitive ability can change at different altitudes, with the highest root:shoot ratio and the highest below-ground competition occurring at the highest altitudes. In arctic tundra environments, Gough (2006) showed that seed germination was higher when neighbouring vegetation had been removed. However, there was little effect of neighbouring vegetation on the survival and growth of adult transplants indicating that the interactive effects of neighbouring vegetation can affect each life-history stage differently.

Overwhelmingly, the few plant interaction studies that deal with seed germination and seedling success in alpine areas show evidence for facilitation via the amelioration of abiotic stress. The occurrence of seedlings clumping together, sheltering on the lee side of neighbours, is common (Carlsson and Callaghan 1991; Kikvidze 1993; Sturm *et al.* 2001; Callaway *et al.* 2002; Gough 2006). Kikvidze (1993) showed that positive spatial associations at high elevations were four times more common than negative ones. Although my results do not fully concur with these results, nor support the hypothesis that seedlings only grow where they can shelter with adjacent vegetation in alpine areas, these findings from the international literature, in addition to the results presented here, show that plant interactions are important in organising alpine plant communities.

The role of plant interactions during climate change in Australia; using the altitudinal gradient in a space-for-time analysis

The predicted future climate scenarios for the Australian alpine zone include higher minimum temperatures, precipitation as rain rather than snow in winter months and an overall reduction of the snow season (Hennessey *et al.* 2003). As a result, changes in the climate may indirectly alter the current balance between positive and negative plant interactions and thereby alter the patterns of dominance and structure in plant communities (Klanderud and Totland 2005). This may occur through the simple effects of areas becoming warmer and more tolerable, where previously plant growth was suppressed by frosts and extended snow cover. Soil nutrients are also expected to become more readily available as higher temperatures facilitate litter decomposition and nutrient mobilization (Klanderud and Totland 2005). Shifts in species interactions, in addition to changes in physiological responses, may lead to changes in abiotic niche suitability for several alpine species (Heegaard and Vandvik 2004). Less stress-tolerant species may be able to migrate up mountains via facilitation, leading to new species assemblages and distributions across the altitudinal gradient (Choler *et al.* 2001). Therefore, if the distribution and abundance of species are facilitated by the presence of other species, their natural organization cannot merely be a co-incidence of similar adaptation to the abiotic environment (Callaway 1997).

In this study, the gradient of environmental factors (including frost events, soil and ambient temperatures) appeared to follow the altitudinal gradient. However, this was only partially reflected in plant interactions. Of course, the interactions are not expected to remain static, as shown in this study by the considerable change in RNE values over only one growing season. As the strength of inter-plant interactions can vary over time, repeated measurements, perhaps over several years, may be important in order to determine the overriding interaction (Olofsson *et al.* 1999).

Experimental warming of an alpine habitat with open-top-chambers (which increase the temperature by 3 to 5 °C, see Arft *et al.* (1999)), has shown that global warming may increase the role of competition in alpine environments because the role of facilitation appears to decrease under the warming treatment (Klanderud and Totland 2005). The natural gradient of high to low alpine peaks in this study can be used in a space-for-time analysis and might reflect the types of changes that may occur in future decades with global warming. Therefore, I anticipate that seedlings growing at high altitudes will face similar pressures that seedlings at low altitudes currently face, which are predominantly neutral or competitive interactions. Seed germination rates are

expected to increase in coming decades, as alpine seeds show high germination rates at temperatures between 20 and 30 °C (Sayers and Ward 1966; Marchand and Roach 1980).

The greatest alterations to plant interactions are predicted for the higher altitudes. In this study at Mt Bogong, the highest site, planted seeds of both species only germinated with close neighbours. If conditions at the highest sites become more favourable, bare ground gaps may become suitable habitats for emerging seedlings as they occasionally do now at the lower elevations. However, the effects of frost-heave, most common in the bare ground gaps, are not likely to be dramatically reduced in future decades, as early-melting snow may leave newly germinating seeds unexpectedly 'out in the cold' when spring-time frosts are common (Bannister *et al.* 2005; Wipf *et al.* 2006). In turn, this may leave the lower sites, which currently experience marginal snow conditions, open for further invasion by typically understorey, subalpine species.

Conclusions

Seed germination and emergence, along with seedling growth and survival, are the life-history stages and recruitment processes most at risk from the environmental pressures of an alpine environment. I showed that the high altitude sites in Victoria were more stressful for these early life history stages than lower peaks, principally because of colder, more frosted conditions causing strong frost-heave of the soil. The results from my short-term experiment indicate that, across an altitudinal gradient, plant-plant interactions can switch from being occasionally competitive or neutral at lower elevations to occasionally facilitative or neutral at higher elevations. No interactions were found between site and treatment on seed germination and therefore, no positive or negative interactions with neighbouring vegetation across the gradient can be confirmed. However, seedling growth and survival were affected by positive, neutral and negative interactions with neighbouring vegetation. The few confirmed positive interactions showed enhanced seedling growth and survival at the higher sites. Should the current balance of interactions across the gradient in future decades change due to climate warming, seed germination and seedling survival in areas previously dominated by neutral or facilitative interactions may be subject to competitive interactions. This may potentially allow new, open areas to be colonized. My study concentrated only on above-ground responses to close neighbouring vegetation; however, the overall response of individuals to their neighbours will ultimately involve the whole organism. In order to decipher the interactions between whole seedlings, close neighbours and environmental factors, future investigations on below-ground processes are required.

Chapter 8 - Synthesis and implications

Introduction

Alpine environments can be harsh, stressful places for plants to grow. Snow cover for several months of the year, short growing seasons, strong winds, frosts and soil heaving from needle ice (Bliss 1962; Brink *et al.* 1967; Billings and Mooney 1968) are just some of the environmental factors present that plants must contend with. At this end of the habitat spectrum, theory predicts that plants will exhibit a life-history strategy that emphasises stasis in the adult stages, at the expense of growth and fecundity (Grime 1977). Hence, many alpine species from around the world are highly clonal, long-lived perennials (Billings and Mooney 1968; Bliss 1971; Körner 1999) that rely on vegetative propagation to maintain populations. This strategy also allows species to survive long periods of unfavourable conditions without the risks that are associated with sexual recruitment. Alpine plants are therefore traditionally viewed as 'stress tolerant' (Grime 1979) and are expected to have low rates of recruitment from seed. Additionally, recruitment from seed is often stated as rare and not important among alpine and arctic tundra species (Billings and Mooney 1968; Bliss 1971; Billings 1973) as the environmental conditions are expected to limit all phases of sexual recruitment (Bell and Bliss 1980). Indeed, the timing of flowering can be controlled by photoperiod, but flowering success can be limited by snowmelt date, ambient temperatures and other environmental phenomenon (Galen and Stanton 1993,1995; Körner 1999; Venn and Morgan 2007). Pollinator visitation rates can also be correlated with environmental factors such as temperatures and snowmelt date (Arroyo *et al.* 1982; Inouye and Pyke 1988). Therefore, pollinator visitation may only peak when ambient temperatures are warmest. In addition, past researchers have found seedling establishment rates to be low (Bell and Bliss 1980) and mortality rates high (Wager 1938) under natural conditions, citing low temperatures and dry soils as the likely causes. Frost events have also been cited as causes of seedling mortality (Billings 1987) as needle ice and soil heave from severe frosts disturb the substrate and damage small plant roots (Inouye 2000; Bannister *et al.* 2005). Therefore, the opportunities for recruitment from seed in alpine plants appear to be limited.

Despite the evidence presented in this early research, which emphasised the apparent lack of sexual propagation in alpine populations, other researchers working

during the same time period were reporting high levels of seed viability and germination rates in laboratory studies (Wager 1938; Bliss 1959; Amen 1966; Sayers and Ward 1966). Considerable variation, however, exists between habitats and locations, as well as within species (Amen 1966). Subsequently, researchers have demonstrated that alpine and arctic species also contribute to germinable seed banks (Freedman *et al.* 1982; Urbanska and Schütz 1986; Cooper *et al.* 2004) and that seedlings can occur in high densities under natural conditions (Jolls and Bock 1983; Welling and Laine 2000a; Forbis 2003) and after disturbance (Chambers *et al.* 1987; Chambers 1995). In addition, seedling establishment among alpine plants can be as successful as below treeline perennial species (Jolls and Bock 1983; Forbis 2003) and hence, sexual reproduction in alpine areas may be no more limited than in other habitats (Forbis 2003; Forbis and Doak 2004).

Therefore, following further observations under natural and experimental conditions, a paradigm shift has occurred in our understanding of alpine plant recruitment processes over the past decades: recruitment from seed in alpine areas can be common and successful. Most of this research has been conducted in the Americas and Europe, whereas research from Australian alpine ecosystems is poorly represented in the literature. Hence, the research presented in this thesis was aimed at contributing to the ideas which are shaping the new paradigm, from an Australian landscape perspective.

Chapter outline

In this final chapter, I bring together the key findings from the six individual studies and the second-order research questions. I follow this with an exploration of how these findings are inter-related using the life-cycle model introduced in Chapter 1 and an ordination of some key life-history stages. I then discuss the present and future of alpine plant recruitment in the context of large- and small-scale disturbances, citing previous research and by building a conceptual model of future scenarios. I conclude the thesis with ideas for future research directions.

Key findings

The overall project goal was to investigate the role of recruitment from seed among plants across a gradient of alpine mountain tops in Victoria. In some instances, the change in climatic and environmental parameters across the altitudinal gradient exerted a significant influence on the patterns and processes of plant recruitment from seed. For the most part, however, the effect was minimal or only seen at the extremes of the gradient, at the highest or lowest sites. Recruitment from seed among alpine plants in this region appears to be significant. Other species may contribute to seed banks and the seedling flora; however, the similarity between these stages and the standing vegetation is often low. In addition, seedlings often never reach maturity and standing populations must therefore continue to reproduce via vegetative regeneration.

Key findings of the second-order study questions

The key findings of this study, as per the second-order study questions introduced in Box 1.1 in Chapter 1, are as follows:

1. Do climate and other environmental variables change across the altitudinal gradient of mountain tops?

Ambient temperatures and, occasionally, soil temperatures, did vary predictably across the altitudinal gradient of sites. Temperatures were generally several degrees lower at high sites when compared to low sites. Temperature measurements, converted into growing degree days, also showed when snowmelt occurred across the gradient, which was up to one month earlier at the low altitude sites. In addition, precipitation was generally higher at the high sites, as estimated by BIOCLIM. Other environmental variables, such as grazing history and soil characteristics, did not always change predictably across the altitudinal gradient of sites. Total soil nitrogen and organic carbon content decreased significantly with altitude, while other minerals in the soil such as copper and manganese increased in concentration with altitude. Altitude can be used as a surrogate to represent the suite of climatic and environmental variables that occur across the gradient.

2. Are there patterns in the vegetation composition across an altitudinal gradient of mountain tops?

Vegetation at the highest sites, Mt Bogong and Mt Hotham, showed the strongest trends with altitude. At these sites, the vegetation was dominated by forb and graminoid species. At the lower altitude sites, shrub species tended to dominate the vegetation and drive the differences between sites. The composition of the vegetation within each site was always

significantly different from every other. However, sites that were most similar in altitude tended to be more similar in vegetation than sites that were least similar in altitude. The similarity of vegetation within some sites varied and hence, some sites did not clump together well in ordination space nor were they positioned together in the dendrogram following cluster analysis. The vegetation at Mt Bogong and Mt Hotham showed the most within-site similarity.

3. Does the mountain top vegetation form a seed bank? If so, how similar is the species composition of the seed bank to that of the standing vegetation?

Seed banks across the altitudinal gradient of sites were extensive, from 180 to over 1400 seeds per m², were similar between sites, and were of a persistent nature. There was little similarity between seed bank species and the standing vegetation. However, only two species found in seed bank samples were not found in the local mountain top flora. The regeneration classes of the seed bank species and the standing vegetation were also mostly dissimilar. The number of species shared by the seed bank and the standing vegetation (qualitative similarity) was usually high compared with the similarity of their abundances (quantitative similarity). Hence, species in the seed bank, therefore, are more likely to come from standing vegetation species which produce large quantities of germinable seed, but are low in their cover abundance.

4. What are the requirements for, and what are the patterns in, seed germination for species which grow across the altitudinal gradient of mountain tops?

Final percent germination values under laboratory conditions were high across all species and temperature manipulations. Some species showed 100% germination. Seed mass had no significant influence on mean final percent germination, lag-times or germination speed. There were no trends of mean final percent germination across the altitudinal gradient. In many of the comparisons where significant differences were found, seed from higher altitudes had a higher probability of germination than seed from lower altitudes. One species, *Aciphylla glacialis*, showed no germination under the generally favourable laboratory conditions. However, after 15 weeks of cold-wet stratification at 2 °C, high final germination rates were recorded. Germination characteristics of this species also showed few trends with altitude.

5. Are there patterns in natural seedling emergence across the gradient of alpine sites? Are there similarities between the seedling flora and standing vegetation?

Seedlings were common at all sites. Seedling density decreased with altitude, but the trends over both years of the study were not significant. The highest mean seedling densities were found at King Billy where, on one occasion, more than 200 seedlings were found in one 0.5 m² plot. At all other sites, the density of seedlings per m² was generally between 7 and 40. Across all sites, most seedlings emerged early in the growing season. Many seedlings survived long enough to become established plants, between 37 and 61%. Seedling mortality roughly matched seedling establishment across sites. There was no significant relationship between the percentage of seedlings that became established plants, nor the percentage of seedling mortality, with altitude. However, most seedlings from shrub species outlived the duration the study. The percentage of forb seedlings increased with altitude, whereas the percentage of shrub and graminoid seedlings both showed slight decreasing trends with altitude.

The similarity between the standing vegetation and seedling vegetation was low. Qualitative similarity was higher than quantitative similarity, indicating that species of new seedlings are likely be the same as the adult vegetation, but high cover-values of mature vegetation are unlikely to result in high seedling densities of that species. The similarity in seedling flora across sites appeared high (from ordination diagrams). The similarity among seedling samples within each site varied between 35 and 45%.

6. Do interactions with neighbouring plants affect seed germination or seedling growth and survival? Do these patterns change across the altitudinal gradient?

The effect of neighbours on seed germination was independent of site and treatment, hence, neither competitive nor facilitative interactions affected seed germination. There were no relationships between seed germination in either treatment across the altitudinal gradient. The survival of seedlings from planted seed was low, regardless of site or neighbouring vegetation.

In contrast, planted seedlings were strongly influenced by the effects of neighbouring vegetation. Across all elevations, facilitative interactions between seedlings and neighbouring vegetation were common. Competitive interactions were more common at lower elevations. At high elevations, seedlings produced more leaves and grew taller when surrounded by intact vegetation. The survival of seedlings without close neighbouring vegetation was reduced. Seedlings growing at high elevations without close neighbouring vegetation were the least likely to survive into their second year.

Key findings and the life-cycle model

The key findings can now contribute to filling the knowledge gaps which were present in the life-cycle model (Figure 8.1) as introduced in Chapter 1. The model shows the inter-relationships between the life-history stages and their subsequent interactions with the recruitment processes that link them.

Although the standing vegetation is predominantly a mixture of species in the 'Mostly Seed' or 'Mostly Vegetative' regeneration classes (see Chapter 3 for definitions), hundreds of viable seeds are regularly produced by even predominantly clonal species. Species of the 'Mostly Seed' class contributed substantially to persistent, germinable seed banks, influencing the high floristic dissimilarity between the seed bank and the standing vegetation. Seeds of all species tested were highly germinable, even those of *Aciphylla glacialis* following cold-wet stratification to break dormancy. High seed germinability was translated into high rates of seedling emergence under natural conditions, although seedlings were mostly from forb and graminoid species. The dissimilarity between the seed bank and the standing vegetation was reflected in further dissimilarities between the seedling flora and the standing vegetation. Seedling mortality appeared to be linked to the timing of snowmelt, with many deaths at the higher sites occurring during the early recording periods of the growing season. Despite the mortality rates, high number of seedlings became established across all sites during the period of study, with some species reaching reproductive maturity. Seed germination showed few interactions with neighbouring vegetation. However, seedling growth and survival was occasionally positively influenced by neighbouring vegetation across all sites. Negative interactions between seedlings and adjacent vegetation were only apparent at the lower elevations. The weak trends in positive and negative interactions across the altitudinal gradient may indicate that the alpine areas of Victoria are relatively benign compared to those in the northern hemisphere.

Discrepancies within the model, such as the differences in species richness between seed bank samples and seedling flora and the standing vegetation, may be an artifact of the differences in sampling size used to quantify each of these, or simply the low contributions some species make to the seed bank and the seedling flora. The differences may also be the result of seed bank and seedling samples being taken from different plots within each site. This could not be avoided as monitoring for seedlings in disturbed plots, following seed bank sampling, may have resulted in biased emergence rates, as seeds present in the soil responded to the disturbance, rather than the environmental and climatic factors present at the site.

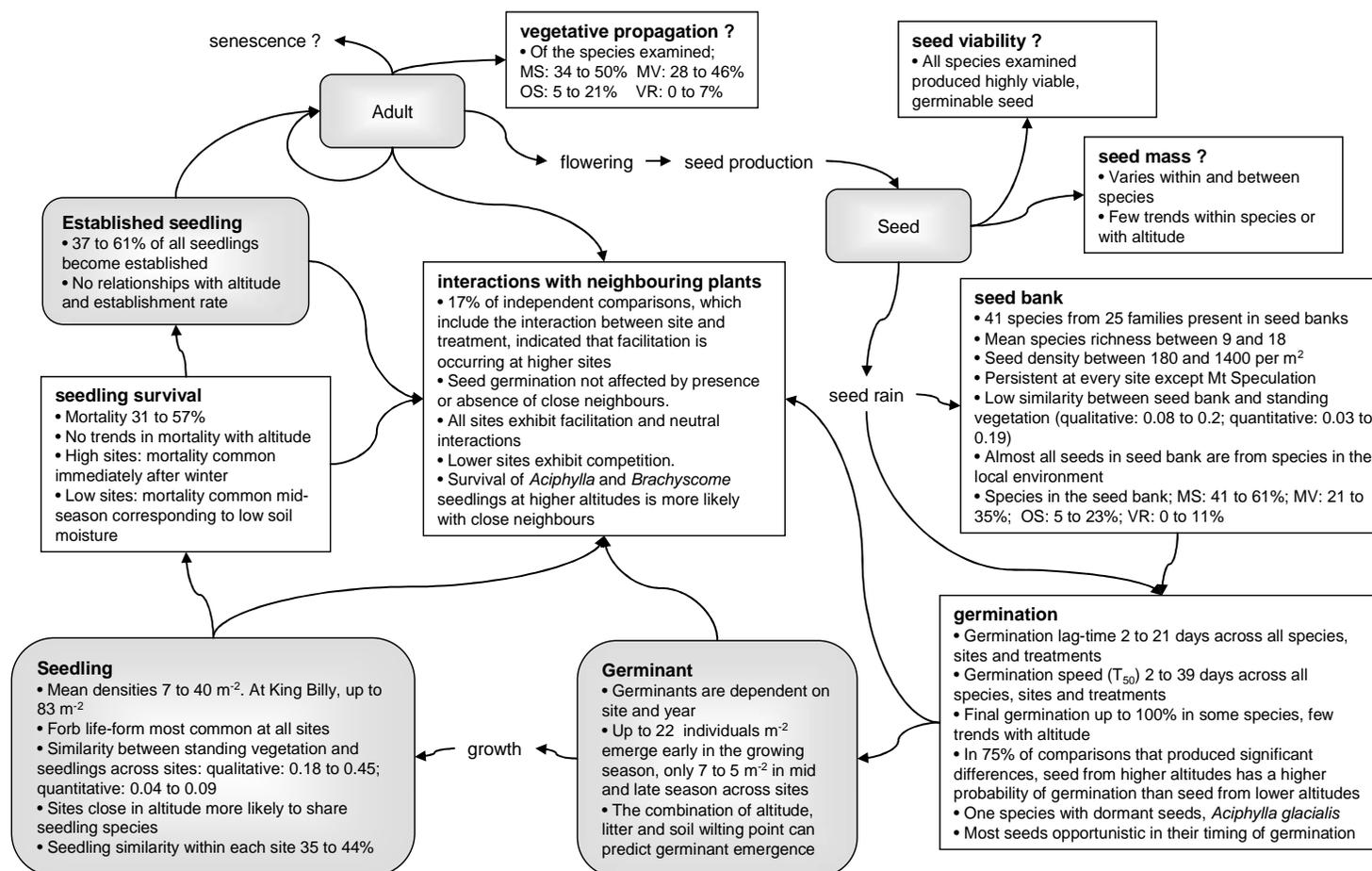


Figure 8.1. The key findings within the life-cycle model. Life-history stages, their properties and recruitment processes that were measured in the study are indicated by **bold** headings. Life-history stages are represented by shaded, rounded boxes. Properties of life-history stages are represented with question marks following the text. Recruitment processes link life-history stages with arrows. Recruitment processes and life-history properties which were measured in this study are bounded by sharp cornered boxes. Mortality can occur during any stage or process in the life-cycle. Adult vegetation may persist for many years without contributing seeds or seedlings to the life-cycle model. MS, mostly seed; MV, mostly vegetative; OS, obligate seeder; VR, vegetative reproduction maintains populations.

Relationships between key life-history stages

The key life-history stages studied here (seeds, seedlings and the standing (adult) vegetation) are linked by recruitment processes such as contributions to the seed bank, germination, seedling emergence and seedling survival. In addition to creating links between these life-history stages, the recruitment processes can act to filter out certain species from the community assemblage whose seeds or seedlings are affected by environmental and climatic constraints (Welling and Laine 2002). Hence, the life-cycle, which refers to the entire process of recruitment from seed to seedlings to adults, can be interrupted or altered at any stage by outside factors, leading to poor correlations between life-history stages in relatively undisturbed vegetation (Chambers 1993). Welling and Laine (2002) speculate that there may be fewer environmental constraints between the stages of standing vegetation and the seed bank, compared to those between the standing vegetation and the seedling stage. There is also evidence that the transition from the seed bank to the seedling stage carries a high mortality risk and thus, species are likely to be more similar in the comparison between seed banks and standing vegetation (Chambers 1993). These trends can also be highly species-specific, as species with particular regeneration strategies, sometimes apparent across life-forms, have evolved to compensate for the risks associated with recruitment from seeds in alpine areas (Chambers 1995). For example, some species may use a masting strategy in response to specific environmental cues in order to saturate the substrate with seed, while others may contribute to the seed bank continually (Körner 1999).

I investigated the similarity between the species present in the standing vegetation, the soil seed bank and the seedling flora, across all sites, using NMDS and subsequent ordination (Figure 8.2). Some distinction was seen between the groups, indicating that the species of each life-history stage are more similar within that stage than between stages. This pattern was confirmed by subsequent ANOSIM analysis, which indicated significant differences between groups (Appendix 8.1). Subsequent pairwise analysis using ANOSIM indicated that the greatest dissimilarity was between the species in the standing vegetation and the species in the seed bank (Appendix 8.1), seen most clearly in the Axis 1 Vs Axis 3 ordination diagram. Seedling vegetation most likely contains a combination of species from the standing vegetation and the seed bank, hence, its wide distribution in the ordination. Life-history groups may tend to clump together because none showed strong trends in species composition with altitude. This gives further evidence to support the idea that sites are relatively similar across the altitudinal gradient in species composition, even across life-history stages. Although the species in the seed

bank and those in the seedling flora were not formally compared with an index of similarity, both these life-history stages showed high dissimilarity with the standing vegetation (see Chapters 3 and 6) and hence, the differences between groups seen in Figure 8.2.

I also compared the relationships between species of these three life-history stages using NMDS and ordination within each site (Appendix 8.2). Within sites, the grouping of life-history stages was varied and many sites showed no group separation along any axis of the ordination. The clearest separation of groups occurred at The Bluff, King Billy and Mt Hotham (Appendix 8.2). Site-specific comparisons showed no evidence for similarities between groups being more frequent at the lower or higher elevation sites.

The weak links between the three stages analysed in the ordination may be due to the initial sampling scale. Across each site, the standing vegetation was recorded as percent cover from each of 20, 1m² quadrats; the seedlings recorded as individuals in 20, 0.5m² quadrats; and the species in the soil seed bank from three bulked soil samples from 20 1m² quadrats. Had the measurements from all three life-history stages been recorded from the same plots, similarities between them may have been higher. However, this was not possible because removing soil samples, for the seed bank analysis, may have altered natural seedling emergence.

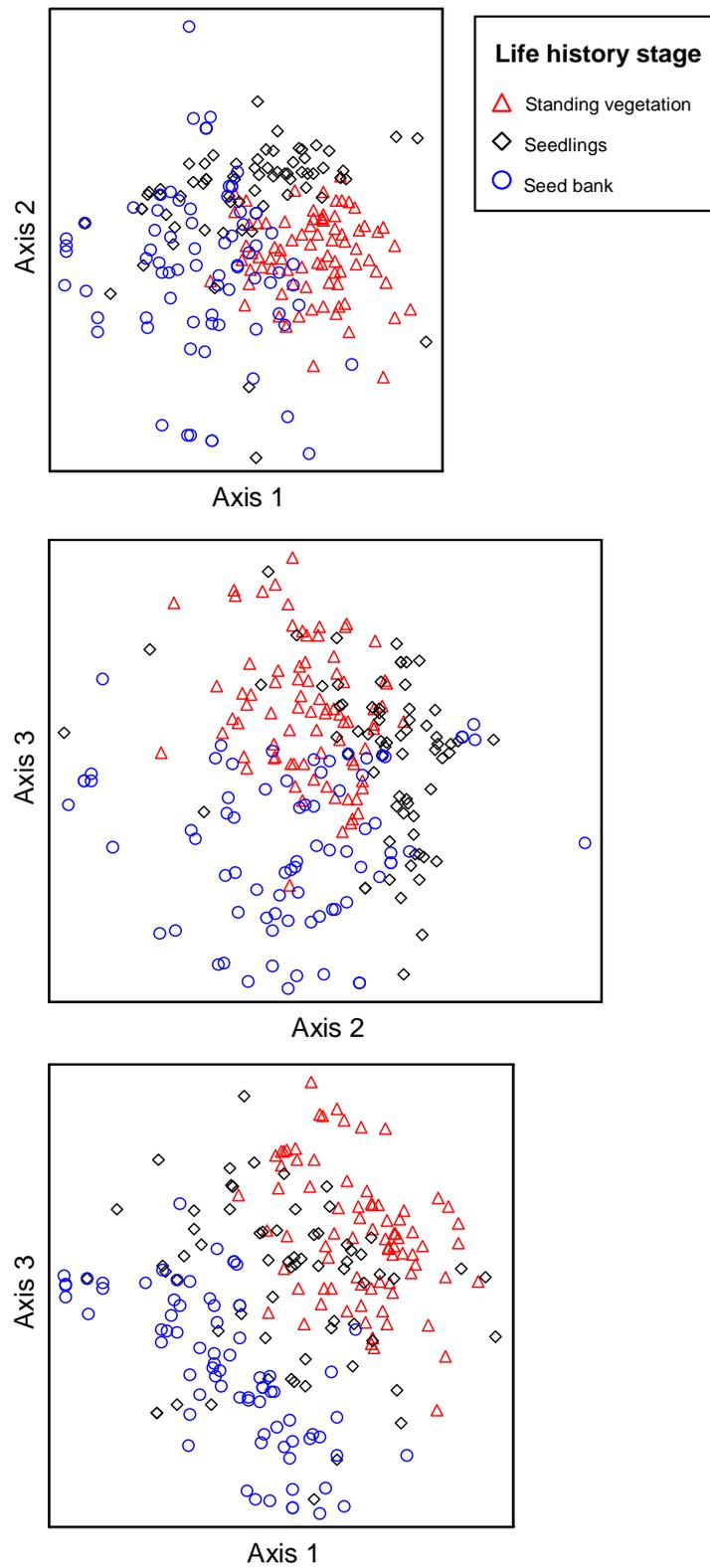


Figure 8.2. The position of standing vegetation, seedling and seed bank samples from all sites within the three dimensional NMDS configuration based on presence/absence data. A random selection of half the available data was used due to computational limitations of the software. Stress 2.1.

Conclusions

The key findings, drawn from the conclusions of the six individual studies presented in this thesis, the life-cycle model, and the additional ordinations of life-history stages, reveal that alpine plant recruitment processes across mountain summits within Victoria are, in the most part, similar to those found in parts of Europe, North and South America. These findings also support the new paradigm in alpine plant ecology: that recruitment from seed in alpine areas can be common and successful. To my knowledge, this study is the first to investigate the landscape-scale patterns in plant recruitment across alpine summits in south-eastern Australia. I confirmed the existence of germinable seed banks, showed that seeds germinate easily, and that seedlings are common, as is the likelihood that some seedlings will become established and mature into reproductive adults. Seedling mortality rates, however, occasionally match establishment rates at some sites. Vegetative regeneration among alpine plants in the study region is prevalent; however, recruitment from seed is an important component of alpine plant regeneration and potentially plays a role in building populations of herb, graminoid and shrub species. The weak links between each life-history stage among many alpine species is also a common phenomenon in other regions (Chambers 1995; Arroyo *et al.* 1999; Welling and Laine 2002). Within a plant community, I showed that the frequency of species contributing to a particular life-history stage can change, as can the prevalence of a life-history stage at a particular site. I found that shrub species may dominate the standing vegetation whereas forb and graminoid species may contribute more substantially to the soil seed banks and the seedling flora. This also implies that the speed of life-cycles and the length of each lifespan can differ greatly between species.

Patterns in climatic and environmental parameters exist across the altitudinal gradient, with cooler temperatures, more frequent frosts and longer snow seasons occurring at the higher altitudes. However, only a few patterns in life-history stages and recruitment processes correlate with these climatic and environmental parameters. The switch towards positive, facilitative plant interactions at higher elevations is also weak. This leads to the conclusion that the altitudinal gradient of sites available for this study may be small and hence, patterns in plant recruitment across the gradient may have been too minor to detect. This small altitudinal gradient of sites within Victoria represents approximately half of the 'window' of the whole gradient of alpine summits within Australia and indeed, the altitudinal range of summits within Australia is only a small window of alpine summits worldwide. Researchers are more likely to detect patterns in plant recruitment across larger altitudinal gradients, as the differences in ambient

conditions also become more pronounced. Therefore, the Victorian mountains may be viewed as one unit with minor patterns in the standing vegetation, but few perceptible differences in plant recruitment between mountains of higher or lower elevation.

Australian alpine vegetation present and future

Outline

In this section, I outline the role of disturbance in alpine areas, and the influence that disturbance can have on plant regeneration. I also discuss the responses of alpine vegetation to previous disturbances. Using a conceptual model, I show how the research presented in this thesis fits into the in the framework of vegetation change and future disturbance regimes in the Victorian alpine zone.

The role of disturbance

The research presented in this thesis has dealt with the patterns and processes of alpine plant recruitment without ongoing or recent disturbances. Disturbance regimes, however, are likely to influence plant recruitment, subsequent succession and community structure following the regeneration niche theory (Grubb 1977). The creation of gaps following a disturbance can cue germination from the seed bank, subsequently influencing seedling recruitment and establishment (Williams and Ashton 1988; Williams 1992; Chambers 1993). Competitors may be removed, in addition to soil nutrients and other limiting factors becoming more available (Chambers *et al.* 1990), leading to succession or changes in community composition. Repeated or large-scale disturbances, however, can lead to losses of top-soil, reduced soil nutrient availability and severe erosion, diminishing successful plant establishment (Johnston and Johnston 2004; Scherrer and Pickering 2006) and significantly reducing species richness and degrading the community structure (McDougall 2001; Scherrer and Pickering 2006). Subsequent recovery following disturbance in alpine landscapes can take decades, as the cold climate acts to slow decomposition and weathering processes (Scherrer and Pickering 2005).

Disturbances in alpine regions

World-wide, disturbances in alpine and arctic tundra landscapes can be severe and of a large-scale, for example, landslides, mining activities, road building and fire (Douglas and Ballard 1971; Miller and Cummins 1987; Chambers 1993). Less severe disturbances can include gopher and other small mammal burrowing and tunnelling (Forbis *et al.* 2004; Sherrod *et al.* 2005), and the impacts of other animals such as reindeer (Cooper and Wookey 2003) and geese (Kuijper *et al.* 2006). Smaller scale disturbance may also include the action of soil frost heave creating areas of bare ground (Johnson and Billings 1962) and recreational disturbances such as camping and trampling on and off trails (Miller and Cummins 1987; Zabinski *et al.* 2000).

In Australia, the history of disturbance in mountainous and alpine areas varies. Since the arrival of Europeans, around 200 years ago, major landscape-scale disturbances include a disruption to the fire regime and the introduction of livestock grazing, dam building and subsequent massive hydro-electric plants and road building (Good 1992; Costin *et al.* 2000; McDougall 2001; Scherrer and Pickering 2005). In the early 19th and 20th centuries, pastoralists introduced large numbers of sheep and cattle into the high country of New South Wales and Victoria in order to feed their livestock in times of drought (Costin 1954). Ineffectively managed livestock resulted in reductions in vegetation cover and an increase in the amount of bare-ground, prompting massive sheet-erosion with subsequent changes in the vegetation patterns and community structure (Costin 1954,1958). Pastoralists also increased the usual fire frequency by deliberately burning alpine grasslands and herbfields to remove the unpalatable native grasses (namely *Poa* spp.) and to promote new growth of the more palatable 'green-pick' (Costin 1954; Carr and Turner 1959). In addition, miners used fire to clear undergrowth and to expose geological features (Lawrence 1999). Before this time, landscape-scale fires are likely to have occurred only once or twice per century (Leigh *et al.* 1987). Accounts of large-scale burning by Aboriginal people in alpine areas remain unclear (Lawrence 1999) but fires were probably few or non-existent. Periods of drought are common in Australia including the alpine zone (Costin 1954; Good 1992). In addition, long dry periods can induce vegetation die-back and also increase the activity of case moth larvae, which eat the bases of native *Poa* species, resulting in patches of dead grasses and occasionally bare ground (Costin 1954; Green and Osborne 1994).

By 1958, all remaining cattle grazing leases had been withdrawn from the Kosciusko State Park (Costin *et al.* 2000) owing to concerns held by the Snowy Mountains Hydro-electric Scheme about the condition of the catchment. In Victoria,

alpine grazing leases were slowly being removed from sensitive areas in the Bogong High Plains and the Wonangatta-Moroka unit during the 1980s and 1990s (A. Markwick, Parks Victoria, pers. comm.). However, in other alpine areas, seasonal grazing continued until the final ban on all grazing in the (now) Alpine National Park announced in 2005.

Nonetheless, disturbances in Australian alpine areas continue, including the effects of recreational activities and tourism, such as ski-area development and maintenance, access roads, walking tracks (McDougall 2001; Johnston and Johnston 2004; Scherrer and Pickering 2006), mountain biking, horse riding and bush camping (Kirkpatrick and Dickinson 1984; Wahren *et al.* 2001a). Other disturbances include the localized effects of soil frost-heave, usually in existing bare ground areas (Chapter 2 and 7) and disturbances from feral horses and deer which can create areas of bare-ground and massive disturbance in and around bog systems (J. Shannon, La Trobe University, pers. comm.). Fires, used as a management tool in sub-alpine areas around logging coupes, private property and those lit by bushwalkers, can also increase the risk and occurrence of fire in the high alpine areas (Kirkpatrick and Dickinson 1984).

Effects of disturbance

Past mechanical disturbances, such as road and trail making, can have lasting effects on the physical and chemical properties of the soil (Johnston and Johnston 2004; McDougall 2001; Scherrer and Pickering 2006). Soils on road verges may have reduced levels of nutrients and organic matter, as well as increased amounts of the coarse material fraction when compared to undisturbed areas (Johnston and Johnston 2004). Soils on disused walking tracks can also have significantly lower levels of organic carbon, nitrogen, phosphorous, potassium and calcium when compared to adjacent undisturbed vegetation (Scherrer and Pickering 2006). Without suitable ameliorating intervention such as revegetation, continued erosion by wind and water on such disturbed areas can eventually result in bare and stony pavements (Brown *et al.* 2006). Roads and similar disturbances can also provide access for weeds into alpine areas (Pickering and Armstrong 2003) as seeds and propagules attach to the increasing numbers of cars, walkers and other visitors to alpine areas.

Fires in alpine areas can completely remove all vegetation cover, including the litter layer, burn the upper soil horizons and reduce soil nutrients (Kirkpatrick and Dickinson 1984). Burnt areas are therefore bare and unstable, and particularly sensitive to wind and water erosion (Costin 1954; Kirkpatrick and Dickinson 1984; Wahren *et al.* 1994; Wahren *et al.* 2001a). Low intensity fires, like many disturbances, can create a

mosaic of gaps in the vegetation (Williams and Ashton 1988; Williams 1992) creating opportunities for colonizing and seed regenerating species (Bliss 1971; Billings 1973).

Vegetation responses to disturbance

Following disturbances, the initial colonisation of bare ground tends to be from the seed bank, rather than from freshly dispersed seeds or vegetative runners (Cooper *et al.* 2004). However, following fires in alpine and sub-alpine areas of Australia, re-sprouting species are more likely to colonise the newly burnt areas (Kirkpatrick and Dickinson 1984; Wahren *et al.* 2001a). These re-sprouting species may have perennating and subterranean organs, for example *Asperula gunnii*, *Craspedia* spp. and *Leptorhynchus squamatus* (Wahren *et al.* 2001). Curiously, the shrub species which recover quickly after fires tend to be obligate seed regenerators (Kirkpatrick *et al.* 2002) rather than re-sprouters (Wahren *et al.* 2001a). However, life-form classes can be poor indicators of the behavior of individual species (Kirkpatrick *et al.* 2002). The first growing season following a fire often shows magnificent pyrogenic flowering displays among many grass and forb species (Wahren *et al.* 2001a), potentially leading to high seed bank inputs.

Successional processes following disturbance in alpine regions are likely to be slow (Billings 1973). Fifty-one years after fire at Mt Wellington, Tasmania, Kirkpatrick *et al.* (2002) report continuing evidence of floristic and structural changes in the alpine vegetation. Similarly, Kirkpatrick and Dickinson (1984) report that 20 to 40 years may be needed for vegetation to completely re-establish at several high peaks in Tasmania. In addition, McDougall (2001) reports that decades may be needed for re-colonisation of a heavily disturbed road verge on the Bogong High Plains, while Roxburgh *et al.* (1988) (followed by Brown *et al.* (2006)) report on continued secondary succession of a high-alpine cushionfield 24 years following road disturbance in Central Otago, New Zealand.

Early colonisers of disturbance induced gaps may possess different life-history and physiological traits compared with the species growing in the more mature successional stages in the undisturbed natural vegetation (Marchand and Roach 1980; Scherrer and Pickering 2006). However, there is evidence that an auto-succession (convergence) model may be appropriate in some alpine landscapes following fire (Kirkpatrick *et al.* 2002). In contrast, Brown *et al.* (2006) suggest that because recent colonisation of new species in a disturbed area occurred, succession may follow a model in which species richness and diversity is maximized at intermediate levels of disturbance (Connell 1978). Fox (1981) tested the intermediate disturbance hypothesis in an arctic-alpine fellfield which was disturbed by frost-heave in the White Mountains, Alaska. He showed that

intermediate levels of disturbance increased species diversity, compared to undisturbed vegetation, by influencing the evenness of species abundances rather than the overall number of species. Hence, succession after disturbance in alpine areas can follow a number of different models, and no single paradigm appears to prevail across all situations.

What appear as recent successional changes in the vegetation, however, should be checked against continual background changes in species' abundances. These may occur over decades, as species' ranges expand and contract in response to historical disturbances and climatic changes (Grabherr *et al.* 1994; McDougall 2003; Scherrer and Pickering 2005). Long-term studies of vegetation change are therefore essential.

Potential responses of Australian alpine vegetation to future disturbance

Australian alpine vegetation may be sensitive to large-scale disturbance, such as repeated landscape-scale fires or cattle grazing, but is likely to have evolved with, and therefore be resilient against, frequent, small-scale, localised disturbances such as frost-heave and insect herbivory (Wahren *et al.* 2001a). There is no evidence that alpine vegetation require fire for regeneration (Kirkpatrick and Dickinson 1984) and fire is generally regarded as rare in the alpine zone (Williams and Costin 1994). Alpine species in Australia are differentially flammable; many shrub species burn well due to their scleromorphic features such as small, hard, leathery leaves with volatile oil producing glands and fire-enhancing architecture (Williams *et al.* 2006). Grasses and many forb species tend not to 'encourage' fire in quite the same manner. Hence, initial post-fire reports of some recent fires in Victoria have concluded that shrub species can determine which areas of the landscape burn preferentially (Wahren *et al.* 2001a; Williams 2003; Williams *et al.* 2006).

Climate change predictions for the Australian alpine zone include higher minimum temperatures, reduced snowfalls and subsequent longer growing seasons (Hennessey *et al.* 2003). The incidence of extreme events, and prolonged droughts, are also expected to increase across Australia, potentially increasing the frequency of fires (Hennessey *et al.* 2005). How the vegetation will respond to rapid and ongoing climate change, in addition to the changes in disturbance regimes, will be determined by the combination of local climatic and environmental factors (see Chapter 2) and the plasticity of species' recruitment processes.

A conceptual model

To help interpret the potential responses of alpine vegetation to future changes, I developed a conceptual model (Figure 8.3). The conceptual model uses a similar framework as the state and transition model as outlined by Westoby *et al.* (1989). In this model, ‘states’ are represented by numbered, grey-shaded boxes; directional ‘transitions’ are represented by straight arrows with associated text indicating the trigger that might initiate the transition. I identify seven states. States 1,4 and 7 are stable, whereas 2,3,5 and 6 are transitory.

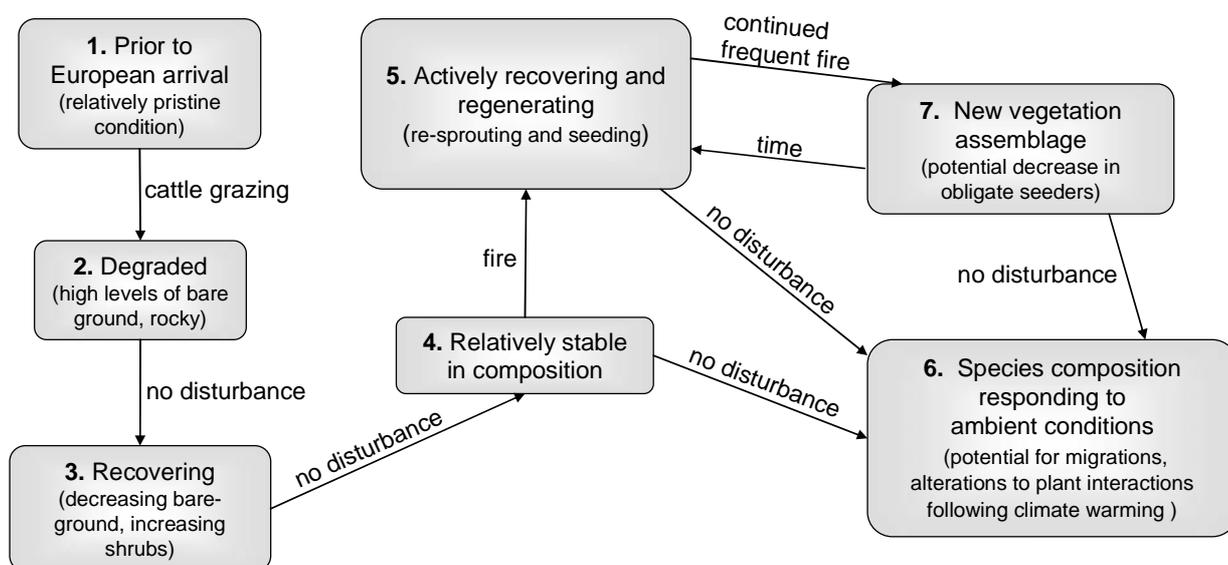


Figure 8.3. Conceptual model of past and future changes of alpine vegetation with respect to disturbance and climate warming. See text for details of each state and transition. The research described in this thesis predominantly focuses upon vegetation in State 4.

Prior to European occupation and settlement, the alpine vegetation was in State 1 and was relatively pristine. Introduced livestock in the 1800s led to a degraded state (State 2) with high levels of bare-ground and exposed rocky soils (Lawrence 1999). After the exclusion of cattle from alpine areas, the recovering vegetation in State 3 showed an increase in the cover abundance of most vegetation types, but especially some shrub species which recruit in bare ground patches (Carr 1962; Williams and Ashton 1988; Williams 1992). With enough time between disturbances, State 3 may transition into State 4. As the extent of the landscape-scale fires in alpine areas during 1939 are unclear (Carr and Turner 1959). I assume that fires did not drastically affect the vegetation at the highest peaks. This, the relatively stable State 4 represents the current vegetation composition and patterns. I consider that the alpine peaks where the research for this thesis was conducted were in State 4. Landscape-scale disturbances such as fire may induce the transitory

State 5, whereby species follow the successional pathways discussed in the previous section. Frequent fires may disrupt auto-successional processes, leading to altered patterns in the vegetation and new species assemblages, shown by State 7. Such fires may occur more frequently in the lower altitude mountains, as flammable shrub species dominate in these areas (see Chapter 2). Some shrub species may also require bare ground gaps for regeneration by seed (Williams 1992) and hence, repeated disturbances, such as fire, may eventually lead to a vegetation assemblage with a higher shrub component. In addition, species without re-sprouting mechanisms (see Chapter 3) may be lost from the vegetation assemblage should fire occur before they mature and set seed. Repeated fire events, however, are more likely to change the composition of vegetation through depleting soil nutrients and encouraging soil erosion in periods of low vegetation cover (Kirkpatrick and Dickinson 1984). Without repeated disturbance, State 7 may move back to State 5 over time and eventually reach State 6. Without major disturbances, I anticipate that all species will need to adapt to the rapidly changing climate, as proposed by State 6, although climate change and disturbances may be linked, drought events and extreme fire weather are predicted to accompany warming temperatures (Hennessey *et al.* 2005).

Ongoing changes in vegetation patterns as a response to climate warming, as in State 6, can be analysed using the natural gradient of mountain summits used in this thesis as a 'space-for-time' analysis. Hence, vegetation patterns and processes which currently dominate at the lower, warmer elevation sites may dominate at the higher elevation sites in the future as the climate warms. Changes may therefore include increased shrub abundances at the higher altitudes (Chapter 2) and more frequent incidences of competitive interactions at the higher elevations (Chapter 7). The seed bank composition (Chapter 3), seed germination (Chapters 4 and 5) and seedling regeneration rates (Chapter 6) are not expected to change dramatically as these processes showed few patterns across the altitudinal gradient. The conceptual model can act as a guide to potential changes in vegetation patterns. Continual, long-term post-disturbance monitoring of alpine vegetation in Victoria will lead to more accurate assessments of species responses to change and their successional strategies.

Elsewhere, alpine vegetation responses to recent climate changes are already apparent. Research from the Swiss Alps shows that warmer temperatures over recent decades are already correlated with migrations in vegetation (Grabherr *et al.* 1994; Walther *et al.* 2002; Walther *et al.* 2005) as the effects of climate, the major limiting factor for altitudinal species richness, is diminished. Similar changes are underway in

Norway where species richness has increased on 19 of the 23 mountains surveyed from 1931 to 1998 (Klanderud and Birks 2003). They showed a mean increase of 10.2 species per mountain over the time period and 25% of species had exceeded their previous altitudinal limits (Klanderud and Birks 2003). Such changes are expected in other mountainous or high latitude regions, assuming there is ample variation in altitude or latitude, available migration corridors and vacant habitat niches (Huggett 1995; Körner 1999). Species are expected to track a shifting climatic envelope (Walther *et al.* 2002; Klanderud and Birks 2003) and sort and sift themselves according to their tolerance ranges and to extreme weather events (Huggett 1995). Long-term studies of this nature offer the chance to unravel the interacting effects of climate, biological interactions, resource availability and extreme events to predict future vegetation responses and subsequent distributions and patterns.

Summary and conclusions

Several recruitment strategies enable Australian alpine species to survive disturbance. Before European settlement, the alpine zone was most likely free of large-scale disturbances and the vegetation composition was more likely maintained by small-scale, localised disturbances such as frost-heave, herbivory and occasional soil erosion. More recently, anthropogenic disturbances in alpine areas have included increased fire frequency, road building and associated trampling following increased visitor access. Disturbances in alpine areas can also have lasting effects on soil structure and composition which, coupled with the cold climate and inherently slow growth rates of alpine plants, may cause slow rates of succession following disturbance. Recruitment from the soil seed bank and vegetative resprouting of surviving individuals are both important mechanisms for responding to disturbance. Succession models among the few local, post-disturbance studies in alpine areas are mixed and dependent on the type of disturbance, vegetation composition and time-since-disturbance. A conceptual model of future vegetation responses can be useful for predicting the outcome of vegetation change in the Australian alpine zone. Knowledge of alpine plant recruitment processes can inform the states and transitions within the model. However research using long-term data sets will no doubt prove essential in unravelling the interactions between disturbance, climate change and vegetation change.

Future research directions

The research presented in this thesis provides a solid base for understanding the current recruitment patterns and processes of alpine plant species. However, this study also highlights the requirement for further investigation into the patterns and processes of plant recruitment in times of change.

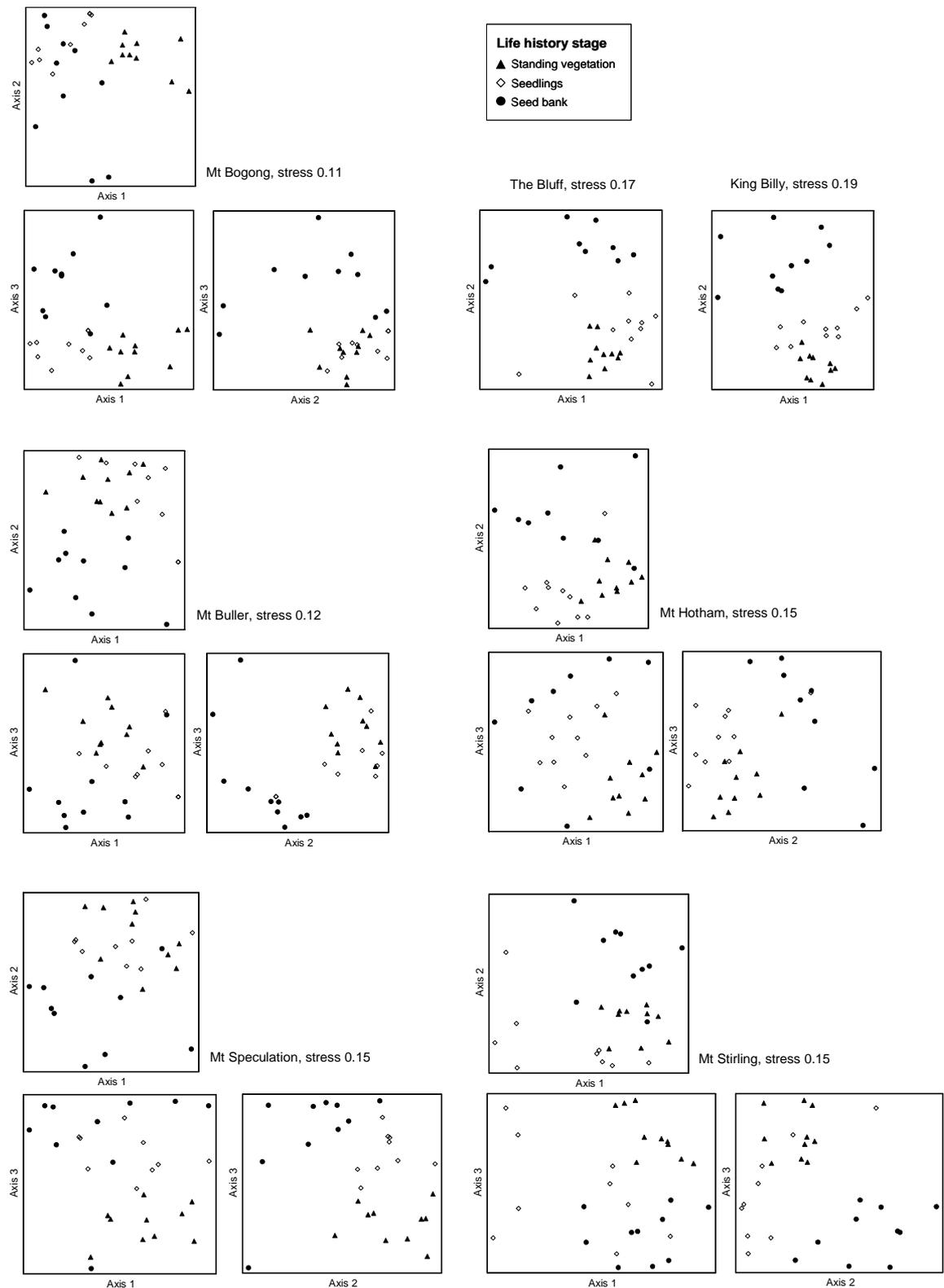
Approximately seven months after the field component of this study was completed, bushfires swept through the Victorian mountain regions (December 2006). Many of the alpine summits in this study were burnt. Therefore, I recommend a comprehensive assessment of the rates, patterns and underlying mechanisms of recovery of the vegetation following fire, which will lead to an improved understanding of these ecosystems. Specifically, such studies should consider seed bank dynamics, seedling emergence and survival, the ongoing and changing role that plant interactions may play in plant regeneration, and the nature of successional states. Detailed species-based demographic studies can be useful in all aspects of this research, as can more generalised community-based approaches.

The stages and processes in the generalised alpine plant life cycle model which were not addressed in this study also deserve research attention. In addition to the background and post-disturbance levels of recruitment, the effects of climate change on alpine plant recruitment also warrant consideration. Reciprocal transplant studies of seeds and seedlings over natural environmental gradients across the alpine landscape may be useful to investigate these research questions. Incorporation of previous research, continuation of long-term studies, knowledge-sharing and inter-disciplinary collaborations will be imperative for improving our understanding of the structure and functioning of Australian alpine ecosystems.

Appendices

Appendix 8.1. ANOSIM results for the similarity between life-history stages within the NMDS ordination. Data was analysed in six randomly selected separate groups owing to computational limitations of the software. Pairwise comparisons of different life-history stages within each ANOSIM are indicated by V, standing vegetation; S, seedling flora; B, seed bank flora.

	Global <i>R</i>	<i>P</i>	Life-history stages	Pairwise comparisons	
				<i>R</i>	<i>P</i>
ANOSIM 1	0.347	0.00	V S	0.27	0.00
			V B	0.6	0.00
			S B	0.16	0.50
ANOSIM 2	0.54	0.00	V S	0.35	0.00
			V B	0.72	0.00
			S B	0.48	0.00
ANOSIM 3	0.239	0.00	V S	0.28	0.00
			V B	0.35	0.00
			S B	0.08	7.80
ANOSIM 4	0.28	0.00	V S	0.22	0.10
			V B	0.44	0.00
			S B	0.15	1.80
ANOSIM 5	0.45	0.00	V S	0.25	0.10
			V B	0.68	0.00
			S B	0.33	0.00
ANOSIM 6	0.27	0.00	V S	0.21	0.10
			V B	0.42	0.00
			S B	0.14	1.00



Appendix 8.2. The position of standing vegetation, seedling and seed bank samples from all sites within either two or three dimensional NMS configurations, based on presence/absence data. A random selection of half the available presence/absence data was used for each site owing to computational limitations of the software. Stress values for each ordination are indicated next to each site name.

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