

## Germination characteristics of Mountain Celery *Aciphylla glacialis* (F. Muell.) Benth. (Apiaceae)

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### Abstract

The germination characteristics of Mountain Celery *Aciphylla glacialis* (Apiaceae) were investigated. This species failed to germinate in conditions that nine other alpine species from the same region found favourable. Seeds were collected from eight mountain peaks in the Victorian alpine zone. These peaks formed an altitudinal gradient of 302 m. The seeds were subjected to a cold-wet stratification treatment in an attempt to overcome what appeared to be seed dormancy. After approximately 15 weeks of the cold-wet stratification treatment, *A. glacialis* seeds began to germinate. Germination rates were fastest among seeds from the mid to high altitude sites, which also had the greatest percentage of seeds to germinate. Mt Speculation (1668 m) and Mt Bogong (1970 m) had the lowest percentage of germination from seeds collected in 2004. Among seeds collected in 2005, the lowest values were from Mt Bogong. Comparing seed collected in 2004 and 2005, there was no significant difference between final per cent germination from any site. There were no significant relationships between altitude and germination characteristics. There were several significant differences in the probability of seed germination between sites. However, there was no overall trend in the probability of seed germination between high and low altitude sites. The role of seed dormancy mechanisms in relation to the alpine environment is discussed and the role of altitudinal gradients in relation to seed germination in this species is speculated upon. (*The Victorian Naturalist* 126 (1), 2009, 4-12)

**Keywords:** seed germination, dormancy, altitudinal gradient, alpine, cold stratification

### Introduction

#### *Seed germination, dormancy and environment*

Seed germination and seedling emergence under natural conditions often are 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. Previously, it was found that nine species from the Victorian alpine zone had high rates of germination (Venn 2007), 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 often above 20°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. Additionally, photoperiodism 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 rela-

tively 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**

This study investigated the germination behaviour of a locally common, but regionally rare, alpine forb that grows in alpine areas in Victoria and New South Wales. The focal species is the Mountain Celery *Aciphylla glacialis* (F. Muell.) Benth. (Apiaceae) (Fig 1 see back cover). 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 40 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).

*Aciphylla* is a dioecious, obligate out-crossing genus dependent on pollinators for fertilisation. It is, therefore, likely to experience some 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* is male biased, with an overall ratio of female to male plants of 1:1.5. Males can also produce four times more flowers than females (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 in reproduction by female *Aciphylla* plants is assumed to decrease their longevity and restrict their growth, especially at higher alpine sites where the conditions for the accumulation of biomass are limited. The costs associated with female function at high altitudes, therefore, could result in females flowering less frequently (Pickering and Arthur 2003), producing fewer seeds and possibly producing non-viable seeds. At lower altitudes, environmental conditions are more favourable (longer snow-free period, warmer temperatures), which could result in an equal flowering ratio between males and females, as well as greater seed production and viability. Phenotypic differences in relation to environmental effects also are common in this genus, making *A. glacialis* a good model species for investigating the differences in germination across an altitudinal gradient. There are few, if any, published studies dealing with germination for any *Aciphylla* species in Australia.

### **Research focus**

This research examines three questions: 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**

Seeds from *A. glacialis* (Fig. 1 see back cover) populations were 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 Hooker Plateau (1970 m) on Mt Bogong. All sites are within 40 km of each other, with most less than 10 km apart (Table 1).

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°C and 27°C in summer, and -6°C and 12°C in

**Table 1.** The seven study site locations and altitude.

Study site	Location	Altitude (m ASL)
Mt Speculation	37°07'30"S 146°38'40"E	1668
King Billy (2)	37°12'45"S 146°36'15"E	1696
Mt Magdala	37°15'30"S 146°37'15"E	1725
Mt Howitt	37°10'30"S 146°38'50"E	1738
Mt Buller (West Knob)	37°08'45"S 145°26'15"E	1762
Mt Hotham	36°58'35"S 147°07'30"E	1860
Mt Bogong (Hooker Plateau)	36°44'27"S 147°17'15"E	1970

winter (Bureau of Meteorology 2007 unpubl.). Frosts are frequent and can occur at any time of year (Williams 1987). The growing season spans approximately seven months, from snow-melt (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). Soils in this region are considered alpine humus and are acidic (pH 4 to 5) (Costin 1962; LCC 1982).

**Germination trial**

Filled and viable seeds were selected by visually assessing each seed using a light box and by gently squeezing each seed. *A. glacialis* seeds did not germinate under conditions that nine other alpine species (*Brachyscome rigidula*, *Brachyscome spathulata*, *Leucochrysum albicans albicans*, *Microseris* sp. 2, *Olearia phlogopappa* var. *subrepanda*, *Xerochrysum subundulatum*, *Luzula acutifolia*, *Trisetum spicatum* and *Rytidosperma nudiflora*) 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, *Aciphylla* seeds were pre-treated with cold-wet stratification. Twenty replicates of ten seeds from each site were arranged in petri dishes on a bed of moist cotton wool with an anti-fungal treatment (10 ml of Mancozeb solution). Petri dishes were 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. 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 per cent germination of the viable seeds present, i.e. those that had not succumbed to fungus attack.

**Data analysis**

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

The shape of each species' per cent germination curve was 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) and comparing those models. This method gives a mean probability of germination at every sampling time and allows whole curves to be compared across sites within each species, rather than only at the sampling times as with more conventional statistics. The K-M product limit estimation function uses germination data from every seed, in the form of elapsed time (days) to germination (right censored data) and also data for seeds that 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  $\chi^2$  statistic and P-value.

Linear regression, and in some cases Pearson/Spearman rank correlations, were performed

across populations between combinations of final per cent 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 collected in 2004 and 2005 showed some germination under the experimental conditions (Fig. 2). The final mean per cent germination ranged from 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 final mean per cent germination in both years ( $95.5 \pm 1.53$ ). Com-

parisons of seeds collected in 2004 revealed that those from Mt Bogong and Mt Speculation (the highest and lowest sites respectively) had significantly lower final mean per cent germination ( $P < 0.05$ ) than seeds from other sites (Fig. 3). Of the seeds collected in 2005, those from Mt Bogong also had significantly lower mean final per cent germination ( $P < 0.05$ ) than the other sites (Fig. 3). Final per cent germination of seeds from Mt Bogong, Mt Hotham and Mt Buller showed no significant differences between years ( $P > 0.05$ ). Linear regression showed there was no significant relationship between mean final per cent germination and altitude.

The time until the first germination for all sites was approximately 15 weeks from the start

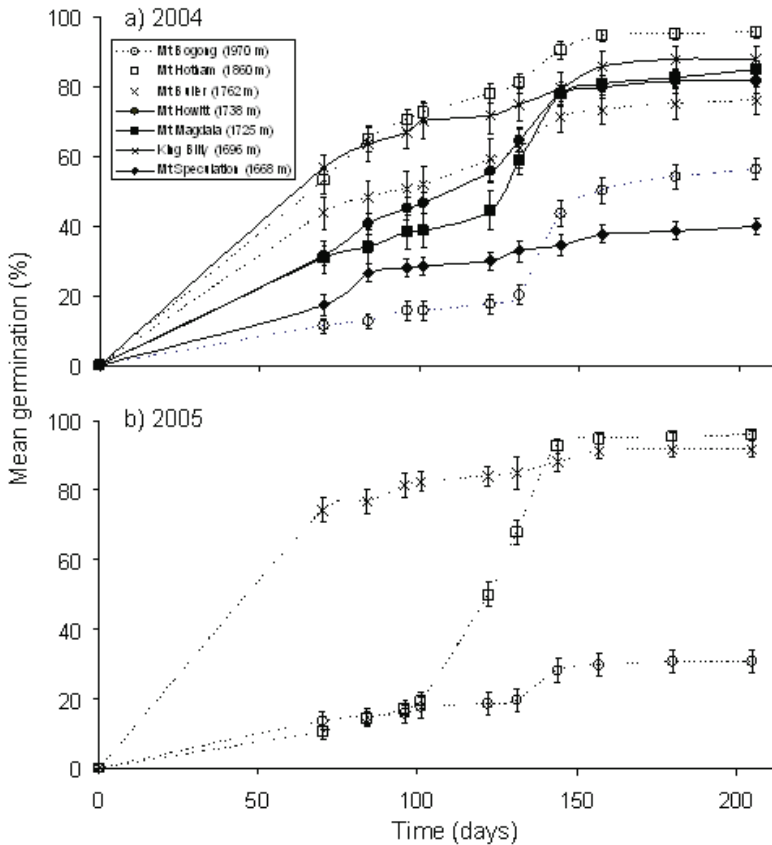
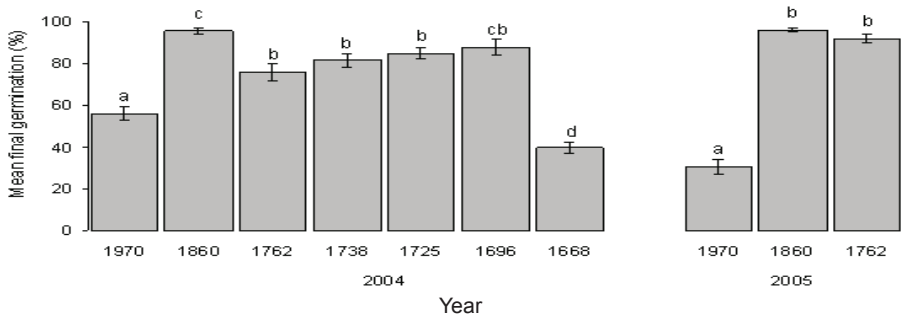


Fig. 2. Mean per cent germination ( $\pm 1$  standard error) of *Aciphylla glacialis* seed collected from the seven alpine sites in (a) 2004 and (b) 2005, over the duration of the experiment (days).



**Fig. 3.** Mean final per cent germination ( $\pm 1$  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.

of the experiment: the exact date fell between observation periods. Germination rate ( $T_{50}$ ) varied across the altitudinal gradient (Table 2). 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 per cent germination ( $R^2 = 0.81$ ,  $P < 0.001$ ) indicating that fast germination rates correlate with high final germination numbers. Linear regression showed that there was no significant relationship between  $T_{50}$  and altitude of seed origin ( $P > 0.05$ ).

The mean probability of germination over time (Fig. 4) indicates there are few trends with altitude of seed origin; however, there are several significant differences between curves of different sites (Table 3). Of the 23 pairwise comparisons of germination probability by site over both years, nine 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.

Between years, the probability of germination was 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  $\chi^2 = 16.264$ ,  $P < 0.001$ ; Mantel's  $\chi^2 = 34.267$ ,  $P < 0.001$  respectively). In contrast, seeds from Mt Buller collected in 2005 had a higher probability of germination than those from 2004 (Mantel's  $\chi^2 = 34.025$ ;  $P < 0.001$ ).

## Discussion

### General interpretation of results

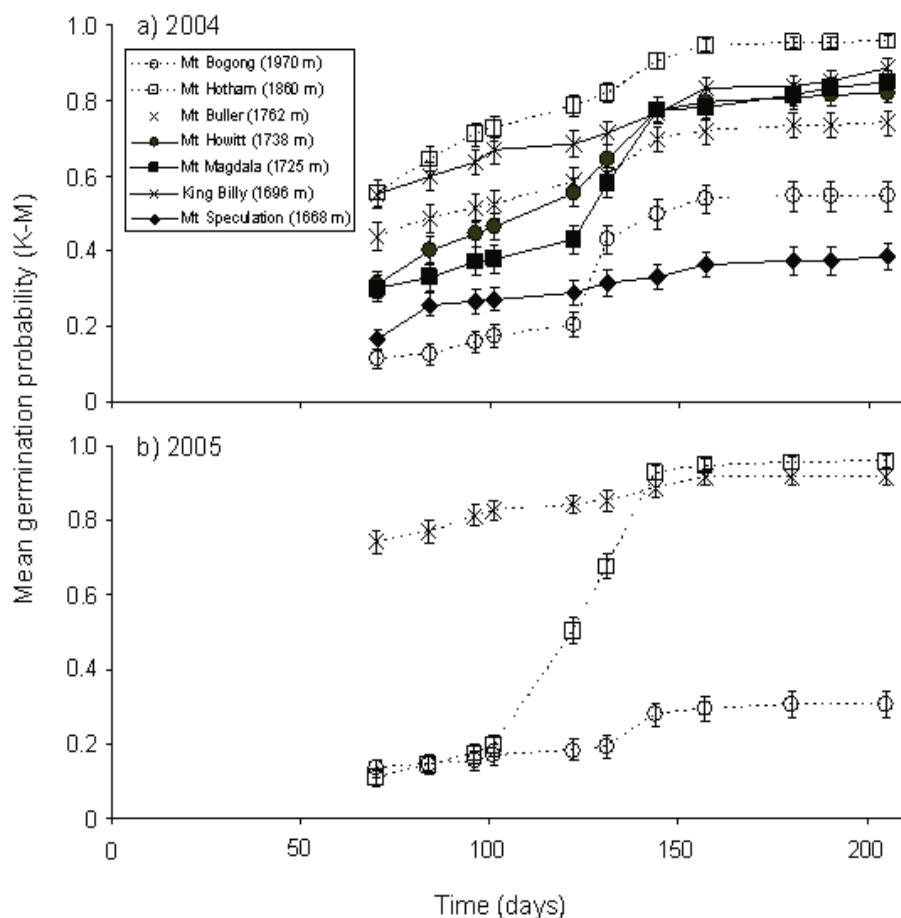
*Aciphylla glacialis* seeds did not germinate under the laboratory conditions that seeds from nine co-occurring alpine species found favourable (Venn 2007). This indicates that *A. glacialis* seeds may experience innate primary seed dormancy. In the current study, seed dormancy was broken by wet-cold stratification, which represents a natural dormancy breaking mechanism (Probert 1992) and implies that this species is a strict spring germinator. Furthermore, the few observations of *A. glacialis* seedlings emerging in the field are restricted to spring and early summer (Venn 2007).

The length of time for *A. glacialis* seeds from all populations to germinate was around 15 weeks, during which conditions were kept at a constant  $2^\circ\text{C}$ . This length of time roughly correlates with the length of a typical Victorian winter, taking into account inter-annual variability in snowfall (Hennessey *et al.* 2003). Seed dormancy and the timing of seed germination in *A. glacialis* under natural conditions, therefore, may be a result of evolutionary experience in this species growing in the Victorian alpine zone.

In this study, considerable variation in germination characteristics between populations from different altitudes was observed. However, final mean per cent 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 adap-

**Table 2.** Germination rate ( $T_{50}$ ) of *Aciphylla glacialis* seeds from seven sites, at various altitudes.

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	1970	2005	205
Mt Hotham	1860	2005	122
Mt Buller	1762	2005	70

**Fig. 4.** Mean probability of germination ( $\pm 1$  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 3.** Pairwise comparisons of the probability of *Aciphylla glacialis* seed germination between sites, based on the probability of germination curves, explained by Mantel's  $\chi^2$ , 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); SP, Mt Speculation (1668 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)				

tations to the changes in environmental factors found across sites. *A. glacialis* seeds also appear to act independently of ambient conditions, thus the timing of germination may be reliant on seed dormancy alone. This restrictive germination pattern may protect *A. glacialis* 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 mean per cent germination was significantly related to fast germination rates. Such inherently fast germination rates 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 and, therefore, species cap-

able 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 per cent 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 germination potential (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.

*Dormancy mechanisms*

Dormancy makes intuitive sense in a landscape where winters are cold and severe. Billings and



Mooney (1968) suggest that the protective layer of snow over winter may serve to insulate seeds sufficiently; hence, they need never fully evolve specific seed dormancy syndromes. Hence, most alpine species lack a seed dormancy mechanism 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 *A. glacialis* 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 this experiment, the length of the cold-wet stratification period required for germination was around 15 weeks. 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 of cold stratification, whereas seed from 3400 m needed three months. This pattern may not be apparent in *A. glacialis* seeds as the altitudinal distribution of this species is relatively small and/or adaptations to annual changes in the snow season length across the altitudinal gradient may be minimal or undetectable.

### Altitudinal gradients

A relationship between germination characteristics and the altitude of seed origin was not found in this study, possibly because the altitudinal differences between sites which support *A. glacialis* populations was 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 per cent germination and shortest germination rate 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 also may have the highest survival rates as seedlings (Holm 1994). No significant relationship between *A. glacialis* seed mass and altitude has been found (Venn 2007), nor has there been any suggestion of significant differences 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, *A. glacialis* 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, no general trends between altitude and final per cent germination or germination probability for *A. glacialis* seeds were found in this study. Therefore, any limitations that the female plants may be experienc-



ing across the altitudinal gradient do not appear to be causing reduced seed germination.

## Conclusions

In laboratory experiments, *A. 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 per cent germination was high, up to 95%, and no differences in germination were found in seeds collected in different years. Fast germination rates were significantly related to high final per cent germination. These germination characteristics of *A. glacialis* did not show significant trends across the altitudinal gradient of sites within the Victorian alpine zone.

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