CURRENT DISTRIBUTION NOT INDICATIVE OF UNDERLYING NICHE REQUIREMENTS OF AN ALPINE FORB: IMPLICATIONS FOR PREDICTING CLIMATE-INDUCED RANGE SHIFTS

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Declaration

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Table of Contents

EXECUTIVE SUMMARY 1

INTRODUCTION 2
  FINGERPRINTS OF CHANGE 2
  MODELLING FUTURE PLANT DISTRIBUTIONS – CORRELATIVE APPROACHES 3
  THE ROLE OF DISPERSAL IN DETERMINING RANGE LIMITS 4
  A MORE ‘IN-DEPTH’ UNDERSTANDING OF RANGE LIMITS 5
  THE ROLE OF BIOTIC INTERACTIONS IN DETERMINING RANGE LIMITS 6
  THE ROLE OF BIOTIC INTERACTIONS IN DETERMINING FUTURE DISTRIBUTIONS 8

METHODS 10
  STUDY SPECIES 10
  STUDY SITE 11
  SITE CONDITIONS 12
  FIELD TRANSPLANT EXPERIMENT 14
  LABORATORY GERMINATION EXPERIMENT 14
  LIGHT LIMITATION EXPERIMENT 15
  FREEZING RESISTANCE EXPERIMENT 16
  DATA ANALYSIS 17

RESULTS 20
  SITE CONDITIONS 20
  FIELD TRANSPLANT RESULTS 22
  LABORATORY GERMINATION RESULTS 24
  LIGHT LIMITATION RESULTS 25
  FREEZING RESISTANCE RESULTS 27

DISCUSSION 28
  GERMINATION CHARACTERISTICS 28
  FROST TOLERANCE IN SEEDLINGS 29
  EFFECTS OF FACILITATION ALONG AN ABIOTIC STRESS GRADIENT 30
  EFFECTS OF COMPETITION ON SEEDLING GROWTH 32
  CONCLUSION 34

REFERENCES 36

APPENDICES 42
  APPENDIX I 42
  APPENDIX II 45
  APPENDIX III 46
  APPENDIX IV 47

List of Figures

FIG 1. Occurrence records of Alpine Podolepis (Atlas of Living Australia) 11
FIG 2. *Podolepis Robusta* in flower (image: J. Morgan) 11
FIG 3. Location of Mt Hotham in Victoria, and study site locations at Mt Hotham (1-10) representing the elevation gradient on south-east and north-west sites 13
FIG 4. Total number of freezing days (temperatures ≤0 °C) recorded at Mt Hotham, in relation to altitude during study period (Nov 2016 – Mar 207) on north-west (solid line) and south-east (dashed line) exposed slopes 20
FIG 5. Growing Degree Days (GDD) recorded for south-east (a) and north-west (b) exposed sites during study period (Nov 2016 – Mar 2017). 21
FIG 6. Effect of treatment and altitude on seedling survival. Mean probability of survival (±95% CI) over one growing season for seedlings planted along an altitudinal gradient in control (solid green line) and gap (solid orange line) treatments. 22
FIG 7. Mean Relative Neighbour Effect (RNE) (±1 SE) for paired transplanted seedlings in gap and control treatments on (a) north-west and (b) and south-east exposed aspects across the elevation gradient. 23
FIG 8. Effect of light and temperature on germination. Fitted values for probability of germination for (a) light conditions and (b) dark conditions (± 95% CI) for the generalised linear model applied on cabinet germination data. 24
FIG 9. Effect of light limitation on net photosynthesis. Fitted mean rate of photosynthesis (± 95% CI) of seedlings grown under full sun, 48% shade and 82% shade. 26
FIG 10. Effect of light limitation on biomass. Fitted mean dry-weight of biomass (± 95% CI) of seedlings grown under full sun, 48% shade and 82% shade. 26
FIG 11. Mean (± 1 SE) variable fluorescence to maximum fluorescence (F_V/F_M) ratios of leaf material used in freezing resistance study, at four temperatures: 4, -5, -11, and -20°C; for Alpine Podolepis leaves of (a) mature plants and (b) seedlings. 27
FIG 12. Shade cast by resident vegetation at north-west sites at Mt Hotham, Victoria. 42
FIG 13. Shade cast by resident vegetation at south-east sites at Mt Hotham, Victoria. 42
FIG 14. Frequency of vegetation (herb, gramminoid, shrub) heights at Mt Hotham on south-east exposed sites (a-e). 43
FIG. 15. Frequency of vegetation (herb, gramminoid, shrub) heights at Mt Hotham on north-west exposed sites (a-e). 44
FIG 16. *Eucalyptus pauciflora* woodland with dense *Podolobium alpestre* understory dominate north-west exposed slopes at Mt Hotham (1670 - 1700 m).. 45

List of Tables

TABLE 1. SUMMARY INFORMATION FOR THE TEN SITES ALONG THE MT HOTHAM TRANSECT INCLUDING LOCATION, ALTITUDE AND ASPECT FOR EACH SITE. 13

TABLE 2. GERMINATION ATTRIBUTES OF ALPINE PODOLEPIS AT 14°C WITH AND WITHOUT A PERIOD OF COLD STRATIFICATION 25

TABLE 3. ANALYSIS OF THE EFFECT OF TREATMENT, ALTITUDE AND ASPECT ON SEEDLING SURVIVAL. 46

TABLE 4. ANALYSIS OF THE EFFECT OF TREATMENT AND ALTITUDE ON SEEDLING SURVIVAL.......... 46

TABLE 5. TABLE OF COEFFICIENTS FOR THE GLM USED TO FIT SEEDLING SURVIVAL AS A FUNCTION OF TREATMENT AND ALTITUDE 46

TABLE 6. STATISTICAL ANALYSIS OF RELATIVE NEIGHBOUR EFFECT FOR NORTH 47

Executive Summary

As the climate warms, plant species are predicted to move upward and poleward in order to remain within their climatic envelopes. These predictions are made by extrapolating current distributions to future climate scenarios under the assumption that plant boundaries are controlled by climate alone. However, species-specific responses to climate change are likely more complex than can be forecast with simple climate modelling. Understanding controls on species geographical range limits, and how these may respond to rapid environmental change has prompted calls for greater 'brute force' experimentation. Here, I investigate controls on the distribution of a model alpine species *Podolepis robusta* (Asteraceae) by conducting a series of field and laboratory experiments. Germination experiments demonstrate a wide germination niche, with no limiting dormancy characteristics or cold stratification requirements. However, when seedlings were subjected to freezing temperatures, leaves suffered significant damage to photosynthetic apparatus compared to adult plants. Hence, it is likely that early seedling establishment is strongly tied to occurrences of early frost during the growing season. Facilitative interactions play a strong role across range edges. As demonstrated by a transplant experiment along a temperature and moisture gradient, close interspecific neighbours significantly increased survival and growth of planted seedlings, compared to seedlings planted in canopy gaps. This pattern was consistent, even below the current distribution, contrary to expectations of stronger competitive interactions. While the field study finds no response to competition on seedling survival, experimental shading indicates intolerance at heavy (82%) light interception. This has consequences for establishment within dense vegetation. Results consistently indicate that *P. robusta* is able to occupy a far greater niche than can be observed currently. These results highlight the importance of facilitative interactions at the seedling stage in the alpine zone, demonstrating that biotic factors act to constrain or widen the theoretical niche. I argue that biotic interactions, dispersal limitation, and recruitment processes may enforce stronger limits to geographic distribution than climatic tolerances *per se*. Predictions on how plant species may respond to climate change will benefit from incorporating these factors.

Introduction

The niche is a fundamental tenet in ecology, and frames our understanding of species range limits (Holt 2009). Climate and other abiotic factors are often demonstrated as having strong influences on plant species distributions (Körner and Paulsen 2004). Hence, responses to climate change are often couched in terms of climatic tolerances. In alpine ecosystems, climate warming is expected to drive species distributions to higher altitudes (Dullinger et al. 2012). These range shifts have important conservation implications, as the upward migration of more competitive, lower-altitude plants, and the reduction of suitable habitat for high-altitude plants, could potentially lead to range contractions and species extinctions (Thuiller et al. 2005; Dullinger et al. 2012; Alexander et al. 2015). However, geographic distributions of plant species result from a combination of abiotic tolerances and biotic factors such as species interactions, dispersal and demographic processes (Holt 2009). The complexity and urgency of predicting the potential impact of climate change on species distributions has been increasingly met with calls for greater 'brute-force' experimentation (Holt 2009; Munier et al. 2010; Hille Ris Lambers et al. 2013; Alexander et al. 2015; Alexander et al. 2016). Experimental assessments of species distributions provide a direct approach in attempting to quantify the niche, and are a powerful tool for making inferences about spatial heterogeneity of abiotic factors and species interactions (Moore 2009).

Fingerprints of change

In mountains, due to an altitudinal temperature gradient, species are expected to migrate upslope in response to climatic shifts involving warming temperatures and longer growing seasons (Pauli et al. 1996). Revisitation of historical sites provides overwhelming evidence for global trends in upward species migration (Pauli et al. 2012), with increases in species richness reported for summits in the European Alps (Parolo and Rossi, 2008; Pauli et al. 2012), the Himalayas (Telwala et al. 2013), the Andes (Feeley et al. 2011) and the Australian Alps (Venn et al. 2012). In particular, species gains are more pronounced on summits of lower altitudes, owing to larger nearby species pools and suggesting that upward shifts are driven largely by leading-edge expansions in response to increasing temperature (Pauli et al.

2012). However, contrasting trends were reported for Mediterranean mountain regions (Pauli et al. 2012), and mountain regions with Mediterranean-type climates (Crimmins et al. 2011), where rather than tracking temperatures, plant species have responded to a decreased water deficit by shifting their optimal elevations downslope. Crimmins et al. (2011) also report that species' entire ranges – including lower boundaries – are shifting, rather than just through upper-boundary extensions as observed in temperate regions. Such contradictory responses to climate change undermine the assumption that temperature is the principle factor in determining species distributions, and highlights the importance of other climatic factors such as energy and water availability (Crimmins et al. 2011; Cahill et al. 2012). Ultimately, the upward trend in species migrations is expected to result in range contraction and extinction of mountain plant species, many of which are rare and endemic (Dullinger et al. 2012). However, long-term revisitation studies are limited in spatial and temporal scope, prompting many ecologists to employ computer modelling in order to predict potential responses to climate change (Brooker et al. 2007).

Modelling future plant distributions – correlative approaches

Typically, climate envelope modelling is employed to predict species ranges in the context of climate change (Brooker et al. 2007). Species range limits are assumed from simple correlations of abiotic conditions within current distributions. These 'climatic envelopes' are then extrapolated to future climate scenarios (Brooker et al. 2007) in order to create a 'statistical niche model' (Holt 2009). Frequently, species distribution models predict substantial impacts on alpine plant diversity, owing to high rates of habitat loss (Dullinger et al. 2012). In a European-scale analysis, a climate-envelope based model predicted habitat losses of approximately 60 per cent of mountain species (Thuiller et al. 2005). However, estimates of habitat loss may depend on the scale of the model. Fine scale (local) models predicted the persistence of all habitats projected to no longer exist at coarse resolutions (European scale) (Randin et al. 2009). This is likely because topography and mean temperature data contain more variability at fine scale than can be expressed at larger scales (Thuiller et al. 2005). Indeed, temperature data collected locally indicates that high topographic variability will conserve the climatic niches of many species in the Swiss Alps

(Sherrer and Körner 2010). Hence, inconsistencies in species distribution modelling demonstrate that estimations of habitat loss depend upon data resolution. This has implications for the accuracy of predictions of habitat loss and species extinctions. Further, predictive models ignore crucial elements affecting species distributions such as dispersal traits and biotic interactions, and as such provide only a rough estimate of possible responses to climate change (Holt 2009; Urban et al. 2012).

Many ecological assumptions and theories can influence predictions of species distributions under climate change (Austin 2002). Brooker et al. (2007) recognise the shortcomings of climate-based modelling, and incorporate biotic interactions such as competition and facilitation between plant species, and plant dispersal ability into a spatial model of a theoretical community. Here, the inclusion of biotic processes provided contrary predictions for future species distributions than those based purely on climatic correlation. However, while this is useful in highlighting the qualitative importance of non-climatic variables in plant distribution, it does so with the use of artificial data. As such, is not necessarily indicative of the patterns and processes found in natural plant communities. Predictive models require greater understanding of the ecological processes that influence species distributions in the context of climate change. While species distribution models assume that realised niches will be retained over time, with species migrating to remain within current climatic envelopes (Thuiller et al. 2005; Brooker et al. 2007), limitations of dispersal and establishment success may prevent a species from shifting its range to keep pace with a changing climate (Urban et al. 2012).

The role of dispersal in determining range limits

With ongoing climate change, certain climatic filters including temperature and snow-duration are relaxed in alpine environments (Alexander et al. 2016). These changes have the potential to open up habitat to plant species at their leading-edge (Alexander et al. 2015). Globally, alpine tree-lines are thought to be strongly temperature-controlled (Slatyer and Noble 1992; Harsch et al. 2009), and therefore potentially responsive to warmer temperatures (Holtmeier and Broll 2005). However, a meta-analysis revealed upward advancements at only half the examined tree-lines (Harsch et al. 2009). In Australia, though warmer temperatures have extended the fundamental niche at the upper boundary of snow gums by 100 m, the tree-line has remained relatively stable (Green 2009). Even after extensive fires in the Australian Alps provided suitable conditions for seedling establishment, most recruitment was seen within and below the tree-line, indicating that upslope migration may be limited by dispersal ability. In the Italian Alps, species that have migrated upslope the farthest since the 1950s are those that possessed light, wind-dispersed diaspores (Parolo and Rossi 2008).

As previously discussed, plant dispersal traits have been incorporated into some species distribution models, with wind-dispersal denoting greater migration success (Austin 2002; Brooker et al. 2007). However, though primarily wind-dispersed, tree-line species in the northern hemisphere show little sign of upslope migration, suggesting post-dispersal mechanisms may influence leading-edge expansions (Hobbie and Chapin 1998). Similarly, though dispersal has been found to be sufficient, there has been little sign of upslope advancement in the Scandinavian mountains by mountain birch, potentially due to the interaction of micro-topography, climate and herbivory (Hofgaard et al. 2009; Speed et al. 2010). Species limited by pre- or post-dispersal processes are therefore at risk of failing to remain within their current climate-envelopes with continued climate warming. Certainly, migration is a process not only tied to traits such as seed size and dispersal ability, but also contingent on propagule availability, germination niche, and seedling establishment.

A more 'in-depth' understanding of range limits

There is little doubt that climate underpins the large-scale distributions of many plant species (Körner 1999), and this is indeed a major assumption in most species distribution models (Brooker et al. 2007; Randin et al. 2009; Dullinger et al. 2012). This is particularly evident for mountain plants where the upper boundary of alpine or subalpine species can be correlated with mean seasonal temperature (Körner 1999). However, the mechanism behind these boundaries are more complex than can be expressed by average growing season temperatures typically used by climate-envelope modelling (Körner et al. 2016). In mountain plants, irregular freezing temperatures during the growing season are more likely to result in tissue death and plant mortality than average minimum temperature (Larcher 1995). Körner et al. (2016) demonstrate that frost damage during bud break and leaf emergence during the growing season are instrumental in establishing the cold-edge range limits of five tree species in Europe. Freezing resistance is also species-specific and related to location, with higher freezing resistance reported for plant populations with increasing altitude (Venn et al. 2013). In addition, different life stages of plants exhibit unequal frost resistance: while adult plants may be able to re-sprout from protected buds, seedlings are much more sensitive to freezing temperatures (Larcher 1995). Indeed, entire cohorts may be devastated by one incidence of early spring frost (Larcher 1995). Hence, individual life-history stages may respond differently to abiotic conditions, and will contribute unequally to population viability beyond current ranges (Warren and Bradford 2011).

The role of biotic interactions in determining range limits

Competition and facilitation also play important roles in the structure and assemblage of alpine plant communities (Holt 2009). The relative importance of such interactions may be distinguished by comparing plant survival or productivity in the presence or absence of benefactors, or when a component (such as the canopy) of the benefactor is altered (Bertness and Callaway 1994). Positive associations with invasive *Taraxacum officinale* and the cushion plant *Azorella monantha* in the Chilean Andes was confirmed, as *T. officinale* seedlings planted within the canopies of *A. monantha* experienced higher survival, net-photosynthesis and stomatal conductance than those planted in bare patches (Cavieres et al. 2005). The acquisition of, and use of resources necessary for plant growth such as nitrogen and water, are linked to photosynthetic performance (Muraoka 2002). Hence, a major limitation of alpine plant growth is photosynthetically active radiation (PAR, 400-700 nm) during the growing season (Körner 1999). A reduction in incident PAR from neighbouring plants, while constituting ‘resource competition’, can be mitigated, or balanced by indirect (positive) effects of reduced solar insolation on topsoil moisture (Körner 1999).

Positive spatial associations between mature adults of one species and the seedlings of another are widely referred to as the ‘nurse plant’ syndrome, and typically occur in stressful habitats (Callaway 1995; Callaway et al. 2002). At high elevations, amelioration of stressors such as strong winds, soil instability and drought by stress-tolerant neighbours, facilitates the persistence of less stress-tolerant species (Bertness and Callaway 1994). While neighbours positively influenced the growth of target species in the Tibetan Plateau, positive responses were related to species density, suggesting that both competition and facilitation were operating in parallel (Wang et al. 2007). This is because the magnitude of positive and negative plant interactions changes across a species range (Bertness and Callaway 1994).

It is generally accepted that a species’ lower boundary is constrained by competitive interactions and extended at upper boundaries by facilitation by more stress-tolerant species (Bertness and Callaway 1994). The apparent inverse relationship between competitive ability and stress-tolerance was popularised by Grime (1977), and is neatly demonstrated with manipulations along an environmental gradient. Plant species responded to neighbour removals according to their position along an altitudinal gradient in the French Alps (Choler et al. 2001). When neighbours were removed from target species at their trailing-edge, biomass increased, while biomass decreased with neighbour removal at the leading edge, where species are typically more constrained (Choler et al. 2001). This stress-gradient hypothesis is supported by evidence from neighbour removal experiments conducted worldwide where generally, interactions shifted from competition to facilitation as elevation and abiotic stress increased (Callaway et al. 2002). These large-scale manipulative experiments highlight the underestimation of plant-plant interactions in ecological theory (Choler et al. 2001). And, while the balance between competition and facilitation shifts across space, it may also shift across time.

Potentially positive or negative responses to neighbours may change depending on the life stages of the interacting species (Callaway and Walker 1997), or temporal fluctuations in the environment (Valiente-Banuet 2008). Indeed, the aforementioned nurse-plant syndrome is typically favourable only for beneficiaries during early life-stages and may switch to a competitive interaction as the seedling matures (McAuliffe 1988; Callaway 1995). Interactions can also shift with variation in climate over the course of a single growing season

(Kikvidze et al. 2006), where abiotic stressors are relaxed or heightened (Bertness and Shumway 1993). Further changes in environmental conditions may alter the balance of facilitative and competitive interactions between plant species. In alpine environments, the relaxation or alteration of certain climatic filters with ongoing climate change is likely to change the direction and strength of plant interactions.

The role of biotic interactions in determining future distributions

As predicted, species have begun to shift their distributions in response to climate change. This is especially evident in alpine systems where steep elevational gradients provide short-distance escapes (Bertrand et al. 2011). Transplant experiments are valuable in teasing out the relative importance of biotic factors beyond a species' current range. In Arctic tundra, the growth and survival of several species transplanted above current elevation limits was limited by below-ground competition from tundra plants (Hobbie and Chapin 1998). Conversely, germination and establishment of sugar maple was lowest beyond its current upper-boundary due to granivory by the southern red-backed vole (Brown and Vellend 2014). In contrast, root pathogens limit upward expansion of sugar maple (Brown and Vellend, 2014), while fungal endophytes extend the range of *Bromus laevipes* due to conferred drought resistance (Afkhami et al. 2014).

Variations in establishment success beyond current ranges will likely result in the reorganisation of community members into novel plant assemblages (Urban et al. 2012). Alexander et al. (2015) test the effects of asynchronous migration on the performance of four target alpine plants. When alpine plants were transplanted to lower altitudes to simulate migration failures, performance was hindered by novel competitors. Conversely, performance of the same species was enhanced when transplanted into novel high-altitude communities. This asymmetry in competitive ability between plants from lower and higher altitudes suggests that species are likely to be affected at the trailing edge of their ranges (Alexander et al. 2015).

Current and future distributions of plant species are controlled by a combination of abiotic and biotic factors, acting in concert. These forces are dynamic, shifting over temporal and spatial scales but are often ignored or minimised in species distribution modelling.
The relative, and simultaneous importance of climate, biotic interactions, and other constraints on current and future distributions, can only be separated by experimental manipulation; however, empirical studies of this type are rare (Holt 2009). I conducted a series of field and laboratory experiments on the ecology and physical tolerances of a model species Alpine Podoelpis (*Podolepis robusta,* Asteraceae). I aimed to investigate how abiotic and biotic factors affect seedling survival, in order to make inferences on constraints to current and future distributions. The type and strength of plant interactions were determined with a transplant experiment above and below the current distribution of Alpine Podolepis at Mt Hotham, along a temperature and moisture gradient. In addition, laboratory experiments assessed germination characteristics, and freezing and shade tolerance of seedlings. Specifically, I tested the following hypotheses:

(i) competition will reduce seedling survival and growth at lower altitudes, and facilitation will increase survival and growth at higher altitudes;

(ii) germination niche for Alpine Podolepis is narrow;

(iii) Alpine Podolepis survival and growth is restricted by light limitation; and

(iv) early seedling survival is constrained by freezing temperatures.

Methods

Study species

Podolepis robusta (Maiden & Betche) J.H. Willis, commonly known as Alpine Podolepis, is a small (20 – 60 cm) erect perennial daisy (Jeanes 1999). Alpine Podolepis is restricted to, and reasonably common throughout the Australian Alps Biogeographic Region (Frood 2015) (Fig. 1). It grows largely in association with snow gum woodland and alpine meadows at the upper limit, or on the edge of inverted tree-lines associated with cold air drainage, at altitudes between 1200 – 1700 m (Jeanes 1999; Frood 2015). At Mt Hotham, plants are largely associated with the warm and dry north-west aspect (J. Morgan, *unpublished data*).

The abundance of Alpine Podolepis was once reduced at least in part through cattle grazing up until the 1950s (Van Rees 1982; Wahren et al. 1994), a disturbance which has since ceased (Wahren et al. 1994). The effect of fire is not thought to have long-lasting influences on the abundance of Alpine Podolepis as, like many alpine forbs and grasses, it responds by resprouting rapidly post-fire (Wahren et al. 2001). In early spring, multiple shoots arise from a basal rosette of glabrous, light green leaves (Frood 2015). Alpine Podoelpis flowers in summer (Dec-Mar) and are characterised by bright yellow capitula (20-35 mm in diameter), clustered in dense cymes (Jeanes 1999) (Fig 2.). Compared to other alpine daisies, seeds are heavy (0.69 mg ± 0.01 mg) (Sommerville et al. 2013). Though presumably wind dispersed, there is currently no experimental evidence concerning the efficacy of wind dispersal by Alpine Podolepis.

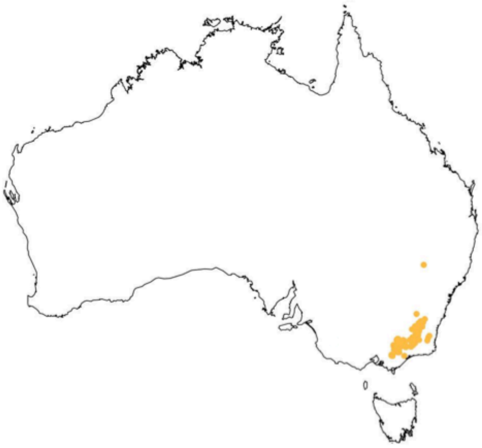


Fig. 1. Occurrence records of Alpine Podolepis (Atlas of Living Australia, 2017).

Fig. 2. *Podolepis robusta* in flower (image: J. Morgan)

Study Site

All laboratory and glasshouse experiments were conducted at La Trobe University, Bundoora, Melbourne, while field experiments were conducted at Mount Hotham (Fig. 3). Mt Hotham (1860 m) is one of Victoria's highest mountains. Mean annual precipitation is ~1480 mm, most of which falls as persistent snow during winter. Mean minimum and maximum temperatures range from 8°C to 16.3°C mid-summer and -0.1 to -3.6 °C mid-winter (Bureau of Meteorology, 2017). Frosts are frequent, even during warmer months (Williams and Ashton 1987).

Ten study sites at Mt Hotham were chosen to represent a gradient of temperature and moisture. Sites range from 1620 m (lowest) to 1855 m (highest), and include five sites on each of south-east and north-west facing slopes (Table. 1). These have different exposure to incident light, which effects temperature, evaporation and hence, snow duration and growing season conditions.

Site conditions

Air temperature at 5 cm above ground during study period (Nov 2016 – Mar 2017) was measured bi-hourly with Thermochron iButtons (Maxim Integrated, California, USA) attached to a wooden stake at each site. From these data, growing degree days (GDDs) were calculated (McMaster and Wilhelm 1997) as an indicator of thermal accumulation (in °C). GDDs were summed for each site in order to represent a cumulative index of available energy for growth and development of seedlings during the study duration, according to the formula:

$$\text{GDDs} = [(T_{MAX} + T_{MIN}) / 2] - T_{BASE},$$

where T_{MAX} and T_{MIN} are the daily maximum and minimum temperatures, respectively, and T_{BASE} = the temperature above which metabolic function is possible. 0°C was chosen as the base temperature, as per Brown et al. (2006) and Venn et al. (2013).

At each site, light interception by dominant vegetation was measured with a quantum light sensor (LI-COR, Nebraska, USA). Photosynthetically active radiation (PAR) was measured a total of ten times above and below the canopy of vegetation along a 30 m transect at 3 m intervals. Along the same transect, vegetation structure was measured at 1 m intervals, whereby canopy interception of herbs, graminoids and shrubs along a structure pole was recorded within height classes of 10 cm increments.

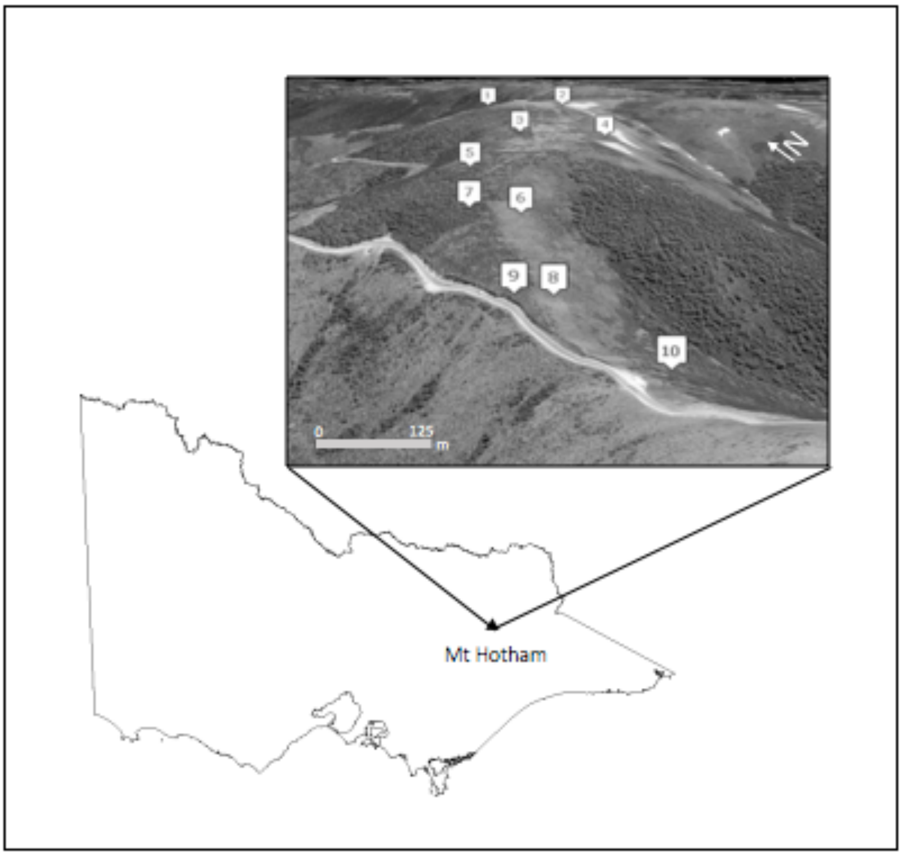


Fig. 3. Location of Mt Hotham in Victoria, and study site locations at Mt Hotham (1-10) representing the elevation gradient on south-east and north-west sites (see Table. 1).

Table 1. Summary information for the ten sites along the Mt Hotham transect including location, altitude and aspect for each site. (UTM = Universal Transverse Mercator coordinate system).

Site	Location (UTM 55H)	Altitude (m)	Aspect
1	511370 E, 5907898 N	1855	NW
2	511433 E, 5907823 N	1860	SE
3	511218 E, 5907696 N	1820	NW
4	511297 E, 5907589 N	1800	SE
5	510990 E, 5907580 N	1780	NW
6	510924 E, 5907434 N	1690	SE
7	510900 E, 5907495 N	1700	NW
8	510816 E, 5907296 N	1660	SE
9	510792 E, 5907329 N	1670	NW
10	510783 E, 5907128 N	1620	SE

Field transplant experiment

To determine the controls on Alpine Podolepis seedling survival and growth, beyond the boundaries of its current distribution, a transplant experiment was undertaken at Mt Hotham. The effects of altitude, aspect and competition were examined.

Seed was germinated from seed collected at Mt Hotham in March, 2016. Seed was surface sown onto a mixture of sterilised perlite, sand and potting mix in October 2016 in a glasshouse. Propagated seedlings were then pricked out into trays with 4 X 4 cm soil plugs and grown for 6 weeks under glasshouse conditions. Prior to planting at Mt Hotham, seedlings were placed outside for 7 days at Bundoora, and were then transported to Mt Hotham, acclimated for 5 days, and then planted over a 3-day period. Seedlings were kept in their trays during transportation to each site. In mid-November 2016, each site received 26 seedlings, one into each gap (cleared) and control plot, arranged along a 26 m transect with alternating treatments at each metre interval. Cleared plots were created for 'gap' treatment by removing above-ground vegetation from within ~15 cm of the transplant site with secateurs and were maintained monthly. The gap treatments were probably conservative. Seedlings planted into gaps were likely still given some shelter from winds by resident vegetation. At planting, the number of leaves, and length of longest leaf was recorded. These measurements were recorded again at the final survey in March 2017. Seedling survival was recorded monthly.

Laboratory germination experiment

To determine whether seed germination of Alpine Podoelpis has a narrow verses wide germination niche, seeds were exposed to different temperature and light availability regimes in a laboratory growth cabinet study.

Treatments spanned a range of diurnal temperatures that represent spring/autumn conditions (14/10 °C), early to mid-summer conditions (20/12 °C, 24/16 °C) and extreme mid-summer conditions (30/20°C). Each treatment was conducted with 12 hr light/dark cycles (Thermoline Growth Cabinets). Within each treatment, seeds were either exposed to light/dark cycles or were kept in constant dark conditions by wrapping petri dishes in two layers of aluminium foil. An additional treatment at 4°C was implemented for two sets of replicates in constant dark conditions. After 30 days, if 0% germination was scored, replicates were moved into growth cabinet at 14/10°C and placed into respective light/dark and constant dark conditions.

For each treatment, there were five replicates, each consisting of 25 seeds placed into 90 mm petri dishes on Whatman #1 filter paper moistened with distilled water and sealed with Parafilm to prevent loss of moisture. These replicates were placed, stacked, into growth cabinets. The order of stacked dishes was randomised after scoring.

Replicates were scored for germination approximately every 4 days for light/dark treatments, and approximately every 8 days for replicates in constant dark treatments in order to minimize light exposure. Seed was considered germinated once the radicle had emerged from the seed coat, and were removed after scoring. Filter paper was re-moistened when required. Once 12 days passed with no new germination from within a treatment, remaining seeds were tested for viability using tetrazolium testing (Moore 1973). At the end of the experiment, germination percentages were adjusted for viability.

Light limitation experiment

The effect of light availability on seedling growth was examined in a glasshouse experiment. In this experiment, net photosynthesis and biomass accumulation were assessed in relation to three light regimes. The treatments were: (i) 0% shade (treated without shade cloth); (ii) 48% shade, (iii) 82% shade. Photosynthetically Active Radiation (PAR) in the glasshouse on a clear day at midday was approximately 1500 µmol m^{-2} s^{-1}.

Treatments were constructed using commercial knitted shade cloth attached to the sides and top of a rectangular enclosure constructed of 2.5 mm fence wire and chicken wire netting. Seed was surface sown onto a mixture of sterilised perlite, sand and potting mix. Propagated seedlings were then pricked out into 40 x 100 mm pots containing sterilised potting mix and grown for seven days for an acclimation period and to control for mortality due to transplant shock. During the acclimation period, seedlings were grown under full ambient light in the glasshouse and irrigated at regular intervals. After this period, three seedlings were allocated at random to each treatment of which there were five replicates. The dry-weight of both above and below ground biomass of 15 seedlings was measured at the commencement of experimental treatments. Treatment replicates were repositioned weekly to control for glasshouse effects, and seedlings were irrigated at regular intervals.

I measured foliar gas exchange with a differential infrared gas analyser (IRGA) (PP-Systems, Massachusetts, USA), 70 to 80 days after seedlings were installed in their respective light regimes. Measurements were taken under ambient temperature conditions, while CO_2 was controlled for each replicate at 400 ppm. Measurements were restricted to the hours between 11:45 am and 1:45 pm on clear days to reduce the influence of passing cloud and sun position. Five recordings were taken manually on three fully expanded leaves from each seedling. Each leaf was inserted inside the leaf cuvette of the IRGA, where records of net-photosynthesis, stomatal conductance, photosynthetically active radiation (PAR) intensity, leaf humidity and temperature were obtained. At the time of final recording, all seedlings were harvested for above and below ground biomass, washed to remove excess substrate and dried at 80°C for 48 h in order to obtain measurements of dry-weight biomass.

Freezing resistance experiment

To assess the sensitivity of seedlings to extreme cold, the effects of freezing temperatures were assessed in the laboratory using chlorophyll fluorescence and the fluorescence yield of Photosystem II.

Plant material for freezing resistance analysis was collected from the population at Mt Hotham in mid-March 2017. During collection, 15 whole rosettes were harvested and sealed in polyethylene bags, and transported to the laboratory in Melbourne in a chilled portable cooler. Upon arrival at the laboratory, plant material was wrapped in damp paper towel in order to maintain hydration of plant material, and stored at 4°C in the dark for 24 h to allow

for cold acclimation. Following pre-treatment, three leaves from each individual were subjected to one of four temperature treatments (-5°C, -11°C, -20°C) for 8 h using thermostatically controlled freezers. Similarly, control samples were held at 4°C. Following the freezing treatment, plant material was wrapped in damp paper towel, sealed in polyethylene bags and placed in the dark in a constant temperature facility at 18°C.
The ratio of variable to maximum fluorescence of the plant material (F_V/F_M) was then determined after three days using a PAM chlorophyll fluorometer (Walz, Effeltrich, Germany). F_V/F_M ratios are reported alongside control (4°C) samples, providing an estimate of photosystem II efficiency during the assay procedure.

The above process was also executed for seedlings. Seed collected from Mt Hotham in 2016 was surface sown on a mixture of sterilised perlite, sand and potting mix. Propagated seedlings were pricked out and transplanted into 40 x 100 mm pots filled with potting mix and grown for three weeks under glasshouse conditions. After this period, seedlings were washed to remove excess substrate from roots. Seedling roots were retained during freezing resistance treatments. Rather than assessing freezing damage to three leaves per plant (as with the mature plants), one leaf was assessed from 15 replicate seedlings for each treatment due to the small number and size of leaves.

Data Analysis

Field transplant experiment

Prediction: If the direction of plant interaction changes among seedlings along a temperature and moisture gradient, I would expect to see higher survival in gaps relative to controls at low altitudes where competitive processes are more likely, switching to higher survival in controls relative to gaps at higher altitudes, where facilitative processes become more common (Callaway 1995). Additionally, if the current distribution of Alpine Podolepis is controlled by climate, I predict that there would be lower survival on the south-east aspect. Therefore, in the modelling, treatment, altitude and aspect were considered as fixed effects. To test whether seedling survival differed among fixed effects, generalised linear models (GLM) were fit using the Laplace approximation in the package *lme4* (Bates et al. 2015) in the 'R' statistical package (R Core Team 2013). Model selection was based on the Akaike information criterion (AIC) (Akaike 1974).

Similarly, plant performance (growth) is expected to change according to treatment (gap or control) along an altitudinal gradient. The net direction of positive and negative interactions was calculated between pairs of transplanted seedlings in gap and control plots using the Relative Neighbour Effect (RNE) Index (Brooker et al. 2005; Venn et al. 2009):

RNE= (Gap – Control / MAX (Gap, Control),

where Gap and Control correspond to the performance of individuals in gaps (neighbours removed) and controls (neighbours left intact), respectively, and MAX (Gap, Control) refers to the highest performance value between the two treatments. Length of longest leaf was the indice used to quantify seedling performance and was calculated as final length / initial length upon the final survey in March 2017. RNE values were modified as per Callaway et al. (2002) such that negative values indicate negative neighbour effects on performance (competition), and positive values indicate positive neighbour effects on performance (facilitation). Presented are mean RNE for seedlings in paired 'gap' and 'control' plots. In the analysis, a death in any pair of seedlings was removed from final calculations. This meant that in one case, on the south-east aspect, a site was removed from analysis due to low replication of paired seedlings. In addition, a site on the north-west aspect was could not be analysed due to missing data. RNE values were analysed with one-way ANOVA according to site whereby the lowest site on each aspect was set as the 'dummy' that all other sites on that corresponding aspect were compared to. North-west and south-east aspects were analysed separately in order to tease out the direction of plant interaction by altitude alone without potential confounding factor of aspect.

Light limitation experiment

Prediction: If competition for light is a key factor limiting the distribution of Alpine Podolepis, then I would expect to see reduced rate of photosynthesis and reduced biomass with decreasing light availability. Rate of photosynthesis and dry-weight biomass were fitted in separate generalised linear mixed effects models (GLMM) using *lme4* (Bates et al. 2015) in the 'R' statistical package (R Core Team 2013). In the first instance, shade-house replicate, plant, and leaf were used as random factors, and seedling was used as a random factor in the latter.

Laboratory germination experiment

Prediction: If specific germination requirements are limiting factors in the distribution of Alpine Podolepis, I would expect to see a narrow range of germination.
The interaction between light and temperature on the germination of Alpine Podolepis seedlings was analysed with a generalised linear model (GLM) using *lme4* (Bates et al. 2015) in the 'R' statistical package (R Core Team 2013). A quasi-binomial error distribution was used in order to account for the over-dispersion evident in germination data (clustering of binary outcomes within treatments). Final germination of seeds in dark and light treatments at 14°C were compared to those that received a period of cold-stratification using Student's t-tests.

Freezing resistance experiment

The extent of tissue damage in response to freezing temperatures (-5°C, -11°C, -20°C) was analysed. If recruitment dynamics are influenced by occurrences of freezing temperatures, seedling tissue is expected to experience higher damage relative to control (4°C) and to adult tissue. Student's t-tests were used for simple comparisons between F_V/F_M ratios of adult and seedling leaves, as a greater temperature range is required in order to calculate level of 'freezing resistance' by linear interpolation as per Bannister (2005) and Venn et al. (2013). Lethal temperatures are considered those at which 50% damage occurs to the photosynthetic apparatus of leaves relative to control (4°C).

Results

Site conditions

South-eastern exposed sites experienced more freezing days (days ≤0°C) than north-west exposed sites during study period (Nov 2016 – Mar 2017). The number of freezing days increased with altitude, and this trend was similar for both aspects (Fig. 4).

Overall, as expected, north-western sites experienced greater cumulative GGDs during the study period than sites on the south-east (Fig. 5). GDDs decreased with increasing altitude on south-east exposed sites. The highest cumulative GDDs was recorded at 1780 m on the north-west, and there did not appear to be a linear trend with GDDs and altitude. This is possibly due to the influence of vegetation cover at sites on the north-west, as dense vegetation cover reduced incident light by 75 – 100% at 1670 m and 1820 m respectively (see Appendices I & II).

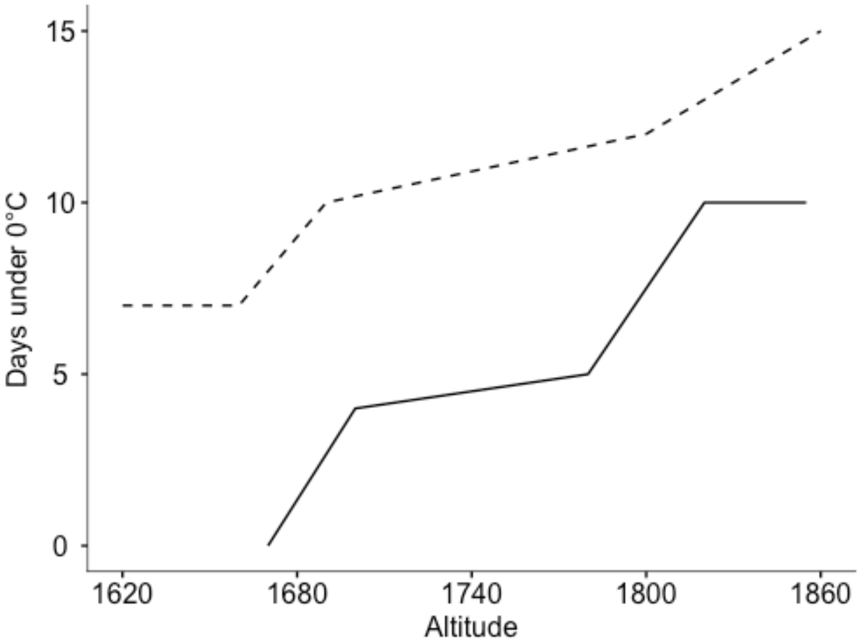


Fig. 4. Total number of freezing days (temperatures ≤0 °C) recorded at Mt Hotham in relation to altitude during study period (Nov 2016 – Mar 207) on north-west (solid line) and south-east (dashed line) exposed slopes.

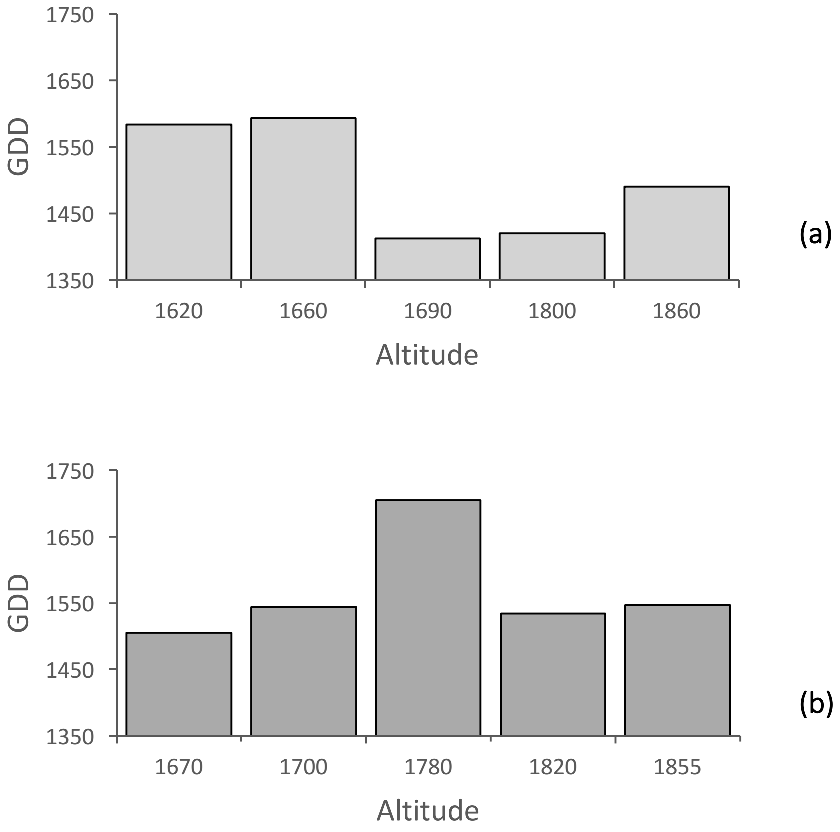


Fig. 5. Growing Degree Days (GDD) recorded for south-east (a) and north-west (b) exposed sites during study period (Nov 2016 – Mar 2017).

Field transplant experiment

Pooled across all sites and treatments, total survival of seedlings over one growing season was 82%. Survival was significantly affected by treatment, with higher mortality for seedlings planted into gaps than controls (p<0.001) (Fig. 6). A trend of increasing mortality with altitude was significant for seedlings in both gap and control treatments (p<0.05). Seedling survival was not significantly different on north-west or south-east exposed sites (p>0.05).

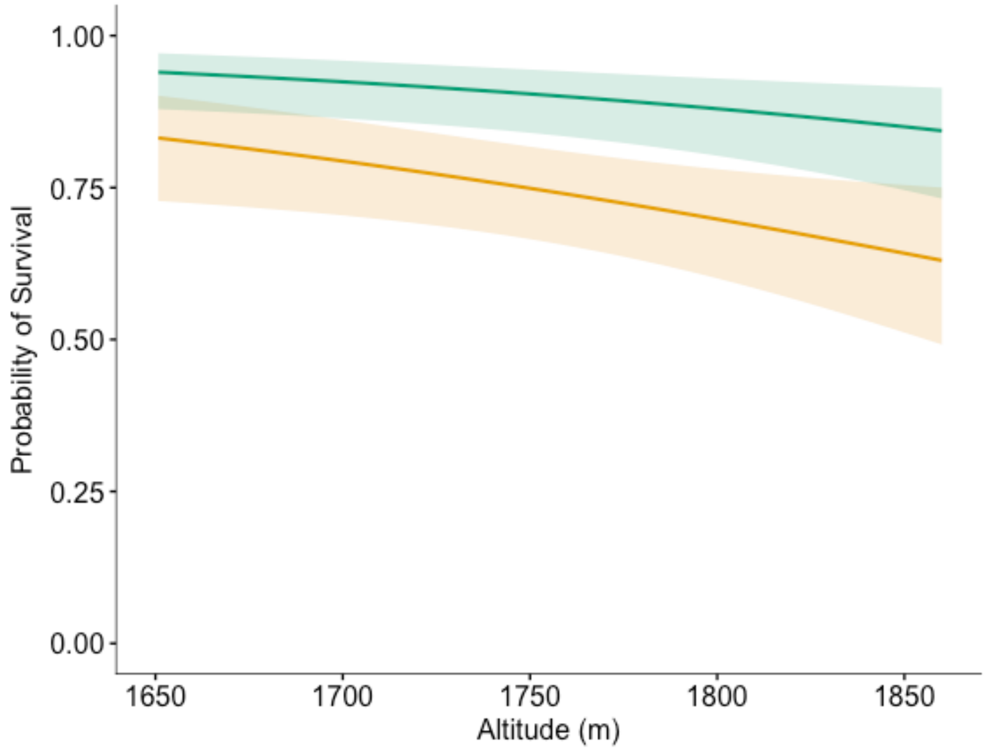


Fig 6. Effect of treatment and altitude on seedling survival. Mean probability of survival (±95% CI) over one growing season for seedlings planted along an altitudinal gradient in control (solid green line) and gap (solid orange line) treatments.

Interaction effects on seedling performance were positive at seven of eight planting sites that varied in altitude and aspect; at the remaining site the interaction was neutral (Fig. 7). The greatest differences in leaf growth occurred at 1820 m on the north-west aspect where seedlings planted into cleared and control plots increased leaf size by 12 and 84%

respectively, hence the positive RNE value. Seedlings at 1670 m showed a 153% increase of leaf size in cleared plots and a 110% increase of leaf size in control plots, hence the neutral RNE value. No statistical differences between RNE values were detected for planted seedlings on the south-east sites; rather, positive interactions with close neighbours were consistent at each site along the elevation gradient. On the north-west aspect, the neutral interaction at 1670 m differed significantly to 1820 m ($p<0.01$) and 1855 m ($p<0.05$) where growth was positively influenced by close neighbours (Fig. 7a; Appendix IV, Table. 6).

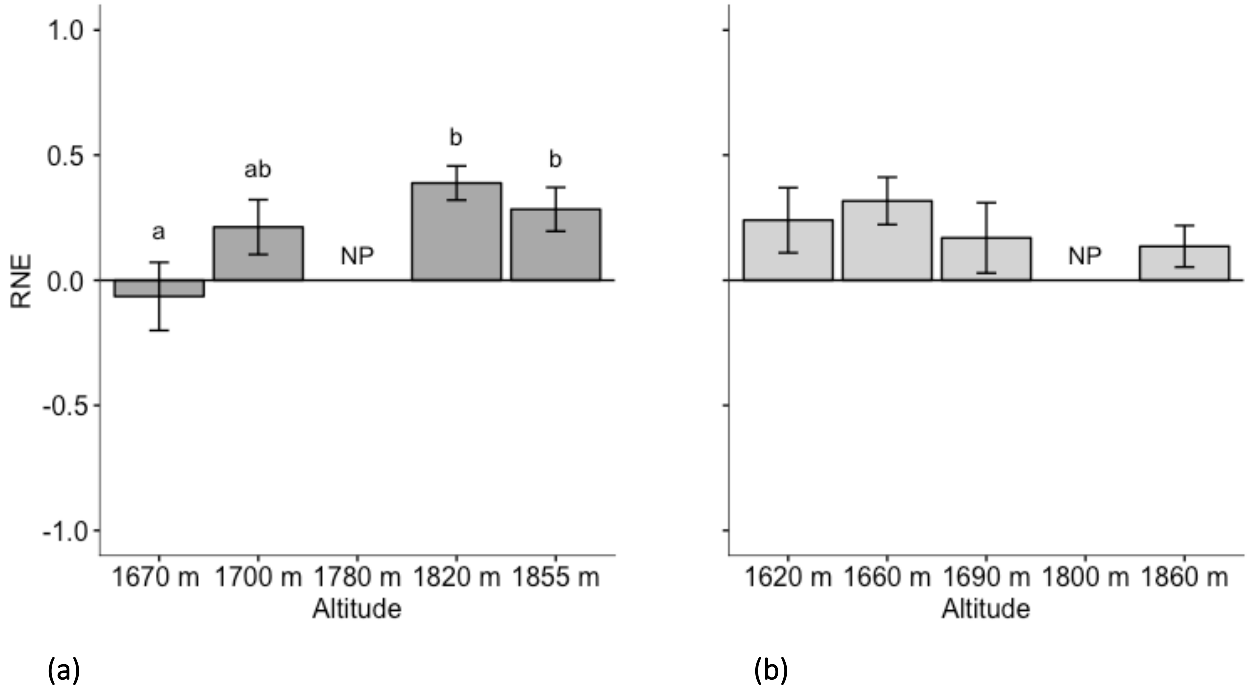
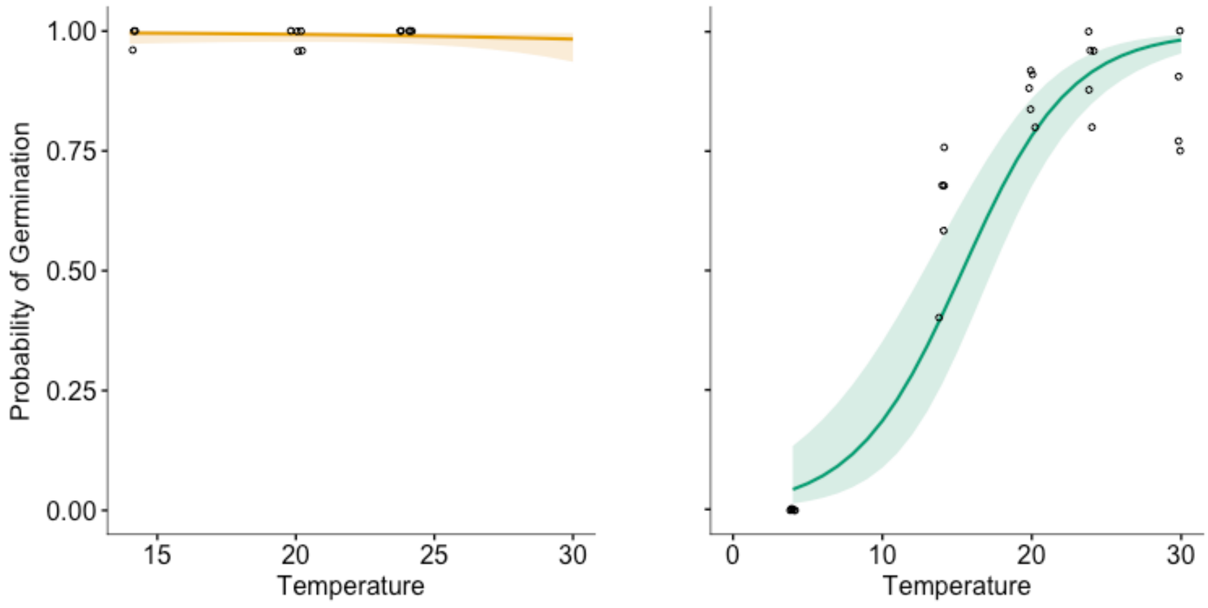


Fig. 7. Mean Relative Neighbour Effect (RNE) (± 1 SE) for paired transplanted seedlings in gap and control treatments on (a) north-west and (b) and south-east exposed aspects across the elevation gradient. Positive values indicate facilitative interactions, and negative values indicate competitive interactions. Neutral interactions are indicated by error bars crossing the y axis at 0. Different superscripts above columns denote significant differences between sites. NP labels indicate that analysis was not possible.

Laboratory germination experiment

Temperature-mediated dormancy is weak, with high germination (>50%) across all diurnal temperature and light conditions, and only constrained at the lowest temperature in the dark (Fig. 8). There was a significant interaction between light and dark treatments with temperature ($p<0.05$), as germination is suppressed in dark conditions ($p<0.01$), but increases with temperature ($p<0.001$), while germination occurred equally well at all temperature regimes in light conditions (14 °C – 30 °C). Time to 50% germination (t_{50}) occurred without stratification and within 30 days for both light and dark conditions ≥ 20°C. At 14°C in the dark, response to cold stratification was positive ($p<0.05$), increasing germination by 21.8% and reducing T_{50} by at least 42 days (Table 2). In the light treatment, T_{50} decreased only marginally by 3 days after cold stratification.



(a) (b)

Fig. 8. Effect of light and temperature on germination. Fitted values for probability of germination for (a) light conditions and (b) dark conditions (±95% CI) for the generalised linear model applied on cabinet germination data. Germination percentages from raw data included as points. Note the different scales for temperature axis.

Table 2. Germination attributes of Alpine Podolepis at 14°C with and without a period of cold stratification. LAG (days) = the number of days from the start of the experiment until germination began. t_{50} (days) = the number of days for 50% of total germination to occur.

Light treatment	Cold stratification period	LAG (days)	t_{50} (days)	Final % germination
Light	30 days	4 - 8	8 - 11	96.8
Light	0 days	7 - 10	14 - 20	99.2
Dark	30 days	11 - 14	13 - 23	83.8
Dark	0 days	10 - 13	62 - 65	62

Light limitation experiment

Both seedling dry mass (above and below ground biomass) and net photosynthesis responded similarly to light limitation treatments (Fig 9. 10.). Values were comparable for seedlings grown in full sun (0% shade) and at 48% shade for seedling biomass ($p>0.05$) and net photosynthesis ($p>0.05$). However, plant biomass (Fig. 10) was reduced significantly in seedlings grown under 82% shade when compared to seedlings grown in full sun (0%) ($p<0.001$) and 48% shade ($p<0.001$). Similarly, net photosynthesis (Fig. 9) was significantly lower for seedlings grown at 82% shade when compared to seedlings grown in full sun ($p<0.01$) and 48% shade ($p<0.05$).

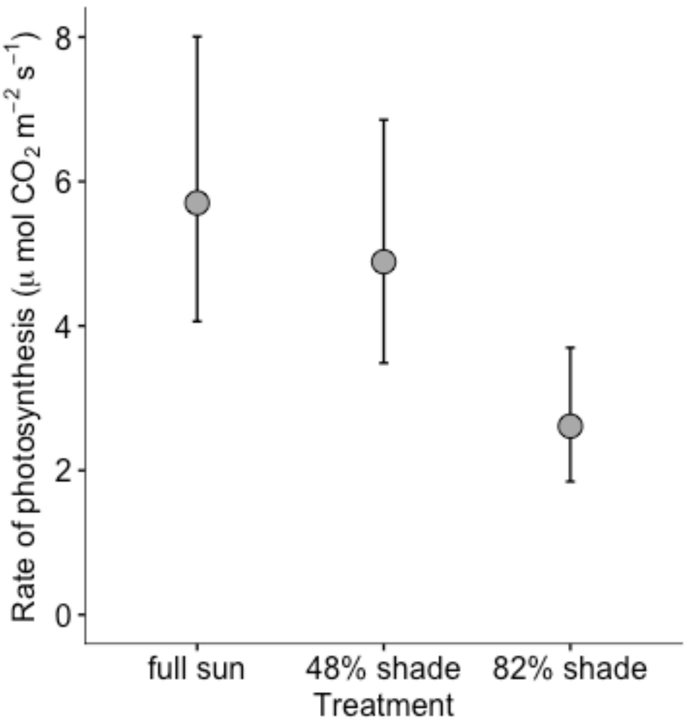


Fig. 9. Effect of light limitation on net photosynthesis. Fitted mean rate of photosynthesis (±95% CI) of seedlings grown under full sun, 48% shade and 82% shade.

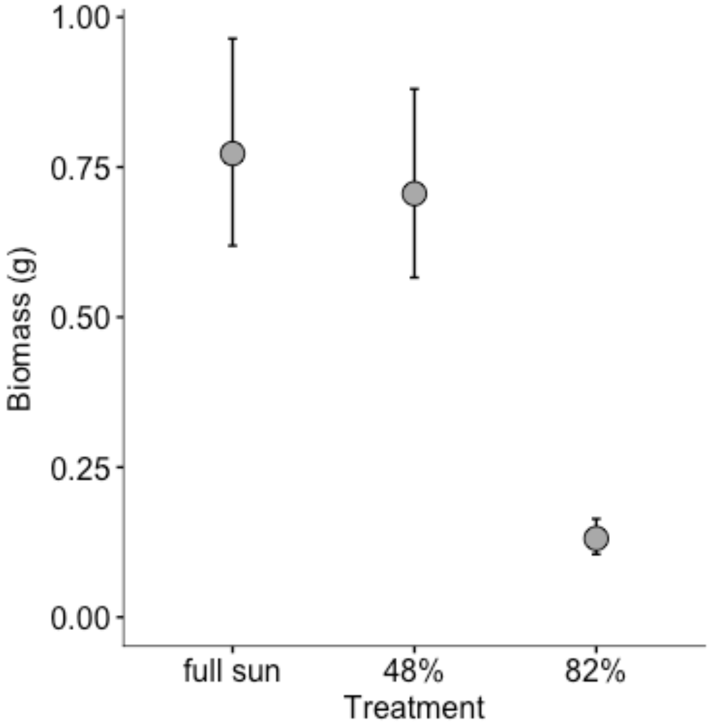


Fig. 10. Effect of light limitation on biomass. Fitted mean dry-weight of biomass (±95% CI) of seedlings grown under full sun, 48% shade and 82% shade.

Freezing resistance experiment

The F_V/F_M ratios of adult and seedling leaves declined dramatically with decreasing temperatures in the laboratory freezers (Fig 11.), with a substantial decrease evident for seedling leaves at -5°C and adult leaves at -11 °C. At -5°C, seedlings experienced significantly greater damage to the photosynthetic apparatus of leaves relative to control (4°C) ($p<0.001$) and to adult leaves exposed to the same treatment ($p<0.001$). Both adult and seedlings experienced almost complete damage at temperatures ≤ 11°C.

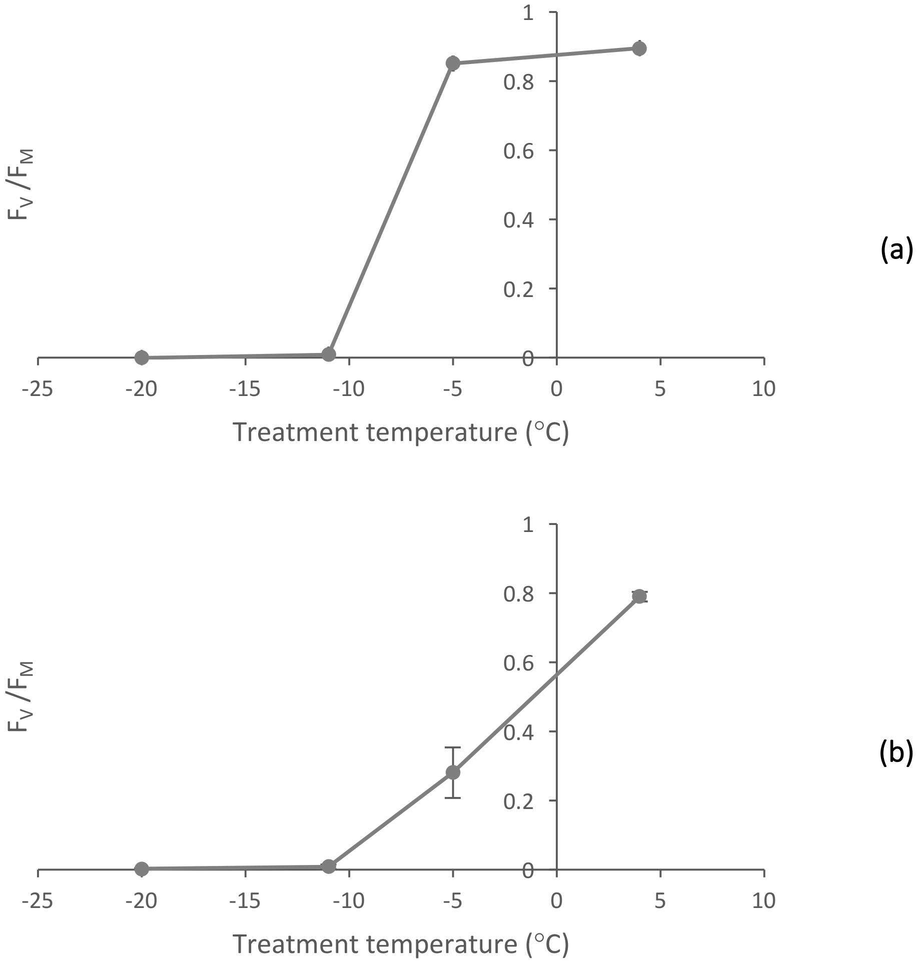


Fig. 11. Mean (± 1 SE) variable fluorescence to maximum fluorescence (F_v/F_m) ratios of leaf material used in freezing resistance study, at four temperatures: 4, -5, -11, and -20°C; for Alpine Podolepis leaves of a) mature plants and b) seedlings.

Discussion

Facilitative (positive) interactions influenced the survival and growth of seedlings over one growing season at Mt Hotham in the Victorian Alps. Seedling survival was not influenced by aspect, but a trend of increasing mortality with altitude was detected. The rate of photosynthesis and biomass accumulation may also be restricted in the field due to competition for light in heavily shaded sites, as suggested by glasshouse experiments. Germination was observed in the laboratory to be broad, at temperatures ≥14°C in light and dark conditions. While cold stratification was not required, the response to stratification was positive in dark conditions, where higher percent germination and faster germination rates likely reflects synchronous germination in the field after snowmelt. Young seedlings suffered greater damage to freezing temperatures than adult plants. As freezing temperatures are common and unpredictable in the alpine zone, vulnerability at the emerging seedlings stage may be a limiting factor in recruitment and distribution. Results suggest that what is observed today as the realised niche of Alpine Podolepis is not reflective of its potential range, and highlights the importance of facilitative interactions in alpine environments.

Germination characteristics

Germination is one of the most fundamental developmental processes in the life cycle of plants, and varies widely among species (Korner 1999). Alpine Podolepis exhibited high germination at a broad range of temperatures; however, it was suppressed in the dark at 4°C. Response to cold stratification was positive, increasing rate of germination and final germination in the dark. Though long-term dormancy is considered rare in alpine landscapes, some alpine species require the experience of low temperatures over winter in order to germinate (Baskin and Baskin 2003). This is the case with Australian alpine species *Aciphylla glacialis* (Venn and Morgan 2009), *Euphrasia collina ssp.* (Sommerville et al. 2013), and *Eucalyptus pauciflora* (Beardsell and Mullett 1984), where unless seeds are subjected to a period of cold-wet stratification, germination is poor or not possible. A lack of dormancy (excluding after ripening), and a wide germination range indicates that Alpine Podolepis are not dependent upon a specific temperature regime for germination, a common trait throughout Asteraceae (Baskin and Baskin 2003; Sommerville et al. 2013).

Positive responses to cold stratification have been reported for a wide array of alpine species, and in some cases widens the germination range and improves final germination (Sommerville et al. 2013). Hence, though germination was reduced in dark conditions, this is likely overcome *in situ* by a cold period experienced over winter. Cold stratification also reduces variability in germination time, synchronising seedling emergence after snow melt (Shimono and Kudo 2005). As such, it is unlikely that Alpine Podolepis are capable of storing dormant seed in the soil. This contrasts with *Carex* species where germination events are spread over two years, reducing the risk of complete recruitment failure (Schütz 2002). Hence, while it is unlikely that the distribution of Alpine Podolepis is controlled by narrow germination requirements seen in other alpine species, an opportunistic and likely synchronous germination in early spring indicates that recruitment hinges upon the amount of seed dispersed in the previous season, and the environmental conditions upon germination.

Frost tolerance in seedlings

Given requirements for germination are relatively broad for Alpine Podolepis, limits to its distribution must be controlled by factors other than a narrow germination niche. Indeed, while germination is common in the Victorian alpine zone, half the amount of naturally emerging seedlings dies before establishment (Venn and Morgan 2009). Alpine Podolepis seedlings were found to be more sensitive to freezing temperatures than adults, suffering significant damage to photosynthetic apparatus at -5°C. Cold-edge boundaries are set by occurrences of frost during the growing season, coupled with species-specific freezing resistance (ability to survive freezing temperatures without damage) (Körner et al. 2016). Freezing temperatures are an important filter on germination, recruitment and persistence in alpine plant communities (Körner and Paulsen 2004) and, as such, are principle determinants of geographic distributions (Sakai and Weiser 1973). Frosts in the Australian Alps are common, even during warmer seasons (Williams and Ashton 1987). During this study, freezing temperatures were recorded as being more common on south-eastern aspects, and increasing with altitude. Resistance to freezing temperatures of alpine plants over the growing season is reportedly quite high in Australian alpine species, with a pattern of increasing tolerance with altitude (Venn et al. 2013). While adults may be less susceptible to spring or summer frosts, seedlings have lower tolerance and limited recuperation ability, as recently emerging seedlings are yet to develop meristematic regions underground (Korner 1999). However, while it is unknown when the threshold for frost resistance is reached for Alpine Podolepis, occurrences of frost during seedling emergence, and during the early stages of establishment, are likely to reduce survival. Hence, seedling establishment may therefore be limited to relatively rare, favourable seasons. However, successful establishment may be possible, given suitable microsites (Venn et al. 2009).

Effects of facilitation along an abiotic stress gradient

During this study, seedling mortality was low, and was not affected by aspect, contrary to expectations, given the current, strongly north-western distribution of Alpine Podolepis at Mt Hotham. While seedling mortality increased slightly with altitude, mortality was low across the entire gradient of beyond-range transplants. Although our altitudinal gradient was small (235 m), the changes in environmental conditions were noticeable with more freezing temperatures recorded on south-eastern aspect, which increased on both aspects with altitude. As indicated by our freezing resistance experiment, early seedling survival is strongly affected by freezing temperatures. Our planted seedlings were six weeks old at time of planting, likely enough time for seedlings to develop root reserves and a level of frost resistance, unlike in newly emergent seedlings (Körner 1999). Hence, if conditions during the early growing season allow for seedling establishment, seedlings are tolerant to a range of conditions at Mt Hotham, contrary to what the current, strongly north-western distribution might suggest. Conclusions can only be based off of one growing season, and perhaps the strength of aspect and altitude may become more apparent with time.

In contrast, similar studies have reported high seedling mortality during the first growing season (Urbanska and Shutz 1986; Venn et al. 2009). Indeed, the seedling stage is critical in the life cycle of plants (Forbis and Doak 2004), and presumably, high survival over a single growing season is indicative of a high tolerance to varied climatic conditions that would be experienced along the altitudinal gradient. In alpine environments, plants are exposed to stressful abiotic conditions including freezing temperatures, needle ice, and scouring winds (Körner 1999). However, substantial variation in microhabitat influences the composition of local vegetation (Sherrer and Körner 2011). Such variation, while driven by topography, altitude, and slope orientation (Sherrer and Körner 2011), is also driven by vegetation (Körner 1999; Venn et al. 2009).

While seedling survival was generally high at all sites, survival was consistently higher in control (uncleared) plots than in gaps. Numerous studies highlight facilitation as an important factor in seedling survival in natural communities (Callaway et al. 1997; Brooker et al. 2007; Venn et al. 2009: Warren and Bradford 2010), as neighbouring plants ameliorate stressful abiotic conditions, creating a microclimate suitable for seedling establishment (Callaway et al. 1997). Indeed, while some species require bare patches for germination and establishment, seedlings in alpine environments are commonly reported clumped together in the lee of larger neighbours (Callaway et al. 2002). In such microsites, ‘nurse plants’ buffer establishing seedlings from scouring winds, increase local temperature and soil moisture (Callaway 1995) and aid in the reduction of disturbances such as soil frost heave (Venn et al. 2012). However, unlike many similar transplant studies which test the stress gradient hypothesis (Choler et al. 2001: Callaway et al. 2002; Cavieres et al. 2005), a switch in the type of interaction (facilitation or competition) was not evident. Instead, consistently positive interactions were demonstrated at all sites, highlighting the importance of positive interactions at one of Australia’s highest mountains. Perhaps this is unsurprising, given the gradients investigated by other ecologists are often greater and transplants are monitored over more than one growing season (see Choler et al. 2001: Alexander et al. 2015). However, Venn et al. (2009) and Alexander et al. (2015) report effects of competition during the first growing season. While competition certainly is an important factor in the distribution of species (Callaway et al. 1997; Dunnett and Grime 1999), it does not appear to be a key driver of Alpine Podolepis establishment during the first growing season.

Facilitative interactions positively influenced the growth of Alpine Podolepis seedlings at most sites over the course of one growing season, consistent with seedling survival response. This is counter to expectations that the direction of plant interactions should shift along an abiotic stress gradient (Callaway 1995; Choler et al. 2001; Callaway et al. 2002). One occurrence of neutral interaction (where seedling growth was not affected by the presence or absence of neighbours) was reported on the north-west aspect at the lowest site. Here, abiotic conditions did not negatively affect seedlings in cleared sites as it did elsewhere, a signal of relatively benign conditions, which is supported by local temperature data. Here, no freezing temperatures were recorded during the study period. Had sites extended to even lower altitudes, competitive interactions may have become the prevailing interaction as reported elsewhere (Callaway et al. 2002; Alexander et al. 2015). The lack of competitive interactions at Mt Hotham may be indicative of abiotic stressors other than temperature. Facilitative interactions are often reported due to low available moisture on dry aspects (Hillier 1990) and heat stress (Korner 1999).

Positive interactions may dominate for Alpine Podolepis during early life stage. Indeed, the patterns and phenomena of 'nurse plant' syndrome are often strongest during early life stages (Callaway 1995). Competitive interactions may dominate once the plant reaches maturity (Callaway 1995) or during mild seasons where abiotic stress is reduced (Kikvidze et al. 2006). Along a similar altitudinal gradient, positive interactions influenced the growth of *Brachyschome ridigula* seedlings, but the strength and balance of interactions shifted temporally (Venn et al. 2009). With environmental variation over the course of one, or many growing seasons, the direction and strength of facilitation and competition is likely to change in a predictable manner (Bertness and Callaway 1994; Brooker and Callaghan 1998). Nurse-plants may become out-competed by benefactors or the reverse (Callaway 1995; Kikvidze et al. 2006), while favourable seasonal conditions may tip otherwise facilitative interactions into competitive ones (Tielborger and Kadmon 2000; Valiente-Banuet 2008). Hence, while positive interactions predominate the growth and survival of Alpine Podolepis, over the first growing season, this trajectory may change through subsequent seasons.

Effects of competition on seedling growth

The mechanisms by which seedlings interact with natural communities are numerous, and can only be separated by experimental manipulation (Bruno et al. 2003). The results suggest that a “suitable” environment for Alpine Podolepis depends on light availability, and indicates that moderate shade is not necessarily negative for seedling growth. The low-light environment that occurs beneath the stand of dominant *Podolobium alpestre* at low-altitude, north-western sites for example, would lead to decreased net photosynthesis and biomass. In contrast, high-light or party shaded environments are equally favourable for growth. Such light conditions can be found within the relatively well-illuminated understory of the upper limits of snow-gum woodlands, and throughout much of the treeless alpine meadows. However, *in situ* conditions are usually not optimal, and net photosynthesis is often below full capacity due to combinations of water stress, temperature extremes or low humidity causing partial stomatal closure (Muraoka et al. 2002). Moreover, damage caused by extreme temperatures, drought, or herbivory also must increase maintenance costs, an added constraint on net growth (Körner 1999).

While certain abiotic stressors can be mediated by microsites created in the lee or canopy of other, more stress-tolerant plants, as the plant reaches maturity, competition for resources becomes more important below-ground (Aguiar and Sala 1994). Wilson (1988) found that root competition was the more intense form of plant interaction, occurring directly through allelochemical exudates, and indirectly through resource depletion. In the Tibetan Plateau, interactions of root competition vary between species (Song et al. 2006). Hence, the effects of competition and may play out in the longer term for Alpine Podolepis seedlings. Indeed, competition may be acting along the gradient in concert with facilitation, such that we are not yet able to observe the effects of above or below-ground competition. How this balance of competition and facilitation will play out through time will be important for understanding how interactions influence the range boundaries of alpine plants.

As demonstrated with laboratory germination and field transplants, Alpine Podolepis appear to have a theoretical niche far greater than can be observed at Mt Hotham currently, indicating possible limitation of dispersal and/or propagule availability. It is common for plants to lose 90-100% of produced seed to seed predation (Louda 1989). Pre-and-post seed predators can determine net fecundity of their plant hosts (Mckone et al. 1998), having consequences for population density (Louda 1982) and distribution (Brown and Vellend 2014). Pre-dispersal seed predation is common among alpine Asteraceae and has been reported for Alpine Podolepis in Mt Kosciuszko (Pickering, 2009). However, the effects of herbivory and soil pathogens are difficult to determine.

There is a paucity of evidence regarding the importance of insects and pathogens in the population dynamics and range limits of host plants. Differential rates of insect or pathogen attack may alter or reverse competitive relationships between plants (Lee and Bazzaz 1980; Rai and Tripathi 1985). In doing so, they have the potential to exclude plant species from communities (Crawley 1989), and therefore may play a major role in the structuring of plant boundaries. In addition, plant response to herbivory is likely to vary with life stage and may interact with resource availability. Seedlings are likely to have lower defense and/or tolerance to attack than established plants (Boege and Marquis 2005) and may also play a role in defining species distributions. Future research might consider how dispersal, seed predation and/or herbivory and pathogens may influence population dynamics and distribution of plants, and how these interactions might change with continued climate warming.

Conclusion

Typically, facilitative interactions are reported as occurring mostly at the extreme limits of a species environmental tolerance, leading to range expansion and altering the realised niche (Bruno et al. 2003). Here, resident plants positively influenced survival and growth of Alpine Podolepis seedlings beyond the current, observed range. However, facilitation occurred not only at the upper limits to its distribution, but also below the trailing edge. Habitat amelioration is an important structuring force in stressful environments (Bruno et al. 2003). For seedling survival in the alpine landscape, this is true for Alpine Podolepis, regardless of the abiotic stress gradient, during the first growing season. Although the consistent trend of positive interactions may change over time, early seedling establishment is a critical stage (Körner 1999). High overall survival indicates a wide range of physiological tolerance along an abiotic stress gradient. High overall survival also highlights possible limitations in dispersal and/or propagule availability. In addition, early seedling survival is likely restricted by occurrences of frost during the early growing season. While there is some evidence of shade intolerance, which may act to restrict distributions at lower altitudes, further experimental research will be required in order to better understand competitive interactions in alpine plants. Simultaneous investigation into propagule availability, dispersal ability and *in situ* recruitment will also aid inferences on the role of population dynamics on distribution and migration rates. Whether consistent, positive interactions reported here will change over time will provide further insight into the mechanisms of species interactions, and their influence on species distributions.

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Appendix I

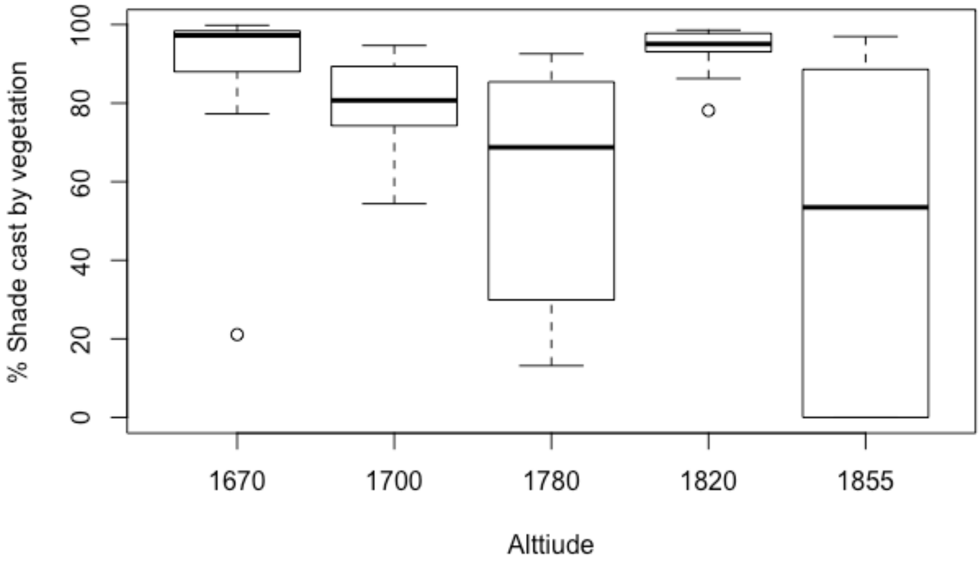

Fig 12. Shade cast by resident vegetation at north-west sites at Mt Hotham, Victoria

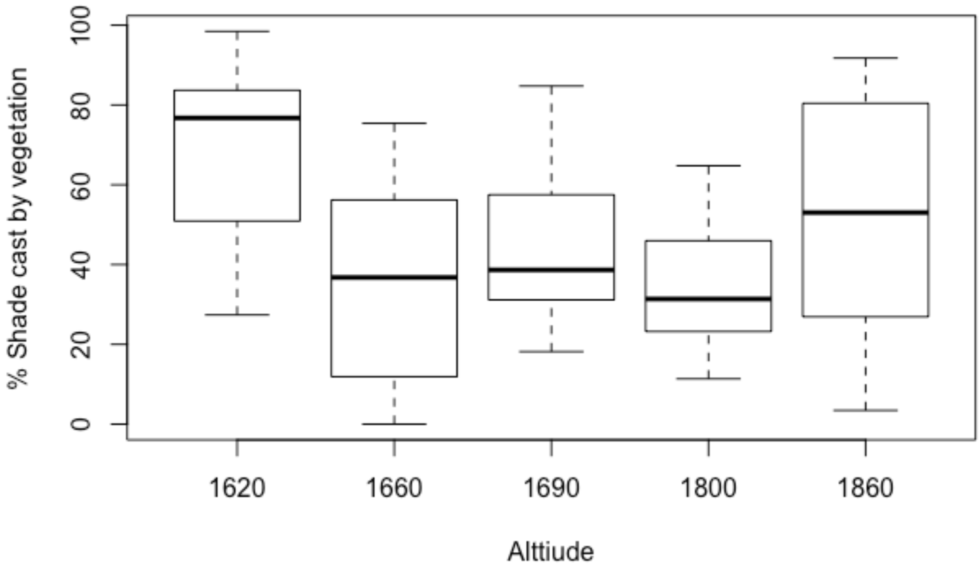

Fig 13. Shade cast by resident vegetation at south-east sites at Mt Hotham, Victoria

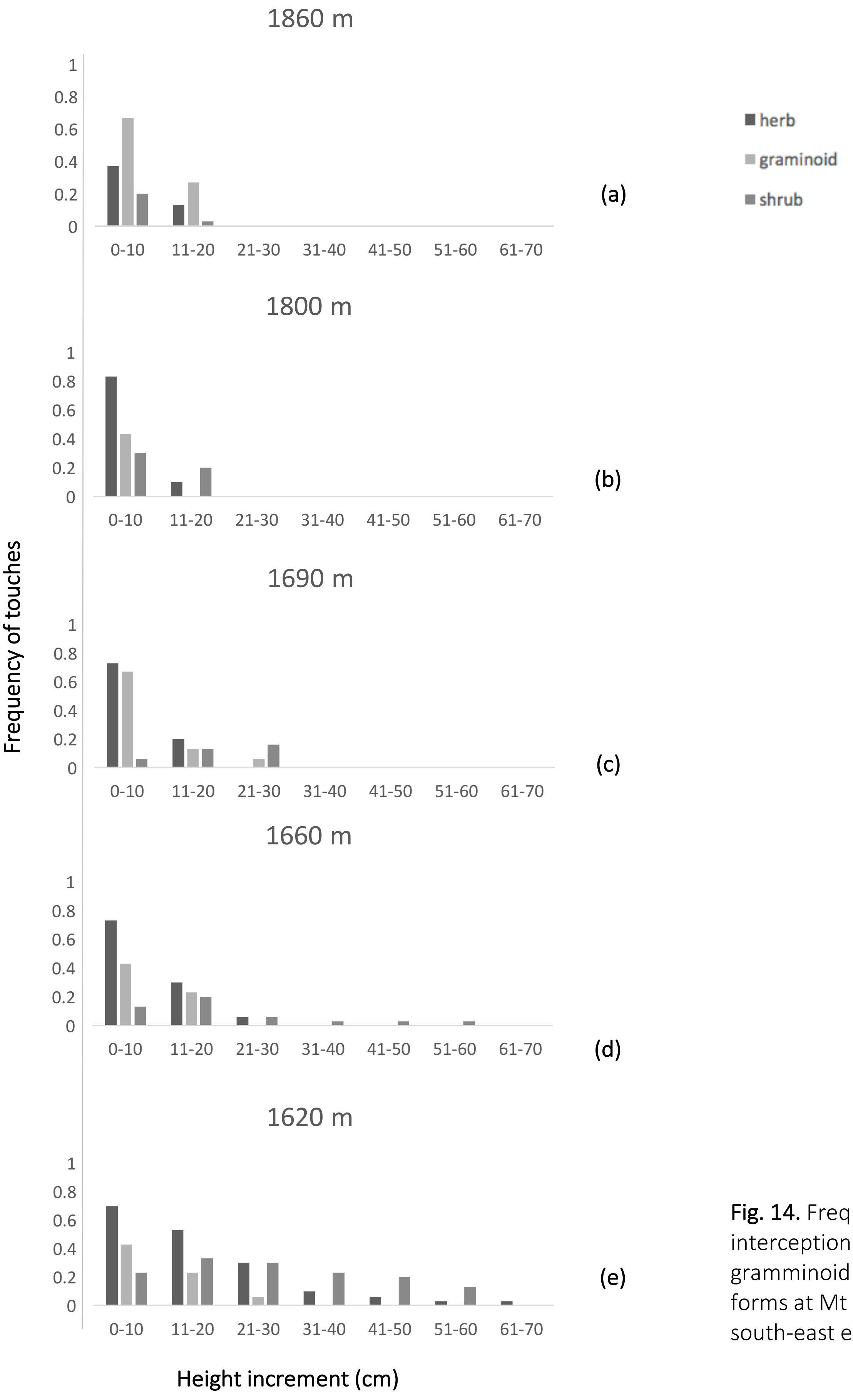

Fig. 14. Frequency of canopy interception of herb, gramminoid and shrub life-forms at Mt Hotham on south-east exposed sites (a-e).

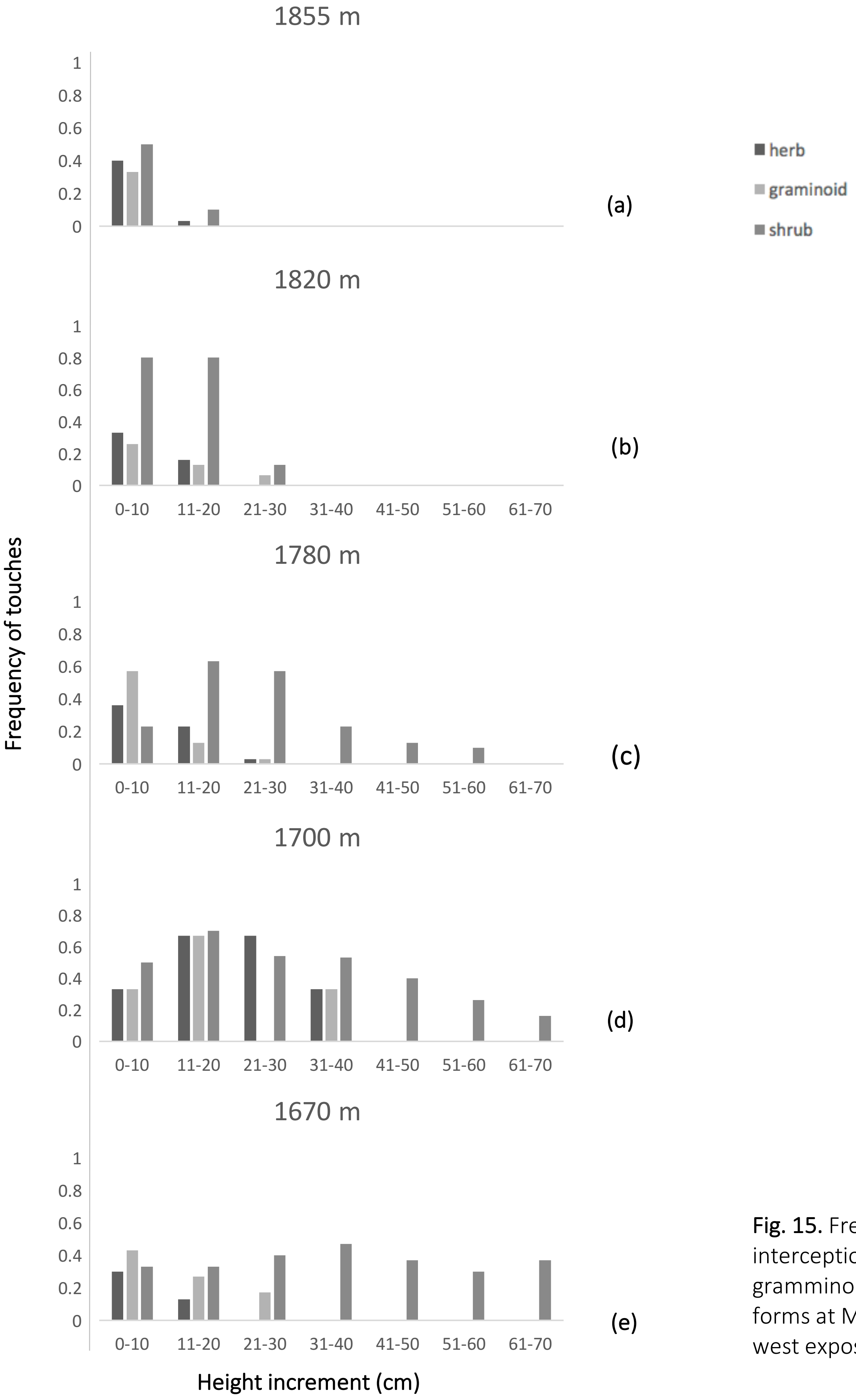

Fig. 15. Frequency of canopy interception of herb, gramminoid and shrub life-forms at Mt Hotham on north-west exposed sites (a-e).

Appendix II

Fig. 16. *Eucalyptus pauciflora* woodland with dense *Podolobium alpestre* understory dominate north-west exposed slopes at Mt Hotham (1670 - 1700 m).

Appendix III

Table 3. Analysis of the effect of treatment, altitude and aspect on seedling survival.

Fixed effect	Chisq	Df	Pr(>Chisq)
Treatment	11.2621	1	0.000791 ***
Altitude	6.4467	1	0.011116 *
Aspect	0.3057	1	0.580321

The effects of treatment, altitude and aspect on seedling survival was assessed with a generalised linear model (GLM). Significant P values indicated by asterisks. Shown are the Chi square, degrees of freedom and P- values of the model. (‘***’ $p<0.001$; ‘**’ $p<0.01$; ‘*’ $p<0.05$; ‘.’ $P<0.1$).

Table 4. Analysis of the effect of treatment and altitude on seedling survival.

Fixed effect	Chisq	Df	Pr(>Chisq)
Treatment	11.2383	1	0.0008013 ***
Altitude	6.1427	1	0.0131952 *

The effects of treatment and altitude on seedling survival was assessed with a generalised linear model (GLM). Significant P values indicated by asterisks. Shown are the Chi square, degrees of freedom and P- values of the model. (‘***’ $p<0.001$; ‘**’ $p<0.01$; ‘*’ $p<0.05$; ‘.’ $P<0.1$).

Table 5. Table of coefficients for the GLM used to fit seedling survival as a function of treatment and altitude.

	Estimate	S.E	z value	Pr(>|z|)
Intercept	11.145130	3.728284	2.989	0.00280 **
Treatment gap	-1.151963	0.359530	-3.204	0.00135 **
Altitude	-0.0052086	0.002097	-2.426	0.01527 *

The survival of Alpine Podolepis seedlings was assessed with a generalised linear model (GLM) fitted with treatment (gap or control) and altitude as additive fixed effects. Significant P values indicated by asterisks. Shown are the model estimates, standard errors and z-values. (‘***’ $p<0.001$; ‘**’ $p<0.01$; ‘*’ $p<0.05$; ‘.’ $P<0.1$).

Appendix IV

Table 6. Statistical analysis of Relative Neighbour Effect for north-west and south-east sites.

RNE north-west	coefficients	estimate	s.e.	z value	Pr(>|t|)
	1670 m - 1700 m	-0.27689	0.16143	-1.715	0.0954
	1670 m - 1820 m	-0.45308	0.14534	-3.117	0.0037 **
	1670 m - 1855 m	-0.34817	0.14968	-2.326	0.0261 *
RNE south-east	1620 m - 1660 m	-0.07716	0.17118	-0.451	0.6547
	1620 m - 1690 m	0.07056	0.16204	0.435	0.6656
	1620 m - 1800 m	0.10457	0.16204	0.645	0.5225

Shown are one-way ANOVA comparisons between sites according to aspect. Asterisks indicate significant P-values. (‘***’ p<0.001; ‘**’ p<0.01; ‘*’ p<0.05; ‘.’ P<0.1).