An empirical study of the dispersal capacity of Australian alpine species.

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For publication in Australian Journal of Botany

A thesis submitted in partial fulfilment of the requirements

for the degree of BScWildConvBio (Hons)

in the

Department of Ecology, Environment & Evolution

La Trobe University

Bundoora, Victoria

23rd of April, 2018

Word count: 9768

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Subject: Wildlife and Conservation Biology (Hons)

Document: An empirical study of the dispersal capacity of Australian alpine species.

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Student Number: 18072684 **Date:** 23rd of April, 2018

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Abstract

Plant species vary dramatically in their ability to disperse, and this will have consequent implications for species to track changes in bioclimatic envelopes. Responses to climatic change are particularly acute for alpine species. In this study, understanding Australian alpine plant species dispersal was addressed in three ways. Firstly by building on published models to predict dispersal distance using a combination of 'soft' and 'hard' plant traits (e.g. terminal velocity). Secondly novel seed traps were used to measure seed dispersal in the field. And thirdly trade-offs between seed dispersal capacity and seedling growth traits were quantified in a laboratory experiment. Seed dispersal models were improved by the inclusion of measured terminal velocity. Its input in models afforded greater discrimination in predicting the species dispersal distance of many Asteraceae. Seed trapping in the field detected 33% of species in traps, suggesting a capacity for only short distance dispersal. One case of long-distance dispersal was found; the exotic daisy, *Cirsium vulgare* (Savi), which was thought to have travelled up to 2 km before being captured. Overall, this study highlights that alpine seed dispersal is likely to be only a few metres for many species. Hence, their capacity to track climate change via dispersal is limited, prompting the need for conservation management to assist alpine species in accessing suitable habitat in a changing climate.

Introduction

Seed dispersal is crucial to the understanding of many ecological processes influencing the composition of local plant communities (Marchand and Roach 1980, Chambers 1995). Plants have extremely limited mobility; therefore, the dispersal of seed is the main mechanism for plants to move around the landscape (Harper et al. 1970, Burrows 1975). Transport away from the parent plant to a location ideal for successful germination, often called a ‘safe site’, is essential for a species to persist (Harper et al. 1965, Gallien et al. 2015). Studies focusing on different aspects of seed dispersal are essential in understanding how dispersal capacity affects a species’ conservation, especially in the face of changing climates (Turnbull et al. 1999, Walther et al. 2005, Morgan and Venn 2017).

Mechanics of seed dispersal

The complete unit of the seed, plus additional plant tissue that assists in dispersal, is known as the ‘diaspore’ (Burrows 1975, Werker 1997). The dried fruit containing a single seed is the ‘achene’ but is commonly just referred to as the seed, a term that encompasses the endosperm, embryo, and the seed coat (Burrows 1975, Werker 1997, Tabassum and Bonser 2017). The main vectors of seed dispersal are water, gravity, wind, explosive dehiscent actions of seed pods and transport by animals (Burrows 1975).

Variation in seed morphology amongst plants has evolved in order for plants to utilise a specific vector and achieve optimal dispersal (Willson and Traveset 2000). In determining the capacity of seeds to move, seed traits such as seed size, shape, mass and dispersal syndrome have been shown to be key predictors of dispersal distance (Burrows 1975, Tamme et al. 2014). Wind-dispersed species invest in diaspore structures that aid in the seed being carried through the air away from the parent plant (Harper et al. 1970). Characteristics of wind-dispersed diaspores include plumed seeds, woolly or hairy seeds, seeds with a membranous winged structure, hair-like pappus structures, dust seeds and seed-carrying tumbleweed (Burrows 1975). Animal-dispersed diaspores may possess hook like structures such as a beak, in order to attach onto animal fur (Fig. 1) (Werker 1997).

Fig. 1 Illustrations showing the morphology of a wind-dispersed and animal-dispersed seed

Within a plant community, seed morphology can vary greatly from species to species (Harper et al. 1970). Among coexisting species, seed mass has been found to differ over five to six orders of magnitude (Leishman et al. 2000). Such a level of variation in seed traits across species demonstrates one process of natural selection allowing species to coexist in a localised area (Dwyer and Laughlin 2017). Seed mass is a useful proxy when examining a species allocation of resources during the development of seeds (Leishman et al. 1995, Turnbull et al. 1999, Moles et al. 2007). Resources are often partitioned between the number of seeds produced and seed size (Harper et al. 1970, Leishman et al. 2000). The advantage for a seed larger in overall size is associated with that seed having a greater reserve for successful germination (Muller-Landau 2010). However, this beneficial aspect is offset by a lower dispersal capacity (Harper et al. 1970, Tabassum and Bonser 2017). The advantageous traits in germination are often seen in seeds that have limited or no dispersal architecture and which rely on gravity to disperse (Leishman et al. 1995, Moles et al. 2007).

Seed transport and terminal velocity

Seed morphology can account for how a seed may be transported across the landscape and is related to the likelihood of seed reaching a safe site (Nathan and Muller-Landau 2000, Tamme et al. 2014). In the case of wind-dispersed seeds, the aerodynamic appendages are the morphological attributes observed to assist with dispersal. Aerial motion can be unique between species due to the evolved variety of diaspore structures (Burrows 1975, Werker 1997). The measuring of diaspore terminal velocity, this being the rate of fall of an object through still air, is gaining momentum within the scientific community as a vital predictor for a species' dispersal ability (Van Oudtshoorn and Van Rooyen 2013). Diaspores with structures highly effective for wind-dispersal fall more slowly than diaspores without appendages or with a greater mass (Tabassum and Bonser 2017). A diaspore's architecture has been found to clearly impact how quickly a seed falls or how long it stays aloft and how far it can travel (Tackenberg 2003, Tackenberg and Stöcklin 2008, Caplat et al. 2012). Therefore, when using terminal velocity as a measure of dispersal distance, a high terminal velocity will limit a seeds dispersal ability (Tabassum and Bonser 2017).

To fully understand seed dispersal patterns, other plant trade-offs also need to be considered (Nathan and Muller-Landau 2000, Dwyer and Laughlin 2017). Variation in dispersal resulting from differences in adult plant characteristics and environmental conditions can impact the spatial patterns of dispersed seed, particularly wind-dispersed seeds (Williams 1992, Nathan and Muller-Landau 2000, Tamme et al. 2014). Plant height has a strong influence on seed dispersal in forest environments (Greene and Johnson 1996, Thomson et al. 2011). However, for plants short in stature, knowing the rate of fall (terminal velocity) for a seed is of less significance, and rather the force needed to produce lift may be considered more influential (Tackenberg 2003). Referred to as ‘updraft’ (inversely related to terminal velocity), could be more useful in understanding the events of dispersal for short stature plants but has had limited investigation (Tackenberg 2003).

Dispersal modelling

The most effective modelling techniques of seed dispersal distances are those that consolidate the plant traits that affect dispersal and can be directly measured. Fortunately, such information about plant and seed attributes are easily obtained, and parameters often include dispersal syndrome, growth form, plant height and seed mass (Jurado et al. 1991, Thomson et al. 2011, Tamme et al. 2014). Morgan and Venn (2017) found that incorporating ‘soft traits’ of seed morphology into dispersal modelling produced meaningful generalisations about alpine species dispersal, concluding that most (75%) are incapable of dispersal beyond 10 m. However, the accuracy of these mechanistic models is difficult to gauge (Tackenberg 2003). With a multiplicity of dispersal syndromes and disparity in the behaviour of each dispersal mechanism, establishing an association between dispersal syndrome and distance of dispersal is difficult (Vittoz and Engler 2007, Muller-Landau et al.

2008). Even dispersal distances calculated from a single dispersal vector can vary greatly (Vittoz and Engler 2007, Muller-Landau et al. 2008). Discrepancies in dispersal distances obtained from models may also exist due to the lack of accountability of the small-scale variation in wind behaviour experienced by a diaspore (Burrows 1975, Tackenberg 2003). Differences in wind-conditions at the time of seed release is also found to be poorly understood and rarely considered in dispersal models (Nathan et al. 2002). Empirical testing of seed dispersal is viewed as an area of study that greatly needs to increase and develop in order to fully understand the process of seed dispersal. In addition, incorporating field assays of localised wind conditions can aide in accurately determining the limitations in dispersal events (Nathan et al. 2001, Clark et al. 2007).

Measuring seed dispersal in the field

Seed dispersal measurements from field trials are scant due a lack of suitable equipment that delivers accurate and quantitative sampling. Studies of seed dispersal have involved the capture of seeds in traps such as funnel traps, mesh traps and sticky traps (Harms et al. 2000, Cottrel 2004, Bullock et al. 2006). Funnel traps, having similarity to the simple sampling methods of pitfall traps, are restricted in only capturing settling seeds and are not inclusive in collecting seeds in flight. Large mesh traps, often used in forests, held above the ground are only efficient in measuring seed rain from the canopy in close proximity to the trap (Harms et al. 2000). For quantifying seeds moving in the air, sticky traps are most frequently used (Chabrerie and Alard 2005). However, this method also has limitations in seed capture efficiency. Retention of seeds on the sticky material can be reduced over time due to the surface becoming saturated; this is especially ineffective for studying seed dispersal over the entire season of seed dispersal (Chabrerie and Alard 2005, Morris et al. 2011). The visual sorting of sticky traps can also produce bias for larger seeds as they are more easily detected when analysing the seed catch (Cottrell 2004). More recently, seed traps have been designed to capture seeds in flight (Morris et al. 2011). Morris et al. (2011) demonstrated the bucket trap design is easy to replicate, cost effective and adequate in providing a broad sampling of seed dispersal.

Varying wind conditions greatly impact the distance of seed dispersal for wind-dispersed species due to the interactions with the aerodynamics of the diaspore (Nathan et al. 2001, Greene 2005). Dispersal distance is also influenced by wind conditions at the time of seed release and the release height (Caplat et al. 2012, Tamme et al. 2014). A major challenge in understanding and modelling the dispersal distance of wind-dispersed species comes from defining the speed and direction of winds experienced by dispersing diaspores. The impacts of small-scale variations in wind behaviour on seed release and travel has been inadequately surveyed in field studies (Nathan et al. 2001). Synchronized events of favourable wind conditions and seed release are considered to be the most effective phenomenon in achieving an increased dispersal distance (Greene 2005, Caplat et al. 2012). Therefore, examining the frequency of effective wind events for dispersal for individual species is a key area of study for understanding dispersal dynamics.

Growth and Establishment

Once achieving seed dispersal to safe sites, the next challenge for plants to thrive in complex communities is to successfully establish (Gallien et al. 2015). Reaching a suitable site for establishment may be more relevant to species survival than the distance a seed travels. (Nathan et al. 2002, Tackenberg 2003). A plant's investment in dispersal capacity often results in trade-offs with other life history traits, such as growth rate and competitive ability, thus impacting a seed's ability to successfully germinate and establish (Chambers 1995, Turnbull et al. 1999). These trade-offs in life-history traits allow for many species to occupy different niches across a landscape (Turnbull et al. 1999, Willson and Traveset 2000). Seed mass is a useful parameter for evaluating the competition colonization trade-off. (Turnbull et al. 1999). In competitive surroundings, larger-seeded species are often more successful in establishing. However, with small-seeded species being certainly present in most ecosystems, the occurrence of small-seeded species is driven by the high abundance of seeds winning establishment sites by weight of numbers (Turnbull et al. 1999).

A higher competitive ability has been observed among alpine plants where a larger seed provides additional growth resources and are beneficial for tolerating environmental stresses (Muller-Landau 2010). In addition, postponed germination is exhibited in many alpine plants as it provides a mechanism to survive extreme weather conditions (Hoyle et al. 2015). Plants of greater seed mass often exhibit a slower relative growth rate (RGR), which may offer benefits for establishing in competitive and stressful environments (Houghton, Thompson, & Rees, 2013).

Small-seeded species generally have higher RGR due to the plant tissues being thinner and lower in density with higher turnover rates (Leishman et al. 2000). Other growth traits such as sturdy tissue construction are associated with being advantageous for competitive ability and are reflected in plants having a lower specific leaf area (SLA) and a greater root system (Leishman et al. 2000).

Australian alpine seed dispersal

Alpine regions are known to harbour a large diversity of plant species with a high level of endemism (Costin et al. 2000, Walther et al. 2005). Seed dispersal mechanisms and dispersal events are considered to be essential processes for alpine ecosystems to be able to withstand changes in climatic temperatures and weather conditions (Guisan and Theurillat 2000, Walther et al. 2005). Life history trade-offs relating to dispersal mechanisms and successful germination also play a critical role in determining which alpine species are most equipped to survive (Chambers 1995).

With rapid changes in temperature, plants might migrate upslope or to cooler areas in order to stay within their climate envelope (Guisan and Theurillat 2000, Walther et al. 2005, Jump et al. 2012). This concept of uphill migration has been derived from studies focused around alpine environments found in the Northern Hemisphere. However, the geological processes between Northern Hemisphere mountainous alpine regions and the Australian alpine landscape are considerably different (Ollier 1986). The Australian Alps are a complex landscape of ancient, eroded and flat-topped mountain ranges with gentle elevation gradients. This contrasts to the Northern Hemisphere in which alpine regions are commonly characterised by steep elevation gradients, having been heavily influenced by glaciation (Ollier 1986, Bell et al. 2018). The increased area and height of mountains found in the Northern Hemisphere, which often include a nival zone, are more likely to provide suitable habitat at higher elevations for alpine flora in the face of climate change. These habitat opportunities are not presented to Australian alpine species (Bell et al. 2018). Therefore, it is important to examine the dispersal range of Australian native plants in order to understand their capacity to locate safe sites with a changing environment, in addition to informing how conservation management may assist the persistence of vulnerable species.

The majority of graminoid and herbaceous species that dominate Australian alpine regions have seeds that rely on wind for dispersal (Tackenberg and Stöcklin 2008, Morgan and Venn 2017), with a high proportion of these wind-dispersed species in the Asteraceae and Poaceae families (Costin et al. 2000). Up to 63% of the flora in the alpine zone shows no inherent dispersal syndrome relying on gravity for dispersal (Tackenberg and Stöcklin 2008, Morgan and Venn 2017). However, being comprised of many small statured species, the capacity for seed dispersal is believed to be constrained by the low release heights from adult plants (Morgan and Venn 2017). This suggests long-distance dispersal events are rare and do not influence seed-dispersal patterns (Nathan et al. 2002).

Study aims

The aim of this study was to evaluate the dispersal capacity of Australian alpine plants, in addition to identifying and examining the competitive ability of species and the relationship between colonization and competition traits. Specifically, this study asks: 1) Does incorporation of the seed dispersal trait terminal velocity improve current dispersal models? 2) Which seeds are dispersing by wind and under what conditions are they dispersing? And, 3) What are the competitive trade-offs for species dispersing in alpine regions?

This study will also add to broader research effort focused on whether alpine plants species will be able to move throughout the landscape and reach safe sites for successful establishment in response to climate change. In particular, it will highlight which species may be more limited in their dispersal or germination strategy and, therefore, more vulnerable to rapidly changing environments.

Materials and Methods

Study site and seed collection

Australian alpine environments occupy approximately 7950 km^2 (Sahukar et al. 2003). Characterised by persistent snow over the winter months, these environments constitute 0.15% of Australia as a whole (Costin et al. 2000). Within Victoria, true alpine environments are found above the treeline at elevations around 1800 m (Sahukar et al. 2003). The vegetation of these regions is made up of a mosaic of heathland, herbfields, grassland and bogs, with exposed rock and rock pavements intermingled throughout the landscape (Mitchell 2002, Sahukar et al. 2003). The alpine zone, being subjected to the coldest temperatures and harshest weather conditions, consists mostly of ground-hugging flora which rarely exceed heights greater than 1 m (Costin et al. 2000).

The study was conducted near the ski resort of Falls Creek, between an elevation of 1210 m and 1830 m (Costin et al. 2000). The mean annual wind speed is approximately 22 km/h, with prevailing winds moving in a north-northwest direction (Australian Government Bureau of Meteorology (BOM), 2018). Sites for fieldwork were representative of true alpine habitat. Eight sites of open grassy shrubland were selected (Fig. 2; UTM co-ordinates can be found in Appendix A). Site selection was chosen using a stratified random method to allow for heavy equipment to be installed near access roads.

Fig. 2 Satellite view of the Falls Creek Resort study site. Red markers numbered 1-8 display the location of each site selected to study seed dispersal in the field.

To characterise and compare the diaspore traits of Australian alpine flora seeds were collected in February to March 2017, from herbfields, grasslands and open heathlands. Mature seeds of 25 species from 10 families were collected from mature flower heads. Seeds were stored in a cool room at conditions of 4 °C for a period of four weeks in order to simulate the alpine winter conditions. The average mass of both the diaspore and diaspore with appendage removed (seed) for each species were calculated from recording the mass of five lots of 10 diaspores for each species. From these measurements, the proportion of investment between the appendage and the diaspore could be calculated (Appendix B). Samples from these collected seeds were used for the terminal velocity and growth studies.

Quantification of terminal velocity

To determine the effect that diaspore morphology has on a species' dispersal potential, the terminal velocity of alpine species was quantified under laboratory conditions. Ten diaspores of each species were individually dropped down a 2 m long clear Perspex tube, 15 cm in diameter (Fig. 3). The tube allowed for a controlled, still air environment and the length of the tube gave a distance long enough for a diaspore to reach a constant falling rate (Sheldon and Burrows 1973). Issues with static attraction of diaspores to the sides of the Perspex tube was minimised by increasing the humidity in the tube. Each diaspore was placed on a platform at the top of the tube and, with a sliding piece of plastic, pushed from the side into the tube. Using stopwatches, two observers recorded the time it took for each diaspore to travel the 2 m. If the times between the two observers differed by 0.15 seconds or more, the time was discarded and the trial run for that diaspore was repeated. This process was repeated, with the same 10 diaspores, to increase trial replication and to give a total of 20 terminal velocity estimates for each species. The average drop time for each species was determined. The terminal velocity was calculated by dividing the drop distance by the average drop time (Riba et al. 2005; Marchetto et al. 2010) (Appendix B).

To ascertain the relationship between terminal velocity and seed morphology, particularly focussing on diaspore mass and the proportion of investment in diaspore appendages, linear regression models were used.

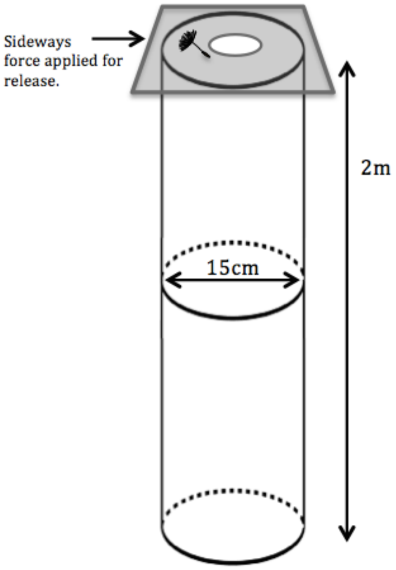

Fig. 3 Terminal velocity testing tube.

Dispersal modelling

To determine whether current predictions of seed dispersal can be improved, the ‘hard trait’ of terminal velocity, based on the method described above, was incorporated into dispersal modelling using the package DispeRsal in the statistical program R (Tamme et al. 2014). DispeRsal is a developed function with an accompanying global taxonomic plant trait data set. DispeRsal uses statistical modelling to calculate maximum distances of dispersal with confidence intervals (CI) for desired species of interest. The input of a combination of plant traits can be used to produce outcomes; these can include dispersal syndrome, growth form, release height, seed mass, and terminal velocity. Morgan and Venn (2017) modelled dispersal, based on soft traits and obtained results suggesting many species have short-distance dispersal. In the current study, predicted dispersal distances were calculated using the basic model combining the soft traits of dispersal syndrome and growth form, and an enhanced model incorporating terminal velocity. The outcomes of the two models were compared to examine whether the addition of hard traits discriminates dispersal capacity more so than models using soft traits alone.

Measuring seed dispersal in the field

Few studies measure seed dispersal in the field, particularly that of height reached by dispersing seed. Hence, modelled dispersal distances have rarely been assessed for their real-world applicability. To overcome this deficiency, seed dispersal in the alpine environment was measured with the use of bucket seed traps. The traps were used in order to quantify the small-distance and long-distance dispersal of their captured seeds. The traps were constructed using readily available materials based on the design of the bucket trap used by Morris et al. (2011) (Fig. 4a). Adjustments to this design included the addition of a wooden frame to provide extra support in the extremely windy alpine conditions. The trap opening was also modified to improve seed retention. A valve structure was affixed to the 22 cm by 22 cm opening of the trap. This maintained the same area for the opening but prevented seeds from being blown back out of the trap after entering.

The traps were placed at field sites in the middle of January 2018 for a total of 35 days, during the optimum period of seed dispersal for the local alpine plants. The 16 traps were placed in pairs, with one trap at a height of 150 cm (top trap) positioned above another at a height of 45 cm (bottom trap) (Fig. 4b). The traps were located at eight sites in the Falls Creek Resort (Fig. 2). The opening of the traps was directed to face the path of the prevailing winds in the region, that being a north-northwest direction. Seeds were collected from the traps every four days. The species and number of filled seed were identified, counted and the height and location of their capture recorded.

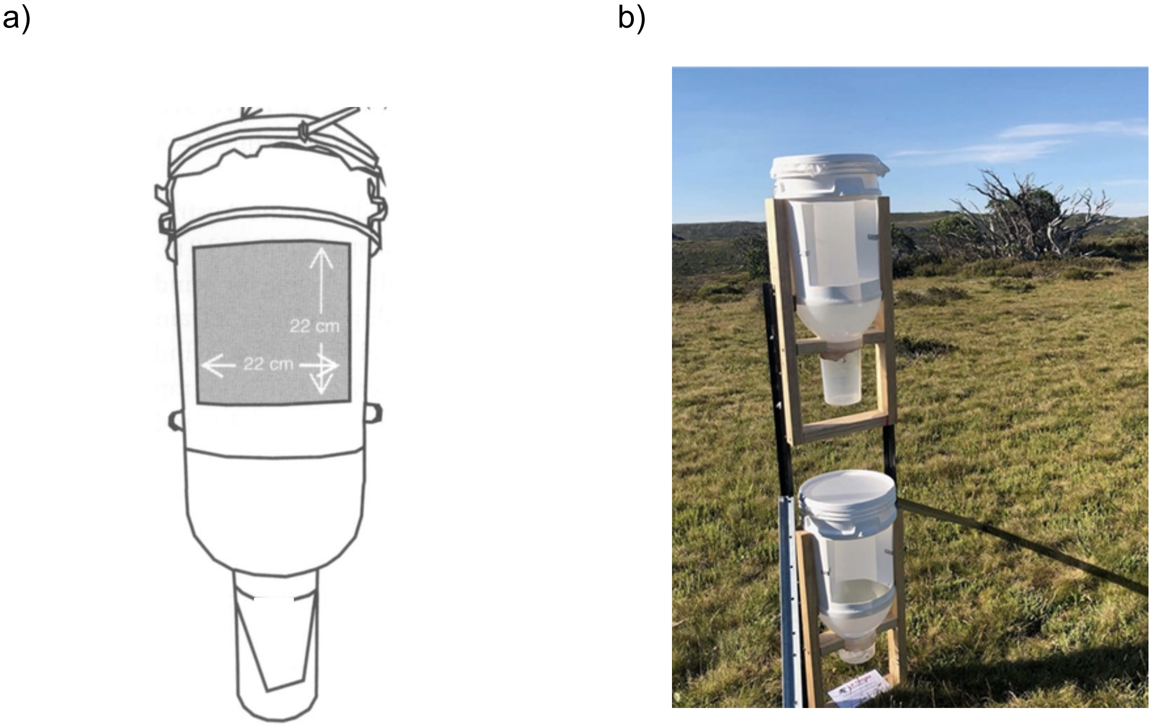

Fig. 4a) Diagram of original seed bucket trap. Image from Morris *et al*. b) a seed bucket trap erected in open grassy shrubland at Site 8 in the Falls Creek Resort.

Floristic surveys

To identify which alpine species in the vicinity of the seed traps were in flower or in seed while the seed traps were deployed a species presences-absence field survey was conducted. The survey quadrat expanded out from the opening of the trap in a semi-circle shape with a radius of 1 m, 5 m, 10 m and 15 m (Fig. 5). Flowering species including those with buds and developing flower heads were noted. This data was used to identify the positioning of the nearest plants with seeds of that species captured in the seed traps.

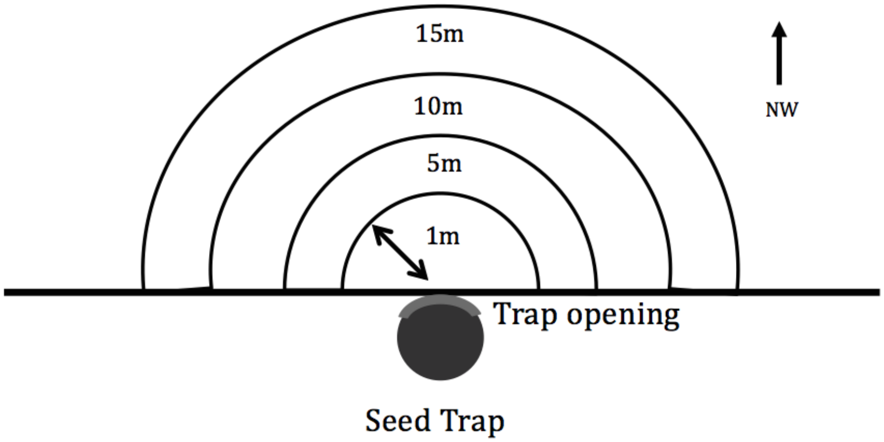

Fig. 5 Arrangement of the floristic survey sampling methods

Wind behaviour

Measurements of the wind column in the alpine landscape were taken to evaluate wind behaviour and the effects of varying wind events on seed dispersal. Anemometers were used to measure the average horizontal and vertical wind speeds over 30 seconds at every 10 cm of height from ground level to a total height of 2 m. Upward vertical wind speeds were used as a measure of updraft events. Wind column measurements were performed on three different days at sites 1, 2, 3 and 7 and twice at sites 4, 5, 6, and 8. This data was used in assessing the difference in wind conditions between sites as well as the difference in horizontal and vertical wind speeds. Importantly, the vertical winds speeds were used in determining the proportion of vertical wind events strong enough to provide diaspore lift for each species depending on their terminal velocity. A paired difference test was run to compare the sets of wind measurements at each trap site and assess whether the mean wind speeds differ. For better statistical and visual evaluation of the wind data, the square-root of wind speeds were calculated to improve the spread of data.

Label-based representation was used to display the significance of the pairwise comparison in vertical wind speed at each trap site. From the measurements of vertical wind speed in the field, the proportion of wind events that were strong enough to produce lift for each species based on the height range of the plant and terminal velocity was calculated.

Growth study

Seed mass and its influences on a species' ability to compete and establish was examined through a growth study. Out of the 25 species of seeds collected, 19 species had sufficient seed numbers to be included in the growth study.

Filled seeds were deemed to be viable and 20 seeds of each species were chosen. Seeds were individually planted into forestry tubes containing an Australian native soil mix. All seeds, excluding those of Asteraceae, were sown at a depth of three times the length of the seed. The soil placed on top of the seed was sifted to eliminate any large pieces of soil matter that would inhibit plant growth. To meet the germination requirements for Asteraceae, all Asteraceae seeds were surface sown; placed on the surface of the soil and completely covered with fine grain sand to a depth of approximately 1 mm.

The seeds were allowed to grow in a temperature-controlled glasshouse (20-25 °C). The forestry tubes were positioned in the centre of the glasshouse to allow for even distribution of light and heat. The seeds were watered daily and the date of emergence for each seed was recorded. Plants were harvested 30 days after emergence.

Seeds that did not emerge after 45 days were subjected to a period of cold stratification. These ungerminated tubes were placed into a cool room at a constant temperature of 4 °C for 28 days to emulate an alpine winter. In addition the plants were covered with black plastic to exclude light and promote germination after the treatment. After 28 days, these tubes were returned to the glasshouse and the harvesting process, as above, was repeated for those seeds which then germinated. The harvesting process consisted of removing the plant from the tube and washing the roots clean of all soil after 30 days of growth. Plants that showed signs of damage or disease such as root rot were discarded and removed from the subsequent analyses.

The below-ground (roots) and above-ground (stems and leaves) biomass of plants were detached and processed separately. The roots were washed, removed from the stems and leaves, placed in a paper envelope and dried at 80 °C, until a constant mass was reached. The above-ground biomass was weighed and the fresh weight (FW) recorded. The leaves were removed from the stems and the stems were placed in the oven to dry under the same conditions as the roots. The area of the total leaf growth was measured using a computer program Leaf Area Measurement (Askew 2003). The leaves were also placed in an 80 °C oven until a constant dry mass was reached. From dry weight measurements, the Specific-Leaf Area (SLA), dry root mass / dry above-ground biomass (shoots) ratio (DR/DS), and relative growth rate (RGR) was calculated.

Growth study data analysis consisted of using the results for the SLA, RGR and DR/DS of different species to produce linear regression models demonstrating the relationship between these competitive traits and seed morphology. The mean SLA, RGR and DR/DS was calculated and individually compared with the seed characteristics of seed mass, diaspore mass and appendage proportion. Regression modelling was able to show which particular seed morphology variable was significant in predicting competition ability.

Results

Terminal velocity

Across the 24 species of diaspores tested, it was found that species with an increase in diaspore mass had a significantly lower terminal velocity (Fig. 6a, $R^2 = 0.1463$, $p = 0.0368$). A similar relationship was found when comparing seed mass and terminal velocity across the species (Fig. 6b, $R^2 = 0.1859$, $p = 0.0204$). When examining the association between terminal velocity and the calculated mass of the proportion of appendages for each species, a non-significant negative trend was found (Fig. 6c, $R^2 = 0.04114$, $p = 0.1727$).

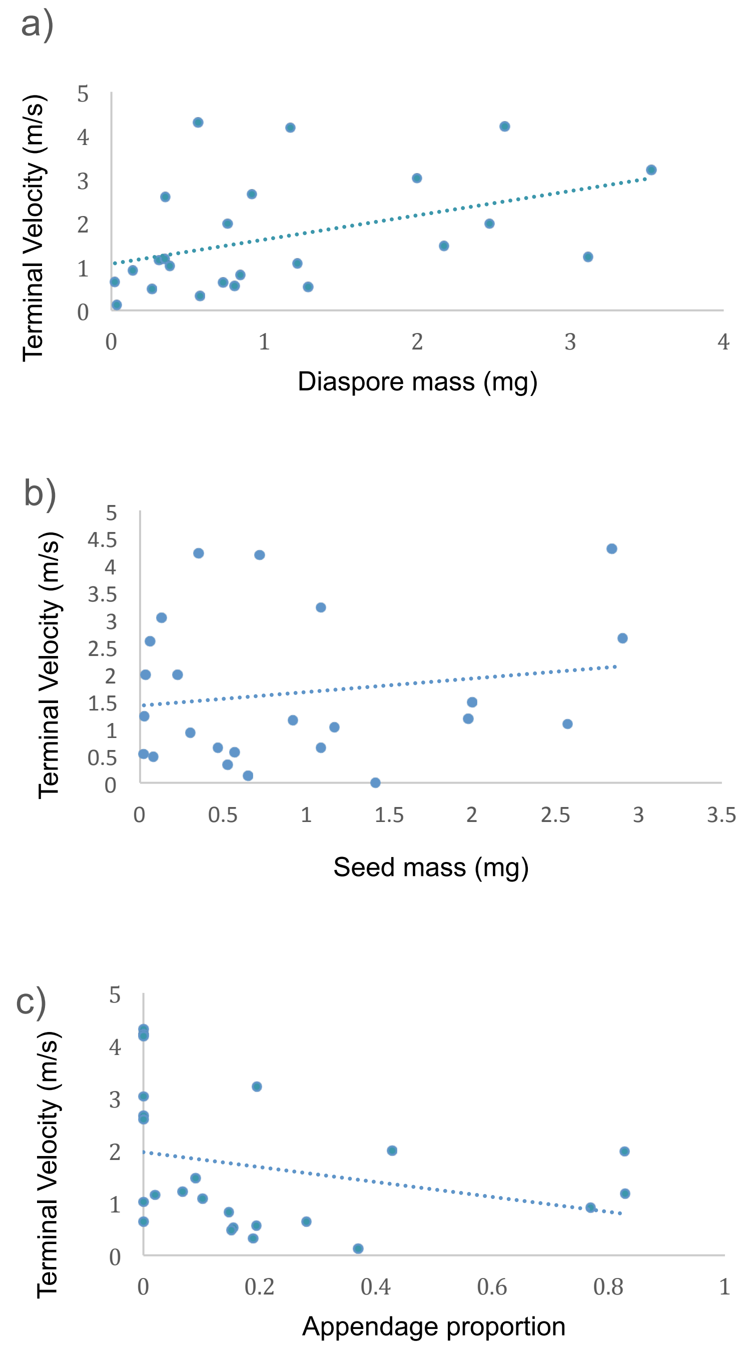

Fig. 6 The relationship between terminal velocity and a) diaspore mass, b) seed mass and c) appendage proportion.

Dispersal modelling

Modelled dispersal distances with and without terminal velocity were compared in order to examine the validation of mechanistic dispersal modelling (Fig. 7). The basic model, without terminal velocity, considered dispersal syndrome and growth form (a proxy to release height) and produced standard dispersal distances for species that shared the same input for those traits. The majority of wind-dispersed species, which were all within Asteraceae, had a modelled dispersal distance of 18.17 m, apart from *Olearia frostii* and *Brachyscome spathulata. Olearia frostii* had the highest modelled dispersal distance at 38.60 m. This is the only plant classed as a shrub in the model. The dispersal distance modelled was 1.90 m for all grass species, whilst gravity dispersed species showed small variation in results from 0.45 m to 2.2 m. When terminal velocity was added into the model, the resultant predicted dispersal distances showed a significant difference for 10 of the 22 species compared. Eight out of the 12 wind-dispersed species evaluated showed significant differences in dispersal distances. Seven of the predicted dispersal distances decreased and one increased. The predicted dispersal distance of *Erigeron bellidioides* more than doubled when its terminal velocity was included, from a distance 18.2 m to 38.4 m. *Microseris lanceolata* and *Celmisia costiniana* both showed over 90% decrease in their predicted dispersal distances, from 18.2 m to 1.1 m and 1.5 m, respectively. All grass species showed an increase in predicted dispersal distance when terminal velocity was included in the model, with two showing a significant difference. *Agrostis venusta* modelled dispersal increased from 1.9 m to 7.1 m, while *Trisetum spicatum* modelled dispersal increased from 1.9 m to 5.9 m; these represent threefold increase in modelled dispersal for both species. All gravity-dispersed species retained similar predicted distances under both modelling conditions. It is noteworthy that the maximum predicted dispersal distance did not exceed 40m for any species.

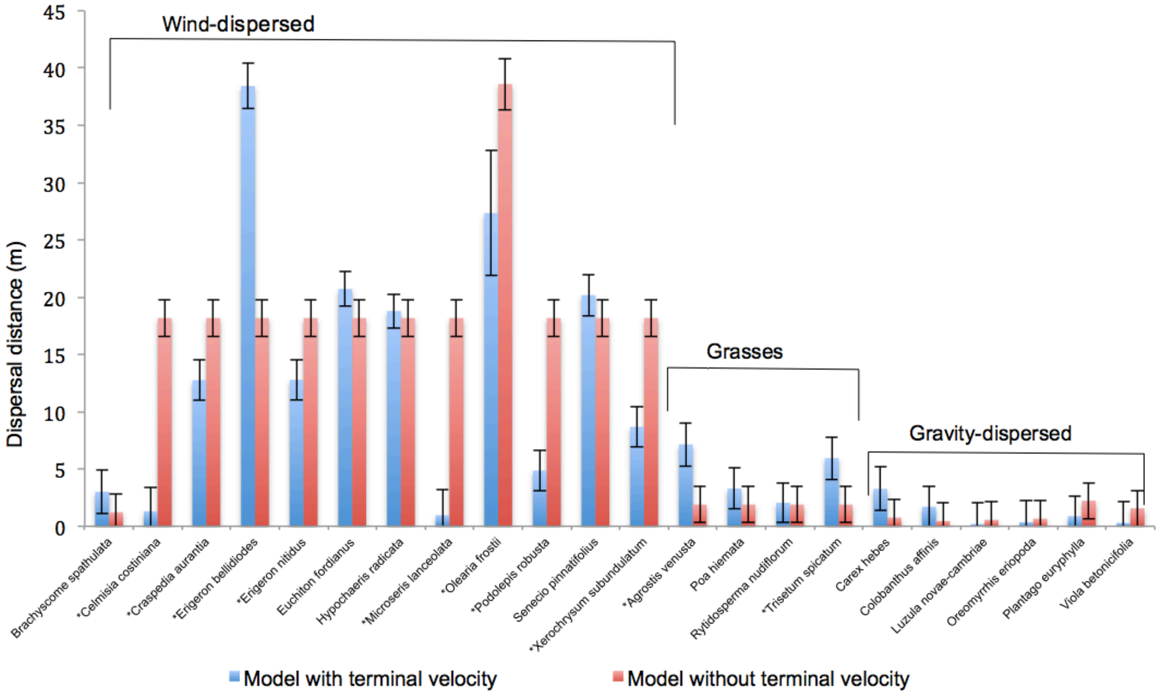

Fig. 7 Modelled dispersal distances with and without terminal velocity for 22 species, 95% confidence intervals included. Species with significant differences in dispersal distances are indicated with an asterisk.

Wind behaviour

The wind measurements performed at each seed trap site and replicated over the summer season provided a sample of the wind conditions experienced at the Falls Creek Resort area. Mean vertical wind speeds were found to be approximately 0.5 m/s (± 0.9) and horizontal wind speeds were measured at 2.2 m/s (± 1.2), independent of the height at which the speed was measured (Fig. 8).

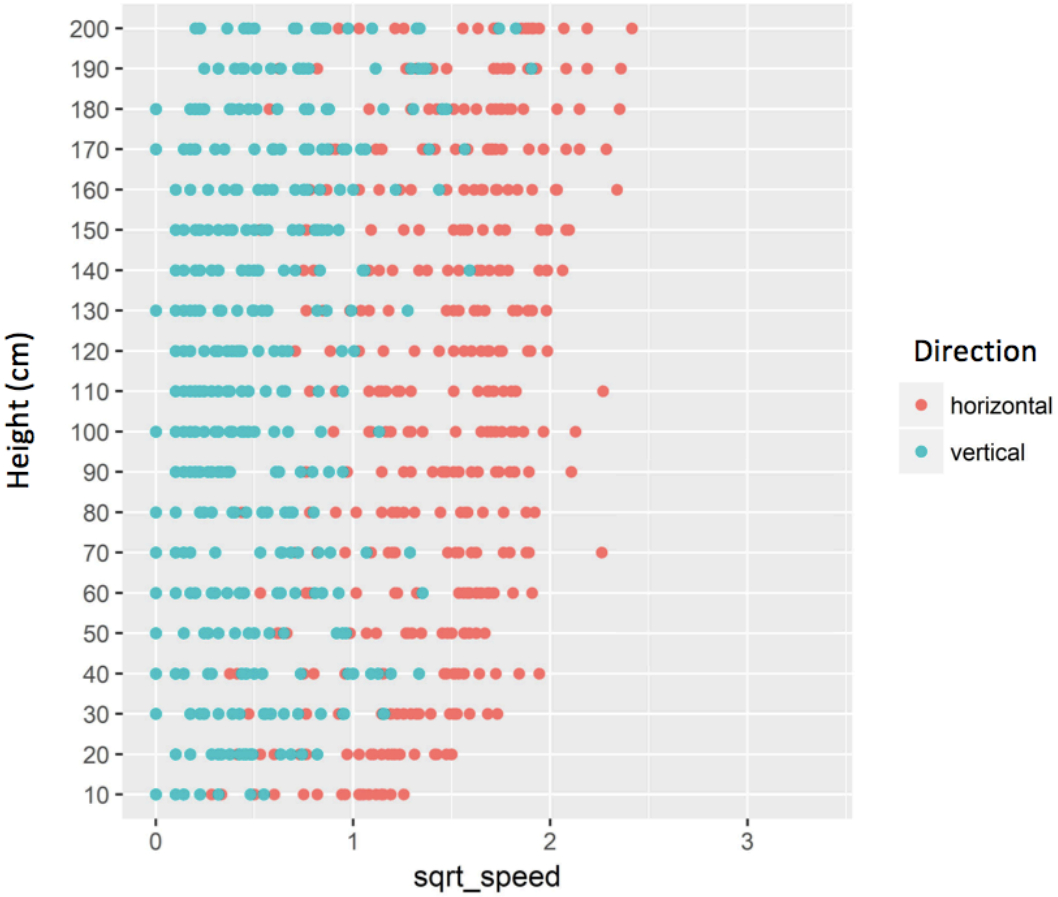

Fig. 8 Square root average vertical and horizontal wind speeds across all sites at a height from 10 cm to 200 cm.

Wind behaviour and terminal velocity

Using the vertical wind speed measurements and the mean terminal velocity of each of the 24 species, the wind events equal to and above the terminal velocity, and therefore considered capable of providing lift for a diaspore, was calculated. To enable the identification of any relationships of wind events with dispersal syndrome, the data was displayed using a key for the species' relative dispersal syndrome. Grasses were categorised separately from gravity-dispersed species due to their low terminal velocity (Fig. 9). Overall known wind-dispersed species experience a higher proportion of updraft events capable of lifting the diaspore. 10% or more of the wind events would have been above the terminal velocity threshold for nine species; seven wind-dispersed and two grasses. No measured wind events were strong enough to provide lift to any animal or gravity dispersed species. The average horizontal wind speed, measured at 2.2 m/s (± 1.2), surpasses the terminal velocity threshold for all but one wind-dispersed species and all grass species

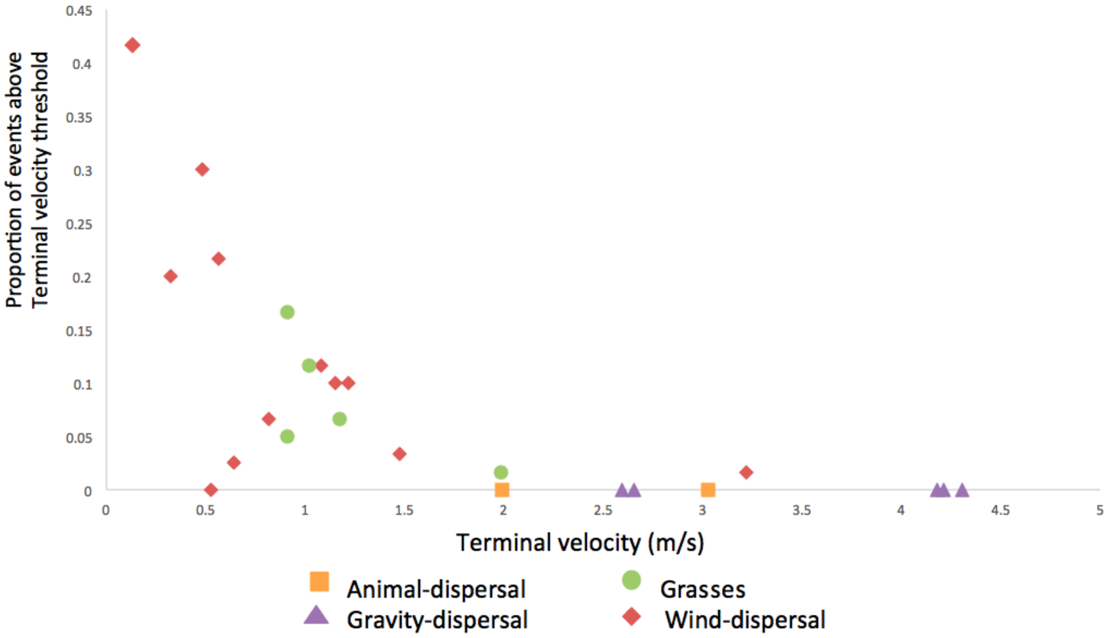

Fig. 9 Proportion of vertical wind events measured in the field above the terminal velocity thresholds measured for the collected samples of 24 species.

Wind behaviour at trap sites

At each trap site, the average horizontal wind speeds were much higher than the average vertical wind speeds and ranged from 3.14 m/s to 1.59 m/s (Fig. 10). The average vertical wind speed measured was highest at trap sites 1 and 4 (Fig. 11). These sites exhibited vertical average wind speeds of 0.61 m/s and 0.75 m/s respectively. All other sites had measured vertical average wind speeds between 0.44 m/s and 0.17 m/s.

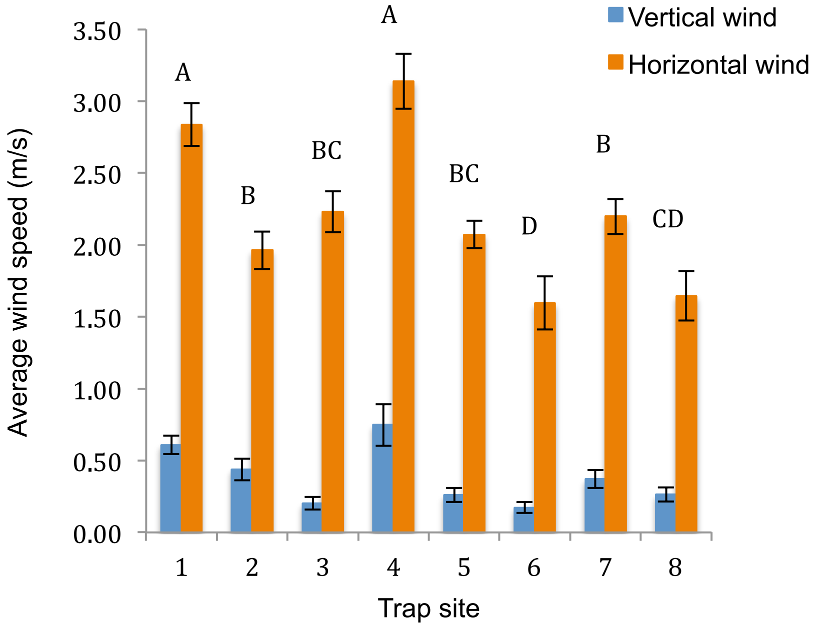

Fig. 10 Mean (±1SE) horizontal and vertical wind speed at each trap site.

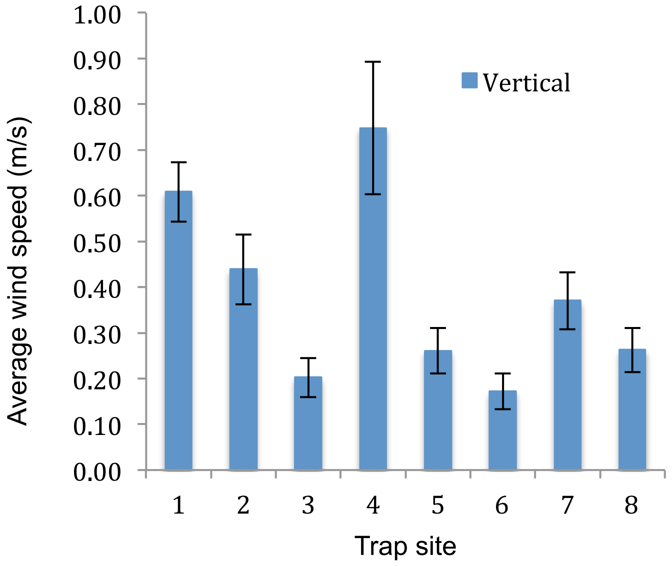

Fig. 11 Mean (±1SE) vertical wind speed at each trap site.

Field seed trap collection

In total, 140 seeds were captured in the seed traps over a period of 35 days; 32 seeds were collected in top traps and 108 in bottom traps (Fig. 12). Twenty different species were observed; 10 wind-dispersed species, 10 gravity-dispersed species. Of the 10 gravity-dispersed species, six were native alpine grass species. No seeds of alpine flora with animal dispersal mechanisms were found in any of the traps.

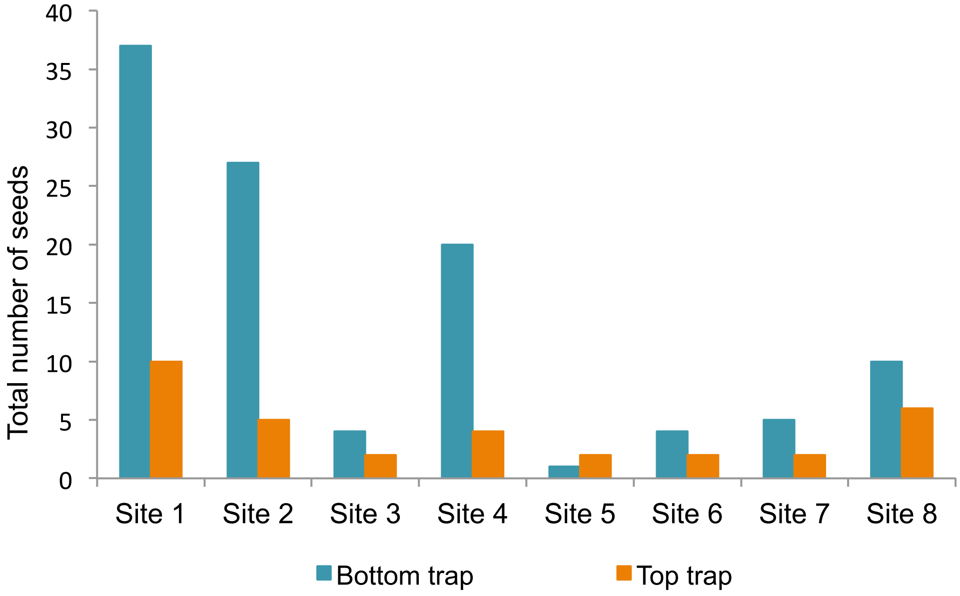

Fig. 12 Seed trap results at each site.

Of the 32 seeds collected in the top traps, 15 seeds were from wind-dispersed species, 15 seeds from grasses species and two seeds from gravity-dispersed species. Of the 108 seeds collected in the bottom traps, 30 seeds were wind-dispersed 42 were grasses and 36 were gravity-dispersed (Fig. 13). Two seeds captured in top traps were wind-dispersed invasive species; *Cirsium vulgare* and *Hypochearis radicata.*

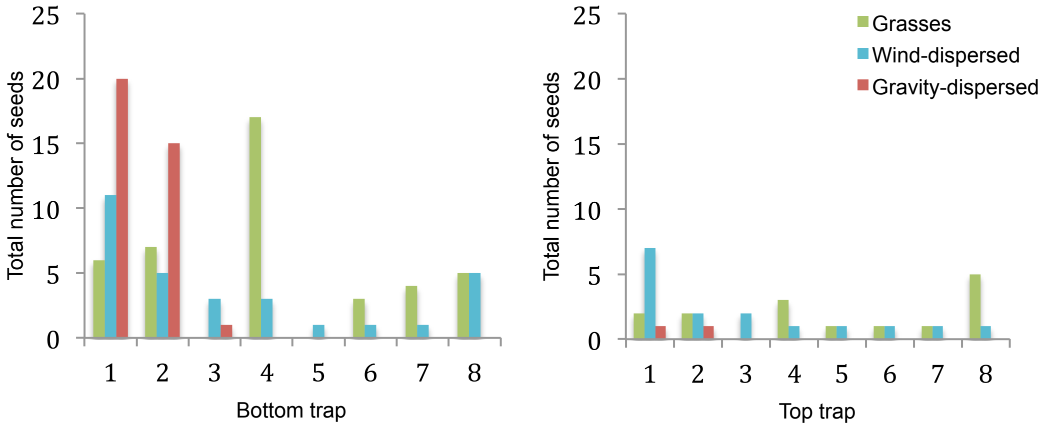

Fig. 13 Distribution of seeds by species dispersal types across top and bottom seed traps

Floristic surveys

A total of 46 species were found to be present in flower or shedding seed across all sites (Appendix C). Of these only 33% of species were found to be dispersing into seed traps. For all the seeds collected in the seed traps the minimum distance of potential seed travel was identified from the floristic survey (Fig. 14). This found 83 of the captured seeds had established plants present within the 1 m radius of the seed trap. 26 seeds travelled from a minimum distance of 5 m, 24 from a minimum distance of 10 m and two from a minimum distance of 15 m. Two species, *Euchiton fordianus* and *Cirsium vulgare,* were found to be dispersing distances greater than 15 m. Four *Euchiton fordianus* seeds were captured, three in bottom traps and one in a top trap. One *Cirsium vulgare* seed was found in a top trap. The only established *Cirsium vulgare* seeding plants were found 2 km away at a decrease in elevation of 212 m.

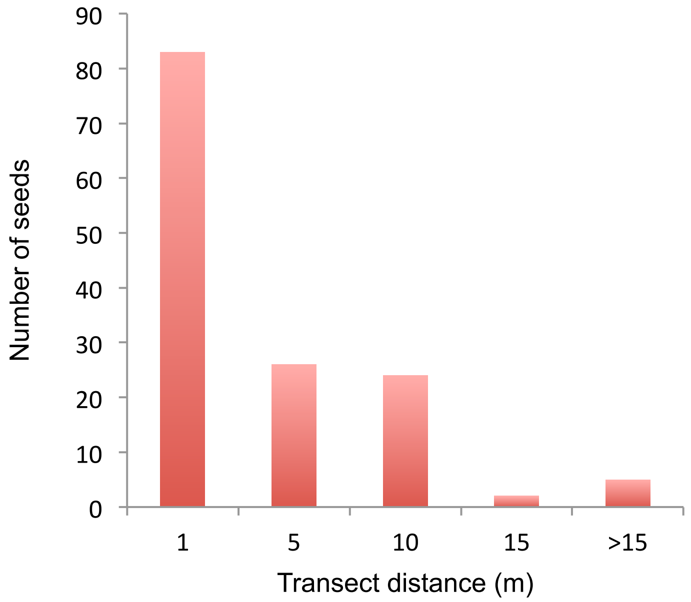

Fig. 14 Minimum distance of dispersal. Total number of seeds collected, relative to the closest flowering or seeding plant found within the florist survey

Growth study

Out of the 20 species used in the growth study, 14 species successfully established, that is they produced seedlings which survived for 30 days and were processed for growth traits (Appendix D). Of these 14 species, nine were wind-dispersed species and five were gravity dispersed-species, two of these being grasses.

When comparing the growth traits of specific leaf area (SLA), relative growth rate (RGR) and dry root to dry shoot mass ratio (DR/DS) to the seed morphology trait of mass for the 14 species, no statistically significant trends were found (Fig. 16 a,b,c). When comparing the growth traits to a calculated value of the seed mass proportion to that of the diaspore mass, a significant positive relationship with SLA was identified ($R^2 = 0.2398$, $p = 0.04334$) (Fig. 16 d). This trend showed that species with a larger seed mass proportion to dispersal appendage had a higher SLA. No statistical relationship was found for seed proportion and RGR and DR/DS (Fig. 16 e,f).

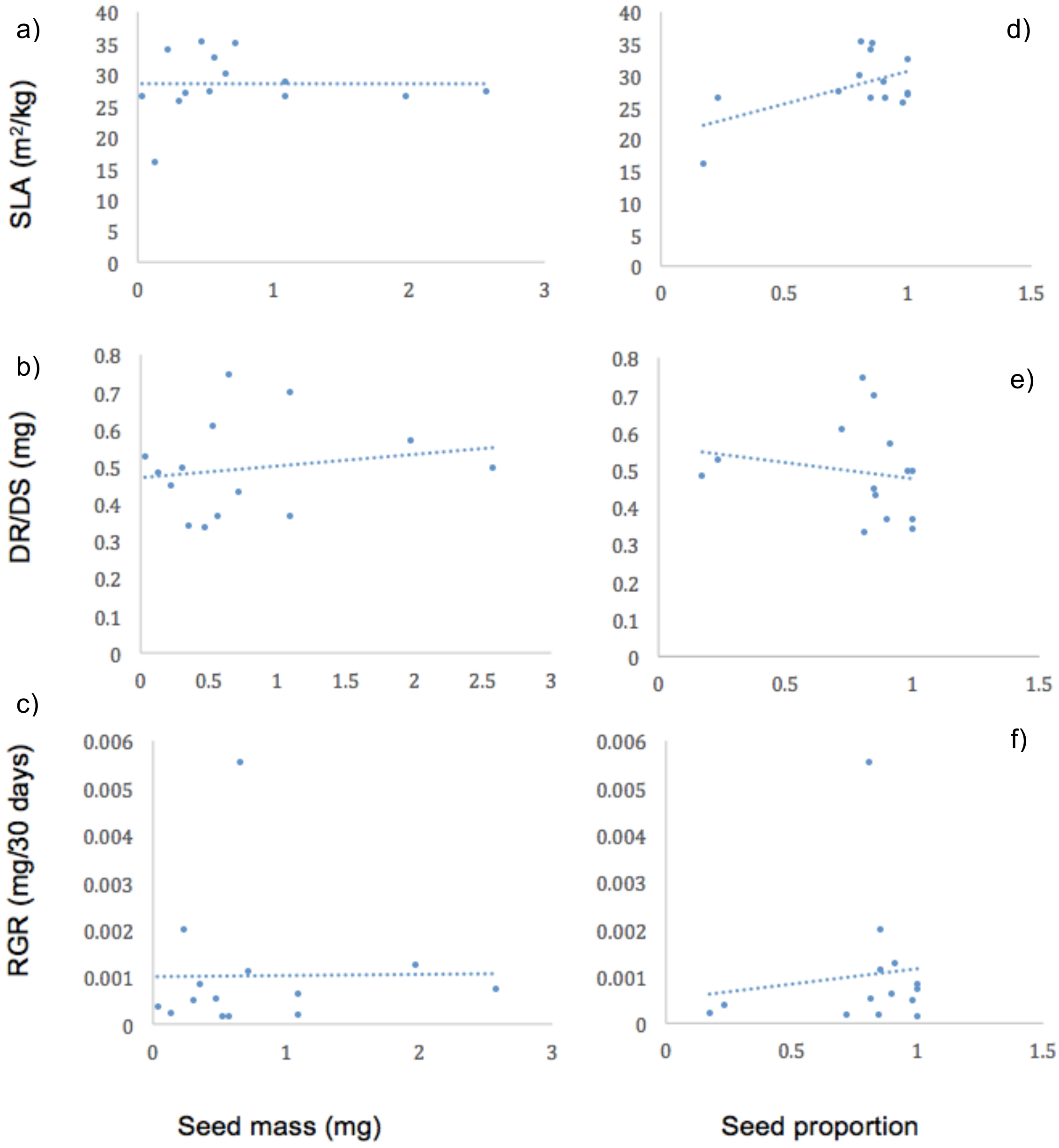

Fig. 15 Comparison of growth traits to seed mass - a,b,c and growth traits to seed mass proportion to diaspore mass - d,e,f

Discussion

Dispersal modelling

Terminal velocity had a strong effect on modelled predicted dispersal distance. When included in seed dispersal models, such as those used by Morgan and Venn (2017), terminal velocity significantly changed the predicted dispersal distance in 10 of 22 species. Hence, terminal velocity appears to be an important (yet rarely included) parameter in dispersal studies that accounts for substantial variation in dispersal capacity (Caplat et al. 2012). Its importance was most obvious in wind-dispersed seeds and grasses. By contrast, terminal velocity has little effect on predicted dispersal in gravity-dispersed species.

There was a positive relationship between diaspore mass and terminal velocity. This is not unexpected (Riba et al. 2005, Tabassum and Bonser 2017). However, when considering the investment into the proportion of the diaspore that constitutes the appendage, it was found that this trait was not a predictor of terminal velocity. This would suggest that the investment into the size of the dispersal architecture is less important and the design of the appendage is of greater consequence (Meyer and Carlson 2001, Riba et al. 2005). Previous studies have used the measurement of a diaspores pappus to achene volume ratio as an indicator of the variation in size and shape to determine dispersal ability (Tabassum and Bonser 2017). This unit of measure was found to be successful in quantifying the specific differences in diaspore morphology when comparing how this affects air resistance between species.

The predictive modelling for grasses found that terminal velocity changes the predicted dispersal distance when included in models. Whilst considered a gravity-dispersed species, the movement of grasses around an alpine ecosystem may be greatly underappreciated. From the modelling all grass species displayed an increase in their predicted dispersal distance when terminal velocity was included. All grasses were found to have a relatively low terminal velocity, particularly in comparison to other gravity-dispersed species. This is most likely due to grass diaspores being comparably small with some species exhibiting hairy structures that affect movement in air (Cheplick 1998, Tackenberg 2003). This may facilitate and provide opportunities for grasses to utilise wind events in alpine environments to disperse seed (Guretzky et al. 2013). Understandably, gravity-dispersed species showed little change in predicted dispersal distances. Due to a lack of aerodynamic appendages, their terminal velocity was high and this produced no significant changes in the predicted dispersal distances from the simpler model (Tabassum and Bonser 2017).

In the future terminal velocity should be considered when investigating wind-dispersal, as the terminal velocity of diaspores is the most informative plant trait in influencing wind-dispersal potential (Tackenberg 2003, Tackenberg and Stöcklin 2008). It can take into account the variation in seed aerodynamics through the morphological differences between species (Riba et al. 2005, Van Oudtshoorn and Van Rooyen 2013). This is particularly important when considering an alpine ecosystem where weather conditions provide more opportunities for dispersal by wind than in other landscapes (Nathan et al. 2001, Tackenberg and Stöcklin 2008).

Wind behaviour

When examining a species dispersal potential, by itself the terminal velocity of seeds in still air as a surrogate for dispersal ability is inadequate (Nathan et al. 2002). Although found to be important in dispersal distance modelling estimates, terminal velocity alone explains only a small fraction of the variation in a species dispersal capacity (Nathan et al. 2001, Tackenberg and Stöcklin 2008). This study found wind to be an important determinant of a species dispersal. Previous studies have found the natural variation in wind speed to be more important in determining dispersal distance than the diaspore trait of terminal velocity (Greene and Johnson 1996, Nathan et al. 2001). However, other traits, such as those associated with differential release of seeds in specific uplift wind events, should not be overlooked, particularly for wind-dispersed species(Nathan et al. 2002). The examination of vertical wind events showed that the specialised architecture allowing for a low terminal velocity in wind-dispersed species increased the probability of experiencing updraft events strong enough to provide lift for those species (Tackenberg 2003). It was also recognized that plant height was not such a limiting factor of dispersal as previously thought. *Euchiton fordianus*, for example, is comparably short in stature (10-20 cm) yet showed that based on its terminal velocity, 42% of updraft events were capable of dispersing diaspores. This was supported by the seed trap study where a proportionally high representation of this species was captured. In total, 15 seeds were captured in the seed traps, with five found in top traps (potentially capturing long-distance seed movements) and 10 in bottom traps (capturing more local dispersal events).

The ‘boundary layer’ effect, where wind conditions are slower closer to the ground due to surrounding vegetation providing some protection and lessening wind speeds, was not obvious in the analysis of the wind data (Smith et al. 2003). Horizontal wind speeds showed a slightly stronger trend in increasing with height, whereas vertical wind speeds remained relatively constant with an increase in height. It is these vertical wind events that are very important in providing dispersal opportunities. Other studies have identified maximum wind speeds to be higher in alpine zones than low lying landscapes (Cain et al. 2000, Nathan et al. 2001). Under these strong alpine conditions, wind is a very effective dispersal vector, even for species not suspected to be wind-dispersed according to their seed morphology (Cain et al. 2000, Nathan et al. 2001).

The measurements of wind events at eight sites in one alpine habitat, during one seed shedding period, may show an underestimation of the updraft events occurring. The conditions for dispersal may be different at other localities with varying slope and aspect. Different seasons may also hold a larger variation in wind events than that captured within the timeframe of this study. Therefore these measurements provide a restricted estimation of the wind dispersal potentials in the area. Although the sample period was short, the need for future studies to incorporate horizontal and vertical uplift events into dispersal examination is evident.

Field seed trap collection

This study is the first to carry out field testing of seed dispersal in the Australian alpine region. The collection of seeds in top traps (150 cm) gives evidence to the height seeds can reach when dispersing even though the plants releasing them have a short stature. Seed numbers captured in the seed traps, over this single seed shedding season, were small. With 33% of recorded species found in to be dispersing into traps, 76% of seeds had established plants within the first 5 metres of the Floristic survey. Only 5 seeds representing 2 species were found to have travelled greater then 15 metres. This suggests the majority or species are only dispersing very short distances. These findings correspond with the dispersal modelling of Morgan and Venn (2017).

Wind-dispersed and grass species were most represented in the seeds captured. For the most part, species found in the traps were also found in the floristic survey in front of the traps. Nevertheless, relatively high numbers of two gravity-dispersed species, *Plantago euryphylla* and *Colobanthus affinis* were also collected. This occurred at sites 1 and 2. The probable explanation for this occurrence is the close proximity of established plants to the seed trap opening. *Plantago euryphylla*, has a height range of 20-30 cm therefore seeds had a short distance to travel into a bottom trap and may have been shaken by extreme weather into the trap. The other species *Colobanthus affinis* has a lower height range of 10 cm or less but seeds from this species were only present in the traps after an extreme rain event. Although not documented, it is hypothesised that this species operates by ombrohydrochoric dispersal, whereby, seed expulsions occur from the force of rain droplets falling into the cup-like structure which holds the seeds (Parolin 2006).

From the seed capture results, grasses were found to have similar dispersal numbers as those species considered to specialise in wind dispersal (Burrows 1975, Guretzky et al. 2013). Native alpine grasses are known to clonally propagate and can dominant alpine communities (Costin et al. 2000, Sahukar et al. 2003).Their strong presence in the florist surveys was mirrored by high numbers of seeds collected in the seed traps. Due to the high abundance of grass seeds dispersing, it increases the likelihood of grass seeds entering a seed trap (Turnbull et al. 1999). This shows wind to be important and an understudied component of their dispersal activity within the alpine area and assists grasses in having a wide spatial patterning and continual dominance in such environments.

The comparison of wind data at each site also provided evidence that wind conditions play a major role in determining what species are able to disperse and reach height in their dispersal travel. This was shown by those species that were collected in the top trap. The most seeds collected per trap site were for sites 1, 2 and 4, with these traps also having relatively higher numbers of seeds in the top traps. The respective average horizontal wind speeds at these sites were not distinctively different to those of other sites. However, the average vertical wind speeds were found to be strongest at these sites. This supports the previously stated importance of wind behaviour in dispersal distance (Nathan et al. 2002, Caplat et al. 2012). Vertical wind, sometimes referred to as ‘turbulent uplift’, has previously been acclaimed as extremely important for herb species of open habitats in being able to disperse up into horizontal wind streams where prolonged flight can occur (Tackenberg and Stöcklin 2008).

Species that were found in the seed traps were represented as species to experience the greatest proportion of wind events to exceed their terminal velocity thresholds and provide lift to a diaspore. Eight out of the 12 species (66%) predicted to experience diaspore lift with 5% or more wind events were found in the seed traps, whereas only four out of 12 (33%) species experiencing less than 5% wind events above their respective terminal velocity threshold were represented in the traps. This clearly highlights the importance of wind behaviour and terminal velocity in a species dispersal capacity, and the need to include these parameters in estimates of potential dispersal (Nathan et al. 2011, Caplat et al. 2012).

Although discovering updrafts to be influential in the dispersal of species around an alpine ecosystem they are only important in the dispersal of species if they occur during the seed shedding period (Greene 2005). Measuring the frequency of updraft events over the entire seed shedding period, and over multiple seasons, would allow for greater clarity as to how important updraft events are in the windy alpine environment (Tackenberg and Stöcklin 2008, Nathan et al. 2011). Measuring vertical wind speeds over days of different temperatures may also capture fluctuations in the presence of updraft events as higher temperatures induce air currents to rise (Soons et al. 2004, Kuparinen et al. 2009).

Invasive plants

Invasive plants are often documented as rapid colonisers in alpine regions. Only two seeds of exotic species were captured in the seed traps, one each of *Hypochearis radicata* and *Cirsium vulgare*. *Hypochearis radicata* is a common weed of the alpine region and was located in many floristic surveys; however, only one diaspore was captured in a seed trap. *Hypochearis radicata* was measured to have a low terminal velocity but has a vast presence in the landscape, which would suggest that this species has a high dispersal capacity (Tabassum and Bonser 2017). Nevertheless, this was not observed in the seed traps. This potentially could be due to the seeds being blown back out of the seed trap after entering them hence, representing a design fault of the trap (Morris et al. 2011). Many of the Asteraceae seeds found in the traps had separated from their pappus. It may be that diaspores that did not detach from their pappus were easily blown back out of the trap instead of falling into the collection container. *Hypochearis radicata* seeds are very different to those of native Asteraceae . The achene of this exotic species extends into a relatively long stem which attaches to the pappus. This structure reduces the abscission of the achene from the pappus and, therefore, this species may not have been retained in the seed traps (Burrows 1975, Greene 2005). Modifications to the seed trap design were made to improve diaspore retention but further modification may be required for use in extremely windy alpine conditions.

Cirsium vulgare is an exotic species not yet documented to be growing above the treeline in alpine habitat at Falls Creek Resort. Nevertheless, a *Cirsium vulgare* diaspore, without pappus, was captured in trap site 4 with the closest established plants being discovered to be approximately 2 km away, 212 m lower in elevation. This is a very long-distance dispersal event and shows the value of trapping seed movements in situ. This finding suggests *Cirsium vulgare* has a diaspore morphology which allows it to disperse upslope and reach alpine zones (Tabassum and Bonser 2017). Although not yet in these habitats with changing climatic conditions the spread of this weed may increase and plants become established above the treeline (Williams et al. 2008, Gallien et al. 2015). No terminal velocity value was measured for this species as it was not present in any of the targeted alpine habitats where seed collections occurred for this study.

Growth and Establishment

Trade-offs between plant traits is well known, reflecting variation in pant strategies to deal with the key drivers of persistence e.g. stress, competition, disturbance (Marchand and Roach 1980, Hoyle et al. 2015). One of the best known trade-offs is the competition-colonisation trade-off whereby traits predicting good colonization (seed dispersal, seed mass, large quantities of seed produced) trade-off against traits that predict competiveness (Turnbull et al. 1999). In this study, dispersal was found to be short-distance for many alpine species. This begs the question. Are poor dispersers better competitors? This question was assessed in a glasshouse experiment that examined rates of growth in alpine plants and how this relates to seed traits such as seed mass. There were no significant trends when comparing the attributes of RGR and DR/DS to seed mass and the proportion of seed mass to diaspore mass. However, when considering the proportion of seed mass to SLA, there was a weak positive trend with a greater proportion of seed mass resulting in a higher SLA. This is contrary to most studies which have found low SLA to be associated with larger seed mass (Leishman et al. 2000). It has been previously concluded that seed size equates to high provisioning for offspring and this improves competitive ability (Jakobsson and Eriksson 2000, Leishman et al. 2000, Coomes and Grubb 2003). A larger seed mass is believed to confer low RGR and increased root mass; these plant traits associated with the production of a sturdy tissue construction (Leishman et al. 2000, Houghton et al. 2013). This strategy is deemed advantageous so that alpine plants can slowly establish in the landscape, tackling the stressful climatic conditions. Typically, small-seeded species generally have a high RGR, high SLA and lower root mass for quick establishment, with seedlings being constructed of lower-density tissues and having high turnover rates. These trends were not apparent in the current study.

Competition ability is often examined in regards to the spatial composition of a community. However, for alpine ecosystem competitive advantages may arise from species being able to persist progressively over time, particularly for combating abrasive weather conditions and snow cover (Angevine and Chabot 1979, Hoyle et al. 2013). High competition ability for larger seeds has been observed for Australian alpine plants in a study which showed a relationship between seed size and postponed germination (Hoyle et al. 2015). Postponed germination is a competitive advantage for alpine plants as it provides a mechanism to survive extreme weather conditions (Hoyle et al. 2013, Hoyle et al. 2015). The growth trends presented in this study may be influenced by postponed germination. This potentially resulted in reduced sample sizes for some species and a true average of the species growth traits may not have been represented. Not all species within the growth study trial had any growth events, suggesting the seeds to be unviable or the requirements to break dormancy for these species were not met.

Implications of this study under climate change

A firm grasp of life history trade-offs, such those between dispersal and growth traits, is needed when forecasting a species' response to climate change; particularly with respect to understanding the specific traits that will prove beneficial (Guisan and Theurillat 2000). Alpine ecosystems are highly vulnerable to the anticipated changes in climate (Jump et al. 2012). Range shift through dispersal is predicted to be a likely response (Nathan 2001, Walther et al. 2005). The most considered scenario, in mountainous landscapes, for species to persist through increasing temperatures is to migrate upslope (Guisan and Theurillat 2000, Walther et al. 2005). However, from the modelled seed dispersal work of Morgan and Venn (2017) and now the empirical validation from the findings of this study, dispersal responses for Australian alpine species are more limited than previously suggested.

Although not widely publicised climate change effects also include changes in wind speeds. Global wind speeds have decreased by 5 -15% during the last 30 years, and are expected to continue to decrease (Vautard et al. 2010, Barton 2014) This will likely impact the frequency and intensity of wind events in Australian alpine regions (McVicar et al. 2008). Wind behaviour was found to be extremely important in producing dispersal opportunities for numerous species. Decreasing wind dispersal events for alpine species will further limit their capacity to disperse to safe sites (Nathan et al. 2002, Trakhtenbrot et al. 2014). Future conservation management techniques may need to involve assisted migration for alpine species to successfully spread and remain present within the landscape.

This study found the exotic species *Cirsium vulgare*, to have the capacity to disperse long-distances. With the impacts of climate change dispersing longer distances gives a species a competitive edge in being able to reach niche habitats more readily. The capturing of the *Cirsium vulgare* seed is a confirming example of the colonization of invasive species from below the treeline into alpine habitats (Gallien et al. 2015). Increasing temperatures are likely to create ideal conditions to enable these species to establish and spread throughout the alpine landscape (Bear et al. 2006, Williams et al. 2008, Hoyle et al. 2013).

Conclusion

This study set out to better understand how Australian alpine species may respond to climate change by quantifying alpine plants' ability to disperse in the field and their potential to establish at safe sites. Alpine species are already at the edge of their climactic range and it is vital seeds reach sites suitable for germination and survival through seed dispersal. Incorporation of terminal velocity into predicted dispersal distance modelling improves current models, and highlighted that there is greater variation in dispersal capacity across alpine species. Localised wind behaviour and wind events were also considered an important contributing factors to dispersal distance. Diaspores require updraft events at speeds above their terminal velocity threshold to provide lift and carriage of the seed. Seed trap results found few species capable of reaching height when dispersing with the majority of species displaying only short-distance dispersal capacity. The capturing of the invasive species *Cirsium vulgare* was found to be an example of exotic species potentially being better equipped in dispersing longer-distance*.* The examination of growth traits did not display any strong trends in competitive ability among differing seed characteristics. Overall this study has shown that empirical testing of seed dispersal is essential in order to fully understand seed dispersal.

Acknowledgments

I would like to thank Dr John Morgan and Dr Susanna Venn for their guidance, knowledge and support for the entire period of this project. Their helpful comments and critics on the manuscript were also greatly appreciated. Nick Moore for his experience and assistance in completing the growth study. Thank you to Dr Peter Green for his enthusiastic involvement with the investigation of updraft events. Falls Creek Resort Management in particular, Environment Officer, Jess Millet-Riley for granting me permission to conduct my study in the Falls Creek Resort. Daniel Miller and Marie Szmalko for their time volunteering in the field. John Szmalko for his hard work and contribution in constructing the seed traps. Mijail Karpyn for his help with the statistical program R.

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Appendix A: UTM coordinates of field sites.

Seed trap site	UTM Coordinates
1	E 0522459, S 5918699
2	E 0522264, S 5918763
3	E 0522489, S 5918597
4	E 0523394, S 5919850
5	E 0523191, S 5919963
6	E 0523635, S 5920509
7	E 0523085, S 5920831
8	E 0523202, S5920884

Appendix B: Seed trait data.

Species	Dispersal Syndrome	Terminal Velocity (m/s)	Diaspore Mass (mg)	Seed Mass (mg)	Modelled dispersal distance (m) (With Terminal Velocity)
Acaena novae-zelandiae	Animal-dispersal	1.99	2.47	1.41	354.53
Agrostis venusta	Gravity-dispersal	0.91	0.14	0.14	7.14
Brachyscome spathulata	Wind-dispersal	1.15	0.31	0.30	3.01
Carex hebes	Gravity-dispersal	2.66	0.92	0.92	3.25
Celmisia pugioniformis	Wind-dispersal	1.22	3.11	2.90	1.31
Colobanthus affinis	Gravity-dispersal	0.64	0.02	0.02	1.71
Craspedia aurantia	Wind-dispersal	0.32	0.58	0.47	12.75
Erigeron bellidiodes	Wind-dispersal	0.64	0.73	0.53	38.43
Erigeron nitidus (nitidius)	Wind-dispersal	0.53	1.29	1.09	12.78
Euchiton fordianus	Wind-dispersal	0.13	0.04	0.02	20.71
***Hypochaeris radicata**	Wind-dispersal	0.56	0.81	0.65	18.78
Luzula novae-cambriae	Gravity-dispersal	4.3	0.57	0.57	0.2
Microseris lanceolata	Wind-dispersal	3.22	3.53	2.84	0.96
Olearia frostii	Wind-dispersal	1.08	1.21	1.09	27.33
Oreomyrrhis eriopoda	Gravity-dispersal	4.21	2.57	2.57	0.35
Plantago euryphylla	Gravity-dispersal	2.59	0.35	0.35	0.88
Poa hiemata	Gravity-dispersal	1.17	0.35	0.35	3.29
Podolepis robusta	Wind-dispersal	1.47	2.17	1.98	4.86
Ranunculus victoriensis	Animal-dispersal	3.03	2	2.00	244.5
Rytidosperma nudiflorum	Gravity-dispersal	1.98	0.76	0.76	2.04
Senecio pinnatifolius	Wind-dispersal	0.48	0.27	0.23	20.18
Trisetum spicatum	Gravity-dispersal	1.02	0.38	0.38	5.94
Viola betonicifolia	Gravity-dispersal	4.18	1.17	1.17	0.29
Xerochrysum subundulatum	Wind-dispersal	0.82	0.84	0.72	8.67

Appendix C: List of species in flower or seeding at all trap sites.

Species captured in seed traps are represented with a ‘1’, absents fro seed capture is represented with a ‘0’.

Species in flower or seeding at trap sites	Presence or absence in seed traps
Acaena novae-zelandiae	0
Acetosella vulgaris	0
Agrostis capillaris	0
Agrostis venusta	1
Euchiton fordianus	1
Asperula gunnii	0
Asterolasia trymalioides	0
Brachyscome decipiens	0
Brachyscome spathulata	0
Carex breviculmis	0
Carex hebes	0
Celmisia costiniana	1
Colobanthus affinis	1
Craspedia aurantia	1
Craspedia coolaminica	0
Erigeron bellidioides	1
Erigeron nitidus	0
Gonocarpus montanus	0
Grevillea australis	0
Helichrysum rutidolepis	0
Hovea montana	0
*Hypochaeris radicata	1
Kunzea muelleri	0
Leptorhynchos squamatus	1
Luzula novae-cambriae	0
Microseris lanceolata	0
Olearia brevipedunculata	0
Olearia frostii	1
Oreomyrrhis eriopoda	0
Orites Lancifolius	0
Plantago euryphylla	1
Poa hiemata	1
Poa hothamensis	1
Podolepis robusta	0
Ranunculus victoriensis	0
Rytidosperma nudiflorum	1
Scleranthus biflorus	0
Scleranthus singuliflorus	0
Senecio gunnii	0
Senecio pinnatifolius	1
Trachymene humilis	0
Trifolium sp	0
Trisetum spicatum	0
Viola betonicifolia	1
Wahlenbergia sp	0
Xerochrysum subundulatum	0

Appendix D: List of species in flower or seeding at all trap sites.

Species used in the growth study	Percentage of successful establishment
Acaena novae-zelandiae	0%
Agrostis venusta	70%
Brachyscome spathulata	25%
Colobanthus affinis	0%
Craspedia aurantia	20%
Erigeron bellidioides	55%
Erigeron nitidus	20%
Euchiton fordianus	0%
*Hypochaeris radicata	50%
Luzula novae-cambriae	55%
Olearia frostii	60%
Oreomyrrhis eriopoda	20%
Plantago euryphylla	35%
Poa hiemata	0%
Podolepis robusta	80%
Ranunculus victoriensis	0%
Rytidosperma nudiflorum	15%
Senecio pinnatifolius	30%
Trisetum spicatum	0%
Xerochrysum subundulatum	90%

Appendix E: Author instructions for submission to Australian Journal of Botany

Title

This should be concise and informative and should contain all keywords necessary to facilitate retrieval by modern searching techniques. Titles including generic or specific names should also contain the name of taxa at higher rank, e.g. Division, Class, Order or Family. Nomenclatural authorities should be omitted from the title. An abridged title that does not exceed 50 characters should also be supplied for use as a running head.

Abstract

This should state concisely, preferably in fewer than 200 words, the scope of the work and the principal findings, and should be suitable for use by abstracting services. Species names mentioned in the abstract should include nomenclatural authorities. Acronyms and references should be avoided.

Text

This should normally be divided into sections, e.g. Introduction, Materials and Methods, Results, Discussion, Acknowledgments, References. All main headings should be in upper and lower case bold type, aligned at the left. Minor headings should be in light italics. The folllowing also should be adhered to: spell out numbers lower than 10 unless accompanied by a unit, e.g. 2 mm, 15 mm, two plants, 15 plants, but 5 out of 15 plants; leave a space between a numeral and its unit; use the ´ise´ construction, not ´ize´; indicate approximate positions of figures and tables on the manuscript.

Synonymies should be indicated by a smaller font size and the first line of each synonymous species should be indented. Where presented, synonymy should immediately follow taxon headings.

Latin diagnoses for new species should be given in English to allow checking by the referees.

Material examined should be the last section presented in each taxon treatment and should be indicated by a minor heading and a smaller font size. Where presented, Etymology and Illustration sections should immediately precede Material examined. For clarity, authors should provide a minor heading, on a separate line, for each section of a taxon treatment, except for the taxon description. This may appear without a heading.

References

In the text, references should be listed in chronological order, separated by semi-colons. Use ´and´ to link the names of two coauthors and ´*et al.*´ where there are more than two. Do not use a comma between the author´s name and the date. References after names of taxa, e.g. in synonymies, should include the author´s name followed by a comma, the journal name (suitably abbreviated) in roman type, the volume number followed by a colon, then the page numbers, and finally the year in parentheses. References occurring only in synonymy should not be given in the reference list. Make sure that all references in the text (except synonymies) are listed at the end of the paper and *vice versa*. At the end of the paper, list references in alphabetical order. Give titles of books and names of journals in full.

E.g *Journal article*

Lucas EJ, Harris SA, Mazine FF, Bellsham SR, Lughadha EMN, Telford A, Gasson PE, Chase MW (2007) Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* **56**, 1105-1128.

Units

The International System of Units (Système International d´Unités, SI units) should be used for exact measurement of physical qualities and as far as practical elsewhere. Measurements of radiation should be given as irradiance or photon flux density, or both, and the waveband of the radiation should be specified. Luminous flux density units (e.g. lux) should not be used. Do not use the double solidus in complex groupings of units, e.g.mmol/m^2/s; use the negative index system instead, i.e. mmol m^{-2} s^{-1}.

Line drawings

The following symbols should be avoided: +, x or *. Explain the symbols used in the caption of the figure or in a legend. State on the axes of a graph what is being measured and give the appropriate units in parentheses.