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Do Facilitative Interactions with Neighboring Plants Assist the Growth of Seedlings at High Altitudes in Alpine Australia?

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Abstract

During the early life-history stages, plants are especially susceptible to the abiotic conditions present in high mountain environments. At high altitudes, facilitative interactions between close neighboring plants may buffer seedlings from these abiotic pressures by providing shelter from frosts and winds. At lower altitudes, seedlings may not be so limited by the abiotic environment, and may therefore compete for resources with close neighboring plants. Using four alpine sites at different elevations (representing an abiotic stress gradient), we investigated how the presence of close neighboring plants influences seedling growth in their first growing season. We experimentally cleared above-ground vegetation and transplanted seedlings of three species into cleared and control plots. We quantified the stress gradient of abiotic conditions across sites by measuring ambient and soil temperatures, soil moisture, and soil frost heave. We used the “Relative Neighbor Effect” index to show the direction of the interaction between transplanted seedlings and their close neighboring plants. *Aciphylla glacialis* seedlings showed neutral interactions across the gradient of alpine sites, with undetectable change across the growing season, compared with *Brachyscome rigidula* seedlings which showed positive interactions with neighbors across the growing season at most sites. *Trisetum spicatum* seedlings showed mostly neutral interactions with neighbors at the higher elevations, and often negative interactions at the lower elevations, particularly midway through the growing season. Our findings highlight the importance of spatial and temporal plant-plant interactions with regard to seedling performance across altitudinal stress gradients.

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Introduction

Harsh ambient conditions, such as soil heaving caused by frosts and subsequent needle ice, short growing seasons, summer soil drought, and large diurnal temperature fluctuations over the summer months combine to make regeneration from seed a risky strategy in alpine and arctic areas (Urbanska and Schütz, 1986; Williams, 1987; Venn and Morgan, 2009). Hence, clonal and vegetative propagation is cited as the most common and successful form of plant regeneration in these environments (Körner, 1999). However, successful seedling establishment is possible provided suitable microsites and ambient conditions (Chambers et al., 1990; Welling and Laine, 2000; Forbis, 2003; Venn and Morgan, 2009). In Australia, for example, Venn and Morgan (2009) found natural seedling emergence between 10 and 85 seedlings m⁻² across mountain summits varying in altitude between 1668 m and 1970 m. Facilitative interactions between close neighboring plants and emerging seedlings may be one mechanism that ensures successful seedling recruitment in these extreme environments (Carlsson and Callaghan, 1991; Moen, 1993; Sturm et al., 2001; Callaway et al., 2002; Cavieres et al., 2002; Acuña-Rodríguez et al., 2006). By clumping together and sheltering from wind or frost on the lee side of neighboring plants (Carlsson and Callaghan, 1991; Moen, 1993; Sturm et al., 2001; Callaway et al., 2002) or sheltering within the canopy of nurse species (Acuña-Rodríguez et al., 2006; Cavieres et al., 2002), alpine seedlings may avoid the

detrimental effects of the ambient environment. Such positive interactions have been reported in numerous alpine locations around the world between adult plants (summarized by Callaway et al., 2002), with the overriding outcome that most plants benefit from close neighbors at high alpine sites and that facilitation is the dominant inter-plant interaction in high mountain environments. However, Cavieres et al. (2006) showed that cushion plants in arid mountains of central Chile facilitated seedling species more frequently at lower elevations by increasing water availability in water-stressed habitats.

Across alpine landscapes and altitudes, abiotic stress can drive the direction and strength of plant interactions (Bertness and Callaway, 1994; Callaway, 1995; Brooker and Callaghan, 1998; Callaway et al., 2002; Kikvidze et al., 2005). Aptly termed the *abiotic stress hypothesis* (Kikvidze et al., 2006), plant productivity is predicted to be highest at the least stressful end of a stress gradient (Grime, 1979), and individual plants may interact negatively, competing for resources such as light, water, and nutrients (Bertness and Callaway, 1994). Here, they may grow to the point where they are limited by competitive neighbors (Wilson and Keddy, 1986; Brooker and Callaghan, 1998). At the stressful end of the gradient, plants may be more limited by the abiotic environment (Bertness and Callaway, 1994; Callaway et al., 2002) and therefore are more likely to show positive interactions with close neighboring plants (Brooker and Callaghan, 1998; Pugnaire and Luque, 2001). Within a stress gradient, plant interactions may

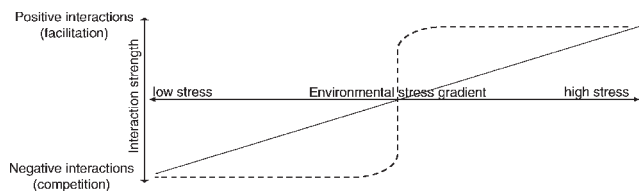


FIGURE 1. Conceptual diagram predicting the relationship between plant interaction type (negative, neutral, positive) and an environmental stress gradient, from low to high. With increasing abiotic stress, positive interactions become predominant, either gradually increasing (solid line) or after reaching ecological thresholds (dashed line), whereby an interaction switch occurs.

also shift seasonally as abiotic conditions improve and deteriorate (Kikvidze et al., 2006). Hence, interactions between plants are spatially and temporally dynamic.

In this study, we test the abiotic stress hypothesis with regard to early seedling growth in the Victorian alpine region in southeastern Australia. The occurrence of seedlings of many species in this region have recently been reported as common (Venn and Morgan, 2009), although our understanding of recruitment processes among alpine plants in Australia remains poor and there is little evidence to provide information on the mechanisms of seedling establishment in these landscapes. Here we investigate the role that facilitative interactions might play in aiding seedling growth of three common alpine species across an altitudinal gradient of mountain peaks, through the course of one growing season. The highest peaks in our study (>1800 m) are dominated by stressful conditions such as strong winds, frequent frosts, extended snow cover, and cool summers (Williams, 1987; Venn and Morgan, 2009). The lower alpine peaks (1500–1700 m), by contrast, have potentially more favorable conditions for plant growth because the snow season is shorter, frosts are less common, and growing seasons are warmer and longer (Venn and Morgan, 2005). Across these alpine peaks, we suggest that facilitative interactions between neighboring plants and seedlings are more likely to occur at the highest elevations where abiotic stress is predicted to be greatest. At lower elevations, however, where plant growth may be less limited by the constraints of the environment, we predicted fewer positive associations between close neighboring plants, and seedlings performing better without close neighbors. The shape of the response curve, however, is not necessarily linear as one descends from high mountain peaks (Fig. 1). Indeed, there may be thresholds for change in interaction type and strength once abiotic limitations have been passed. We also predicted temporal changes in plant interactions throughout the growing season as soil moisture availability and the frequency of frost heave events change throughout the growing season. We predicted that seedling success, measured by relative growth rate across the snow-free season, is related to facilitative interactions, especially at the highest altitudes; however, we did not predict the results to be consistent across study species as differences in resource allocation, growth form, and leaf area all affect how plants perceive their local environment.

Methods

STUDY SITES AND SPECIES

The study was conducted in the Alpine National Park, approximately 350 km northeast of Melbourne, Australia. The area comprises several high peaks, including Victoria's highest

mountain, Mt. Bogong (1986 m), which can be covered by snow for four to five months of the year. The mean annual rainfall is >1800 mm (LCC, 1982) with much of this precipitation falling as snow on the high peaks during winter. Average air temperatures follow seasonal variations with typical daily minima and maxima of between 2 and 27°C in summer (November to April) and –6 and 12°C in winter (May to October). Frosts are frequent and can occur at any time of year (Williams, 1987). The growing season spans approximately seven months from snowmelt, usually the end of September, until late April, when the first substantial snowfalls of the winter begin.

We chose sites on four mountain peaks to represent a gradient in elevation from high to low: Mt. Bogong (1970 m), Mt. Hotham (1860 m), Mt. Magdala (1725 m), and King Billy (1696 m). The sites are approximately 8–50 km from each other, with King Billy and Mt. Magdala being the closest and King Billy and Mt. Bogong the most distant. By only using the summit areas of each peak, and thereby keeping the effects of aspect (wind, rain, and snow direction) and topography constant across sites, we were able to focus on the abiotic differences which occur at the different altitudes. All sites are classed as “Steep Alpine Mountains” after Costin (1957), are above the natural treeline, and are dominated by tall alpine herbfield vegetation (McDougall, 1982; Walsh et al., 1986) consisting of short-statured forbs (*Celmisia pugioniformis*, *Celmisia costiniana*, *Stellaria pungens*, *Asperula gunnii*) and tussock grasses (*Poa fawcettiae*, *Poa hiemata*) interspersed with sprawling shrubs (*Grevillea australis*, *Hovea montana*) up to 0.6 m in height. The relative proportions of the dominant species remain the same across the sites and bare ground in these communities is typically 20–30%. Despite the underlying geological variation (LCC, 1982), in these regions parent material rarely influences soil type and all soils are considered to be of the “alpine humus” type and are acidic (pH 4.0–5.0) (Costin, 1962). Cattle are currently excluded from all sites, but grazing has occurred to varying degrees in the past (Lawrence, 1999). None of the sites examined have experienced wildfires since 1939 or, in some cases, well before this time.

We chose three study species: *Aciphylla glacialis* (Apiaceae), a robust, dioecious perennial herb, 20–50 cm high, with leathery dissected leaves; *Brachyscome ridigula* (Asteraceae), a leafy, clumping perennial daisy up to 30 cm high; and *Trisetum spicatum* (Poaceae), a variable, tufted perennial grass, 20–40 cm high; hereafter, these are referred to as *Aciphylla*, *Brachyscome*, and *Trisetum*. Although none of these species is considered dominant, all are locally abundant at each site and their occurrence has been confirmed at most of the other mountain peaks in the region (Walsh et al., 1986; McDougall and Walsh, 2007). In addition, all three species flower annually, have highly germinable seeds, are present as seedlings at the study sites (Venn and Morgan, 2009) and are not regarded as vegetatively spreading species; rather, they rely on seedling recruitment for regeneration.

EXPERIMENTAL DESIGN

At each of the four study sites, 24 cleared plots (for each species) were created by clipping above-ground vegetation to ground level to create a 225 cm² plot. Adjacent uncleared control plots of the same size were paired with each cleared plot, 0.5 m away, giving a total of 48 plots at each site for each species (144 plots in total at each site using three species). These paired plots were positioned randomly at each site, in and around particularly low (<20 cm) grass tussocks and shrubs present at each site. Plots were also placed in areas of similar species composition across

sites. We did not separate the above-ground vegetation removals from below-ground interactions, as we left the existing roots in both control and cleared plots undisturbed. Competitive or facilitative interactions were therefore only measured from above-ground parameters, although below-ground parameters may have also indicated additional plant interactions. Seedlings were grown from local seed collected during the 2003/2004 and 2004/2005 growing seasons. The seed was germinated in Melbourne at La Trobe University in controlled glasshouse conditions during early 2005. Propagated seedlings were then moved outside to a shadehouse to continue growing for 10 weeks in trays with 4 × 4 cm soil plugs. We kept the seedlings in their trays during transportation to each site, acclimatized the seedlings over 2–4 nights at each site, and kept each seedling's plug of soil and roots intact while planting and watering each seedling. One seedling was planted into each cleared and control plot in April 2005, before the onset of the winter snows. At planting, we counted the number of leaflets for every *Aciphylla* seedling and leaf blades for every *Trisetum* seedling, and we measured the height of every *Brachyscome* seedling as an initial measurement for the start of the experiment. We repeated these measurements for every seedling at three sampling intervals (early, mid, and late) during the following growing season. The early season sampling interval was between 5 and 18 November 2005, the mid-season sampling interval was between 11 and 26 January 2006, and the late season sampling interval was between 16 March and 13 April 2006. Due to seedling mortality in the shadehouse, there were insufficient seedlings to plant every species at every site. Thus, *Aciphylla* seedlings were not planted at Mt. Bogong, and *Brachyscome* seedlings were not planted at Mt. Hotham.

DATA ANALYSIS

We calculated the relative competitive intensity between pairs of seedlings, in cleared and control plots across the altitudinal gradient of sites, using the Relative Neighbour Effect (RNE) index (Markham and Chanway, 1996; Brooker et al., 2005):

$$\text{RNE} = (\text{P}_{\text{Cl}} - \text{P}_{\text{Co}}) / \max(\text{P}_{\text{Cl}}, \text{P}_{\text{Co}}), \quad (1)$$

where P_{Cl} and P_{Co} refer, respectively, to the performance of seedlings grown in cleared and control plots, and $\max(\text{P}_{\text{Cl}}, \text{P}_{\text{Co}})$ refers to the maximum of either P_{Cl} or P_{Co} . The RNE index makes the data interpretation clear and informative, allowing for the expression of the intensity of both facilitative and competitive interactions. To make more intuitive sense, we present the RNE values in reverse, so that positive values indicate a positive interaction (facilitation) and negative values indicate a negative interaction (competition), as per Callaway et al. (2002). We calculated the term for “performance” in the RNE index using the number of leaflets for *Aciphylla* and leaf blades for *Trisetum* seedlings and the height (cm) of *Brachyscome* seedlings in paired cleared and control plots at every sampling interval. We present the overall mean RNE value for seedlings from each pair of cleared and control plots, for each site at three intervals across the growing season in 2005/2006. We can therefore assume that differences in leaf number or height of seedlings, between pairs of cleared and control plots, constitute a relevant indicator of the direction and strength of a biotic interaction between the seedlings and the neighboring plants. Low RNE values indicate a weak interaction, whereas high RNE values (positive or negative) indicate a relatively stronger interaction. In our analysis, a death in any pair of seedlings was removed from the calculations to give

a conservative estimate of competitive or facilitative interactions with neighboring plants. The differences between RNE values at each site, within each species and sampling interval, were compared with one-way ANOVA and Bonferroni post-hoc tests. Assumptions of normality and homogeneity of variance were met by log-transforming the data. SYSTAT version 10 (copyright SPSS Inc., 2000) was used for all statistical analyses.

CLIMATE AND ENVIRONMENTAL VARIABLES

In order to assess the degree of environmental stress experienced at each of the study sites, and to demonstrate the physical differences between experimentally cleared and control plots, we measured air and soil temperatures, soil moisture, frost frequency, and soil frost heave.

Soil and air temperatures were measured hourly with TinyTag data loggers at Mt. Bogong (1970 m) and King Billy (1696 m) during the 2005/2006 growing season. Measurements from Mt. Hotham and Mt. Magdala were discarded due to logger failure. The soil temperature probes were inserted into cleared (15 × 15 cm) and control plots at 10 cm depth. The air temperature probes were housed in a Stevenson screen mounted at 1 m height.

Temperature data were converted to mean monthly growing degree-days (GDDs) in order to produce a single metric per month that is easily comparable between sites. GDDs were calculated as a measure of accumulated degrees Celsius above a base temperature to represent a cumulative index of energy available for growing plants, according to McMaster and Wilhelm (1997):

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

The daily GDDs were then summed for each month. We chose 0°C as a conservative base growing temperature as alpine plants are generally varied in their absolute base growing temperature and this value encompasses this variability (Bliss, 1962; Körner, 1998; Brown et al., 2006).

Soil moisture (%) was measured using a Theta-Probe and HH2 reader (Measurement Engineering, Australia) in cleared and control plots at every site over the 2005/2006 growing season and at every sampling interval (early, mid, and late). Readings were calibrated against gravimetrically determined soil moisture measurements from the four sites. The relative change in soil moisture over the growing season in cleared and control plots at each site was analyzed by repeated measures ANOVA. In cases where the sphericity assumption was violated we used the more conservative Greenhouse-Geisser epsilon corrected *p*-value (Quinn and Keough 2002). Differences in soil moisture between sites, in the same sampling interval and treatment, were analyzed with two-way ANOVA. Data were log-transformed in order to meet the assumption of homogeneity of variance.

We measured the impact of frost events on soil stability using vertical displacement pins (Brown et al., 2000). This method records the height that frozen soil reaches during a frost event, and frost heave is inferred from the change in height of a rubber washer on a 5 mm stainless steel rod (see Brown et al., 2000). In 10 cleared and 10 control plots, near the experimental plots, a vertical displacement pin was erected and frost heave recorded during the early, mid, and late sampling intervals. Pins were only erected at Mt. Bogong, Mt. Hotham, and King Billy. Frost heave data were analyzed by two-way ANOVA on log +1 transformed data to compare site and treatment effects.

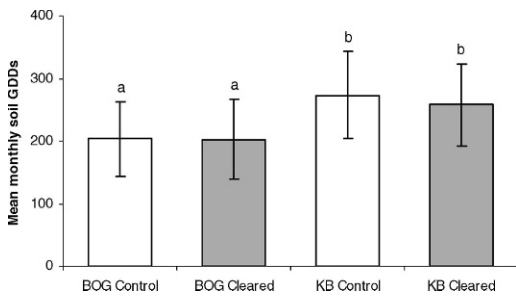


FIGURE 2. Mean monthly growing degree days (GDDs) (± 1 se) derived from soil temperatures recorded at Mt. Bogong (1970 m) (BOG) and King Billy (1696 m) (KB) between June 2005 and November 2006 in cleared and control plots. Symbols indicate significant differences between treatments within sites from paired *t*-tests.

Results

ENVIRONMENTAL VARIABLES

Air and Soil Temperatures

Over the growing season, air temperatures were high at King Billy (the lowest site at 1696 m), with daytime maximum temperatures regularly between 20 and 30°C and overnight temperatures rarely below 10°C (between January and March). At Mt. Bogong (the highest site at 1970 m), during the same period, maximum daytime temperatures were between 15 and 20°C and overnight temperatures were always below 10°C and often below 0°C. Monthly GDDs between June 2005 and February 2006 revealed that more degrees were accumulated at the lowest site (King Billy, 1696 m) than the highest site (Mt. Bogong, 1970 m) with a mean difference of 80 GDDs per month. During this period, 2341 GDDs were accumulated at King Billy compared to 1629 at Mt. Bogong. Air temperatures at Mt. Bogong remained lower for longer, mostly due to the extended duration of snow cover at this site.

Soil temperatures converted into GDDs between June 2005 and February 2006 at King Billy (1696 m) and Mt. Bogong (1970 m) followed the patterns in air temperatures, with significantly higher GDDs at King Billy in both treatments (*t*-tests between cleared and control plots at Mt. Bogong and King Billy, $P < 0.001$) (Fig. 2). Soil temperatures in control plots were significantly higher than cleared plots at King Billy (*t*-test, $P < 0.05$), although there were no significant differences between treatments at Mt. Bogong (*t*-test, $P = 0.96$). The mean difference between treatments over this period at Mt. Bogong was 0.29 GDDs, whereas at King Billy this difference was 15.12 GDDs.

Soil Moisture

Soil moisture over the growing season was rarely constant, with the lowest values recorded during the mid-sampling interval (Fig. 3). Additionally, we noticed rainwater tending to pool in the cleared plots rather than the control plots. Polynomial contrasts within site and treatment (cleared or control) indicated significant quadratic differences in soil moisture over the three sampling intervals at all sites ($P < 0.001$). During the early sampling interval, there was a significant effect site and treatment on soil moisture, but no significant interactions between these two sources of variation (site: $F = 104.2$, $P < 0.001$; treatment: $F = 6.89$, $P = 0.009$; interaction: $F = 1.081$, $P = 0.36$). During the mid-sampling interval, there was a significant effect of site and a significant interaction between site and treatment on soil moisture (site: $F =$

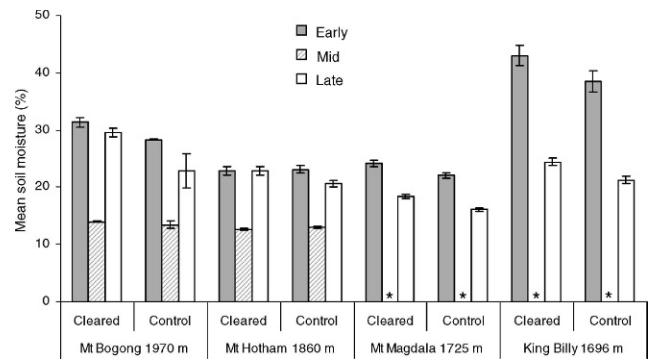


FIGURE 3. Mean soil moisture (%) (± 1 se) for soil in cleared and control plots at the four study sites, at three sampling intervals (early, mid and late) for the 2005/2006 growing season. *No data available.

37.54, $P < 0.001$; treatment: $F = 0.74$, $P = 0.39$; interaction: $F = 9.507$, $P = 0.002$). During the late sampling interval there were significant effects of all three sources of variation on soil moisture (site: $F = 88.69$, $P < 0.001$; treatment: $F = 74.09$, $P < 0.001$; interaction: $F = 6.12$, $P < 0.001$) (Fig. 3).

Frost Heave

We recorded 31 frost events (air temperatures below 0°C) at the lowest site (King Billy, 1696 m), and 41 frost events at the highest site (Mt. Bogong, 1970 m) during the snow free season in 2005/2006, even though snow thawed almost a month later at the highest site compared to the lowest site. These frost events caused strong soil frost heave which tended to mostly occur early during the growing season at these three sites (Fig. 4). Frost heave was more frequent and significantly stronger in areas of bare ground compared with areas of intact vegetation ($P < 0.001$). There was also a significant effect of site, pooling over treatment ($P = 0.040$), although there was no interaction between site and treatment (two way ANOVA, $F = 1.829$, $P = 0.164$) (Fig. 4).

SEEDLING EXPERIMENT

Rather than showing absolute growth rates and numbers of leaves or height for each species, we used the RNE index to show the relative interaction between seedlings with their neighbors, based on growth parameters. However, seedlings of all species generally showed poor growth regardless of treatment and many



FIGURE 4. Mean (± 1 se) vertical displacement of rubber washers on vertical displacement pins (mm) in cleared (gray bars) and control (white bars) plots at three sites, Mt. Bogong (1970 m), Mt. Hotham (1860 m), and King Billy (1696 m), during the 2005/2006 growing season. Different labels above columns indicate significant within-site differences ($P < 0.05$). Higher mean vertical displacement indicates stronger and higher frost-heave of the soil.

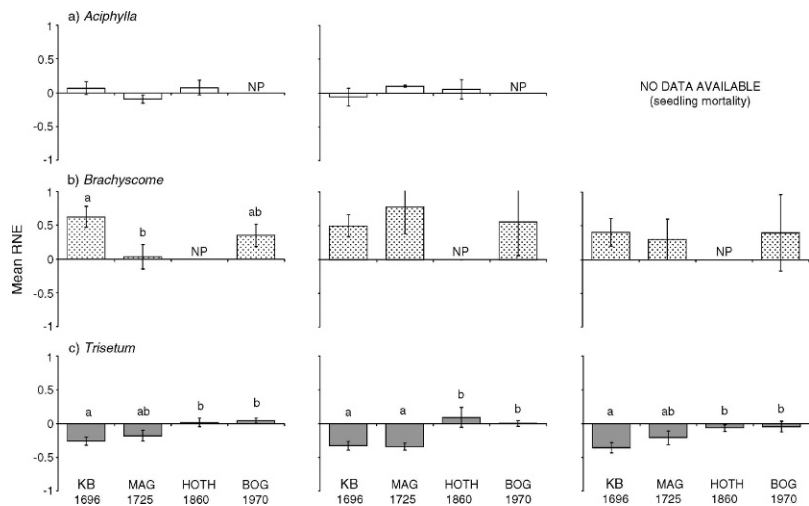


FIGURE 5. Mean Relative Neighbor Effect (RNE) (± 1 se) for (a) *Aciphylla*, (b) *Brachyscome*, and (c) *Trisetum*, for pairs of planted seedlings at King Billy (1696 m) (KB), Mt. Magdala (1725 m) (MAG), Mt. Hotham (1860 m) (HOTH), and Mt. Bogong (1970 m) (BOG), across three sampling intervals (early, mid, and late) during the 2005/2006 growing season. Positive values indicate a facilitative interaction and negative values indicate a competitive interaction. Different labels above columns indicate significant differences between sites during that particular sampling interval. NP: *Aciphylla* seedlings were not planted at Mt. Bogong, nor were *Brachyscome* seedlings at Mt. Hotham.

seedlings died. For example, *Aciphylla* seedlings showed up to 90% decrease in number of leaflets in both cleared and control plots by the end of the experiment, whereas *Brachyscome* and *Trisetum* seedlings showed mixed results. The greatest change in growth during the experiment occurred in the height of *Brachyscome* seedlings at King Billy, where in cleared and control plots there was an increase in height of 259 and 270%, respectively, and hence a positive RNE value during the late sampling interval, indicating positive interactions with neighbors at this site (Fig. 5). *Trisetum* seedlings at King Billy showed a 169% increase in leaf blade numbers in cleared plots and a 72% decrease in control plots, hence the negative RNE value during the late sampling interval at this site. By the late sampling interval, many *Aciphylla* seedlings had died, especially those at Mt. Hotham where less than five paired plots with both seedlings remained alive, leaving too few pairs on which to calculate meaningful RNE values. Hence, no values for the last sampling interval for this species are presented (Fig. 5). Among *Brachyscome* and *Trisetum* seedlings, the variability in mean RNE values tends to increase toward the end of the growing season, again due to the decreasing sample size following seedling deaths. Low RNE values, or those close to zero, indicate weak or neutral interactions between each seedling in the pair with their neighbors, rather than overall low growth. Conversely, if both seedlings in the pair show high growth rates, the RNE value will also be low as the seedlings are not, again, responding strongly to the presence or absence of close neighbors.

No statistical differences between RNE values throughout the growing season were detected for *Aciphylla* seedlings; rather, neutral interactions with neighboring plants, at high and low elevations, appear to dominate for this species. The growth (measured as height) of *Brachyscome* seedlings was facilitated by the presence of neighboring vegetation throughout the growing season, although this was somewhat inconsistent across altitudes (Fig. 5b), with neutral interactions occurring at Mt. Magdala (1725 m) early in the growing season. The growth (number of leaves) of *Trisetum* seedlings appeared not to be strongly influenced by neighboring vegetation at the two highest sites; rather, neutral interactions were present throughout most of the growing season. At the lower sites, however, competitive interactions with neighboring vegetation appeared to dominate (Fig. 5c). Midway through the growing season, the effect size of these interactions increased, becoming more negative, but then

weakening late in the growing season. The negative interactions midway through the growing season corresponded with particularly low soil moisture values at this time.

Discussion

Facilitative (positive), competitive (negative), and neutral interactions influenced the growth of seedlings over one growing season at alpine peaks in southeastern Australia, but the effects appear to be mostly species-specific. Competitive interactions appeared to influence the growth of *Trisetum* seedlings substantially, and this was mostly at the lowest elevations. Temporally, the balance and strength of these plant-plant interactions changed over one growing season. *Trisetum* seedlings were more negatively affected by near neighbors in the middle of the growing season when temperatures were highest and soil moisture lowest, suggesting that competition for limiting resources may be a key limitation to plant recruitment in low altitude alpine peaks. By contrast, *Brachyscome* growth seems to be positively affected by close neighbors during their initial growth stages, even at the lower end of the altitude gradient. This species grew taller when near neighbors were present, suggesting a buffering from winds and perhaps frosting. Finally, the relative growth rate of *Aciphylla* seedlings were rarely affected by near neighbors at any altitude. This species is slow growing (relative to *Trisetum* and *Brachyscome*) and hence, positive and/or negative interactions may be more difficult to detect over the course of one growing season. Alternatively, the balance between positive (sheltering) effects of neighbors on growth, and the competitive effects of those neighbors, may cancel out plant gains/losses, ensuring no overall effects are detected.

Although our altitudinal gradient was rather small (274 m), the changes in environmental conditions across the gradient were substantial, confirming that changes in the intensity of abiotic stress can occur over short spatial scales in alpine environments. The stressful conditions that we documented at the higher sites (i.e. lower air and soil temperatures, stronger frost heave and more frequent frosts), combined with the differences in frost heave and soil moisture between treatment plots, appear to have reduced potential competitive interactions between seedlings and neighboring plants rather than promote strong facilitative ones. Hence, many neutral interactions were detected in this study. The

exception to this rule is seen in the relatively consistent facilitative interactions with regard to growth between *Brachyscome* seedlings and neighboring vegetation across the whole stress gradient. However, high variability due to low sample sizes across the experiment may have decreased our ability to detect strong differences between interactions.

Most plant-plant interaction studies from alpine regions have emphasized the beneficial effects of close neighboring vegetation on adult plant growth and survival, where environmental factors such as low temperatures, wind, and soil disturbances limit plant growth more so than resource availability (Callaway, 1995; Kikvidze, 1996; Callaway, 1997; Choler et al., 2001; Pugnaire and Luque, 2001; Callaway et al., 2002; Klanderud and Totland, 2005). Studies such as ours, on the very early life-history stages of alpine plants, in relation to competitive and facilitative interactions, have been relatively few both in the Australian and the international literature (Brooker et al., 2008). However, in the Snowy Mountains, Australia, Wilson (1993) showed that neighbors promoted survival in one species, but suppressed growth in all other study species. Wilson (1993) also showed that the degree of below-ground competitive ability can change at different altitudes, with the highest root:shoot ratio and the highest below-ground competition occurring at the highest altitudes. In arctic tundra environments, Gough (2006) showed that seed germination was higher when neighboring vegetation had been removed. Consistent with our results, there was little effect of neighboring vegetation on the survival and growth of adult transplants, indicating that the interactive effects of neighboring vegetation can affect each life-history stage differently.

Overwhelmingly though, published plant interaction studies that deal with seedling success in alpine areas show evidence for facilitation via the amelioration of abiotic stress (Carlsson and Callaghan, 1991; Kikvidze, 1993; Sturm et al., 2001; Callaway et al., 2002; Cavieres et al., 2002; Acuña-Rodríguez et al., 2006; Gough, 2006; but see Cavieres et al., 2006, for an exception). Kikvidze (1993) showed that positive spatial associations at high elevations were four times more common than negative ones. Our results do not fully concur with those of others, nor support the hypothesis that alpine seedlings only grow where they can shelter with adjacent vegetation in alpine areas. Perhaps the small size of our cleared experimental plots (i.e. 15 × 15 cm) may have contributed to these results, as foliage adjacent to the plot had potential to provide partial shelter from wind and frost.

Importantly, we showed that the balance and strength of plant interactions can change over one growing season. Although almost half the number of naturally emerging seedlings in the Victorian alpine zone die before establishment (Venn and Morgan, 2009), our findings indicate that some seedlings would benefit from close neighbors during their initial growth stages, even at the lower end of the altitude gradient, as neutral and facilitative interactions were common across the three study species. As these seedlings develop, the direction and strength of interactions with neighboring vegetation are likely to change. However, the positive effects of aerial protection provided by shrubs and grasses appear most important at the early seedling stages. Subsequently, as seedlings develop into juveniles and adults, below-ground competition for resources becomes overridingly important (Aguiar and Sala, 1994). If a neighbor is to be facilitative, the advantages of the association must be sufficiently large to compensate for below-ground competition and generate a net benefit for the co-existing species (Carlsson and Callaghan, 1991). Hence, at our high elevation study sites, close neighbors may not always act as beneficiaries, nor will the environmental conditions at these sites (the frequent frosts and lower temperatures) always constrain

plant growth. As demonstrated here, above-ground facilitation is not the rule in determining successful recruitment from seedlings in alpine regions in Australia, even at the high elevation sites, as interactions with neighboring plants appear to be species-specific at the seedling stage.

Conclusions

Positive, neutral, and competitive plant-plant interactions were detected in our study, suggesting that close neighboring plants can play an important role in the early life-history stages of alpine plants. These interactions can change during one growing season as the relative importance of abiotic stress changes in response to temperatures, soil moisture, and frost frequency. Future research might consider the effects of neighboring vegetation on seed germination, in addition to effects of longer-term seedling survival. In order to decipher the interactions between seedlings, close neighbors, and environmental factors, future investigations should include below-ground processes and interactions with neighbors across stress gradients. However, above-ground plant interactions, especially those involving seedling growth, remain important in the organization of alpine plant communities.

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