

Negative Associations between Seedlings and Adult Plants in Two Alpine Plant Communities

Author: Forbis, Tara A.

Source: Arctic, Antarctic, and Alpine Research, 41(3) : 301-308

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: <https://doi.org/10.1657/1938-4246-41.3.301>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Negative Associations between Seedlings and Adult Plants in Two Alpine Plant Communities

Tara A. Forbis*†

*Niwot Ridge Long-Term Ecological Research Program

†USDA-ARS Exotic and Invasive Weeds Research Unit, 920 Valley Road, Reno, Nevada 89512, U.S.A.
tforbis@unr.edu

Abstract

Plant species' requirements at seed and seedling stages are critical in determining their distributions. Proximity to adult plants, as well as the presence of litter or rocks on the soil surface can influence seedling success. By comparing the microsite characteristics of points occupied by naturally occurring seedlings to the characteristics of unoccupied points in fellfield and dry, moist, and wet meadow alpine plant communities on Niwot Ridge, Colorado, U.S.A., this study addresses the following questions: Are seedlings more likely to be near an adult plant or in litter than are unoccupied points? Does the proximity of seedlings to adult plants vary among communities? In the fellfield community, are seedlings more likely to be located next to a rock than are unoccupied points? I found that seedlings were farther from adult plants than were unoccupied points in the wet meadow, a community with dense vegetation cover and wet soils. Contrary to expectation, I also found that seedlings were farther from adult plants than were unoccupied points in the fellfield, the driest, most barren community. Seedlings were not more likely than unoccupied points to be located in areas of litter buildup, and fellfield seedlings did not occur disproportionately within the protection of a rock. This study suggests that competition between adult plants and seedlings may be taking place both in highly productive and in very unproductive alpine plant communities.

DOI: 10.1657/1938-4246-41.3.301

Introduction

Plant species' requirements at seed and seedling stages are critical in determining species distributions. Seeds require sites that are appropriate for entrapment and retention, and sites where conditions allow their survival of abiotic stresses and avoidance of granivory and pathogen-caused mortality (Harper, 1977). Seedlings require sites where there is a reasonable probability of avoiding herbivory and seedling pathogens (Harper, 1977), and where necessary resources, including water and light, are available, and not entirely preempted by competitors (Aguilera and Lauenroth, 1993). Thus, the characteristics of the sites that are ultimately occupied by seedlings depend on the cumulative microsite requirements of a species across all these stages (Galen and Stanton, 1999; Schupp, 1995).

NEGATIVE VERSUS POSITIVE INTERACTIONS WITH NEIGHBORS

Competition between plants is defined as a reduction in fitness due to the shared use of a limited resource (Gurevich et al., 2002). Competition has long been considered an important force shaping plant community dynamics. Competition with adult neighbors has been shown to result in seedling mortality (Aguilera and Lauenroth, 1993; Gordon and Rice, 1993). In communities with dense vegetation cover, the reduction in competition provided by gaps (i.e. openings in the vegetation) can benefit seedlings. Even small (1 cm) gaps between adult plants have been shown to favor seedlings (Silvertown, 1981) in some situations. For many species, gaps create a regeneration niche (*sensu* Grubb, 1977) by providing decreased competition for space,

light, water, and nutrients. For example, treefall gaps in tropical forests are key sites for seedling establishment (Connell, 1989). In aspen forests, seedlings establish primarily in openings caused by forest fires (Romme et al., 1997), and in grasslands, fire and animal disturbances create openings that facilitate seedling establishment (Reader, 1993; Edwards and Crawley, 1999; Eriksson and Eriksson, 2000). In the alpine tundra, disturbance has been shown to increase seedling establishment rates (Oloffson and Shams, 2007). Gaps are often caused by burrowing mammals, and can facilitate establishment over the long term (Forbis et al., 2004). Gaps would be expected to facilitate seedling establishment in communities in which competition is an important factor.

Facilitation is also an important process in plant communities and refers to positive interactions between physiologically independent plants (Hunter and Aarssen, 1988, Callaway and Walker, 1997). This can occur in a successional context (Clements, 1916) or in stable plant communities (Hunter and Aarssen, 1988). The facilitation of seedlings by established plants (Pugnaire et al., 1996; Eccles et al., 1999) is called nurse plant syndrome (Niering et al., 1967; Cavieres et al., 2008), which can occur either through biotic interactions or due to changes in the structural environment. Nurse plant syndrome has been most often identified in arid systems (Went, 1942) and is likely useful during ecosystem restoration (Gómez-Aparicio et al., 2004).

Bertness and Callaway (1994) proposed a conceptual model suggesting that as abiotic stress increases, the relative importance of facilitation should increase and the relative importance of competition should decrease. A global study (Kikvidze et al., 2005) supported the stress gradient hypothesis with spatial patterns of plants in productive habitats being overdispersed,

while less productive, colder sites had aggregated spatial patterns of plants. The hypothesis was also supported by work in the European alpine showing that facilitation dominates plant interactions at high, xeric sites, and competition dominates at lower, more mesic sites (Choler et al., 2001). However, across biomes, a rigorous meta-analysis of the stress gradient hypothesis was unable to find unequivocal support for it (Goldberg et al., 1999), and indicated that the relationship depended on the life history stage in question. Therefore, the application of the stress gradient hypothesis to the seedling stage is a separate question which has been addressed only in a few systems.

ROCKY MOUNTAIN ALPINE COMMUNITIES

Though sexual reproduction among alpine plants had been thought to be rare (Marchand and Roach, 1980; Archibold, 1984; Bauert, 1996; Totland, 1997; Gugerli, 1998), a previous study showed that seedlings are present in the four major Rocky Mountain alpine plant communities (Forbis, 2003). In general, these communities are above-treeline sites dominated by low-growing grasses, sedges, and forbs (Billings and Mooney, 1968). Factors affecting suitability for seedling establishment are likely to include productivity and canopy cover (Kitajima, 1994), soil moisture and precipitation (Forbis, 2003), and date of snowmelt (Galen and Stanton, 1999), all of which vary among these communities.

Of these communities, fellfield sites are the driest, are generally snow-free throughout the winter due to high wind speeds, and have the longest growing season and the greatest fluctuation in soil temperature (May and Webber, 1982). These exposed sites have equal cover of bare rock and plants (Komárková, 1979) with approximately 50% cover of rock and bare ground (Table 1). In winter, exposed plants experience scouring by ice crystals. Dominant species in these communities are four forbs with the cushion growth form: *Silene acaulis*, *Minuartia obtusiloba*, *Trifolium nanum*, and *Paronychia pulvinata*. (Table 1; nomenclature follows Weber, 1976).

Dry meadows are slightly moister than fellfields and have slightly shorter growing seasons due to some winter snow cover. Dry meadow sites are dominated by the sedge *Kobresia myosuroides*, the clubmoss *Selaginella densa*, and the perennial forb *Acomastylis rossii*, and have about 89% plant cover (Table 1). Moist meadows have deeper snow cover, higher soil moisture, and shorter growing seasons than fellfield or dry meadow and are dominated by the forbs *A. rossii*, *Artemisia scopulorum*, *Trifolium parryi*, and the grass *Deschampsia caespitosa* (Table 1). Wet meadows have the latest-lying snowbanks, shortest growing season, and soils that remain saturated throughout much of that growing season, which lasts half as long as that of fellfield sites on average. Wet meadows are dominated by the forb *Caltha leptosepala* and by the sedge *Carex scopulorum* (Table 1; May and Webber, 1982).

If the stress gradient hypothesis holds for seedling establishment in the Rocky Mountain alpine, I would predict that the highest-stress community, the fellfield, would be dominated by facilitative interactions among plants, evidenced by positive spatial associations. I would also expect that the community at the least stressful end of the gradient, the wet meadow, would be dominated by competitive interactions among plants, evidenced by negative spatial associations.

LITTER AND ROCK EFFECTS ON ESTABLISHMENT

In addition to productivity, soil moisture, growing season length, and other among-community differences, the abundance of

litter and rocks would be expected to affect seedling establishment. In some situations, litter facilitates seedlings (Suding and Goldberg, 1999), while in others, litter is inhibitory (Dalling and Hubbell, 2002). Litter affects the chemical and physical (Downs and Cavers, 2002) as well as the biological (Garcia-Gunman and Benitez-Malvido, 2003) environments of seeds and seedlings. Generally, seeds tend to be deposited in the same places that litter is deposited (Facelli and Pickett, 1991). Litter can affect the seed's fate by promoting fungal pathogen infection, preventing granivory, or affecting seed burial (Rotundo and Aguiar, 2005). One might expect litter to facilitate seedlings where protection from desiccation is critical, and to inhibit seedlings where litter promotes seedling pathogens or prevents germination. In alpine dry, moist, and wet meadows, desiccation is an important factor in seedling mortality (Forbis, 2003). Therefore, one might expect litter to facilitate seedlings in the fellfield and dry meadow, where soil moisture values are low (Taylor and Seastedt, 1994). However, one previous study from an alpine site indicated that litter did not influence seedling density (Welling and Laine, 2000).

Rocks are abundant in the Rocky Mountain fellfield (but not in the other communities) and may provide protection to seedlings in this driest and most exposed alpine community. In the alpine in general, availability of rocks can be important in promoting seedling establishment. For example, working in Iceland, Elmarsdottir et al. (2003) found more seedlings near rocks, and concluded that this could be due to either increased seed entrapment or enhanced seedling survival. In the tropical alpine, Kleier and Lambrinos (2005) found that seedlings of two species occurred in the protection of boulders. Therefore, the availability of rock sites in the fellfield may be important to seedling establishment.

OBJECTIVES

This study addresses the following questions for alpine seedlings on Niwot Ridge, Boulder County, Colorado: Are seedlings more likely to be located closer to or farther away from an adult plant than are points unoccupied by seedlings? Are seedlings more likely to be located in areas of litter buildup? Do these relationships vary among communities? And, in the fellfield community, are seedlings more likely to be located closer to or farther away from a rock than are points unoccupied by seedlings?

Methods

This study was conducted at several sites on Niwot Ridge (elevation ~3500 to 3700 m) in the Front Range of the Colorado Rocky Mountains (40°03'N, 105°36'W). Plots were located in the four major alpine plant communities; fellfield, dry meadow, moist meadow, and wet meadow (described above).

In 1998, 11 permanent plots were created to monitor germination and survival of seedlings in the four community types described above. There were three fellfield plots of 1 m² and two wet meadow plots of 0.5 m². The smaller wet meadow plots were determined to have seedling densities that did not differ from 1 m² plots using a seedling density area⁻¹ curve, and two rather than three plots were used because of the high density of wet meadow seedlings relative to seedlings in the other communities studied. The sizes of the 3 dry meadow and 3 moist meadow plots varied between 0.25 and 1.25 m² because these plots were scaled to pocket gopher disturbance plots as part of a separate study (Forbis et al., 2004).

Only newly germinated seedlings were marked. Individuals were identified as new seedlings by the presence of cotyledons

TABLE 1

Species composition and cover of bare ground and rock in the four alpine plant communities studied here. Only species with $\geq 2.0\%$ cover in at least one community are included in this table. Total species numbers per community were 38 for dry meadow, 19 for fellfield, 39 for moist meadow, and 23 for wet meadow. Values shown are percent cover; 0.01 was the cover value assigned species that were present but not encountered.

Species	DM	FF	MM	WM
bare ground	6.7 \pm 2.8	17.5 \pm 5.8	5.0 \pm 2.3	6.1 \pm 1.7
rock	4.7 \pm 1.3	31.9 \pm 7.5	0.2 \pm 0.2	1.1 \pm 0.2
<i>Acomastylis rossii</i> ssp. <i>turbinata</i>	9.5 \pm 3.3	7.2 \pm 5.0	23.3 \pm 3.5	7.5 \pm 2.7
<i>Artemisia scopulorum</i>	1.0 \pm 0.7	0.6 \pm 0.5	11.1 \pm 3.8	7.4 \pm 4.7
<i>Bistorta vivipara</i>	3.8 \pm 3.1		0.6 \pm 0.6	3.2 \pm 0.6
<i>Caltha leptosepala</i>			0.01	27.3 \pm 8.8
<i>Carex rupestris</i> ssp. <i>drummondiana</i>	11.6 \pm 2.3	6.5 \pm 3.4	5.1 \pm 2.8	
<i>Carex scopulorum</i>				11.6 \pm 2.5
<i>Castilleja occidentalis</i>	0.01	0.01	1.7 \pm 0.8	0.2 \pm 0.2
<i>Deschampsia caespitosa</i>			8.7 \pm 3.6	4.8 \pm 2.5
<i>Erigeron simplex</i>	0.01	0.01	5.0 \pm 0.7	
<i>Festuca baffinensis</i>		3.3 \pm 0.2		
<i>Festuca</i> sp.	0.4 \pm 0.4		2.5 \pm 1.9	1.6 \pm 0.8
<i>Gentianodes algida</i>		0.2 \pm 0.2		6.5 \pm 2.6
<i>Kobresia myosuroides</i>	35.3 \pm 1.8		2.8 \pm 1.9	
<i>Lloydia serotina</i>	4.4 \pm 1.4		2.4 \pm 1.5	
<i>Minuartia obtusiloba</i>	2.2 \pm 0.7	8.4 \pm 2.2	1.9 \pm 1.3	
<i>Oreoxis alpina</i>	5.2 \pm 0.5		0.7 \pm 0.7	
<i>Paronychia pulvinata</i>		13.2 \pm 3.2		
<i>Phlox sibirica</i> ssp. <i>pulvinata</i>	1.2 \pm 0.9		2.3 \pm 2.3	
<i>Poa glauca</i>			4.5 \pm 4.5	
<i>Polygonum bistortoides</i>	1.6 \pm 0.5	0.3 \pm 0.3	2.1 \pm 0.5	2.4 \pm 2.1
<i>Salix nivalis</i>				4.5 \pm 1.6
<i>Sibbaldia procumbens</i>			3.7 \pm 3.1	5.2 \pm 4.8
<i>Silene acaulis</i>	1.6 \pm 1.1	2.7 \pm 1.3	0.01	
<i>Tonestus pygmaeus</i>		2.4 \pm 0.2		
<i>Trifolium dasyphyllum</i>	4.4 \pm 1.6			
<i>Trifolium nanum</i>		3.2 \pm 0.7		
<i>Trifolium parryi</i>			11.1 \pm 5.6	6.8 \pm 3.7

(forbs) or by the dispersed floret at the base of the seedling and/or the presence of the coleoptile (graminoids). Examples of ambiguous seedlings were excavated from outside the plots to verify that they were not vegetative ramets. Using a gridded point frame, seedlings were assigned coordinates that mapped them to within 0.5 cm², and the frame was anchored to permanent corner markers so that individuals could be relocated in successive years. Dates of germination and mortality and species identity, when possible, were recorded for each individual. Identifications were made using photographs of laboratory-germinated seedlings.

Vegetation cover by species was estimated. Sampling was carried out in each of the plots in July 2001 using a modification of the point intercept method as described by Barbour et al. (1999) with 100 sampling points located 20 cm apart within each plot. Cover sampling plots were 1 m², even in cases in which the seedling plot was slightly smaller or larger. A pin was inserted vertically into the vegetation and all species touched (aerial or basal cover) were recorded for each point. Species that were not hit but that were present were given an arbitrary cover value of 0.01%.

In July 2000, litter and gap characteristics were recorded for all sites occupied by naturally occurring seedlings that were at least one year old ($n = 508$; by community fellfield = 81, dry meadow = 43, moist meadow = 72, wet meadow = 312). For each seedling, presence/absence of leaf litter surrounding the seedling and distance from the seedling to the nearest adult plant were recorded. Spatial pattern is often used in the study of competition

and facilitation (Callaway, 1995), with distance indicating negative interactions and proximity indicating positive interactions. To generate representative distributions of litter abundance and vegetation density, a point not occupied by a seedling ("unoccupied point") 20 cm north of each real seedling was also sampled. The location of each seedling and each unoccupied point in fellfield plots was recorded as being adjacent (within 1 cm) to a rock or not. The fellfield has high cover of gravel; the minimum size for a rock was set at 1 cm diameter, as this appeared to be larger than the pieces of the ubiquitous gravel. Because the plots varied in slope and aspect, I do not anticipate that using nonseedling points in a consistent, rather than random, direction from the seedling point will bias the estimated abundance of plants, litter, or rocks.

Another method for characterizing the distribution of adult plants, litter, and rocks would have quantified the density of these features in the plots and used randomization tests to compare the characteristics of the seedling sites to the expectations generated from random samples of the density data. However, the paired seedling/unoccupied point method that I used is more powerful because the paired points should be more similar to one another than they would be to a random point, reducing the variation in other factors and increasing the power to detect differences in distance to plant, and presence of litter, and rock.

To determine whether seedlings were found near adult plants more often than were unoccupied points, I used mixed-models ANOVA with rank-transformed distance to the nearest adult as

the response variable. Plot (nested within community), community, litter, and the binary variable seedling point/non-seedling point were independent variables. The community term asked whether seedlings in different communities differ in their tendency to be near adults and the litter term asks whether there is a relationship between distance to the nearest plant and tendency for seedlings to occur in litter. Seedling and non-seedling sites were compared within communities using least squared mean differences. To determine whether seedlings occur in litter more often than do unoccupied points, logistic regression with litter/no litter as the response variable and seedling/unoccupied point and community as predictors was used. Analyses were done assuming observations within a plot were nonindependent, using the repeated statement in PROC GENMOD (SAS Institute, 2001).

Separate analyses were performed to determine whether fellfield seedlings were found next to (within 1 cm of) rocks more often than were nonseedling points. A logistic regression was performed with adjacent to rock/not adjacent to rock as the response variable and seedling/unoccupied point as the predictor. Again, observations were assumed to be non-independent within plots. Type III SS were used in all analyses.

Results

Table 1 shows the species composition of the four communities studied. Table 2 shows the composition of the seedlings. Most abundant overall were *Artemisia scopulorum*, *Polygonum bistortoides*, and *Erigeron melanocephalus*, all of which were most abundant in wet meadow.

The seedling and unoccupied point distances from an adult plant are shown in Figure 1. In general, seedlings were located farther from adult plants than were unoccupied points (mixed models ANOVA, $F_{1,1015} = 23.99$, $P < 0.0001$). On average the seedling distance–unoccupied point distance (\pm SE) was 6.0 ± 1.7 cm for fellfield, 3.4 ± 0.7 cm for wet meadow, 2.2 ± 2.0 cm for dry meadow, and 1.3 ± 1.0 cm for moist meadow. There were differences between communities in distance to the nearest plant within levels of seedling/unoccupied point ($F_{3,1015} = 42.33$, $P < 0.0001$). Specifically, seedlings were farther from adult plants than were unoccupied points in the fellfield and the wet meadow (least squares mean differences, $F_{1,81} = 19.35$, $P < 0.0001$; and $F_{1,312} = 23.83$, $P < 0.0001$, respectively). The trend was the same in the dry and moist meadows, but these trends were not significant ($P > 0.1$ in both cases; Fig. 1). There was also among-plot variation in distance to the nearest plant (mixed models ANOVA, plot nested within community, $F_{7,1015} = 3.38$, $P = 0.0014$). Species did not differ widely in their distances from adult plants; no species' mean fell outside the 95% confidence limits for distance to the nearest plant (Fig. 2).

Seedlings were not located in litter more often than were unoccupied points (logistic regression; $\chi^2 = 1.23$, $P = 0.2673$). There were no differences between communities in the likelihood of a seedling occurring in litter, given the abundance of litter in each community ($\chi^2 = 5.27$, $P = 0.1533$).

In the fellfield, seedlings did not occur more often near rocks than did unoccupied points ($\text{Pr} > \chi^2 = 0.2241$). The mean probability of occurrence of rocks at unoccupied points was 0.20 ± 0.054 , while for seedlings it was 0.35 ± 0.045 .

Discussion

Seedlings on Niwot Ridge were farther from adult plants than were unoccupied points both in the wet meadow, a community with dense vegetation cover and soils that are wet throughout the

TABLE 2

Seedling count by species and community. Seedlings ranged from 0 to 2 yr old.

Species	Dry meadow	Fellfield	Moist meadow	Wet meadow
<i>Acomastylis rossii</i>				
<i>ssp. turbinata</i>		4		5
<i>Androsace chamaejasme</i>				
<i>ssp. carinata</i>	1		1	
<i>Arenaria fendleri</i>	2	4	1	1
<i>Artemisia scopulorum</i>		1	8	86
<i>Clemensia rhodantha</i>				10
unknown composite	2	1		
<i>Eritrichum aretioides</i>		3		
<i>Erigeron melanocephalus</i>				44
<i>Erigeron simplex</i>			31	
<i>Gentianodes algida</i>				15
<i>Cimicifuga prostrata</i>				20
<i>Tonostylis pygmaeus</i>		11		
<i>Lloydia serotina</i>	1			
<i>Luzula spicata</i>		1		
<i>Minuartia obtusiloba</i>		13		
unknown monocot		1		4
<i>Paronychia pulvinata</i>		8		
<i>Polygonum bistortoides</i>		3		56
<i>Primula parryi</i>				1
<i>Ranunculus pedatifida</i>			12	
<i>Salix</i> sp.				1
<i>Sedum lanceolatum</i>	10		7	
<i>Sibbaldia procumbens</i>			3	2
<i>Silene acaulis</i>	1	17	1	
<i>Thlaspi montanum</i>	23		8	
<i>Trifolium dasyphyllum</i>	2			
<i>Trifolium nanum</i>		14		
<i>Trifolium parryi</i>				16
unidentified	1			20

growing season and in the fellfield, the driest, most barren community. However, this was not true for the two intermediate communities, dry and moist meadow. Additionally, seedlings were not more likely to be located in areas of litter buildup or near rocks in the fellfield than were unoccupied points.

NEGATIVE ASSOCIATIONS IN THE WET MEADOW

I predicted that negative spatial associations between adult plants and seedlings would be seen in the wet meadow, and that prediction was supported by the data. In sites with lower abiotic stress, it is generally expected that competition will play a larger role in plant community dynamics (Callaway and Walker, 1997) and one would expect gaps to improve conditions for seedlings in cases where vegetation is dense and canopy cover is almost complete. Resources that might be driving competition in this environment include light, due to the high plant cover (Table 1), nutrients, which are known to be limiting (Theodose and Bowman, 1997), or possibly water, though that is less likely to be limiting in the wet meadow because soil moisture remains high throughout the growing season and plants are unlikely to ever experience water stress (Taylor and Seastedt, 1994).

NEGATIVE ASSOCIATIONS IN THE FELLFIELD

I predicted positive associations between seedlings and adult plants in the fellfield due to high levels of abiotic stress. Other

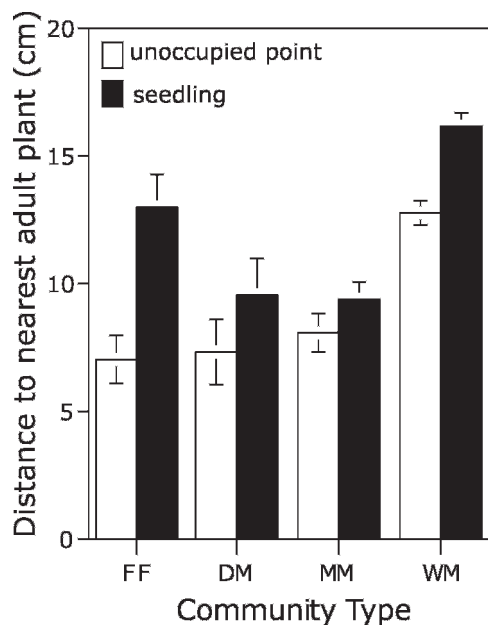


FIGURE 1. Distances from seedlings to the nearest adult plants were greater than distances from unoccupied points to the nearest adult plants. This difference was significant only for fellfield and wet meadow plots. Values are means \pm 1SE. FF = fellfield, DM = dry meadow, MM = moist meadow, WM = wet meadow.

researchers have found both positive and negative associations, many of them site- or species-specific. In the Rocky Mountain fellfield, two previous papers predicted opposing patterns. An early study by Griggs (1956) suggested that seedlings occur disproportionately within cushions of adult plants, but Bonde (1968) found that seedlings occurred just as often in open sites. The most extensive research into interactions among plants in high-elevation, cushion-dominated communities has been done in the Andes (e.g. Cavieres et al., 2002; Arroyo et al., 2003). These researchers have found that cushion plants are usually positively and occasionally negatively associated with other plants (Cavieres et al., 2005; Fajardo et al., 2008) and that the presence of negative associations varies among species and sites (Fajardo et al., 2008).

One factor that may have contributed to the negative associations in the Rocky Mountain fellfield is the predominance of the cushion growth form among both seedling and adult populations. Four of the ten most abundant plants in the fellfield are cushions (Table 1) and among seedlings, five of the ten most abundant species were cushions (Table 2). In general, one would expect plants within a functional group to inhabit a similar niche due to similarities in structure and resource use, and facilitative interactions would be expected within functional groups, while competitive interactions might be expected within a functional group (Brooker et al., 2007).

This study failed to support the stress gradient hypothesis (Bertness and Callaway, 1994) for interactions between adult plants and seedlings. This may be due to the extreme nature of this community relative to most terrestrial plant communities. Michalet et al. (2006) proposed that under very severe conditions, biotic interactions become unimportant relative to the level of stress, and species traits (i.e. stress tolerance) play the most important role in determining species' niche boundaries. Neither the study of Fajardo et al. (2008) nor this study elucidate mechanisms responsible for negative associations between plants in high-elevation cushion-plant dominated communities. Future studies

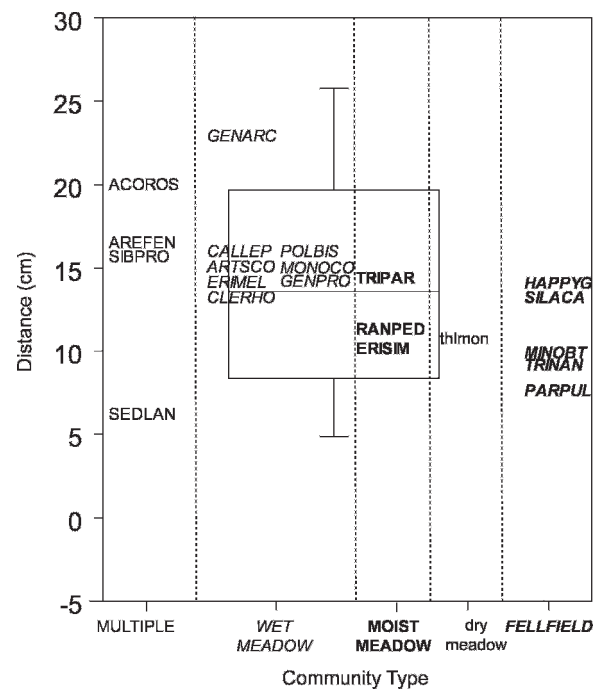


FIGURE 2. Species differed little in their average seedling's distance to the nearest plant. Species shown were represented by at least 7 individuals. Fonts and x-axis label indicate the community in which at least 75% of the individuals of each species were found. MULTIPLE means that a species was found equally distributed among multiple communities. ACOROS = *Acomastylis rossii*, AREFEN = *Arenaria fendleriana*, ARTSCO = *Artemisia scopulorum*, CALLEP = *Caltha leptosepala*, CLERHO = *Clementsia rhodantha*, ERIMEL = *Erigeron melanocephalus*, ERSIM = *Erigeron simplex*, GENARC = *Gentiana arctica*, GENPRO = *Gentiana prostrata*, HAPPYG = *Happlopappus pygmaea*, MINORT = *Minuartia obtusiloba*, MONOCO = unidentified monocot, PARPUL = *Paronychia pulvinata*, POLBIS = *Polygonum bistortoides*, RANPED = *Ranunculus pedatifida*, SEDLAN = *Sedum lanceolatum*, SIBPRO = *Sibbaldia procumbens*, SILACA = *Silene acaulis*, THLMON = *Thlaspi montanum*, TRINAN = *Trifolium nanum*, TRIPAR = *Trifolium parryi*.

should include experimental manipulations of seed entrapment, seed retention, seed survival, germination rates, and seedling survival rates. Such mechanistic studies would separate seedling-plant interactions from pre-germination processes, discussed below.

SEED ENTRAPMENT

Because this study used naturally-occurring seedlings rather than following planted seeds, the explanation for spatial distribution of seedlings may be a combination of pre- and post-germination processes. Patterns of seed entrapment can explain much of the variation in spatial distributions of seedlings, particularly in high-wind environments like the alpine tundra (Chambers et al., 1991).

Seed-trapping studies have found that most seeds without specialized dispersal mechanisms have primary dispersal (dispersal directly from the plant) of 15 cm or less from the parent plant (Stöcklin and Bäumler, 1996; Scherff et al., 1994), but secondary dispersal (horizontal or vertical movements of the seed subsequent to primary dispersal) is likely more important in the ultimate spatial pattern of plants in a community (Chambers and MacMahon, 1994), and the high winds of the alpine make it

likely that even species without specialized dispersal mechanisms are traveling some distance from the parent plant. In general, surface roughness, soil particle size (Chambers et al., 1991), and the presence of rocks and/or litter enhance entrapment (Harper, 1977), and smooth surfaces that are free of obstacles trap few, if any, seeds (Fort and Richards, 1998). Average cover of bare ground and bare rock in wet meadow, moist meadow, and dry meadow ranged from 5.6 to 11.4%, but in fellfield, average cover of bare ground and bare rock was 49.4%, so the surfaces available for seed entrapment differ markedly in the fellfield.

Expectations based on what is known about seed entrapment would suggest that in the fellfield, seedlings should occur disproportionately within cushion plants, rather than in open spaces. Therefore, both pre- and post-germination processes of seedling establishment suggest that seedlings should be positively associated with adult plants. Our results are surprising, and highlight the need for mechanistic studies of seed entrapment, germination, and seedling survival in the alpine fellfield.

DISTURBANCE AND SEEDLING ESTABLISHMENT IN DRY AND MOIST MEADOW

In the two highest-cover Rocky Mountain alpine communities, the dry and moist meadows, my previous work has shown that gopher disturbances enhance seedling establishment over the long term (~20 yr), suggesting that some reduction in canopy cover is beneficial for establishment of seedlings in Rocky Mountain alpine tundra (Forbis et al., 2004). Given this result, I would have expected dry and moist meadow seedlings to be located in gaps. However, this study found no significant relationship between seedling occurrence and distance to the nearest adult plant in dry and moist meadows; therefore, there was no evidence for amelioration of competition by gaps.

The difference between these results may be explained by the fact that the sites I sampled had not been disturbed by gophers at all, or at least not for so long that disturbance effects were not detectable. Gaps between plants were small (the dry and moist meadows had 88.6 ± 2.8 and $94.8 \pm 3.6\%$ cover, respectively) and the gaps I sampled did not have the characteristics of sites disturbed within the last decade by mammal burrowing, which include disturbed soils as well as a more open structure (Sherrod and Seastedt, 2001; Forbis et al., 2004). Facilitation of seedlings in these relatively dense communities may require larger openings in the vegetation, or it may be dependent on processes associated with soil disturbance.

EFFECT OF LITTER AND ROCKS ON SEEDLINGS

I found no effect of litter on spatial patterning of alpine seedlings, and no among-community differences in litter effects. Litter quantity varied widely among communities ($30 \pm 48\%$ cover in fellfield to $92 \pm 27\%$ cover in moist meadow) but did not have a discernable effect on seedling establishment. Experimental manipulation of litter abundance within communities might uncover patterns that this observational study did not.

Rocks did not appear to be an important factor allowing seedling establishment in the fellfield. This result differs from what has been found by others (e.g. Kleier and Lambrinos, 2005), and from expectations given abiotic conditions in the fellfield. Mechanisms of seed entrapment have been discussed above; enhanced seedling survival would be expected to come along with the shade, protection from wind, and reduced soil evaporation in these microsites. However, the interaction of seed entrapment,

germination, and seedling survival processes in rock-protected sites do not appear to favor seedling establishment in these sites.

CONCLUSION

Expectations based on our current understanding of seed entrapment, and on the stress-gradient hypothesis would suggest that alpine fellfield seedlings should be positively associated with adult plants. However, our data indicate that the opposite is true. Future studies should focus on species-specific associations, as well as on the mechanics of seed entrapment, germination, and seedling survival in this intriguing alpine plant community.

Acknowledgments

I thank J. Krieger and R. Marlin for assistance with field work and A. de Queiroz for discussions. A. de Queiroz, W. Longland, L. Turner, and W. D. Bowman provided comments on the manuscript. Funding came from the Niwot Ridge LTER Program (NSF DEB-9810218) and a fellowship from the University of Colorado Department of Environmental, Populational and Organismic Biology.

References Cited

- Aguilera, M. O., and Lauenroth, W. K., 1993: Seedling establishment in adult neighborhoods: intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. *Journal of Ecology*, 81(2): 253–261.
- Archibold, O. W., 1984: A comparison of seed reserves in arctic, subarctic, and alpine soils. *Canadian Field-Naturalist*, 98: 337–344.
- Arroyo, M. T. K., Cavieres, L. A., Peñaloza, A., and Arroyo-Kalin, M., 2003: Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology*, 169(1): 121–129.
- Barbour, M. G., Burk, J. H., Pitts, W. D., Gilliam, F. S., and Schwartz, M. W., 1999: *Terrestrial Plant Ecology*. Menlo Park, California: Benjamin/Cummings.
- Bauert, M. R., 1996: Genetic diversity and ecotypic differentiation in arctic and alpine populations of *Polygonum viviparum*. *Arctic and Alpine Research*, 28: 190–195.
- Bertness, M. D., and Callaway, R., 1994: Positive interactions among plants. *Trends in Ecology and Evolution*, 9(5): 191–193.
- Billings, W. D., and Mooney, H. A., 1968: Ecology of arctic and alpine plants. *Biological Reviews*, 43(4): 481–529.
- Bonde, E. K., 1968: Survival of seedlings of an alpine clover (*Trifolium nanum* Torr.). *Ecology*, 49(6): 1193–1195.
- Brooker, R. W., Maestre, F. T., Callaway, R. M., Lortie, C. L., Cavieres, L. A., Kunstler, L., Liancourt, P., Tielbörger, K., Travis, J. M. J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, A., Olofsson, J., Pugnaire, F., Quiroz, C. L., Saccone, K., Seifan, M., Touzard, B., and Michalet, R., 2007: Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96: 18–34.
- Callaway, R. M., 1995: Positive interactions among plants. *Botanical Reviews*, 61: 306–349.
- Callaway, R. M., and Walker, L. R., 1997: Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, 78(7): 1958–1965.
- Cavieres, L., Arroyo, M., Peñaloza, A., Molina-Montenegro, M., and Torres, C., 2002: Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science*, 13(4): 547–554.
- Cavieres, L. A., Badano, E. I., Sierra-Almeida, A., and Molina-Montenegro, A. M., 2005: Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not

- increase with elevation in the Andes of central Chile. *New Phytologist*, 169: 59–69.
- Cavieres, L. A., Quiroz, C. L., and Molina-Montenegro, M. A., 2008: Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: Are there differences between nurses? *Functional Ecology*, 22: 148–156.
- Chambers, J. C., and Macmahon, J. A., 1994: A day in the life of a seed—Movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics*, 25: 263–292.
- Chambers, J. C., Macmahon, J. A., and Haefner, J. H., 1991: Seed entrapment in alpine ecosystems—Effects of soil particle size and diaspore morphology. *Ecology*, 72(5): 1668–1677.
- Choler, P., Michalet, R., and Callaway, R. M., 2001: Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82(12): 3295–3308.
- Clements, F. E., 1916: *Plant Succession: an Analysis of the Development of Vegetation*. Washington, D.C.: Carnegie Institution of Washington.
- Connell, J. H., 1989: Some processes affecting the species composition in forest gaps. *Ecology*, 70(3): 560–562.
- Dalling, J. W., and Hubbell, S. P., 2002: Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology*, 90(3): 557–568.
- Downs, M. P., and Cavers, P. B., 2002: Physical and chemical factors associated with the reduction or delay of seed germination and seedling emergence of bull thistle, *Cirsium vulgare* (Savi) Ten. under leaf litter. *Ecoscience*, 9(4): 518–525.
- Eccles, N. S., Esler, K. J., and Cowling, R. M., 1999: Spatial pattern analysis in Namaqualand desert plant communities: evidence for general positive interactions. *Plant Ecology*, 142: 71–85.
- Edwards, G. R., and Crawley, M. J., 1999: Effects of disturbance and rabbit grazing on seedling recruitment of six mesic grassland species. *Seed Science Research*, 9: 145–156.
- Elmardottir, A., Aradottir, A. L., and Trlica, M. J., 2003: Microsite availability and establishment of native species on degraded and reclaimed sites. *Journal of Applied Ecology*, 40: 815–823.
- Eriksson, A., and Eriksson, O., 2000: Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. *Nordic Journal of Botany*, 17(5): 469–482.
- Facelli, J. M., and Pickett, S. T. A., 1991: Plant litter—Its dynamics and effects on plant community structure. *Botanical Review*, 57(1): 1–32.
- Fajardo, A., Quiroz, C. L., and Cavieres, L. A., 2008: Spatial patterns in cushion-dominated plant communities of the high Andes of central Chile: How frequent are positive associations? *Journal of Vegetation Science*, 19: 87–96.
- Forbis, T. A., 2003: Seedling demography in an alpine ecosystem. *American Journal of Botany*, 90(8): 1197–1206.
- Forbis, T. A., Larmore, J., and Addis, E., 2004: Temporal patterns in seedling establishment on pocket gopher disturbances. *Oecologia*, 138: 112–121.
- Fort, K. P., and Richards, J. H., 1998: Does seed dispersal limit initiation of primary succession in desert playas? *American Journal of Botany*, 85(12): 1722–1731.
- Galen, C., and Stanton, M. L., 1999: Seedling establishment in alpine buttercups under experimental manipulations of growing-season length. *Ecology*, 80(6): 2033–2044.
- García-Gunman, G., and Benítez-Malvido, J., 2003: Effect of litter on the incidence of leaf-fungal pathogens and herbivory in seedlings of the tropical tree *Nectandra ambigens*. *Journal of Tropical Ecology*, 19: 171–177.
- Goldberg, D. E., Rajaniemi, T., Gurevitch, J., and Stewart-Oaten, A., 1999: Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, 80: 1118–1131.
- Gómez-Aparicio, L., Zamora, R., Gómez, J. M., Hódar, J. A., Castro, J., and Baraza, E., 2004: Applying plant facilitation to forest restoration in Mediterranean ecosystems: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, 14: 1128–1138.
- Gordon, D. R., and Rice, K. J., 1993: Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology*, 74(1): 68–82.
- Griggs, R. F., 1956: Competition and succession on a Rocky Mountain fellfield. *Ecology*, 37(1): 8–20.
- Grubb, P. J., 1977: Maintenance of species-richness in plant communities—Importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society*, 52(1): 107–145.
- Gugerli, F., 1998: Effect of elevation on sexual reproduction in alpine populations of *Saxifraga oppositifolia* (Saxifragaceae). *Oecologia*, 114: 60–66.
- Gurevich, J., Scheiner, S. M., and Fox, G. A., 2002: *The Ecology of Plants*. Sunderland: Sinauer Associates, Inc.
- Harper, J. L., 1977: *Population Biology of Plants*. Oxford: Academic Press.
- Hunter, A. F., and Aarssen, L. W., 1988: Plants helping plants. *Bioscience*, 38: 34–39.
- Kikvidze, Z., Pugnaire, F. I., Brooker, R. W., Choler, P., Lortie, C. J., Michalet, R., and Callaway, R. M., 2005: Linking patterns and processes in alpine plant communities: a global study. *Ecology*, 86: 1395–1400.
- Kitajima, K., 1994: Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, 98: 419–428.
- Kleier, C., and Lambrinos, J. G., 2005: The importance of nurse associations for three tropical alpine life forms. *Arctic, Antarctic, and Alpine Research*, 37(3): 331–336.
- Komárková, V., 1979: *Alpine Vegetation of the Indian Peaks Area, Front Range, Colorado Rocky Mountains*. Vaduz: Cramer, 655 pp.
- Marchand, P. J., and Roach, D. A., 1980: Reproductive strategies of pioneering alpine species: seed production, dispersal, and germination. *Arctic and Alpine Research*, 12: 137–146.
- May, D. E., and Webber, P. J., 1982: Spatial and temporal variation of the vegetation and its productivity on Niwot Ridge, Colorado. In Halfpenny, J. C. (ed.), *Ecological Studies in the Colorado Alpine: a Festschrift for John W. Marr*. Boulder: University of Colorado, Institute of Arctic and Alpine Research Occasional Paper, 37: 35–62.
- Michalet, R., Brooker, R. W., Cavieres, L. A., Kikvidze, Z., Lortie, C. J., Pugnaire, F. I., Valiente-Banuet, A., and Callaway, R. M., 2006: Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, 9: 767–773.
- Niering, W. A., Whittaker, R. H., and Lowe, C. H., 1963: The saguaro: a population in relation to environment. *Science*, 142: 15–23.
- Oloffson, J., and Shams, H., 2007: Determinants of plant species richness in an alpine meadow. *Journal of Ecology*, 95: 916–925.
- Pugnaire, F. I., Haase, P., Puigdefábregas, J., Cueto, M., Clark, S. C., and Incoll, L. D., 1996: Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos*, 76: 455–464.
- Reader, R. J., 1993: Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology*, 81: 169–175.
- Romme, W. H., Turner, M. G., Gardner, R. H., Hargrove, W. W., Tuskan, G. A., Despain, D. G., and Renkin, R. A., 1997: A rare episode of sexual reproduction in aspen (*Populus tremuloides* Michx.) following the 1988 Yellowstone fires. *Natural Areas Journal*, 17: 17–25.
- Rotundo, J. L., and Aguiar, M. R., 2005: Litter effects on plant regeneration in arid lands: a complex balance between seed retention, seed longevity and soil-seed contact. *Journal of Ecology*, 93(4): 829–838.

- SAS Institute, 2001, *SAS*. Cary, North Carolina: SAS Institute, Inc.
- Scherff, E. J., Galen, C., and Stanton, J. L., 1994: Seed dispersal, seedling survival and habitat affinity in a snowbed plant: limits to the distribution of the snow buttercup, *Ranunculus adoneus*. *Oikos*, 69: 405–412.
- Schupp, E. W., 1995: Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, 82(3): 399–409.
- Sherrod, S. K., and Seastedt, T. R., 2001: Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. *Biogeochemistry*, 55(2): 195–218.
- Silvertown, J. W., 1981: Micro-spatial heterogeneity and seedling demography in species-rich grassland. *New Phytologist*, 88: 117–128.
- Stöcklin, J., and Bäumler, E., 1996: Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science*, 7: 45–56.
- Suding, K. N., and Goldberg, D., 1999: Variation in the effects of vegetation and litter on recruitment across productivity gradients. *Journal of Ecology*, 87: 436–449.
- Taylor, R. V., and Seastedt, T. R., 1994: Short- and long-term patterns of soil moisture in alpine tundra. *Arctic and Alpine Research*, 26: 14–20.
- Theodose, T. A., and Bowman, W. D., 1997: Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology*, 78(6): 1861–1872.
- Totland, Ø., 1997: Limits on reproduction in alpine *Ranunculus acris*. *Canadian Journal of Botany*, 75: 137–144.
- Weber, W. A., 1976: *Rocky Mountain Flora*. Boulder: Colorado Associated University Press.
- Welling, P., and Laine, K., 2000: Characteristics of the seedling flora in alpine vegetation, subarctic Finland, I. Seedling densities in 15 plant communities. *Annales Botanici Fennici*, 37: 69–76.
- Went, F. W., 1942: The dependence of certain annual plants on shrubs in southern California deserts. *Bulletin of the Torrey Botanical Club*, 69: 100–114.

MS accepted April 2009