H. Elizabeth Kirkpatrick[1], Jeremy W.S. Barnes[2], and **Barbara A. Ossowski,** Department of Biology, University of Puget Sound, 1500 N. Warner, Tacoma, Washington 98416

Moss Interference Could Explain the Microdistributions of Two Species of Monkey-flowers (*Mimulus*, Scrophulariaceae)

Abstract

Two species of monkey-flowers (*Mimulus guttatus* and *M. lewisii)* differ in their microdistributions along small slow-moving streams in western Washington state: *M. guttatus* generally grows in the streambeds with moss mats whereas *M. lewisii* generally grows on the streambanks where moss does not occur. Interactions with the moss might help explain these differences in microdistribution. Moss mats that occupy the streambeds might have differential effects on either the establishment or subsequent growth of these monkey-flowers. Alternatively, different tolerances of inundation could help explain the differences in microdistribution. We carried out greenhouse experiments designed to understand the potential for moss and inundation to explain the differences in microhabitat occupation of the two *Mimulus* species. Moss mats essentially eliminated successful seedling establishment in *M. lewisii* but allowed establishment of a reduced number of *M. guttatus* seedlings. Growth of established seedlings of *M. lewisii* was enhanced by surrounding moss mats whereas growth of *M. guttatus* was unaffected or reduced. Inundation increased growth rates of both species similarly. Therefore, differential effects of moss on seedling establishment might explain the observed differences in microdistribution.

Introduction

Many studies have demonstrated competitive effects of neighbors on the distributions of plants (Goldberg and Barton, 1992). Although positive effects were recognized very early as important mechanisms in a few interactions [e.g., primary succession (Connell and Slatyer, 1977)], facilitation had received little attention in general plant community processes until recently. Several recent studies and theoretical explorations have shown the potentially widespread importance of positive interactions and the potential for interactions to have both positive and negative effects (Callaway, *et al*. 1991; Callaway, 1994; Bertness and Callaway, 1994; Berkowitz, *et al*., 1995; Callaway and Walker, 1997; Holmgren, *et al*. 1997; Levine, 1999). Recent work suggests that facilitative effects are more likely to be predominant in harsh environments whereas competitive effects are more likely to be predominant in benign environments (Hacker and Gaines, 1997; Callaway and Walker, 1997; Callaway, *et al*., 2002; Maestre, *et al*., 2003). Moreover, the same species can have simultaneous positive and negative effects and variation in abiotic conditions may alter the net effect (Levine, 2000; Maestre, *et al*., 2003). Mosses have been shown to interfere with (Keizer *et al.*, 1985; Kotorová and Leps, 1999; Delach and Kimmerer, 2002; Overbeck, *et al.,* 2003) or facilitate (Keizer *et al.*, 1985; Ryser, 1990; Santiago, 2000; Delach and Kimmerer, 2002; Sedia and Ehrenfeld, 2003) the establishment and survival of vascular plants. Although the mechanisms have generally not been elucidated, light reduction, moderation of temperature and soil moisture, allelopathic effects, and seed trapping have been suggested.

The local distribution of a plant species likely results from a complex interplay of both positive and negative effects of other species, as well as locally varying abiotic factors. On the western slopes of the Cascade mountains of Washington, both *Mimulus lewisii* DC (great purple monkey-flower) and *M. guttatus* Pursh. (common yellow monkey-flower) occur along slow-moving streams (Waser, *et al.,* 1982). Their microdistributions differ, however, in that *M. lewisii* typically occurs on the stream banks whereas *M. guttatus* typically occurs in the streambed, especially in the presence of mats of hydric mosses (H. E. Kirkpatrick, *personal observation*). In the absence of a moss mat, *M. lewisii* can occasionally be found in the streambed.

[1]Author to whom correspondence should be addressed.
E-mail: kirkpatrick@ups.edu

[2]Current address: Nova Southeastern University Oceanographic Center, 8000 North Ocean Dr., Dania Beach, Florida 33004

The exclusion of *M. lewisii* from the streambed could result from a combination of positive and negative effects of neighbors (the mosses and other plants in the community) as well as abiotic factors. The climate of the western Washington Cascades typically includes a summer drought from July through September, and mountain stream flow during the summer drought generally depends on melt water. Especially during summer, when temperatures are relatively high and water availability is lower, there is the potential for moss in the streambed to facilitate growth of the *Mimulus* species by increasing humidity and retaining soil moisture. However, a thick moss mat may also interfere with the seed establishment of these *Mimulus* species.

We proposed three non-exclusive hypotheses that might explain the difference in the ability of the *Mimulus* species to occupy the streambed. The first two hypotheses explore the potential positive and negative effects of moss; the third explores an abiotic explanation: 1) *M. lewisii* may be rare in the streambed because moss reduces the establishment from seed of *M. lewisii* more than that of *M. guttatus*, 2) the presence of moss facilitates the post-establishment growth of *M. guttatus* more than that of *M. lewisii*, and 3) *M. lewisii* may be confined to the streambed because it is intolerant of inundation.

Methods

All experiments were conducted in the greenhouse at the University of Puget Sound. Seeds of both species of *Mimulus* were collected in October 1998 and mats of moss were collected in November 1998 from a site southeast of Mt. Rainier National Park in the Gifford Pinchot National Forest (46° 42' 00" N, 121° 29' 30" W). At this site, the associated streambed mosses were identified as a mixture of *Philonotis fontana* and *Brachythecium frigidum* (Lawton, 1971) growing in a continuous mat 6 cm or more in depth. We were unable to move moss mats intact; instead we gathered sufficient moss for the experiment without trying to maintain the mat structure. Because ambient temperatures were cool, the moss was held until it was needed in opaque plastic bags outside the greenhouse in shade.

We carried out three experiments, one to test each of the three hypotheses, in the greenhouse at the University of Puget Sound. Temperatures in the greenhouse during the experiment varied from approximately 18°C to 25°C, and no supplementary light was supplied. Because it was necessary to use an artificial soil mixture rather than field soil, we used two soil mixes, a peat mixture and a perlite mixture, that spanned a range of water-holding capacities. The temperature range within the greenhouse likely had a narrower range than in the field, and the light levels were likely somewhat lower than field conditions.

Establishment Experiment

To test the effects of moss on establishment, a factorial experiment (2 species x 2 moss treatments x 2 soil types) compared the two *Mimulus* species, moss presence or absence, and two soil types. Eight (54 cm x 26 cm) shallow trays were filled with either a 50:50 mixture of sterile potting medium and peat or a 50:50 mixture of sterile potting medium and perlite. The two soil mixtures were similar in aeration and nutrient content, but the peat mixture had higher water water-holding capacity than the perlite mixture. Approximately 1500 seeds (30 mg of *M. lewisii* seeds; 25 mg of *M. guttatus* seeds) of the assigned *Mimulus* species were scattered evenly over the soil on each tray, over which a 3 cm deep mat of moss was spread in the "moss" treatments. Seeds were left uncovered in the "no moss" treatments. The trays were watered gently to capacity at regular intervals. Seeds were sown in November 1998, and after six weeks, the number of *Mimulus* seedlings established, above the moss cover (when present), was counted for each tray. Quite unexpectedly, many *M. guttatus* seedlings became established in the moss-covered peat soil *M. lewisii* tray, apparently introduced by the moss cover since no *M. guttatus* seedlings appeared in the *M. lewisii* tray without moss. Therefore, in December 1998, we reinitiated the experiment with moss mats from which *M. guttatus* seedlings had already germinated and been removed; in this second experiment, no *M. guttatus* seedlings were found in the *M. lewisii* trays. Because the counts of seedling number were unreplicated, they were compared using Chi-squared goodness of fit tests (with equal expected numbers) for the main effects of moss treatment, soil type, and species and Chi-squared tests of independence for the interactions.

To assess the amount of shade induced by the moss, we measured light penetration through the wet and dry moss mat using tandem LI-COR LI-189 Quantum/Radiometer/Photometers, one below a glass plate supporting the moss mat and the other under only the glass plate. This technique allowed us to express light depletion as percent of ambient light. We found that the presence of a moss mat reduced incident light by more than 99% in both wet and dry conditions.

Post-establishment Growth Experiment

To test the effects of moss on post-establishment growth, we designed a second factorial experiment (2 species x 2 moss treatments x 2 soil types x 15 replicates = 120) using 10 cm plastic pots in which individual seedlings of each *Mimulus* species had been established. About four weeks after germination, a 3 cm deep mat of moss was added to the top of the moss treatment pots, surrounding, but not covering, the *Mimulus* seedling. The pots were randomly arranged on the greenhouse bench and watered regularly to capacity for 10 more weeks after which the above-ground *Mimulus* tissue for surviving seedlings was harvested, dried for three days at 60°C and weighed. After square-root transformation to attain homogeneous variances, absolute biomasses were analyzed in separate two-way ANOVAs, one for each species, to compare the effects of moss and soil type for each species (Goldberg and Scheiner, 1993).

Inundation Experiment

To test the responses of each species of *Mimulus* to inundation, we compared germination and growth of the *Mimulus* species in the greenhouse under two soil moisture regimes: moist and saturated. Twenty-five individuals of each *Mimulus* species were started from seed in each of two 50-compartment seed-starting trays (6 cm depth) that were set into solid trays to maintain the water treatments. In the moist treatment, water was maintained at approximately 1 cm depth throughout the experiment. In the saturated treatment, water was maintained at the soil surface throughout the experiment. In all treatments, we used the same peat soil mixture previously described. Seeds were planted at the end of December 2000 and allowed to grow for 21 weeks, harvested (both roots and shoots), dried for three days at 60°C, and weighed. Because *M. guttatus* gained almost twice as much biomass as *M. lewisii*, we compared effects of inundation relative to the biomass in the moist soil treatment. The relative biomass values compared proportional effects of inundation. The relative biomass data were square-root transformed prior to analysis to attain homogeneity of variances. In all cases, the level of significance was set at P=0.05 prior to beginning the experiments.

Results

Establishment Experiment

The presence of moss drastically reduced establishment from seed of both *Mimulus* species compared to the treatments without moss [*M. lewisii* was reduced by 99.8% (998 seedlings without moss vs. 2 seedling with moss), χ^2 = 992.0, P<0.001; *M. guttatus* was reduced by 90.0% (170 seedlings without moss vs. 17 seedlings with moss), χ^2=125.2, P<0.001, Figure 1], with establishment reduced significantly more for *M. lewisii* than for *M. guttatus* (χ^2=79.1, P<0.0001). More seedlings established in the peat mixture than in the perlite mixture for *M. lewisii* (χ^2=739.6, P< 0.001), but more seedlings established in the perlite mixture than in the peat mixture for *M. guttatus* (χ^2= 3.9, P<0.001). This difference between the species in their response to the soils was significant (χ^2=377.6, P<0.001).

Post-establishment Growth Experiment

The presence of moss surrounding the stems affected the two species differently (P<0.001). Moss enhanced the aboveground biomass of established *M. lewisii* plants (P=0.001), and did so similarly in the two soil types (Table 1, Figure 2). Compared to the no moss treatment, the mean biomass of *M. lewisii* was 68% higher in the peat mixture (P=0.005) and 79% higher in the perlite mixture (P=0.084) when moss was present. In constrast, the effect of moss surrounding *M. guttatus* stems depended on soil type (P<0.001): in the peat mixture, the moss had no significant effect on biomass (although the mean biomass was 35% higher in the presence than in the absence of moss), but in the perlite mixture, the moss reduced biomass of *M. guttatus* by 73% (P<0.001).

Inundation Experiment

Both species survived similarly well under inundation conditions, and in fact, both gained more total biomass in saturated soil than in moist soil (P= 0.004, Figure 3).

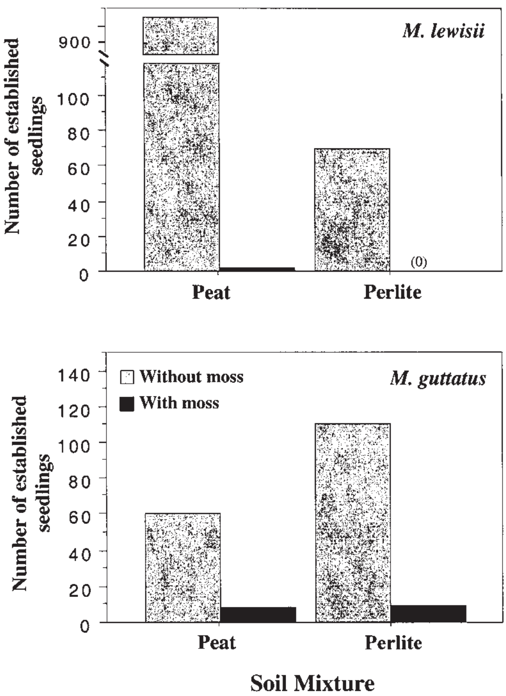

Figure 1. *Establishment experiment*—Total counts of *Mimulus* seedlings established in peat and perlite soils, with and without a moss mat placed on the surface of the seed trays.

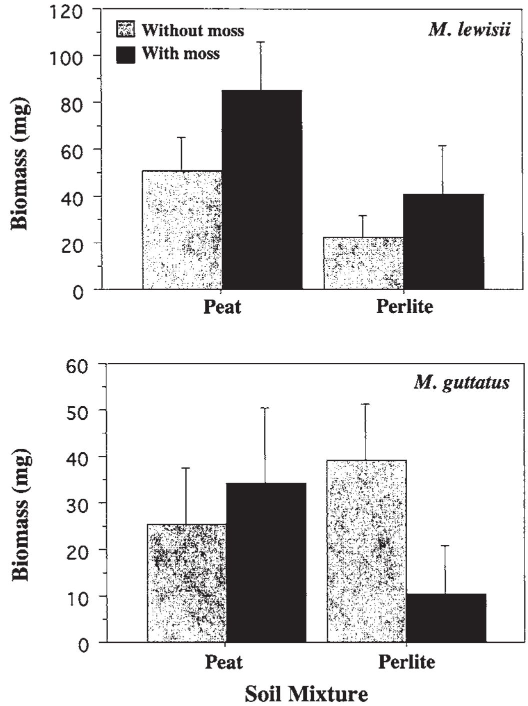

Figure 2. *Post-establishment growth experiment*—Aboveground biomass (+ 95% CI) of *Mimulus lewisii* and *M. guttatus* grown on peat or perlite soil mixtures, with or without moss. Sample sizes ranged from 10 to 15 surviving replicates per treatment group; biomass values were square-root transformed before analysis to achieve homogeneity of variances.

TABLE 1. *Post-establishment growth experiment*—ANOVA results for the effects of moss mats and soil type on growth of *M. lewisii* and *M. guttatus* (square-root transformed aboveground biomasses).

Source	df	MS	F	P
M. lewisii				
Moss treatment	1	45.854	11.416	0.0014
Soil type	1	107.144	26.668	< 0.0001
Moss*Soil type	1	1.936	0.482	0.4907
Residual	51	4.018		
M. guttatus				
Moss treatment	1	15.716	3.747	0.0595
Soil type	1	4.764	1.136	0.2925
Moss*Soil type	1	59.271	14.130	0.0005
Residual	43	4.195		

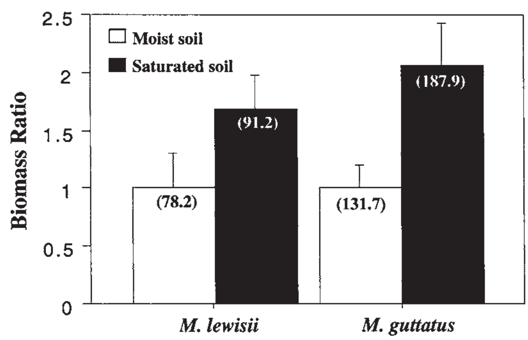

Figure 3. *Inundation experiment*—Ratio (+ 95% CI) of growth in saturated soil to the mean growth in moist soil (aboveground biomass only) of *M. lewisii* and *M. guttatus*. Absolute dry biomass means (mg) are shown within the bars (N = 23 to 25).

Discussion

Effects of Moss on Establishment

We tested the hypothesis that rarity of *M. lewisii* compared to *M. guttatus* in streambeds might be caused by more severe negative effects of moss mats on establishment of *M. lewisii* from seed. This hypothesis was supported in that our moss mats essentially eliminated *M. lewisii* but allowed a small number of *M. guttatus* to establish. The essential elimination of *M. lewisii* seedlings suggests a mechanism by which *M. lewisii* would be excluded from steambeds in which moss was abundant. Moreover, in our experiments, the moss mats apparently functioned as a seed bank for *M. guttatus* but not *M. lewisii.* However, this difference in seed storage capacity mght have been biased by a lack of a *M. lewisii* seed source in the vicinity. Because our experiment was not designed to test the differential seed storage capacity of the moss mat, this was not a variable that we controlled. For seeds of either species, germinating in the midst of the moss mat rather than beneath it would likely reduce any negative effects of the moss cover. It is possible that *M. lewisii* seeds would successfully establish if they germinated in the moss mat rather than under it. Nevertheless, *M. guttatus* apparently has a greater capacity to establish through the moss mat given that 8.5 times as many *M. guttatus* seedlings as *M. lewisii* seedlings established from under the moss mat. These results support the hypothesis that moss mats exclude *M. lewisii*, but not *M. guttatus*, from streambeds.

Similar differential effects on the establishment of vascular plants under moss mats have been found by other authors. Keizer *et al.* (1985) found that seedling emergence of some forbs but not others was negatively correlated with moss cover in a Dutch chalk grassland. Zamfir (2000) found that emergence of forb seedlings was more inhibited by the presence of a moss mat than were grasses, and that thicker moss mats inhibited forb emergence more than thinner moss mats. She also found, however, that dead moss did not have the same inhibitory effects as living moss, suggesting some biotic mechanism for the effects she documented.

The difference between the *Mimulus* species in their ability to establish in the presence of a moss mat may derive from differences between the species in either their germination or their early growth characteristics. The majority of *M. lewisii* seeds may not have germinated at all under the moss mat, or they may have germinated and been unable to sustain themselves to reach the top of the moss; there was no evidence of etiolated or dead *M.lewisii* seedlings below the moss when it was removed. The stems of successful *M. guttatus* seedlings within the moss mat were curved and twisted, suggesting that they were able to respond to tiny gaps in the moss canopy to reach the surface.

The difference in ability of the two *Mimulus* species to establish in the presence of a moss mat could explain the exclusion of *M. lewisii* from streambeds where a thick layer of moss is present. Thus, although we found that moss had a negative direct effect on establishment of both *Mimulus* species, it could have a positive indirect effect on *M. guttatus*, preserving the streambed as *M. guttatus* habitat by preventing the establishment of *M. lewisii* and perhaps other plants as well. Vascular plant establishment has been shown to be reduced in the presence of moss in several habitats: *Pinus sylvestris* in a boreal forest (Dahlberg *et al*., 1997), forbs in a subarctic meadow (Pietikäinen *et al*., 2005), forbs in an oligotrophic wet meadow (Spacková and Leps, 2004), and five tree species in Pacific northwest cedar-hemlock forests (Wright *et al.,* 1998; Weber *et al.,* 2003). If similar reductions in establishment occur among other vascular plants in stream habitats, this reduced competition would indirectly benefit *M. guttatus*, but only if the effect were relatively more severe on the other plants. It would be useful to compare the relative abilities of other plants to establish in the presence of a moss mat with that of *M. guttatus* to assess this indirect benefit. Despite rather severe impacts of moss on establishment from seed, the ability of *M. guttatus* to spread vegetatively would minimize the direct negative effect of moss on its population dynamics. However, because vegetative propagation results in genetically identical individuals, the chance of inbreeding is increased. Recent evidence indicates that inbreeding in *M. guttatus* can result in a fitness decline via herbivore interactions (Carr and Eubanks, 2002).

Effects of Moss on Post-establishment Growth

We tested the hypothesis that moss mats more positively affected post-germination growth of

M. guttatus than that of *M. lewisii.* This hypothesis was clearly not supported: averaging across both soil types, biomass gained by *M. lewisii* seedlings increased by almost 80% because of positive responses in both soil types, whereas biomass gained by *M. guttatus* seedlings was reduced by almost 40% in the presence of moss because of a strong negative response to moss in the perlite soil and very little response in the peat soil. Because of the enhanced growth of both *Mimulus* species on saturated soil (see response to inundation below), the somewhat drier perlite mixture may have represented a more stressful environment. The neutral or negative post-germination response of *M. guttatus* to moss contrasts with the clearly positive response of *M. lewisii* to moss. We observed one possible explanation for this difference. *Mimulus guttatus* has a stoloniferous growth form, establishing adventitious roots where the stems come in contact with the soil. In the moss-treated pots with perlite soil, *M. guttatus* initiated many adventitious roots in the moss layer. Although we included all of these roots in the aboveground biomass total, this tissue presumably did not increase the photosynthetic biomass of the plant. This allocation of energy to root production may have reduced the total photosynthetic area dedicated to energy acquisition, potentially limiting total biomass. This increased allocation to root biomass was not apparent in the peat mixture, perhaps because water availability in the peat soil was higher, reducing the need for allocation to root biomass overall. This potential explanation of the negative effect of moss on biomass gain of *M. guttatus* in perlite soil awaits further testing.

Response to Inundation

The hypothesis that soil saturation prevents *M. lewisii* from occupying the streambed was clearly refuted, since both species gained more biomass under saturated soil conditions than under moist conditions and there was no suggestion of any difference in the species proportional responses. Therefore, the hypothesis *M. lewisii* does not tolerate inundation and requires the better-aerated sites on the streambank was not supported.

The joint negative and positive effects of moss shown in the current experiment are echoed in the literature. Moss increased the germination of various forb seedlings on iron mine tailings in New York (Delach and Kimmerer, 2002), and has been associated with higher seedling establishment of a *Cypripedium* orchid species in Estonia (Kull, 1998), an epiphytic fig in the tropics (Laman, 1995), and with higher forb seedling densities on woody debris in a Hawaiian cloud forest (Santiago, 2000). Moss cover has been associated with higher vascular plant cover in the New Jersey Pinelands (Sedia and Ehrenfeld, 2003), better recruitment of white fir in the Jura Mountains of France (Tan, 1987), and better recruitment of white spruce after fires in the western Great Lakes region (Purdy *et al*., 2002). However, moss presence has been implicated in reduced success of tree seedlings in the forests of central Argentina (Enrico *et al.,* 2004) and of Scots pine in a Scottish moorland forest (Hancock *et al*., 2005). Moss had negative effects on germination, but positive effects on seedling growth, in a fen meadow in Germany (Overbeck *et al.,* 2003). Similarly, *Polytrichum* moss reduced germination but enhanced survival during drought of white spruce seedlings in southern Canada (Parker *et al.,* 1997).

As this brief review suggests, mosses can have both positive and negative effects on the success of young vascular plants. Positive effects on germination and early establishment seem to result from increased water availability, decreased temperatures, or protection from seed and seedling predators. Negative effects seem to result from decreased light, preventing contact with mineral soil, and possibly nutrient competition. These generalizations suggest that mosses should have had the most benefit to *Mimulus* seedling growth on the drier perlite soil, which was the case for *M. lewisii* but not for *M. guttatus*. Clearly, soil texture can alter the potential benefit of moss association.

The balance of positive and negative effects of mosses on the two *Mimulus* species differed due to the species' differences in their ability to establish under the moss mat. Because *M. lewisii* was unable to establish in the presence of moss, moss can potentially prevent its occupation of streambeds. However, if *M. lewisii* were to establish in a streambed prior to the colonization of mosses, the growth of those established individuals might be enhanced by subsequent colonization of moss, but seeds from these individuals would perhaps not be able to establish. In contrast, the ability of *M. guttatus* to establish through a moss mat allows it to occupy streambeds previously colonized by moss.

Acknowledgements

We thank the University of Washington Herbarium for access to the bryophyte collection to confirm our moss identifications. We also thank the University of Puget Sound for undergraduate research funding and access to facilities and equipment. This manuscript benefited greatly from the insightful comments of Elizabeth Binney, David Morgan, Fred Rhoades, and Suzzane Schwab.

Literature Cited

Berkowitz, A. R., C. D. Canham, and V. R. Kelley. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology 76:1156-1168.

Bertness, M. D. and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191-193.

Callaway, R. M. 1994. Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals. Ecology 75:681-686.

Callaway, R. M. and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958-1965.

Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. Ecology 72:1484-1499.

Callaway, R. M. R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. I. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844-848.

Carr, D. E. and M. D. Eubanks. 2002. Inbreeding alters resistance to insect herbivory and host plant quality in *Mimulus guttatus* (Scrophulariaceae). Evolution 56:22–30.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:119-1144.

Delach, A. and R. W. Kimmerer. 2002. The effect of *Polytrichum piliferum* on seed germination and establishment on iron mine tailings in New York**.** The Bryologist 105:249–255.

Dahlberg, A., O. Zackrisson, A. Jaderlund, and M. C. Nilsson. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. Oikos 78:209-220.

Enrico, L., G. Funes, and M. Cabido. 2004. Regeneration of *Polylepis australis* Bitt. in the mountains of central Argentina. Forest Ecology and Management 190:301-309.

Goldberg, D. E. and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. American Naturalist 139:771-801.

Goldberg, D. E. and S. M. Scheiner. 1993. ANOVA and ANCOVA: field competition experiments. In: Design and Analysis of Ecological Experiments, S.M. Scheiner and J. Gurevitch (eds.), Chapman and Hall, New York.

Hancock, M., S. Egan, R. Summers, N. Cowie, A. Amphlett, S. Rao, and A. Hamilton. 2005. The effect of experimental prescribed fire on the establishment of Scots pine Pinus sylvestris seedlings on heather *Calluna vulgaris* moorland. Forest Ecology and Management 212:199-213.

Hacker, S. D. and S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. Ecology 78:1990-2003.

Holmgren, M. M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology 78:1966-1975.

Keizer, P. J., B. F. Van Tooren, and H. J. During. 1985. Effects of bryophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. Journal of Ecology 73:493-504.

Kotorová, I. and J. Leps. 1999. Comparative ecology of seedling recruitment in an oligotrophic wet meadow. Journal of Vegetation Science 10:175-186.

Kull, T. 1998. Fruit-set and recruitment in populations of *Cypripedium calceolus* L. in Estonia. Botanical Journal of the Linnean Society 126:27-38.

Laman, T. G. 1995. *Ficus stupenda* germination and seedling establishment in a Bornean rain forest canopy. Ecology 76:2617-2626.

Lawton, E. 1971. Moss Flora of the Pacific Northwest. Journal of the Hattori Botanical Laboratory, Supplement no. 1.

Levine, J. M. 1999. Indirect facilitation: evidence and predictions from a riparian community. Ecology 80:1762-1769.

Levine, J. M. 2000. Complex interactions in a streamside plant community. Ecology 81:3431-3444.

Maestre, F. T, J. Cortina, S. Bautista, and J. Bellot. 2003. Does *Pinus halepensis* facilitate the establishment of shrubs in Mediterranean semi-arid afforestations? Forest Ecology Management 176:147-160.

Overbeck, G., K. Kiehl, and C. Abs. 2003. Seedling recruitment of *Succisella inflexa* in fen meadows: Importance of seed and microsite availability. Applied Vegetation Science 6:97–104.

Parker, W. C., S. R. Watson, and D. W. Cairns. 1997. The role of hair-cap mosses (*Polytrichum* spp.) in natural regeneration of white spruce (*Picea glauca* (Moench) Voss). Forest Ecology and Management 92:19-28.

Pietikäinen, A., M. M. Kytöviita , and U. Vuoti. 2005. Mycorrhiza and seedling establishment in a subarctic meadow: Effects of fertilization and defoliation. Journal of Vegetation Science 16:175-182.

Purdy, B. G., S.E. Macdonald, and M. R. T. Dale. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest Silva Fennica 36:289-306.

Ryser, P. 1990. Influence of gaps and neighbouring plants on seedling establishment in limestone grassland. Experimental field studies in northern Switzerland. Veröffentlichungen des Geobotanischen Institutes der Eidg. Technischen Hochschule, Stiftung Rübel in Zürich 104:1-71.

Santiago, L. S. 2000. Use of coarse woody debris by the plant community of a Hawaiian montane cloud forest. Biotropica 32:633–641.

Sedia, E. G., and J. G. Ehrenfeld. 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. Oikos 100:447-458.

Spacková, I. and J. Leps. 2004. Variability of seedling recruitment under dominant, moss, and litter removal over four years. Folia Geobotanica 39:41-55.

Tan, B.S. 1987. Influence of some ecological factors on the first stages of fir regeneration in the mountain forests of the Jura. Revue D'Ecologie et de Biologie du Sol 24:623-635.

Received 15 July 2004
Accepted for publication 14 January 2006

Waser, N. M, R. K. Vickery, Jr. and M. V. Price. 1982. Patterns of seed dispersal and population differentiation in *Mimulus guttatus*. Evolution 36:753-761.

Weber, A., B. Gilbert, J. P. Kimmins, and C. E. Prescott. 2003. Factors limiting the early survivorship of *Thuja plicata* on northern Vancouver Island, British Columbia. Canadian Journal of Forest Research 33:854-861.

Wright, E. F., K. D. Coates, and P. Bartemucci. 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. Canadian Journal of Forest Research 28:1352-1364.

Zamfir, M. 2000. Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. Oiko*s* 88:603-611.