

FACILITATION ACROSS STRESS GRADIENTS: THE IMPORTANCE OF LOCAL ADAPTATION

E. K. ESPELAND¹ AND K. J. RICE

Ecology Graduate Group, Department of Plant Sciences, Mail Stop 1, University of California, Davis, California 95616 USA

Abstract. While there is some information on genetic variation in response to competition in plants, we know nothing about intraspecific variation in facilitation. Previous studies suggest that facilitation should increase fitness in stressful environments. However, whether a plant experiences an environment as stressful may depend on prior adaptive responses to stressors at a site. Local adaptation to stress at a site may reduce the likelihood of facilitation. Seeds of *Plantago erecta* from stressful (serpentine soil) and non-stressful (non-serpentine soil) edaphic environments were reciprocally planted into these two soil types. Although competition did not differ significantly among seed sources, there was evidence for a local adaptation effect on facilitation. Non-serpentine seeds planted into serpentine soil exhibited greater individual plant biomass at higher densities. The interaction between population source and growth environment indicates a role for evolutionary processes such as local adaptation in the expression of facilitation in plants.

Key words: annual plants; competition; density dependence; facilitation; intraspecific; local adaptation; *Plantago erecta*; serpentine.

INTRODUCTION

In recent years, facilitation has been recognized as an important ecological interaction, and more experiments have examined facilitation and its strength relative to competition (Bruno et al. 2003). In this nascent experimental field, there have been three primary research foci: comparing the strength of facilitation vs. competition (see Callaway and Walker 1997 and Holmgren et al. 1997 for reviews), examining the spatial scale at which facilitation is important (Dickie et al. 2005), and testing whether the facilitative effect increases as environmental stress increases (Lortie and Turkington 2002, Liancourt et al. 2005). However, the influence of evolutionary processes on facilitative effects has not been explored. It is usually assumed that whether or not a plant experiences an environment as stressful is a species-wide phenomenon. However, one might expect that differing adaptive responses at the population level to environmental stress would generate within-species variation in facilitation. Although relatively few, competition experiments that have explored intraspecific variation in competitive response (Shaw and Platen-

kamp 1993, Dudley and Schmitt 1995, Shaw et al. 1995) indicate that competitive response varies among populations within species. Thus, it seems reasonable to expect that facilitative responses also vary among populations within a species. Our study is the first that we know of to examine intraspecific variation in facilitative effects on plant fitness.

Facilitation occurs when interactions among plants produce greater plant fitness or abundance than when plants are grown alone. Most of the facilitation literature has focused on the benefits of interspecific interactions (reviewed in Hunter and Aarssen 1988 and in Callaway and Walker 1997). Well-studied “nurse plants” in deserts show that, via shading and hydraulic lift, established plants can promote the recruitment of other plants (Caldwell et al. 1998). Within the intertidal environment, other species can promote establishment of a focal species through the amelioration of the physical stress of wave impact (Bertness et al. 1999). Plant establishment and survival can be assisted by the presence of other plants via nutrient sharing either by root grafting (found in trees, Hunter and Aarssen 1988) or mycorrhizal networks (Chiariello et al. 1982). The presence of other plants can also stimulate beneficial soil bacterial activity (Hunter and Aarssen 1988). The above mechanisms are direct in that they involve plant-on-plant interaction. Indirect mechanisms of facilitation

Manuscript received 18 July 2006; revised 7 December 2006; accepted 13 February 2007. Corresponding Editor: J. J. Stachowicz.

¹ E-mail: ekespeland@ucdavis.edu

depend upon mobile biota: increasing plant density resulting in a lower predation pressure (Hulme and Hunt 1999, Parmesan 2000) or increased likelihood of cross-pollination (Groom 1998).

There has been considerable debate about the strength of facilitation vs. competition along productivity gradients. Bertness and Callaway (1994) propose that direct facilitation should be strongest at high levels of abiotic stresses while indirect facilitation should be strongest at low levels of stress. Within environments with intermediate levels of stress, competition is predicted to dominate. This conceptual model appears as the most common cited view within the facilitation literature (Callaway and Walker 1997, Holmgren et al. 1997, Bruno et al. 2003). It should be noted, though, that the majority of the facilitation literature focuses on inter-specific interactions.

If one views all plant interactions as predominantly competitive (Tilman 1988, Goldberg and Novoplansky 1997), then one would expect competition to be strongest in the least physically stressful environment where plant density or biomass is the highest. Weldon and Slauson (1986) reviewed the long-running debate about the importance of competition in stressful environments and determined that while competition may be intense in harsh environments, it may have less effect on fitness than other environmental stresses. Many plants fail to reproduce in stressful environments, and if facilitation increases the likelihood of reproduction, then facilitation may have a large effect on plant fitness in stressful environments, particularly for annual species where a failure to reproduce may result in local extinction.

The serpentine grasslands of California are an excellent system for testing the importance of competition and abiotic stress within plant communities (Huenneke et al. 1990, Jurjavcic et al. 2002, Williamson and Harrison 2002). While serpentine soils are nutritionally stressful, they can support varying amounts of biomass, depending on soil depth (Jurjavcic et al. 2002).

Our study examined the relative strength of below-ground intraspecific facilitation and competition in plants growing under nutrient stress compared to plants growing in more fertile soils. The experiment examined direct facilitation among annual plants of the same species and was designed to test whether facilitation increases when edaphic stress increases. Competitive and facilitative effects were tested at three aspects of life history: germination, mortality, and biomass accumulation. A unique aspect of our design was to consider how the evolutionary history of a plant species (e.g., adaptation to serpentine soil) might modulate the expression of facilitation in plants exposed to low nutrient conditions. The hypotheses were these:

(1) Facilitation is more important for plants exposed to physical stress in the low nutrient growth environ-

ment of serpentine soil. Competition is more important in the less stressful environment of non-serpentine soil.

(2) Facilitation is more important for plants from nonlocal seed sources because of a lack of adaptation to local stressors. In contrast, competition will predominate among locally adapted genotypes.

METHODS AND MATERIALS

Plantago erecta (E. Morris) is an annual plant with a native range extending from Baja California and Arizona north through the California Floristic Province to southern Oregon (see Plate 1). Although completely self-compatible, some outcrossing is likely in this species (E. Espeland, *unpublished data*). Seeds are ballistically dispersed and travel long distances only rarely. *Plantago erecta* can grow at high densities (up to 1 plant/cm²) and occurs in shallow, low-fertility soils (serpentine outcrops, road cuts) as well as in deep, more fertile soils.

In spring 2004, seeds were collected from six populations of *P. erecta* at McLaughlin Reserve within the University of California Natural Reserve System. The Reserve is located within the California coastal range at the junction of Lake, Napa, and Yolo counties in northern California (38°31'12" N, 122°14'24" W). Within grassland areas of the reserve, three populations were located on serpentine soil and three on non-serpentine soil. The landscape of the McLaughlin Reserve is patchy so that sampled serpentine and non-serpentine populations were completely interspersed. Soil was collected from an area within 100 m where *P. erecta* plants were found (at one serpentine population and one non-serpentine population), but none occurred at the soil collection locations, thus collected soil was unlikely to have a *P. erecta* seed bank already present. Serpentine soils have very low calcium:magnesium ratios, often toxic levels of nickel, and are low in nitrogen, phosphorous, and molybdenum (Kruckeberg 1984). The serpentine soil collected for this experiment has a low calcium:magnesium ratio (0.2) typical of serpentine soils (Kruckeberg 1984), but average, non-toxic, nickel levels (17.5 ppm, Proctor and Woodell [1975]; soils data provided by J. Gerlach). We thus assumed that plants growing in the serpentine soil treatment would be nutrient-stressed, but not necessarily suffering from nickel toxicity.

Seeds were stored at room temperature until March 2005, at which time they were weighed and placed in a 4°C cold room for 19 days. Seeds were bulked across collection sites by their population source type (serpentine or non-serpentine) before sowing. Seeds were sown into pots on 28 March and 29 March 2005. To restrict competitive and/or facilitative effects to belowground interactions, each pot (2 × 3 × 10 cm deep) was divided aboveground into six equal parts by foil separators extending 7 cm above the soil surface. Pots were spaced so that each plant had access to 3 cm² of aboveground

TABLE 1. Effects of plant density, seed source soil, and planting soil on average plant biomass for *Plantago erecta*.

Independent variable	df	Type III SS	MS	F	P
Density	1	8000.55	8000.55	9.64	0.003
Maternal soil	1	29.33	29.33	0.04	0.851
Density \times maternal soil	1	249.66	249.66	0.30	0.545
Planting soil	1	1536.39	1536.39	1.85	0.177
Density \times planting soil	1	64.23	64.23	0.08	0.782
Maternal soil \times planting soil	1	4817.76	4817.76	5.80	0.018
Density \times maternal soil \times planting soil	1	3340.26	3340.26	4.02	0.048
Error	92	76 380.71	76 380.71		

light area. Because the average height of container-grown plants in a previous experiment was 7 cm (E. Espeland, *unpublished data*), we expected aboveground interactions from canopy overlap to be minimal. No more than a single seed was sown into each of the six sectors of the pot. Seeds were sown in the same positions within the pot for each treatment combination. For seeds collected from non-serpentine populations, the non-serpentine soil was designated as their "local" soil whereas for seeds collected from serpentine populations, the non-serpentine soil was considered to be their "nonlocal" soil. Seeds were sown in a factorial arrangement at three planting densities (two, four, and six seeds) in two soil types (local or nonlocal) for two source population types (serpentine and non-serpentine). Each treatment combination was replicated 15 times.

Pots were kept indoors until the first emergence was recorded on 1 April 2005, and then pots were placed outdoors in Winters, Yolo County, California (38°30' N, 122°0' W). Plants were regularly watered so that water stress did not occur. Plant canopies did not grow taller than the foil separators over the course of the experiment. Aboveground plant biomass was collected on 1 June 2005 after all the plants had senesced. After collection, the aboveground biomass of each plant was dried and weighed. Roots appeared to fully exploit the pot space in almost all pots.

Data analysis

Four models were tested, each determining the interactive effects of seed source soil type and planting soil type with (1) *P. erecta* sowing density on percent mortality within each pot, (2) sowed *P. erecta* density on percent germination, (3) emergent *P. erecta* density on average plant weight within each pot, and (4) planted *P. erecta* density on average plant weight within each pot. Sowed seed density per pot (for the emergence analysis) and emerged plant density per pot (for the mortality and biomass analyses) were treated as continuous variables in the analysis. Due to variable germination, each emerged density occurred in two to eleven pots. Percent germination and percent mortality data were arcsine-square root transformed prior to analysis. Average biomass data were ranked to meet the assumption of

normality (Conover and Iman 1982) and to increase homogeneity of variances. Data were ordered by pot from lowest average plant biomass to highest average plant biomass (pot biomass divided by number of plants in the pot), and ranks were assigned based on this order. Ranking has been shown to increase homogeneity of variance (Iman and Conover 1979), and this was the case for our data as well. For untransformed data in our four treatments (seed source by planting soil in a factorial design), variances ranged from 5% to 33% whereas, in transformed data, this range was reduced to 17–34%. Plant biomass is linearly and positively related to seed output in this species (number of seeds = $0.437 + 342.917$ [biomass, in mg], $R = 0.8$; E. Espeland, *unpublished data*). We used PROC GLM in SAS (version 9.1; SAS Institute 2005) for all analyses.

RESULTS

Plant mortality did not respond to increasing plant density. There was no main or interactive effect of sowing density, seed source soil type, or planting soil type on plant mortality over the growing season ($P > 0.3$). Survivorship over the growing season was high, averaging $92\% \pm 21\%$ (mean \pm SD). Plant densities ranged from 0.17 to 1 plants/cm², which approximates the range of densities found in natural populations (E. Espeland, *unpublished data*).

Increasing sowed seed density decreased emergence. There was a significant effect of sowing density on percent emergence, with lower emergence at higher densities (0.687–0.033 number sown, $R^2_{\text{adj}} = 0.03$, $P < 0.001$). Planting soil type also had a significant effect on percent emergence with lower emergence from serpentine soil ($44\% \pm 27\%$) than from non-serpentine soil ($69\% \pm 38\%$, $P < 0.025$). These emergence rates are comparable to those for field-planted seed which ranges from 28% to 75% (E. Espeland, *unpublished data*).

The significant three-way interaction among density, seed source soil type, and planting soil type for average plant biomass (Table 1, $P < 0.05$, $R^2 = 0.18$, $df = 7, 92$, $F = 2.96$) indicates that the relationship between plant density and average plant biomass is affected by the growing soil as well as plant seed source. We partitioned this interaction by separating local and nonlocal seed sources for further analysis. Plants growing on their

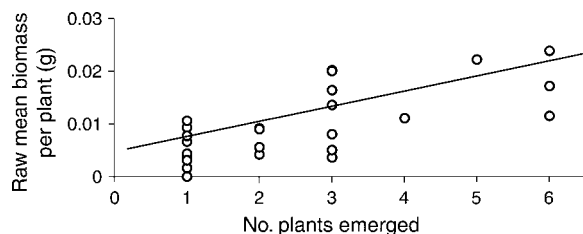


FIG. 1. Plant biomass (pot biomass divided by number of emergent *Plantago erecta*) for nonlocal seed source is positively related to plant density on serpentine soil. Raw mean plant biomass (g) = $0.0029 + 0.0027 \times \text{density}$; rank-transformed data, $R^2_{\text{adj}} = 0.46$, $P < 0.001$.

“local” soil type had no detectable response to plant density ($P = 0.60$). Plants growing on their “nonlocal” soil type showed a significant interaction between soil type and plant density ($P < 0.008$). Average plant biomass in non-serpentine plants growing in serpentine soil had a highly significant positive response to increasing plant density (Fig. 1, biomass rank = $17.8 + 10.7 \times \text{density}$, $R^2_{\text{adj}} = 0.46$, $P < 0.001$) whereas serpentine plants growing in non-serpentine soil did not have a significant response to plant density ($P = 0.08$), although the trend in response was still positive.

There was evidence of overall local adaptation in these seed sources in that regardless of the number of plants per pot, there was a significant interactive effect of planting soil and seed source on final plant biomass (Table 1, $P < 0.02$). Biomass was highest for plants from non-serpentine populations grown in non-serpentine soil and lowest for plants from non-serpentine populations grown in serpentine soil (Table 2).

To test the net competitive or facilitative effect over all life history stages, ranked final average plant biomass was regressed against planted *P. erecta* density. The model was not significant ($P > 0.2$).

DISCUSSION

Plant mortality was not affected by emergent plant density, thus there was no net effect of either facilitation or competition on mortality. An overall net competitive effect was expressed at the emergence stage and was not

affected by variation in edaphic stress simulated by the soil type treatments. *Plantago erecta* seeds sown at high densities had lower emergence percentages than seeds sown at low densities, although the effect was small (i.e., sowing density explained only 3% of the variance in emergence rates). This result supports previous studies on other annual plants that report competition at the emergence stage in arid and semiarid systems (Lortie and Turkington 2002, Shilo-Volin et al. 2005). Because *P. erecta* populations maintain seed banks (E. Espeland, unpublished data), ungerminated seeds are not necessarily lost to the population but may emerge in subsequent years if they escape predation. Buffering by the seed bank may thus reduce the relative importance of competition at emergence.

To determine whether competition or facilitation was the stronger net effect on plant biomass accumulation, average plant biomass was regressed against the number of emergent plants: a positive slope would indicate a net facilitative effect, while a negative slope would indicate a net competitive effect. Facilitation was extremely important for non-serpentine seed sources growing on the low nutrient soil ($R^2 = 46\%$). The mechanism for this net facilitative effect among non-serpentine plants occurs belowground, as aboveground plant structures were kept separate during this experiment.

The lack of relationship between planted, rather than emerged, *P. erecta* density and biomass accumulation may indicate a balance between competition (at the emergence stage) and facilitation (during biomass accumulation) so that no net effect is observed. This lack of a relationship may also indicate an overriding influence of mortality that had no relationship to plant density.

The underground facilitation observed in this experiment is most likely related to nutrient uptake and could occur via root grafting (although observed only in trees and not yet tested in annual plants [Hunter and Aarssen 1988]), mycorrhizal networks (Chiarriello et al. 1982), increased soil bacterial activity (Hunter and Aarssen 1988), or increased concentration of root exudates that make nutrients more biologically available (Vance et al. 2003).

TABLE 2. Plant biomass by seed source soil and planting soil.

Seed source soil type	Planting soil	Ranked biomass†	Raw biomass (g)	No. plants
Local	non-serpentine	$62.2^a \pm 33.8$	0.017 ± 0.014	27
Nonlocal	non-serpentine	$54.7^{ab} \pm 35.4$	0.016 ± 0.014	27
Local	serpentine	$50.08^{ab} \pm 23.9$	0.012 ± 0.008	25
Nonlocal	serpentine	$45.2^b \pm 26.2$	0.010 ± 0.007	26

Note: Values are means \pm SD.

† Average biomass data were ranked to meet the assumption of normality (Conover and Iman 1982) and to increase homogeneity of variances. Data were ordered by pot from lowest average plant biomass to highest average plant biomass (pot biomass divided by number of plants in the pot), and ranks were assigned based on this order. Different letters indicate significant differences between treatments (Fisher's LSD, $P < 0.05$).



PLATE 1. Serpentine outcrop with *Plantago erecta* population. Photo credit: E. K. Espeland.

If we consider that facilitation increased fitness of nonlocal seed sources in “unfamiliar” soil environments, we may infer that each seed source is adapted to their home soil in such a way that a locally-adapted individual can access most of the soil resources without assistance (direct or indirect) from other plants. Endomycorrhizal fungi have been shown to be effective in enhancing plant fitness of a related, perennial species, *Plantago lanceolata* (Ayres et al. 2006), but only when plants cannot exhaust soil nutrient resources without the presence of fungi. In this experiment, plants may have been limited in their ability to fully exploit the nutrient resources of an unfamiliar soil type.

Other work has predicted that the balance between competition and facilitation should change over stress gradients (Bertness and Callaway 1994). Thus, we expected net facilitative effects to be more evident on the stressful, serpentine soil. This was partially the case in that facilitation on stressful soil was detected, but only for the nonlocal seed source. The degree of facilitation changed according to the evolutionary history of the plants, and thus evolutionary history is an important component of how plants experience stress.

This experiment only compared the relative effects of belowground competition and facilitation under nutrient stress when water was not limiting. There is evidence that serpentine soils lose water more rapidly than non-serpentine soils (Macnair et al. 1989). Competition for water in natural populations of *P. erecta* may override the positive belowground density effects on growth observed in this experiment because other studies have shown that intraspecific facilitation in plants is less likely

to occur in xeric environments (see Holmgren et al. 1997 for review).

Our observation that facilitative effects were strongest for the non-serpentine seed sources growing in serpentine soil supports the hypothesis that facilitation is most important when organisms are growing under conditions far from their environmental optima. This hypothesis has been explored at the species level (see Bertness and Callaway 1994 and Liancourt et al. 2005 for examples) and our study supports viewing environmental optima within an evolutionary context at the population level (suggested by Bijlsma and Loeschcke [2005]). If we view environmental optima as the product of the interaction between stress as an agent of selection and the historic adaptive response of the population, we will gain a more realistic “plant’s eye” view of stress.

The influence of evolutionary history on intraspecific facilitation has strong implications for invasive species as well as for ecological restoration. Our findings suggest that in colonization of physically stressful sites, an increase in intraspecific densities may lead to greater population persistence and growth. With facilitation occurring in dense populations, high immigration rates actually increase the likelihood of local adaptation (Holt et al. 2004), and thus may increase the probability of colonization success. This hypothesis is supported by work at the species level where high densities may increase the likelihood of invasion success in introduced species because of intraspecific facilitation (Taylor and Hastings 2005). On the negative side, intraspecific facilitation may also increase genetic load within populations by allowing less fit plants to survive and reproduce.

ACKNOWLEDGMENTS

This work was performed in part at the McLaughlin Reserve of the University of California Natural Reserve System (UCNRS) and partially funded by a Mildred E. Mathias Grant for work at the UCNRS to E. K. Espeland and a Packard Foundation Interdisciplinary Science Grant (2000-01607) to K. J. Rice. Thanks to S. Mueller for field assistance and to S. Harrison, J. Harding, K. Moore O'Leary, S. Elmendorf, M. Schlesinger, K. Jones, J. Weiner, J. Grace, and two anonymous reviewers for helpful conversations and comments on previous versions of the manuscript.

LITERATURE CITED

- Ayres, R. L., A. C. Gange, and D. M. Aplin. 2006. Interactions between arbuscular mycorrhizal fungi and intraspecific competition affect size, and size inequality, of *Plantago lanceolata* L. *Journal of Ecology* 94:285–294.
- Bertness, M. D., and R. M. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–193.
- Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80:2711–2726.
- Bijlsma, R., and V. Loeschke. 2005. Environmental stress, adaptation and evolution: an overview. *Journal of Evolutionary Biology* 18:744–749.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Caldwell, M. M., T. E. Dawson, and J. H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113:151–161.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965.
- Chiariello, N., J. C. Hickman, and H. A. Mooney. 1982. Endomycorrhizal role for interspecific transfer of phosphorus in a community of annual plants. *Science* 217:941–943.
- Conover, W. J., and R. L. Iman. 1982. Analysis of covariance using the rank transformation. *Biometrics* 38:715–724.
- Dickie, I. A., S. A. Schnitzer, P. B. Reich, and S. E. Hobbie. 2005. Spatially disjunct effects of co-occurring competition and facilitation. *Ecology Letters* 8:1191–1200.
- Dudley, S. A., and J. Schmitt. 1995. Genetic differentiation in morphological responses to simulated foliage shade between populations of *Impatiens capensis* from open and woodland sites. *Functional Ecology* 9:655–666.
- Goldberg, D., and A. Novoplansky. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85:409–418.
- Groom, M. J. 1998. Allee effects limit population viability of an annual plant. *American Naturalist* 151:487–496.
- Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975.
- Holt, R. D., T. M. Knight, and M. Barfield. 2004. Allee effects, immigration, and the evolution of species' niches. *American Naturalist* 163:253–262.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources and plant invasion and community structure in California serpentine grassland. *Ecology* 71:478–491.
- Hulme, P. E., and M. K. Hunt. 1999. Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of prey. *Journal of Animal Ecology* 68:417–428.
- Hunter, A. F., and L. W. Aarssen. 1988. Plants helping plants. *BioScience* 38:34–40.
- Iman, R. L., and W. J. Conover. 1979. The use of the rank transform in regression. *Technometrics* 21:499–509.
- Jurjavec, N. L., S. Harrison, and A. T. Wolf. 2002. Abiotic stress, competition and the distribution of the native annual grass *Vulpia microstachys* in a mosaic environment. *Oecologia* 130:555–562.
- Kruckeberg, A. R. 1984. California serpentine: flora, vegetation, geology, soils and management problems. University of California Press, Berkeley, California, USA.
- Liancourt, P., R. M. Callaway, and R. Michalet. 2005. Stress tolerance and competitive response ability determine the outcome of biotic interactions. *Ecology* 86:1811–1818.
- Lortie, C. J., and R. Turkington. 2002. The effect of initial seed density on the structure of a desert annual plant community. *Journal of Ecology* 90:435–445.
- Macnair, M. R., V. E. Macnair, and B. E. Martin. 1989. Adaptive speciation in *Mimulus*: an ecological comparison of *Mimulus cupriphilus* with its presumed progenitor, *Mimulus guttatus*. *New Phytologist* 112:269–279.
- Parmesan, C. 2000. Unexpected density-dependent effects of herbivory in a wild population of the annual *Collinsia torreyi*. *Journal of Ecology* 88:392–400.
- Proctor, J., and S. R. J. Woodell. 1975. The ecology of serpentine soils. *Advances in Ecological Research* 9:255–365.
- SAS Institute. 2005. SAS version 9.1. SAS Institute, Cary, North Carolina, USA.
- Shaw, R. G., and G. A. J. Platenkamp. 1993. Quantitative genetics of response to competitors in *Nemophila menziesii*: a greenhouse study. *Evolution* 47:801–812.
- Shaw, R. G., G. A. J. Platenkamp, F. H. Shaw, and R. H. Podolsky. 1995. Quantitative genetics of response to competitors in *Nemophila menziesii*: a field experiment. *Genetics* 139:397–406.
- Shilo-Volin, H., A. Novoplansky, D. E. Goldberg, and R. Turkington. 2005. Density regulation in annual plant communities under variable resource levels. *Oikos* 108:241–252.
- Taylor, C. A., and A. Hastings. 2005. Allee effects in biological invasions. *Ecology Letters* 8:895–908.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.
- Vance, C. P., C. Uhde-Stone, and D. L. Allan. 2003. Phosphorous acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytologist* 157:423–447.
- Weldon, C. W., and W. L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. *Quarterly Review of Biology* 61:23–44.
- Williamson, J., and S. Harrison. 2002. Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications* 12:40–51.